Vegetation of Non-alluvial Wetlands of the Southeastern Piedmont

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Abstract

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Non-alluvial wetlands play an important ecological role for many plant and animal species, providing a contribution to regional and landscape-scale biodiversity. Despite their ecological significance, non-alluvial wetlands in the southeastern Piedmont have received little research attention. The purpose of this study is to develop a quantitative classification and description of non-alluvial wetland plant communities for the southeastern Piedmont. Vegetation was surveyed in 123 plots from central Virginia to northern South Carolina selected to represent high-quality examples of Piedmont non-alluvial wetlands. Cluster analysis and ordination techniques were used to identify and describe community types in terms of their species composition and environmental settings. Ten non-alluvial wetland community types were identified for the southeastern Piedmont, five for seepage wetlands and five for depressional wetlands. These results provide a baseline quantitative classification that may be used for conservation planning or to refine and improve documentation for existing plant community concepts.

To my loving parents and brother for their endless support and

to Matty for always believing in me

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Chapter 1. Introduction

Non-alluvial wetlands are known to provide an important contribution to both biodiversity and ecological services. However, in the last decade they have received reduced legal protection under federal laws and this change has highlighted the need to develop a scientific basis for understanding the ecological role of these unique wetlands. The Clean Water Act (CWA) provides regulations for the protection of water quality in United States. This law has historically been interpreted to provide protection for streams and wetlands in the U.S. However, the law uses language such as “navigable waters” and “waters of the United States” to define the scope of coverage. Following a 2001 Supreme Court decision in Solid Waste Agency of Northern Cook County (SWANCC) v. United States Army Corps of Engineers, federal protection was substantially reduced for isolated wetlands and non-navigable waters. Since that time, the role of CWA protection of such waters has been debated, but isolated wetlands remain largely unprotected by federal regulation and protection is left to individual state regulation (Tiner 2003a; Whigham & Jordan, 2003; Marks 2006; Meyer et al. 2007). This has left many isolated wetlands unprotected, particularly wetlands such as prairie potholes of the Midwest and isolated wetlands of the Mississippi River Valley. Some states have adopted wetland regulation policies to supplement CWA regulation and provide protection for isolated wetlands, but may still exclude small wetlands from protection. For example, in a pending South Carolina bill providing protection for isolated wetlands, only wetlands larger than 0.5 acre are subject to protection (South Carolina S. 116 2007). Also, these regulations protect wetlands from dredging and filling but may not protect wetlands from other manipulations such as removal of vegetation.

In Virginia it is estimated that more than 180,000 acres of the state's wetlands are geographically isolated (Hershner et al. 2000). In a study of regional landscapes across the U.S., isolated wetlands were estimated to account for between 20-50% of each region's total wetland acreage and typically more than 50% of each region's total number of wetlands (Tiner 2003b). The extent of isolated wetlands may be systematically underestimated because these often small habitats can be difficult to identify from remotely-derived map data. In a watershed study in the Southern Appalachians, Hensen (2001) found that of all existing perennial, intermittent, and ephemeral waters, only 14-21% were accounted for on USGS topographic maps. In a study of Carolina Bays, the lower limit for remote detection was found to be 0.2 ha (~ 0.5 acre) and within detectable wetlands, abundance on the landscape increased with decreasing size (Semlitsch & Bodie 1998). Wetlands less than 0.5 acre may still contribute a great deal of wetland habitat and cumulative ecological services due to their frequency on the landscape. Nationally, approximately 50% of wetland area has been lost since European colonization (Dahl 1990) and an additional 58,000 acres of wetlands are lost each year (Marks 2006). Small isolated wetlands, particularly those that are shallow and easily drained, have been subject to some of the most intensive destruction. In agricultural and urbanizing landscapes such wetlands may be essentially eliminated (Marks 2006).

While non-alluvial wetlands are often considered "isolated wetlands" under wetland regulation, they occupy a range of positions along an isolation-connectivity continuum

(Leibowitz 2003). Non-alluvial wetlands are found in many landscape settings and have diverse ecosystem dynamics. These wetlands are often effective as nutrient sinks and can trap sediment transported from adjacent uplands. However, because of the diverse dynamics and settings in which non-alluvial wetlands are found, they can provide a wide array of ecological functions (Whigham & Jordan 2003). Non-alluvial wetlands provide a significant contribution to both local and regional diversity by supporting a different suite of species than the surrounding landscape, while also supporting some regionally rare species. Geographically isolated wetlands have been found to support 274 at-risk plant and animal species in the U.S. and more than one-third of those species depend exclusively on isolated wetlands. Most of these at-risk species are plants, which are even more likely than animals to be isolated wetland specialists. Isolated wetlands also support unique communities. Approximately 13% of the ecological systems recognized by NatureServe are geographically isolated wetlands (Comer et al. 2005). Non-alluvial wetlands are the primary breeding habitat required for many species of amphibians, where the typically fish-free conditions of non-alluvial wetlands offer a reduced risk of predation (Marks 2006). In a comprehensive study of these wetlands comparing a range of sizes, results suggest that small wetlands have similar amphibian richness to large wetlands and support unique faunal assemblages (Snodgrass et al. 2000). Isolated wetlands can also function as valuable stepping stones and food sources for many species that are not isolated wetland specialists. Migratory waterfowl depend on the rich invertebrate food supply of seasonal, isolated wetlands during migration (Marks 2006). In a simulation of the loss of small, unprotected wetlands on the population dynamics of animals, Gibbs (1993) found that many otherwise stable populations of turtles, small mammals, and small birds would face significant risk of local extinction if small wetlands were lost.

In the southeastern U.S., several types of non-alluvial wetlands have been recognized for their ecological importance. Non-alluvial wetlands of the southern Blue Ridge Mountains, often called mountain bogs, support many rare and endemic taxa as well as several unique plant communities. It is estimated that approximately 85% of mountain bog wetland area has been lost or severely degraded, and the remaining wetlands have been targeted for conservation (Weakley & Schafale 1994; Warren et al. 2004; Wichmann 2009). Carolina bays are a type of non-alluvial wetland characteristic of the southeastern Atlantic Coastal Plain. These species-rich depressions can be very numerous on the landscape and range widely in size. They support rare species and a remarkable variety of ecological communities, from pond cypress savannas, pond cypress ponds, depression meadows, and hardwood swamps to bay forests and ombrotrophic pocosins (Sharitz & Gibbons 1982; Nifong 1998; Sharitz 2003). The importance of Carolina bays and other Coastal Plain depressions for breeding amphibians and maintaining amphibian diversity has been studied extensively (Snodgrass et al. 2000; Russell et al. 2002; Sharitz 2003; Gibbons et al. 2006).

In comparison to non-alluvial wetlands of the Mountains and Coastal Plain of the southeastern U.S., research on non-alluvial wetlands of the Piedmont is lacking. This may be driven by the relative rarity of non-alluvial wetlands in the Piedmont compared with other regions. Some forms of non-alluvial wetlands are less common in the Piedmont because it is a geologically mature landscape and supports fewer examples of natural depressions, as is evidenced by the absence of natural lakes. The Piedmont, a transitional ecoregion between the Mountains and Coastal Plain, is one of the fastest growing regions in the country and experiencing rapid urbanization. Four and a half percent (7368 km^2) of all Piedmont land was converted to urban use during the period from 1973-2000 and most of that land was converted from forests (Fonseca and Wong 2000; Brown et al. 2005). Many non-alluvial wetlands in the Piedmont are found in urbanizing areas, often on privately owned land, which places them at high risk for development or alteration.

Non-alluvial wetlands of the Piedmont have been treated in two broad categories in state classifications based on hydrologic setting. Piedmont seeps or “bogs” are groundwater seepage-fed wetlands that often occur on slopes or at topographic breaks. Such seepage wetlands vary in landscape setting from isolated, upland positions to floodplain-edge seeps with alluvial influence. Depression wetlands are topographic low-points, often closed basins, that fill seasonally from precipitation and surface runoff (Schafale and Weakley 1990; Fleming et al. 2010). They are characterized by moisture conditions that change dramatically during the course of the growing season, creating a stressful environment of extremes for which many species are not well adapted. The concept of a non-alluvial wetland is a somewhat artificial category that has been developed for organizational convenience. However, in reality non-alluvial wetlands as a group encompass a broad variety of wetlands with widely divergent ecosystem dynamics. This is true for seepage wetlands and depression wetlands, which are driven by very different hydrodynamics and support distinct suites of species.

In an effort to contribute to our basic understanding of the ecology of these isolated wetlands of the Piedmont, vegetation patterns and environmental settings were examined using a dataset of 123 plots from Piedmont non-alluvial wetlands, ranging from central Virginia to northern South Carolina. Detailed descriptions of non-alluvial wetland communities and an understanding of the relationships between vegetation and environmental drivers may aid in their protection and restoration. In a preliminary analysis of vegetation patterns, Piedmont non-alluvial wetlands appeared to split into two distinct groups that correspond to the two previously documented hydrologic settings: seeps and depressions. This clear distinction can be seen in a Non-metric Multidimensional Scaling (NMS) ordination of vegetation composition. NMS was performed in PC-ORD 5.31 for all taxa using Sørensen distance and cover classes as the measure of abundance, with 20 random starting configurations in autopilot mode. The optimal result using autopilot mode was a two-dimensional solution (Figure 1.1). Two depression wetland plots appear in the two-dimensional ordination to be outliers relative to the other depression wetlands, and closer in compositional space to seepage wetlands. A second NMS ordination was performed with a three-dimensional solution selected. In the three-dimensional ordination, the two outlier depression wetland plots can be seen to be distinct from seepage wetlands along a third axis. Vegetation in seepage wetlands is dominated by a red maple (*Acer rubrum*) canopy with characteristic understory species like cinnamon fern (*Osmundastrum cinnamomeum*), winterberry holly (*Ilex verticillata*), possumhaw (*Viburnum nudum*) and netted chainfern (*Woodwardia areolata*). Plant assemblages of depressional wetlands are species poor in comparison and strongly dominated by willow oak (*Quercus phellos*), along with species such as overcup oak (*Quercus lyrata*), cypress swamp sedge (*Carex joorii*), winged elm (*Ulmus alata*), and trumpet creeper (*Campsis radicans*). There are also distinct environmental differences between the two hydrologic wetland types: depressional wetlands have higher clay content and are more acidic than the comparatively sandy, base-rich seepage wetlands (Figure 1.1). Due to their distinct character and their traditional treatment as different wetland types, the vegetation patterns of seepage wetlands and depressional wetlands are explored in separate chapters. Chapter 2 is an analysis of seepage wetland vegetation and Chapter 3 provides an analysis of depression wetland vegetation.

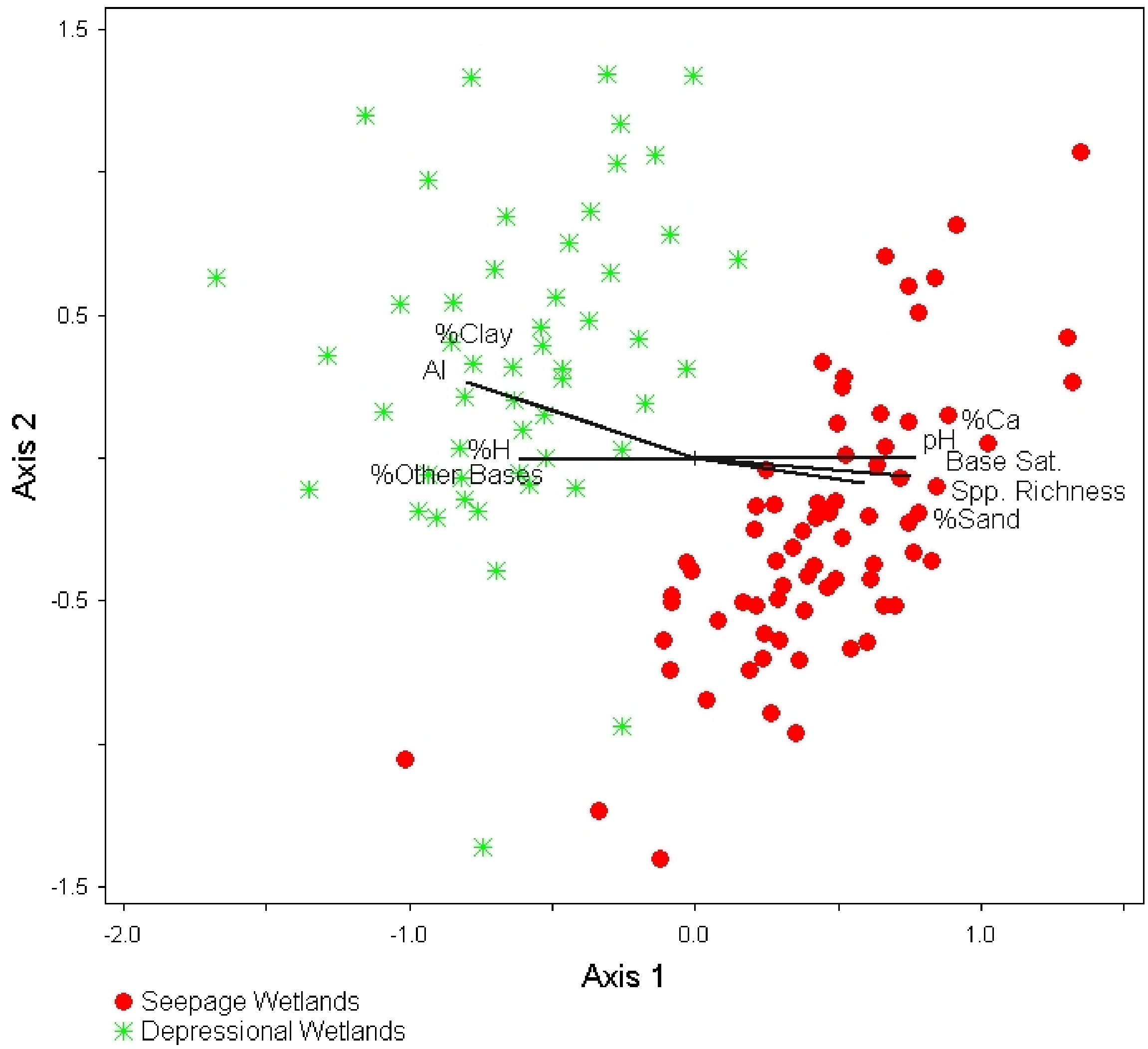

Figure 1.1. Two-dimensional non-metric multidimensional scaling (NMS) ordination of vegetation from 123 plots of Piedmont non-alluvial wetlands. Color coded symbols represent hydrologic setting. Correlation of environmental variables with ordination axes (cutoff r = 0.6) are displayed by joint-plot overlays, where the length and direction of the vector represent the strength and the direction of correlation with the axes, respectively.

Chapter 2. Classification and Description of Piedmont Seepage Wetland Plant Communities

Introduction

Seepage wetlands form in locations of groundwater discharge, often at springheads, where the water supply is sufficient to support the development of wetland communities. These wetlands are often small (typically less than 1000 m^2) and can be easily overlooked. As a consequence, seepage wetlands have not been well studied and many of their dynamics are poorly understood (Hall et al. 2001). The few studies available for seepage wetlands in the U.S. suggest that they have a number of potentially important ecological functions. Seepage wetlands play an important role in contributing to regional and landscape-level biodiversity (Harrison et al. 2000; Morley & Calhoun 2009). In the southeastern Piedmont of the U.S., seepage wetlands support several plants of conservation concern, including the federally endangered bunched arrowhead (*Sagittaria fasciculata*), as well as species of state concern such as shortleaf sneezeweed (*Helenium brevifolium*), Baldwin's yelloweyed grass (*Xyris baldwiniana*), and purple fringeless orchid (*Platanthera peramoena*). Piedmont seepage wetlands are also home to several ecological communities that are considered to be vulnerable or imperiled (Nelson 1986; Schafale & Weakley 1990; Fleming & Patterson 2010; NatureServe 2010). A relatively constant water supply and lack of deep pools make seeps ideal breeding sites for many species of amphibians and insects (Schafale & Weakley 1990). The four-toed salamander (*Hemidactylium scutatum*) and Thorey's grayback dragonfly

(*Tachopteryx thoreyi*), which are North Carolina species of concern, use seeps as their primary breeding sites (Steve Hall, pers. comm.).

Groundwater-fed wetlands may also provide a number of ecosystem services. As groundwater travels along subsurface flowpaths, it is exposed to subsoil and bedrock. This can impart distinct chemical properties to groundwater, which often has higher leached mineral content and higher pH (Rice & Bricker 1995; Richardson & Vepraskas 2001; Bedford & Goodwin 2003). A study on the nitrogen budget of a seepage-fed stream in New York found that the stream effectively removed nitrate during the growing season through nitrogen uptake and denitrification (Burns 1998). In groundwater-fed fens of the Northeast, the mineral-rich content of groundwater can occlude phosphorus in biologically unavailable forms. Depending on the substrate through which it flows, groundwater can provide a steady supply of minerals like iron, calcium bicarbonate, or calcium sulfate, which all react with phosphate and cause it to precipitate, providing a sink for phosphorous in the watershed (Bedford & Godwin 2003). Wetlands provide much of the dissolved organic carbon (DOC) that enters the aquatic environment, and Creed et al. (2003) found that small forested wetlands, such as seeps, accounted for most of the variation in DOC exported from watersheds. Research indicates that water entering streams during storms often comes from “old” subsurface water that is flushed from the ground through sites of groundwater discharge, such as at seeps (Hornberger 1998). During the summer, when surface runoff is reduced, seeps have been found to be primary sources of baseflow. From these headwater positions, seeps could be in a unique position to have a disproportionately large impact on watershed processes relative to their small size (Burns et al. 1998; Alexander et al. 2007; Morley et al. 2011).

Hydrology is one of the primary drivers of wetland ecosystem structure and function. Many wetland processes are determined by the chemical composition and characteristics of water supply (Brinson 1993; Mitsch & Gosselink 2007). Seepage hydrology can be created through a variety of landscape features. Topographic breaks or concavities, as well as features of stratigraphy, are primary mechanisms that may act independently or in conjunction (Richardson & Vepraskas 2001; Winter 1988). Breaks in slope create a hydraulic gradient that promotes the upward flow of water (Hornberger 1998). Even subtle topographic breaks can promote the formation of wetlands on slopes when hillsides join to form a topographic cove or hollow, where subsurface flowlines converge. In order to form wetlands in this context, the soil must be thick enough to allow the slow movement and long storage of groundwater (Richardson & Vepraskas 2001). Slope wetlands with these characteristics sometimes act as the origination point for streams and may be called zero-order basins (Sheridan and Spies 2005). In seeps created by stratigraphy, the presence of layers in soil or bedrock that have sharply divergent hydraulic conductivities (where water flows freely through one statum and is restricted by another) can create horizontal or upward water flow. This may result in surface discharge in zones of upwelling or where the permeable stratum intersects a slope (Richardson & Vepraskas 2001; Winter 1998). Clay lenses, that commonly underlie seepage wetlands of the otherwise sandy Sandhills ecoregion, are one example of stratigraphy driven seepage wetlands (Nelson 1986; Schafale & Weakley 1990). Some geologic features that have been found to promote seepage include: heterogenous geologic terrains, bedrock landslides, faults in impermeable bedrock, and alluvial or colluvial deposits. Each unique hydrologic setting may access aquifers of different depth and size, driving variation in constancy of water supply and response to precipitation (Burns et al. 1998; Winter 1998; Stein et al. 2004; Springer & Stevens 2009).

Although seeps can form channels and often contribute water to streams or rivers, they are typically considered non-alluvial wetlands (Schafale & Weakley 1990; Fleming et al. 2010). As a consequence of the concern over reduced legal protection, combined with awareness of their contribution to regional biodiversity, seepage wetlands have become a priority for conservation (Fleming et al. 2010). Despite the concern for these wetlands, there have been very few studies of their biological communities and no studies from the southeastern Piedmont. Knowledge of community composition and its drivers is necessary to develop a basic understanding of seepage wetland ecosystems and it also provides a foundation for conservation and restoration efforts. Vegetation plays a structuring role for biological communities, where plant assemblages provide habitat for many organisms and interact in numerous biogeochemical processes (Tabacchi et al. 1998). Plant communities can also function as an easily recognizable unit for classification or conservation purposes.

The U.S. National Vegetation Classification System (NVC) is developing a nationwide classification of natural communities based on vegetation. It is cross-linked with state-level community classification systems and provides a common language that can be used for many conservation, restoration, and management applications (Jennings et al. 2009). However, the NVC communities developed for seepage wetlands in this region are based primarily on qualitative assessments and often lack plot data. An independent state classification of natural communities for North Carolina has been developed based on a qualitative synthesis of environmental setting and floristics. According to this system, seeps are classified as either fire-prone, hillside seeps with a flora characteristic of bogs ("Hillside

Seepage Bog"), seep vegetation along banks of small headwater streams ("Piedmont Boggy Streamhead"), or seeps that occur at breaks in slopes ("Low Elevation Seep") (Schafale 2003). In a Virginia classification, three community types are recognized for seepage wetlands in the study area based on a numerical analysis of floristic composition. The three Virginia concepts are distinguished by the presence of boggy flora ("Coastal Plain/Piedmont Seepage Bog") or by soil fertility ("Coastal Plain/Piedmont Acidic Seepage Swamp" and "Coastal Plain/Piedmont Basic Seepage Swamp") (Fleming et al. 2010). The purpose of this study is to develop a region-wide numerical classification of seepage wetland vegetation in the southeastern Piedmont that provides descriptions of recognizable plant communities. Detailed summaries of vegetation and community setting could be used to inform and refine NVC associations as well as to provide a framework for integrating national and state concepts of seepage wetlands. In addition to documentation and description of community types, this research also attempts to investigate the important environmental gradients that are associated with compositional variation and may act as drivers of seepage wetland community composition.

Methods

Study area

Vegetation was surveyed in the eastern Piedmont physiographic province of the southeastern U.S., spanning a zone from the southern Piedmont of Virginia through the Piedmont of North Carolina and into the northern Piedmont of South Carolina. This area represents much of the Piedmont Seepage Wetland Ecological System (CES202.298) recognized by NatureServe (2010). The eastern Piedmont is an ancient peneplain characterized by erosional forces (Oosting 1942; Markewich et al. 1990). It is geologically complex and consists of broad regions of igneous or metamorphic rock with areas of volcanic intrusion as well as several basins of Triassic sedimentary rock. There are occasional inselbergs, formed from erosion resistant rock or from ancient weathered mountain chains that contribute areas of sharp topographic relief (Stuckey 1965). As a sloping peneplain, topography and soils of the Piedmont vary along a gradient in descending elevation from the boundary with the Southern Blue Ridge, where thinner soils and high relief are predominant, to the fall zone, where soils are thickest and topographic relief is minimal (Markewich et al. 1990). Topographic relief and the formation of stream networks are controlled primarily by differences in the resistance of bedrock to erosive forces (Markewich et al. 1990; Woodruff & Parizek 1956).

The combination of varied bedrock and longitudinal trends gives the Piedmont a moderately complex topography, creating localized differences in stream valley geomorphology. There are four major geologic landscapes in this region of the Piedmont: the felsic crystalline terrains, the Carolina Slate belt, the Triassic Basins, and a complex mixed mafic and felsic unit. The felsic crystalline terrains are composed of granite, granite gneiss, biotite gneiss, and mica schist, with common intrusions of more mafic rock, such as gabbro. There are eastern and western sections of this landscape, each with different characteristic soil series. The Carolina Slate Belt is underlain primarily by volcanic agrillites, as well as mafic and felsic metavolcanic rock. Soil series in this landscape often have comparatively high silt content and thin saprolite. There are four Triassic Basin bands that are characterized by low topographic relief and are underlain by shales, sandstones, and other sedimentary rocks. The mixed mafic felsic unit is very complex, where soils of very different character, derived from either mafic or felsic rock, occur as complexes in close proximity. (Daniels 1984).

Climate is humid subtropical, but there is considerable variation in both temperature and precipitation across the relatively large study area (Markewich et al. 1990). Mean annual temperature of study sites ranges from 12-16 degrees C. Mean annual temperature is lower in the northern and western reaches of the study area and higher in the southern and eastern reaches. Mean annual precipitation of study sites ranges from 1074-1475 mm/year. Precipitation rates are highest near the southern Blue Ridge and decline to the north and towards the Coastal Plain. The Piedmont has a long history of disturbance in the form of urban development and agriculture. Beginning with the settlement of Europeans, most locations in the Piedmont suitable for agriculture were cleared. Early agricultural practices resulted in substantial topsoil erosion throughout the region. The transported sediment has been deposited along stream drainages and in some areas the depositional layer is extensive (Trimble 1974). Land cover is currently a mix of developed land, agriculture, and forest used for silviculture or natural areas (Markewich et al. 1990). Remaining natural forests are second-growth and often exist within a patchwork of other land uses (Oosting 1942).

Site selection

Sampling locations were selected in an attempt to capture a large proportion of the remaining examples of high-quality, natural seepage vegetation known from the study area. Seepage wetlands were defined as sites supporting wetland vegetation that had visible evidence of seepage hydrology. This was often seen in the form of groundwater discharge issuing from springheads but also included evidence of saturated soil in a sloping, non-alluvial landscape position. Because much of the Piedmont has been subject to anthropogenic disturbance, sites were sought that showed signs of minimal disturbance and that were large enough to be sampled by our standard protocol. Beyond those criteria, all known seeps where site access could be obtained during the primary field season were sampled. Many of the seeps included in this study were located by reference to the North Carolina Natural Heritage Program element occurrence database. Additional high quality wetlands were located through consultation with regional agencies, biologists, and conservation organizations. Several sites in South Carolina were identified from known locations of the seep specialist, *Sagittaria fasciculata*. Sites included in this study were restricted to the Piedmont province, except for one location near the fall line of the Upper Coastal Plain, in a transitional area where both Coastal Plain sediments and igneous Piedmont bedrock are present. Seeps from Virginia were not sampled directly for this project but were included from an archive database of plots sampled by the Virginia Natural Heritage Program (VANHP: Fleming et al. 2010). Plots from sites described as seepage wetlands and from locations in Virginia's "Southern Piedmont" ecoregion were selected for inclusion from the database. In total, 71 plots were analyzed: 61 from North Carolina, 6 from South Carolina, and 4 from Virginia (Figure 2.1).

Field methods

The primary fieldwork for this study was conducted from May-August 2009. During the primary field season, 56 permanent vegetation plots were established in seepage wetlands using the Carolina Vegetation Survey (CVS) protocol (Peet et al. 1998). Data from 11 additional CVS-style plots were obtained from the CVS archive database. Plots from the archive database were sampled in June and September 1994, July 2000, and May 2010. Plots from the VANHP database were established following Virginia's DCR-DNH plot data collection protocol (Virginia Dept. of Conservation and Recreation 2011) and were sampled in October 1992, and May or June of 2002, 2005, or 2006.

The CVS protocol allows plots to range in size from 100 m^2 to 1000 m^2, comprised of between one and ten 100 m^2 modules, in order to accommodate stands of different size and configuration. Plots completed during the primary field season were all sampled at the 100 m^2 size (typically 10 m x 10 m) due to the small extent of most seepage wetlands. The 11 additional plots obtained from the CVS archive ranged in size from 100 m^2 to 1000 m^2 (most frequently 200-400 m^2). Plots from Virginia were 400 m^2 or 100 m^2, the standard DCR-DNH plot sizes for forest/woodland or for shrubland/herbaceous vegetation, respectively. Plots were placed in stands of relatively homogenous vegetation and an attempt was made to establish the plot within the wetland boundaries. In some plots, either due to the shape of the wetland or to internal heterogeneity caused by mosaic microtopography, patches of upland vegetation were incidentally captured. Seepage wetlands encountered in this study were typically small enough for one plot to capture the majority of the site's compositional variation but in occasional circumstances, when the wetland was very large or included patches of distinct vegetation, multiple plots were established.

Within each plot, all vascular plant taxa were recorded and the aerial cover of each taxon was estimated using cover classes. Several low-resolution bryophyte taxa were also recognized in many plots, including *Sphagnum* spp., *Mnium* spp., *Climacium* spp., *Thuidium* spp., *Leucobryum* spp., and *Marchantiophyta* spp. Aerial cover was estimated for each taxon as total plot cover and cover by strata. The CVS protocol uses the following cover class scale: 1 = trace (<0.1%), 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%. Virginia DCR-DNH protocol follows the same cover class scale, except the scale ranges from 1-9, with 9 representing 75-100%. There were no examples of taxa occurrences given cover class 10 from the CVS plots, so for this dataset the two scales are functionally equivalent. For each stratum, the height and percent aerial cover were estimated. The diameter at breast height (dbh) of woody stems was tallied by taxa in the following diameter classes: 0-1 cm, 1-2.5 cm, 2.5-5 cm, 5-10 cm, 10-15 cm, 15-20 cm, 20-25 cm, 25-30 cm, 30-35 cm, and 35-40 cm (Virginia plots do not have tallies for stems <2.5 cm). Diameter of trees larger than 40 cm was recorded to the nearest 1 cm.

Plants were identified to the finest taxonomic resolution possible, most frequently to species or variety. However, due to the vegetative condition of most specimens, the difficulty of distinguishing some species in the field, the need to standardize taxonomic concepts across several data sources, and species complexes encountered from archived plots, some occurrences were treated as lower resolution taxonomic complexes for analyses (*Viola* spp., *Vitis* subgenus *Vitis,* and *Chelone [glabra + obliqua]*, *Nyssa [biflora + sylvatica* swamp variety*]*). For example, *Chelone glabra* and *C. obliqua* both occur within the study area but cannot be identified beyond the genus level without flowering or fruiting characteristics, and the specimens of *Chelone* that were encountered in this study were in vegetative condition. Within *Nyssa sylvatica,* there appears to be several races or varieties that have been documented throughout its range. This variation is not well-understood and several informal concepts have been recognized. One form of *Nyssa sylvatica* that appears to be very similar to *Nyssa biflora* in both appearance and habitat has been noted by taxonomists and ecologists in the region of the Carolinas (Weakley 2010; Alan Weakley, pers. comm.; Robert Peet, pers. comm.). This race of *Nyssa sylvatica* is similar to *Nyssa* *sylvatica* var. *typica* (*sensu* Fernald 1935). It was termed *Nyssa sylvatica* swamp variety in this study and was combined with *Nyssa biflora* in analyses due to the difficulty of distinguishing the two taxa and the many historical changes that have occured in treatment of *Nyssa sylvatica* varieties. Plots are archived in VegBank along with a full index of lower resolution taxonomic concepts used in analyses that links these concepts to species listed in the plots. Nomenclature follows Weakley (2010) except for *Nyssa sylvatica* swamp variety, which is discussed, but unnamed, in Weakley (2010).

Additional descriptive and environmental data were collected for each plot including geographic coordinates, slope, aspect, hydrologic regime class, soil drainage class, estimated stand size, landform, and topographic position. Field soil samples were collected and analyzed for nutrients and texture. For CVS plots, a soil sample was collected from the A horizon (top 10 cm of mineral soil) of each intensive module (number of intensive modules ranged from 1-4, depending on plot size). One sample from the B horizon (approximately 50 cm below the surface) was also collected from the center of each plot. Soil samples from Virginia plots were collected in multiple locations from the A horizon and combined. All soil samples were analyzed by Brookside Laboratories, Inc. in New Knoxville, Ohio. Total cation exchange capacity (CEC) (meq/100 g), pH, exchangeable cations (Ca, Mg, K, Na ppm), percent base saturation, estimated nitrogen release, easily extractable P, soluble sulfur, extractable micronutrients (B, Fe, Mn, Cu, Zn, Al ppm), percent organic matter, and bulk density values were determined for each sample. Extractions were carried out using the Mehlich III method (Mehlich 1984) and percent organic matter was determined by loss on ignition. Soil texture was determined as percentage sand (2 mm – 63 μm), silt (63 μm – 2 μm), and clay (<2 μm). Values from the A horizon samples were used in the analysis because B horizon data were not available for all plots. If multiple A horizon samples were collected, the values were averaged to provide a single set of soil data from each plot prior to analysis.

An estimate of seep wetness was generated using a hydrophytic vegetation index. The index was developed with data from region 2 (Southeast) of the U.S. Fish and Wildlife's wetland indicator lists (U.S. Fish and Wildlife Service 1988). The wetland indicator lists place species of plants in one of five wetland indicator categories according to frequency of occurrence in wetland habitat (estimated probability of occurring in wetland habitat: UPL = <1%, FACU = 1%-33%, FAC = 34%-66%, FACW = 67%-99%, OBL = >99%). The wetland indicator categories were converted to a hydrophytic scale as follows: OBL = 5, FACW+ = 4.25, FACW = 4, FACW- = 3.75, FAC+ = 3.25, FAC = 3, FAC- = 2.75, FACU+ = 2.25, FACU = 2, FACU- = 1.75, UPL = 1. Hydrophytic scale values for each species were weighted by cover class and averaged by plot to generate a hydrophytic vegetation score for each plot (Wentworth et al 1988).

In addition to the data collected on site, some environmental data were derived remotely using a Geographic Information System (ArcGIS 9.3: ESRI 2008). Bedrock geology was obtained from USGS state digital geology maps for Virginia, North Carolina, and South Carolina (U.S. Department of the Interior, U.S. Geological Survey: http://tin.er.usgs.gov/geology/state/). A hydrogeologic map of the Southern Blue Ridge and Piedmont of North Carolina (Daniel and Payne 1990) was used to assign a hydrogeologic unit to each site. For Virginia and South Carolina plots, a hydrogeologic unit was assigned based on the known bedrock geology for those locations. The hydrogeologic unit that corresponds to each bedrock geology type was found by cross-referencing the hydrogeologic units assigned to each bedrock geology type mapped for North Carolina. Estimates of average water yield of the mapped hydrogeologic units were obtained from Daniel and Dahlen (2002) and assigned to each plot. Soil series and soil taxonomic classification were determined using digital SSURGO soil maps from USDA Natural Resource Conservation Service (http://soils.usda.gov/survey/geography/ssurgo/). Plot distance to nearest stream was calculated from 1:100,000-scale NHDFlowline feature class of the USGS National Hydrography Dataset (http://nhd.usgs.gov/). Spatial stream data were supplemented with attribute data from NHDPlus, which provided mean annual watershed temperature and precipitation, Strahler stream order, as well as slope, volume, and velocity of the nearest stream (Horizon Systems Corporation: http://www.horizon-systems.com/nhdplus/index.php). Distance to 100-year floodplain and width of nearest floodplain were calculated for North Carolina sites using digital floodplain maps (DFIRM) produced by FEMA, obtained through North Carolina Floodplain Mapping Program (http://www.ncfloodmaps.com/). Floodplain data for South Carolina and Virginia were estimated using FEMA's online Map Viewer (https://hazards.fema.gov/wps/portal/mapviewer).

Numerical Analyses

A community classification was developed using a hierarchical agglomerative cluster analysis. A hierarchical approach was employed because it has been widely used in community classification and provides a flexible framework for creating hierarchical clusters (McCune et al. 2002). Rare taxa (those that occur in three plots or fewer, which represents 5% of all plots) were removed from the analysis because rare taxa create noise in calculations of inter-plot similarity and can obscure relationships between composition and the environment (McCune et al. 2002). However, rare taxa that may be important to stand composition, here defined as taxa with aerial cover greater than 5-10% or with a restricted habitat (those that are found in 6 or fewer community associations in the CVS archive database), were included in the analysis. A distance matrix, using Sørensen distance, was created for 71 plots x 231 taxa, representing inter-plot similarity in taxa composition and abundance. Several different measures of taxa abundance were employed in the calculation of the distance matrix, including cover classes, percentage cover mid-points, percentage cover mid-points relativized by species maximum, and presence-absence. The final distance matrix was calculated using cover classes, which represent a log scale of percentage cover estimates, because cover classes provided a means of de-emphasizing the dominant aspect of tree and shrub growth-forms, which has been found to be useful in other community classifications (McCune et al. 2002) and produced the most ecologically interpretable results. A clustering dendrogram was created using the distance matrix with flexible beta linkage method ($\beta = 0.25$) in PC-ORD 5.31 (McCune and Mefford 2006). Flexible beta linkage ($\beta = 0.25$) is compatible with Sørensen distance and is a space conserving approach (McCune et al. 2002). Dufrêne -Legendre (DL) indicator species analysis (calculated in PC-ORD 5.31) was used in conjunction with cluster analysis to determine the optimal number of clusters to recognize based on maximization of the number and representation of significant indicator species ($p < 0.05$) in each group (Dufrêne & Legendre 1997; McCune et al. 2002). Higher-level groups were also recognized from the hierarchical dendrogram structure. A hierarchical framework of vegetation concepts allows for flexibility in the resolution with which vegetation patterns in seepage wetlands may be viewed, ideally providing broader utility for various classification, conservation, or restoration initiatives that may have different scopes and goals.

Synoptic vegetation tables were created for each cluster using JUICE 7.0, which provided an efficient means for compiling synoptic information and was used to calculate fidelity using the phi-coefficient method (Tichý 2002). Synoptic tables provide the constancy, average cover, fidelity, diagnostic value, and DL indicator species value for prevalent taxa in each cluster. Constancy was calculated as the percent frequency of taxon occurrence within a cluster. Fidelity is a measure of cluster faithfulness and was calculated using phi-coefficient, which accounts for differences in cluster size. Values greater than zero indicate that the taxon-cluster co-occurrence is more frequent than expected by chance (Chytrý et al. 2002). Diagnostic value (DV = constancy * fidelity/100) and DL indicator species value (IndVal) both highlight taxa that are characteristic of a cluster, where values increase as a given taxon is both increasingly common and faithful to a cluster. Prevalent taxa (*sensu* Curtis 1959) were identified by ranking cluster taxa by constancy and selecting the N most common taxa, where N is the cluster average species richness. Average cover, followed by diagnostic value, was used as a secondary selection criterion in the case of ties in constancy. Cluster homoteneity, calculated as mean constancy of prevalent taxa, is a measure of cluster compositional constancy. Community types were named following standards used in the NVC. Names are composed of species found from numerical analyses to have high constancy in the community and that also have high cover and diagnostic value when possible. Species are listed by growth form, with hyphens ("-") separating species within the same stratum and slashes ("/") distinguishing species of different strata (NatureServe 2010).

The relationship of vegetation composition to environmental variables was explored with non-metric multidimensional scaling (NMS) ordination using varimax rotation and

Sørensen distance of taxa cover classes with rare species removed. One plot (FPMR002) included in other analyses was removed from the final ordination because it occupied an outlier position in compositional space and was lacking soils data. The ordination was implemented in PCORD 5.31 using all defaults, for both two and three-dimensional solutions. Each resulting ordination represents the solution with the lowest stress from 20 random starting configurations. The two-dimensional ordination was selected for its graphical clarity and because the three-dimensional solution provided very little additional information. Joint-plot overlays were created using Pearson correlation values of environmental variables with ordination axes. A generalized additive model surface of environmental variables fitted to the NMS ordination was created in R 2.10.1 with the function 'surf' from the package 'labdsv' (R Development Core Team 2009; Dave Roberts 2010). The function "surf" provides a graphical representation that is ideal for examining non-linear patterns of environmental variation across compositional space.

Results

Cluster analysis, combined with indicator species analysis, indicated five optimal clusters or community types. The clustering dendrogram can be seen in Figure 2.2 and a synoptic vegetation table for the five community types is presented in Table 2.1. A list of plots included in the analysis and their assignment to community type is included in Table 2.5. The five community types can be considered within three higher-level groups. The three broader groups appear to be distinguished by landscape setting or watershed position and are termed "Headwater Seeps", "Lowland Seeps", and "Floodplain Seeps". Most seeps known from this study area are to some extent associated with a stream network, but the degree of the stream's bottomland development and the proximity of association with alluvial processes appear to be related to compositional patterns in vegetation. Seeps in headwater positions, either isolated from stream-networks or occurring along small first-order streams, are distinct from those that occur in larger stream valley lowlands, and seeps on well-developed floodplains are distinct from those that occur within valley bottoms but in positions above the floodplain. The results of the NMS ordination show a suite of landscape and edaphic variables that are correlated with the primary axis of variation (Figure 2.3). Stream order and velocity are positively correlated, while distance to floodplain and slope are negatively correlated with the first axis of variation. Soil pH, Ca, Cu, and Mn are also positively correlated with the first ordination axis. Soil texture varies along the first axis but in a non-linear pattern that can be seen in Figure 2.4. Sand content is low at either end of the first axis and peaks near the mid-point, while clay and silt show the reverse pattern. Canopy height and elevation are correlated with the second axis of variation. The cumulative R^2 of the NMS ordination was 0.795.

I. Headwater Seeps

The Headwater Seeps group includes wetlands in zero-order basins, seepage vegetation that occurs along small, first-order streams and seeps surrounded by uplands that are disconnected from stream networks. Because of their higher position in the watershed, many seeps in this group occur in sloping terrain, often in gentle topographic concavities with evidence of saturation. Topographic break settings and distinct springheads are not common features of this group. Soils have relatively high silt content (mean = 51.3 %; see Table 2.2) but are nutrient-poor, with the lowest pH (mean = 4.52) and lowest values for most soil nutrients, including Ca, Mg, Mn, Zn, Cu, Al, and Fe.

Upland forest is the primary matrix community that surrounds Headwater Seeps and neighboring streams are typically too small to support floodplain vegetation. As a result, intrusion of upland species is common in this group. This group is characterized by some upland species such as *Quercus alba* and *Oxydendrum arboreum,* as well as a number of wetland species including *Osmunda regalis* var. *spectabilis*, *Vaccinium fuscatum,* and *Osmundastrum cinnamomeum*. The headwater group has the lowest average hydrophytic vegetation score (mean = 3.38), suggesting these sites may be the driest or that they are intermittently wet. There is a Coastal Plain influence in the flora of this group, which occurs predominantly in the Slate Belt of the southeastern Piedmont of North Carolina, in the vicinity of the Uwharrie Mountains. The Uwharrie Mountains region is near the fall line and is known to have a Coastal Plain component to its vegetation (Wells, 1974). The Uwharries region also supports the majority of the Piedmont's representation of longleaf pine (Schafale 2003), which is a fire-dependant ecosystem and its presence indicates that this region likely experienced chronic wildfire. The examples of this group that occur in Virginia are also found near the eastern edge of the Piedmont (Figure 2.5).

The Headwater Seeps group includes two community types: Streamhead Seeps and Headwater Boggy Seeps. Although Streamhead Seeps and Headwater Boggy Seeps do not cluster together in the dendrogram, there is a great deal of compositional affinity in ordination space and similarity in environmental factors (see Figure 2.3). Headwater Boggy Seeps do not join with any other community type in the dendrogram. This is most likely because they contain many unique species not otherwise found in the dataset. Although Headwater Boggy Seeps are found in similar landscape settings to Streamhead Seeps, all sites included in Headwater Boggy Seeps are burned with some regularity. Burning creates an open physiognomy and allows the Headwater Boggy Seeps to support a number of distinct species. In many ways Headwater Boggy Seeps could be considered a specialized subtype of Streamhead Seeps that is burned regularly and occupies a more remote headwater position.

Headwater Boggy Seeps: (4 plots)

Acer rubrum / Gaylussacia frondosa / Andropogon spp. (A. glomeratus) - Osmundastrum cinnamomeum - Eupatorium rotundifolium Woodland

Environmental Setting:

Headwater Boggy Seeps are found somewhat distant from stream networks, in locations where the closest surface waters are first-order streams. This community type may occupy the most extreme headwater position along the watershed-position gradient. Neighboring streams have the lowest volume and velocity as well as the highest slope. Soils are silty (mean = 72.1%) and very low in sand (mean = 11.8%). This type has the lowest average values for most measures of soil fertility, such as pH, CEC, base saturation, Ca, Mg, K, Na, Mn, Zn, and Fe. In contrast to the Streamhead Seeps, Headwater Boggy Seeps have higher clay content and occur in locations with greater plot slope.

Vegetation:

The tree stratum is poorly developed; low canopy height (mean = 8 m) and low woody stem density are characteristic. This creates an open, woodland physiognomy with dense cover in the herb layer. The nominal *Acer rubrum,* as well as *Nyssa sylvatica* and *Liquidambar styraciflua,* occur as small trees and are also represented in the shrub stratum. Headwater Boggy Seeps are often set in a matrix of longleaf pine forest and consequently may have *Pinus palustris* overhanging in the canopy or as seedlings in the herb stratum. The shrubs *Alnus serrulata* and *Gaylussacia frondosa* are both common and significant indicators. Other common shrubs include *Vaccinium [corymbosum + fuscatum + formosum]*, *Aronia arbutifolia*, and the occasional *Morella caroliniana*. The herb layer is dominated by *Osmundastrum cinnamomeum* and *Andropogon* spp., particularly *A. glomeratus* but also including *A. gyrans* and *A. virginicus*. Other grasses are common in this community and some may have high cover such as *Saccharum* sp., *Danthonia spicata*, *D. sericea*, and *Dichanthelium scoparium*, *D. chamaelonche* and *D. lucidum*. Common herbs, many of which are significant indicators, include *Eupatorium [pubescens + rotundifolium]* as well as *Xyris* sp., *Symphyotrichum dumosum*, *Eupatorium pilosum*, *Rhexia* spp., and *Scleria [nitida + triglomerata]*. Most occurrences of carnivorous plants encountered in this study were found in this community type and include *Drosera brevifolia* and the occasionally dominant *Sarracenia* spp. (*S. purpurea* ssp. *venosa*, *S. flava*, and *S. ×catesbaei*). A synoptic vegetation table for Headwater Boggy Seeps is provided in Appendix 2A.

Classification:

The Headwater Boggy Seeps community type is approximately equivalent to the NVC association *Acer rubrum* var. *trilobum / Morella caroliniensis - Gaylussacia frondosa / Andropogon glomeratus - (Sarracenia flava)* Woodland (CEGL004781). See the Discussion for further details.

Streamhead Seeps: (19 plots)

Acer rubrum / Vaccinium fuscatum - Eubotrys racemosa / Osmundastrum cinnamomeum - Osmunda regalis var. spectabilis - Chasmanthium laxum Forest

Environmental Setting:

Streamhead Seeps are broader in terms of floristics and environmental setting than Headwater Boggy Seeps. They occur along first and second-order streams, distant from floodplains, in positions adjacent to streams or isolated from other surface waters. This type shares many of the environmental features of Headwater Boggy Seeps, including silty soils and low pH. However, Streamhead Seeps have intermediate values between Headwater Boggy Seeps and the rest of the dataset for most measures of stream size, soil texture, and soil fertility. Also, this type has a more forested physiognomy than Headwater Boggy Seeps and it appears to be infrequently exposed to fire.

Vegetation:

Acer rubrum, *Liriodendron tulipifera*, and *Liquidambar styraciflua* are characteristic canopy species. The canopy also commonly includes the upland trees, *Quercus alba* and *Oxydendrum arboreum*, which are both significant indicators of this community type. These trees are likely to occur in peripheral positions in the wetland and may largely be overhanging, rather than rooted in the seep. *Ilex opaca* var. *opaca* is common in the understory. The shrub stratum is well-developed, relatively diverse, and consistent with an acidic setting. *Vaccinium [corymbosum + fuscatum + formosum]*, *Viburnum nudum*, *Eubotrys racemosa*, *Ilex verticillata*, and *Gaylussacia frondosa* all have relatively high constancy. *Vaccinium [corymbosum + fuscatum + formosum]* and *Eubotrys racemosa* are also significant indicators. Several vine species are also common in this community, including *Vitis rotundifolia* var. *rotundifolia*, *Toxicodendron radicans*, *Smilax rotundifolia* and *Smilax glauca*. The herb stratum is moderately developed and dominated by ferns that are characteristic of seepage wetlands, *Osmundastrum cinnamomeum* and *Osmunda regalis var. spectabilis*. In addition, *Chasmanthium laxum*, *Euonymus americanus*, *Lycopus virginicus*, *Arisaema triphyllum*, *Mitchella repens*, *Scutellaria integrifolia*, and *Eutrochium fistulosum* are common. A synoptic vegetation table for Streamhead Seeps is provided in Appendix 2B.

Classification:

The Streamhead Seeps community type overlaps with the NVC association *Acer rubrum* var. *trilobum - Liriodendron tulipifera / Ilex opaca var. opaca / Osmunda cinnamomea* Forest (CEGL004551), but is somewhat broader in environmental setting and geographic range. See the Discussion for additional details.

II. **Lowland Seeps**

Seeps in this group are found along stream valleys in lower watershed positions than Headwater Seeps, where streams and valley bottoms are larger, often with well-developed floodplains that are able to support alluvial wetland vegetation. However, seeps in this group do not occur on the active floodplain itself and are unlikely to be exposed to flooding. In contrast to headwater seeps that often emerge along the length of gentle slopes, seeps in this group commonly occur at topographic breaks, some of which are quite sharp. The topographic break usually occurs in a foot-slope position where the break may represent a boundary that constrains the valley bottom. Most seeps in this group emerge at springheads that form small braided channels and rivulets, creating a hummock-hollow microtopography. Lowland Seeps have soils that are much higher in sand content (mean = 71.4%) than the Headwater or Floodplain seeps. The pH in this group is still acidic (mean = 5.01), but is higher than that of Headwater Seeps and similar to the pH found in Floodplain seeps. The soils are intermediate in fertility between Headwater and Floodplain seeps. Cation exchange capacity is low but percent base saturation is comparatively high, although soils in this group have a higher proportion of Mg and Na and lower proportion of Ca relative to Floodplain Seep soils.

As a consequence of the lowland setting, matrix vegetation surrounding these seeps has a more mesic character than vegetation surrounding headwater seeps and is more likely to have floodplain vegetation within a dispersable proximity. Some of the significant indicator species for Lowland Seeps are *Platanthera* spp., *Arisaema triphyllum*, *Ilex verticillata*, *Chelone [glabra + obliqua]*, and *Euonymus americanus.* Seeps in this group tend to have a relatively tall canopy (mean = 28 m) and high species richness (mean = 55 species/plot). Two community types, Infertile Swampy Seeps and Rich Foot-slope Seeps, were identified in this group. These communities can be distinguished primarily based on soil fertility and neighboring stream size. Infertile Swampy Seeps occur along smaller streams, with smaller floodplains, and also occur at greater distances from floodplains than do Rich Foot-slope Seeps. Infertile Swampy Seeps are also sandier than Rich Foot-slope Seeps and have corresponding low soil fertility (mean values for Na, Mn, Mg, and CEC in particular are lower). There is also a strong geographic distinction between the two community types. Infertile Swampy Seeps occur in the Inner Piedmont and Rich Foot-slope Seeps are more common in the Outer Piedmont (Figure 2.5). This geographic division is also consistent with the difference in elevation between the two community types along the second axis of the NMS ordination (Figure 2.3).

Infertile Swampy Seeps: (16 plots)

Acer rubrum - Nyssa sylvatica swamp variety *(Nyssa biflora) / Viburnum nudum – Aronia arbutifolia / Smilax laurifolia / Carex allegheniensis* Forest

Environmental Setting:

Infertile Swampy Seeps are wet, sandy, and nutrient-poor, developing in valleys along small to medium streams, with some floodplain influence. Sites are found in the felsic crystalline terrain, underlain primarily by mica-rich igneous rocks of the western Piedmont. Seeps in this type appear to be wetter than Rich Foot-slope Seeps and both headwater community types, based on the hydrophytic vegetation scores. A number of species diagnostic of this type are also characteristic of infertile, peaty wetlands in other areas of the state (Weakley 2010). There is a Coastal Plain element to the flora of acidic seepage swamps and several species typically found on the Coastal Plain extend into the Piedmont in seeps of this type.

Vegetation:

The tree stratum is typically well-developed and dense. The canopy is dominated by *Acer rubrum*, sometimes with *Nyssa [biflora* + *sylvatica* swamp variety], which has high cover when present. *Liriodendron tulipifera* is also common in the canopy but is more likely to grow on the edge of the seep and may to some extent reflect matrix vegetation. *Fraxinus pennsylvanica* is often found in the canopy or subcanopy with moderate cover. *Ilex opaca* var. *opaca* is abundant in the understory. The shrub stratum is also well-developed and diverse compared to other types, with the highest woody stem density (mean = 1.2 stems/m^2). *Viburnum nudum* is very common and typically has a high cover. Other common shrub species include *Ilex verticillata*, *Aronia arbutifolia*, *Vaccinium [corymbosum + fuscatum +*

formosum], *Alnus serrulata*, *Itea virginiana*, *Xanthorhiza simplicissima*, and *Toxicodendron vernix*. *Viburnum nudum*, *Aronia arbutifolia,* and *Toxicodendron vernix* are significant indicators. Vines, which may be part of the shrub or tree stratum, are abundant in this type as well. *Toxicodendron radicans, Parthenocissus quinquefolia*, *Decumaria barbara,* and *Smilax* spp., particularly *S. laurifolia*, *S. walteri* and *S. rotundifolia*, are prevalent. *S. walteri* is a significant indicator. The herb stratum can be diverse and typically contains several *Carex* spp., including *C. allegheniensis*, *C. leptalea*, *C. lurida*, *C. atlantica* and *C. howei*, along with the ferns *Osmundastrum cinnamomeum* and *Woodwardia areolata*. Other common or diagnostic herbs include *Platanthera* spp., *Lycopus virginicus, Leersia virginica*, *Mitchella repens*, *Arisaema triphyllum*, *Chelone [glabra + obliqua]*. Liverworts, division *Marchantiophyta*, are also common. Two significant indicator species, *Helenium brevifolium* and *Sagittaria fasciculata*, while not prevalent in Infertile Swampy Seeps, were found exclusively and with some frequency in this community type. Both are species of conservation concern; *Sagittaria fasciculata* is a federally endangered species and *Helenium brevifolium* is endangered in North Carolina and Tennessee. A synoptic vegetation table for Infertile Swampy Seeps is provided in Appendix 2C.

Classification:

The Infertile Swampy Seeps community type partially overlaps with the NVC association *Acer rubrum* var. *trilobum / Viburnum nudum var. nudum / Osmunda cinnamomea* - *Saururus cernuus* - *Impatiens capensis* Forest (CEGL004426), of the *Acer rubrum* - *Nyssa sylvatica* Saturated Forest Alliance. However, some of its composition and unique features are not represented in this association. The Infertile Swampy Seeps community type also overlaps with the description for the *Nyssa biflora* - *Acer rubrum* -

(Liriodendron tulipifera) Saturated Forest Alliance, but is not represented by any of the associations within that alliance. See the Discussion for additional details.

Rich Foot-slope Seeps: (20 plots)

Acer rubrum / Ilex verticillata / Arisaema triphyllum - Saururus cernuus – Platanthera spp. Forest

Environmental Setting:

Rich Foot-slope Seeps issue from lowland positions in stream valleys that vary in size but are typically larger (mean stream order = 2.8) than those of Infertile Swampy Seeps (mean stream order = 1.4). They are found predominantly in the eastern Piedmont, on bedrock such as meta-argillite and felsic metavolcanic rock. In general, soils of Rich Foot-slope Seeps are fairly sandy (mean = 65.8%) but higher in many soil nutrients than Infertile Swampy Seeps. This type has intermediate hydrophytic vegetation scores and the highest species richness (mean = 56.5 species/plot). Seeps in this type typically occur close to developed floodplains and may have more floodplain propagule availability than Infertile Swampy Seeps.

Vegetation:

Acer rubrum is the dominant canopy tree, but *Liquidambar styraciflua, Liriodendron tulipifera* and *Fraxinus pennsylvanica* also occur frequently. The subcanopy is characterized by the significant indicator species, *Carpinus caroliniana*, and occasionally by *Magnolia virginiana*. *Fagus grandifolia* is significant indicator of this type, although typically not rooted in the seep. Both *Carpinus caroliniana* and *Fagus grandifolia* are widespread species common in other ecosystems as well and may be more indicative of matrix vegetation. The shrub stratum is less well-developed than in Infertile Swampy Seeps; mean stem density is 0.81 stems/m^2. Few shrubs have high constancy except *Ilex verticillata*, which is common but with low cover. Other occasional shrubs include *Lindera benzoin*, *Ilex opaca* var. *opaca*, and *Vaccinium [corymbosum + fuscatum + formosum]*. Other common vines include *Smilax rotundifolia*, *Toxicodendron radicans*, *Parthenocissus quinquefolia*, *Lonicera japonica*, and the indicator species *Bignonia capreolata*. The herb stratum is typically well-developed and diverse. Dominants, *Arisaema triphyllum* and *Athyrium asplenioides*, are also both significant indicators. *Osmundastrum cinnamomeum*, *Woodwardia areolata*, and *Saururus cernuus* are all common and have relatively high cover. Grasses such as *Leersia virginica* (a significant indicator), *Glyceria striata*, *Microstegium vimineum*, and *Dichanthelium dichotomum var. ramulosum* are also common constituents of this community type. Herbs with high constancy include *Lycopus virginicus*, *Carex debilis*, *Platanthera* spp. (a significant indicator), *Boehmeria cylindrica*, and *Solidago caesia*. A synoptic vegetation table for Rich Foot-slope Seeps is provided in Appendix 2D.

Classification:

The Rich Foot-slope Seep community type partially overlaps with the NVC association *Acer rubrum* var. *trilobum / Viburnum nudum var. nudum / Osmunda cinnamomea - Saururus cernuus - Impatiens capensis* Forest (CEGL004426), but is narrower and more constant in environmental setting and composition. See the Discussion for additional details.

III. **Floodplain Seeps**

Floodplain Seeps occur within the boundaries of active floodplains. Like Lowland Seeps, they often occur at topographic breaks that constrain valley bottoms, however in this group the active floodplain extends to the location of the seepage so that there is more interaction between groundwater seepage and alluvial processes. Some examples of this type also occur in locations of groundwater sheetflow along floodplains of mid-sized streams. This group is distinguished from Lowland Seeps edaphically. Floodplain Seep soils have higher clay (mean = 15.5%) and silt (mean = 46.4%) content, with low sand (mean = 38.1%), compared to the soils of Lowland Seeps. Soils in this group are relatively nutrient rich, with the highest average values for CEC, N, P, Ca, Mg, K, Fe, Mn, Cu, and Al as well as the highest average Ca/Mg ratio. However, base saturation and pH (mean = 4.99) are similar to that of the Lowland Seeps group. Sites in this group are also found near streams of larger orders (mean stream order = 3) that have high stream velocity and low slope. This group contains only one community type.

Floodplain Seeps: (12 plots)

Acer rubrum / Alnus serrulata - Lindera benzoin / Glyceria striata - Impatiens capensis – Carex atlantica Forest

Environmental Setting:

Floodplain Seeps are found on active floodplains with loamy, nutrient-rich soils. They are the most distinct community in the cluster analysis but also have a notable degree of internal heterogeneity. They do not appear to be geographically constrained and occur scattered throughout the study area (Figure 2.5). With the highest average hydrophytic vegetation score (mean = 3.78), floodplain seeps appear to have well-developed wetland hydrology. Examples of this community have a somewhat open physiognomy, with a short canopy height (mean = 19.8 m) and low woody stem density (0.72 stems/m^2).

Vegetation:

The tree stratum is moderately to poorly developed and of less constant composition than the other seepage wetland community types. *Acer rubrum*, *Fraxinus pennsylvanica*, and *Liquidambar styraciflua* are the most constant tree species, but other species, such as *Betula nigra*, may also be occasionally abundant, particularly on large floodplains. Development of the shrub stratum is also somewhat variable. Some sites develop an open canopy of small trees with a limited or absent shrub layer, while other sites have a relatively dense shrub layer. In seeps with dense shrub cover, *Alnus serrulata* is usually the dominant shrub. This dense cover of *Alnus* may represent a successional response to disturbance, as several of these sites had some evidence of disturbance. Sites with moderate shrub cover are likely to have *Lindera benzoin*, possibly in combination with *Alnus serrulata*. Vines such as *Toxicodendron radicans*, *Lonicera japonica*, and *Parthenocissus quinquefolia* are commonly present but with low cover. The herb stratum is typically dense, somewhat species poor, and dominated by graminoids. The grasses *Glyceria striata*, *Cinna arundinacea*, and *Microstegium vimineum* all have high constancy. Numerous species of *Carex* are also common, including *C. lurida*, *C. atlantica*, *C. howei*, *C. laevivaginata*, *C. crinita*, *C. tribuloides*, and *C. radiata*, several of which are also significant indicators for this community type. Other fairly constant constituents of the herb stratum include *Impatiens capensis*, *Lycopus virginicus*, *Boehmeria cylindrica*, *Sagittaria latifolia*, and *Persicaria sagittata*, along with the mosses *Mnium* spp. and *Sphagnum* spp. A synoptic vegetation table for Floodplain Seeps is provided in Appendix 2E.

Classification:

The Floodplain Seeps community type partially overlaps with the NVC association *Acer rubrum* var. *trilobum / Viburnum nudum var. nudum / Osmunda cinnamomea - Saururus cernuus - Impatiens capensis* Forest (CEGL004426), but is narrower and more constant in composition and environmental setting. See the Discussion for additional details.

Discussion

Landscape Setting

Compositional variation in seepage wetlands of the southeastern Piedmont is related to a number of co-varying environmental factors that appear to reflect landscape position. The position within a watershed along the gradient from upland to lowland and from source to mouth seems to be of particular importance. Landscape position is likely to determine site geomorphology and many edaphic characteristics. Wetlands have been classified by various methods but one approach that incorporates landscape position and may be particularly suitable for seepage wetlands is the hydrogeomorphic (HGM) wetland classification system developed by Brinson (1993). The HGM wetland classification system provides a framework for categorizing wetlands based on landscape position, water source, and wetland hydrodynamics. Seepage wetlands correspond well with the concept of a "slope wetland" in the HGM system. Slope wetlands are found in sloping landscape positions, such as on hillsides, often at topographic breaks that allow the groundwater table to intersect the surface or where groundwater is forced up to the surface (Brinson 1993). A study of slope wetlands in the Mid-Atlantic Piedmont found three subclasses of slope wetlands (headwater, seep face, and floodplain), which were found to correspond well to vegetation patterns. The term “headwater type” was used for wetlands that occur along gentle upland slopes and in incised valleys created by first or second-order streams in a backslope position. “Seep faces” were found in foot/toe-slope positions, in areas with sharp topographic breaks. “Floodplain type” wetlands were found in toe-slope positions at the base of steep slopes on floodplains (Whelchel 2006). These subclasses do not correspond directly with the community types found here, but there is considerable overlap and the results further suggest that such landscape-driven geomorphology is an important driver of variation in seepage wetlands. Sheridan & Spies (2005), in a study of the hill-slope vegetation of zero-order basins in Oregon, also found that the distribution of plants follows gradients in geomorphology.

Some properties of soil composition and moisture availability vary predictably with landscape position due to continual processes of erosion and deposition. Sediment and water are transported downslope along hillsides and in drainages, and sediment is repeatedly being repositioned in bottomlands during flooding events. In general, upland interfluves tend to have soils dominated by clay, with low pH and low Ca and Mg, whereas transportational and depositional zones (backslope, Foot-slope, toeslope, and alluvial positions) tend to have greater sand content and higher pH, Ca, Mg (Hole & Campbell 1985; Brubaker et al. 1993). Flooding also influences soil properties, and alluvial soils are often highly fertile with texture that varies with floodplain geomorphology. Fine sediment is deposited in backswamps, which may extend to topographic breaks at the edge of the floodplain, giving them relatively high clay content (Mitsch & Gosselink 2007). Nutrient availability also appears to be an important driver for vegetation in many wetlands and has been studied extensively across the minerotrophic gradient in fens (Malmer 1986; Johnson & Leopold 1994; Wheeler & Proctor 2000). In a study of seepage wetlands in New York, Hall et al. (2001) found that pH, Ca, Mg, and nitrate were all strongly correlated with plant species composition. All examined ions, except Al, were found to be positively correlated with pH.

Seeps in different landscape positions may also be more likely to be supplied by water from different sources of seepage water. There are numerous mechanisms that lead to the development of seepage hydrology, including bedrock fractures, topographic convergence, as well as permeable or impermeable strata. Each mechanism is likely to be associated with distinct water chemistry and hydrodynamics (Stein et al 2004; Burns et al 1998; Winter 1998). Headwater seeps typically do not occur at topographic breaks, but instead are found in gentle concavities where saturation may be driven by topographic convergence combined with the presence of an impermeable stratum, such as a clay layer in the soil, as has been described for the Piedmont Seepage Wetland Ecological System defined by NatureServe (NatureServe 2010). Seeps in foot-slope or colluvial positions with very sandy soil may be associated with a highly permeable layer of sand or gravel. A fen in the North Carolina Mountains with sandier soil than neighboring fens was found to be underlain by a gravel deposit (Moorhead et al. 2000). Seepage that develops at the base of break in slope on the edge of a floodplain may arise from a combination of intersection with the water table, intersection with a stratum that creates horizontal water flow, upward force on groundwater water driven by the break, and permeable alluvial or colluvial deposits. In a study of the geologic settings of slope wetlands, Stein et al. (2004) found that seeps associated with alluvial and colluvial deposits had the most constant water supply and largest water reservoirs. The source of seepage water is important for vegetation because the constancy and quantity of water supplied have been found to be important drivers for vegetation across many types of wetland ecosystems (Hupp & Osterkamp 1994; Hall et al.

2001; Battaglia & Collins 2006). The source of wetland water is also likely to affect the nutrient supply available for wetland vegetation. The Infertile Swampy Seeps type has particularly low CEC, Mg, Mn, Zn, Na compared to Rich Foot-slope Seeps. Infertile Swampy Seeps are predominantly underlain by felsic, silica-rich rock, which occurs as complexes of biotite gneiss, mica schist, and granite. Such bedrock can produce groundwater with a low concentration of dissolved solids due to the resistance of silicate minerals to chemical weathering (Daniel & Dahlen 2002; Bedford & Godwin 2003). If characteristics of the composition of Infertile Swampy Seeps reflect a geologic driver, then the distribution of this community type, which is primarily restricted to the inner Piedmont, may be an artifact of the regional distribution of the bedrock with which it is associated.

Seeps as Inclusions

The seepage wetlands encountered in this study were frequently less than $1000m^2$ and occurred as inclusions in a matrix of upland forest or riparian vegetation. As small inclusions surrounded by different habitat, seepage wetlands function in some ways as habitat islands. Seepage wetlands are usually highly recognizable as distinct communities, particularly in upland settings, because they support a markedly different suite of species than the surrounding landscape. The dramatic species turnover, combined with the high species richness typical of seeps, allows seepage wetlands to significantly contribute to the diversity of a landscape despite their small size. High species turnover and contribution to local diversity has been found in studies of seeps from other regions of the U.S. and Canada (Morley & Calhoun 2009; Harrison et al. 2000; Sheridan & Spies 2005; Flinn et al 2008). Habitat islands are often influenced by the matrix in which they are embedded. The influence of matrix vegetation can be seen in this study, where some of the indicator species for each of the three broad groups are typical of the matrix vegetation that might be expected for that landscape position. This has implications for conservation and suggests that seepage wetlands may be susceptible to invasion by exotic species, as has been found for other patchy habitats if the matrix becomes modified. Conservation of the matrix community in conjunction with the seep should be expected to be important for maintaining natural vegetation in seepage wetlands (Wiser & Buxton 2008).

Compositional Variation

Classification of natural communities provides units of organization that serve as the foundation for many conservation and management activities. Without such a classification, the natural variation that exists within these communities would be difficult to operationalize. However, as can be seen in the ordination, composition of seepage wetlands varies fairly continuously and a classification necessarily imposes sharp boundaries on this continuum. The classification provides a representation of the characteristic variation found in seepage wetlands, but it should be recognized that because species tend to be distributed individualistically, the lines between community types are not absolute and there may be examples of seepage wetlands transitional between community types. In the Headwater Seeps group, it appears from historical records that several of the seeps that are here classified as a Streamhead Seep previously had vegetation characteristic of Headwater Boggy Seeps. Because these sites have not been recently burned, they may be undergoing a successional transition away from an open physiognomy and boggy flora. It is possible that if fire was returned to these sites, that composition characteristic of Headwater Boggy Seeps would return. Dynamic processes of disturbance or hydrologic change may also prompt successional changes in community composition. It is important to note that there was some evidence of disturbance in many of the sites sampled for this study. Some seeps in the Floodplain type, in particular, appeared to have been subject to anthropogenic or natural disturbance, which may contribute to the heterogeneity seen in that type.

Seep Classification

Seepage wetlands are small and widely ignored. One possible source of their limited recognition is the lack of a consistent, unifying definition implemented for seepage wetlands. Seepage wetlands have been conceptualized in a wide variety of frameworks that vary regionally and with discipline. Some examples of terms used for these habitats are: springs, seeps, groundwater discharge wetlands, fens, bogs, headwater wetlands, isolated wetlands, non-alluvial wetlands, slope wetlands, zero-order streams (Weakley & Schafale 1994; Bedford & Goodwin 2003; Whigham & Jordan 2003). Each concept overlaps partially and in different ways, so that in some ways seeps seem to have "fallen through the cracks" of wetland concepts. Seeps have a long tradition of being termed "bogs" in the Southeast, despite being groundwater driven. Because seeps are groundwater-fed wetlands, they may deserve inclusion in the concept of fens. While this term has been historically used in glaciated regions for wetlands with high pH and mineral content, the comparatively acidic seeps of the unglaciated Southeast could still fit well within the concept of a "poor fen" (Weakley & Schafale 1994).

The classification and community descriptions presented here may be used to supplement or refine community concepts for Piedmont seepage wetlands recognized by the U.S. National Vegetation Classification and state classifications. The seep community types identified here have been developed to be compatible with NVC associations (Jennings et al. 2009) and to contain a similar degree of compositional variation. Some community concepts presented here are broader than recognized NVC associations, while others are narrower. Many of the current NVC associations for Piedmont seepage wetlands are rated as having moderate confidence. The plot data and systematic classification over a large geographic area developed in this study should serve to refine and increase the confidence of association concepts. In an effort to facilitate the refinement of NVC concepts, a summary of the relationships between the community types found in this study and recognized NVC concepts has been developed along with recommendations for the revision of several NVC associations. A comparison of the relationships between the community types described here and NVC associations is also summarized in Table 2.3.

Acer rubrum var. *trilobum - Liriodendron tulipifera / Ilex opaca var. opaca / Osmunda cinnamomea* Forest (CEGL004551) is a fairly narrow association defined from four plots (004-01-0146, 004-01-0147, 004-04-0147, 004-05-0153) and is rated as having moderate confidence. The plots were sampled along several low-gradient, seepage-fed streams in the Uwharrie Mountains of North Carolina and the association is described as being restricted to the North Carolina Piedmont. The four plots used in defining this association were included in this analysis and are contained within the Streamhead Seep community type. The Streamhead Seep community type represents a similar, but expanded and more fully developed, concept than the *Acer rubrum* var. *trilobum - Liriodendron tulipifera / Ilex opaca var. opaca / Osmunda cinnamomea* Forest association. It is recommended that this association be retained but expanded in concept to include seepage wetlands in a broader range of headwater positions than solely those that occur along the banks of small, seepage-fed streams. Several plots in the Streamhead Seeps community type are located in other portions of North Carolina as well as Virginia, which suggests that the geographic range of this association should be expanded to include much of the outer Piedmont and extreme inner Coastal Plain from North Carolina to Virginia. The compositional description should be broadened to include important and diagnostic species such as *Vaccinium fuscatum, Eubotrys racemosa*, and *Chasmanthium laxum*.

Acer rubrum var. *trilobum / Morella caroliniensis - Gaylussacia frondosa / Andropogon glomeratus - (Sarracenia flava)* Woodland (CEGL004781) is a narrow association defined from two plots (004-02-0158 and 004-06-0153) and is rated as having moderate confidence. Both plots are from the Uwharrie Mountains of North Carolina. The two plots used to define this association were included in Headwater Boggy Seep community type, along with another location from the Uwharries and a location from the outer Piedmont of Virginia. The Headwater Boggy Seeps community type is approximately equivalent to the *Acer rubrum* var. *trilobum / Morella caroliniensis - Gaylussacia frondosa / Andropogon glomeratus - (Sarracenia flava)* Woodland association, but slightly broader. It is recommended that this association be retained but expanded in geographic coverage to include fire-maintained seeps from the outer Piedmont of North Carolina and southern Virginia. The association currently has very little description of its environmental setting so the environmental settings found for Headwater Boggy Seeps could be used to more fully develop the association's description. Because this community type was defined based on only two plots, the compositional description should be altered to include more species and reduce the importance of species such as *Sarracenia flava*, which only occurs in one plot. Important species such as *Eupatorium rotundifolium, Gaylussacia frondosa*, and *Xyris* spp. should be included in the compositional description.

Acer rubrum var. *trilobum / Viburnum nudum var. nudum / Osmunda cinnamomea - Saururus cernuus - Impatiens capensis* Forest (CEGL004426) is a somewhat broad association that encompasses much of the variety of seep settings found in the Piedmont and inner Coastal Plain of North Carolina and adjacent areas. The classification confidence is moderate and it is not tied to quantitative plot data. Details on the association's hydrology, soils, and geomorphology are mostly lacking. The compositional description is generalized, with rather limited detail, and the shrub stratum is not defined. Infertile Swampy Seeps, Rich Foot-slope Seeps, and Floodplain Seeps all overlap with this association concept, although they are each narrower in circumscription. Rich Foot-slope Seeps and Floodplain Seeps could be considered to be mostly contained within this association. This association also characterizes some, but not all, of the composition of Infertile Swampy Seeps. The importance of shrub species such as *Aronia arbutifolia, Ilex verticillata*, *Vaccinium fuscatum*, *Xanthorhiza simplicissima*, and *Toxicodendron vernix* for Infertile Swampy Seeps is not represented in the current description. Other important species in Infertile Swampy Seeps, such as *Smilax walteri*, *S. laurifolia*, as well as the endangered species, *Sagittaria fasciculata* and *Helenium brevifolium*, are also not included. It is recommended that a new association be developed for Infertile Swampy Seeps that covers its unique environmental features and its assemblage that is only minimally represented in the *Acer rubrum* var. *trilobum / Viburnum nudum var. nudum / Osmunda cinnamomea - Saururus cernuus - Impatiens capensis* Forest association. It is also recommended that this association be replaced by two new associations that capture the more consistent physical settings and compositional patterns associated with each of the Rich Foot-slope Seeps and Floodplain Seeps community types.

The above associations are found within either the *Acer rubrum - Nyssa sylvatica* Saturated Forest Alliance or the *Acer rubrum* Saturated Woodland Alliance. An additional alliance of interest is the *Nyssa biflora - Acer rubrum - (Liriodendron tulipifera)* Saturated Forest Alliance. This alliance is found in the southeastern U.S., primarily on the Coastal Plain, but it is also described as occurring in the Piedmont within seepage wetlands. In the alliance description, there is a comment that it is found at the Bunched Arrowhead Preserve in the Piedmont of South Carolina. Several plots from the Bunched Arrowhead Preserve were included in this analysis and constitute a portion of the Infertile Swampy Seeps community type. However, the associations within this alliance are all restricted to the Coastal Plain and do not occur in the Piedmont. While the *Nyssa biflora - Acer rubrum - (Liriodendron tulipifera)* Saturated Forest Alliance, as it is described, overlaps with the Infertile Swampy Seep concept, none of the associations within the alliance overlap with the community concept. It is recommended that a new association be developed to represent Infertile Swampy Seeps and that this association be placed in the *Acer rubrum - Nyssa sylvatica* Saturated Forest Alliance, along with the other Piedmont seepage wetland associations, particularly because *Nyssa sylvatica* swamp variety may be more important in this community type than is *Nyssa biflora*.

There are several other associations for seepage wetlands recognized by the NVC reported from the Piedmont of Virginia that have some compositional similarities to the concepts found in this study. However, these associations occur predominantly in other geographic regions and have some floristic differences that help to distinguish the concepts of this study from associations in adjacent areas. The *Acer rubrum - Nyssa sylvatica - Magnolia virginiana / Viburnum nudum var. nudum / Osmunda cinnamomea - Woodwardia* *areolata* Forest association (CEGL006238) is described for seepage wetlands of the Mid-Atlantic Coastal Plain, from Pennsylvania to Virginia. It is also reported to extend into the extreme eastern portion of the Piedmont of Virginia. This association is, in substance, a Coastal Plain type and appears to have minimal overlap geographically with the Piedmont. It is characterized by a number of common seepage wetland species as well as a suite of Coastal Plain species not found in this study, such as *Persea palustris, Triadenum virginicum, Bartonia paniculata, Carex collinsii,* and *Helonias bullata.* The association also differs environmentally and is described as supporting pools of standing water with deep or moderately deep muck, which is inconsistent with the seepage wetlands encountered in this study. The association appears to have limited overlap with Streamhead Seeps but it is possible that there are some seepage wetlands transitional between the two concepts in the outer Piedmont of southern Virginia.

The *Acer rubrum - Nyssa sylvatica / Ilex verticillata - Vaccinium fuscatum / Osmunda cinnamomea* Forest association (CEGL007853) occurs from Pennsylvania to North Carolina. It is described for the Mountains and western Piedmont, but within the Piedmont is only known from locations north of southern Virginia. In this study area, seepage wetlands of the western Piedmont were encountered south of southern Virginia, so there may be no geographic overlap between this association and the community concepts developed here. The association does share some compositional similarities with community types described in this study, but is fundamentally more montane floristically. Species such as *Viburnum cassinoides*, *Kalmia latifolia*, and *Carex gynandra* are dominant in examples of this association, while rarely encountered and of low abundance in this study. Additionally, the seepage wetlands encountered in the western Piedmont belong predominately to the Infertile

Swampy Seeps community type, which has a floristic affinity with the Coastal Plain rather than the Mountains, and has very limited compositional overlap with this association.

Acer rubrum - Fraxinus (pennsylvanica, americana) / Lindera benzoin / Symplocarpus foetidus Forest (CEGL006406) is a broad seepage swamp association found from southern New England to Virginia. This association appears to encompass seeps in similar settings to Rich Foot-slope Seeps and Floodplain Seeps, but the species assemblage is distinct and floristically more northern. Species such as *Quercus bicolor, Quercus palustris, Betula lenta, Ulmus americana,* and *Ulmus rubra* as well as *Lyonia ligustrina, Ilex montana* are common in this association while rare or absent in this study. Because this association has been described as occurring south to the northern-most portion of this study area, there may be some transitional locations between this association and Floodplain Seeps or Rich Foot-slope Seeps in the central Piedmont of Virginia.

State specific classifications often recognize somewhat broader community concepts and may incorporate a hierarchical format for community types, depending on the scale of resolution that is most appropriate for the state. This study provides rather comprehensive coverage of the North Carolina Piedmont, but contains relatively limited geographic coverage of South Carolina and Virginia. While the results of this study will likely be informative for state classifications in Virginia and South Carolina, specific recommendations for refinement of seepage wetland community concepts in those states would have limited utility without more complete geographic coverage of the state. This is particularly true for Virginia, where many of their seepage wetland communities are described for both the Piedmont and Coastal Plain, and moreover the Coastal Plain was not included in this study. The results of this study are most directly comparable to the North

Carolina state classification. The Classification of the Natural Communities of North Carolina: Fourth Approximation (Fourth Approximation; Schafale 2003) describes community concepts for North Carolina. The community concepts of this work have been developed to be congruent with NVC associations, although some of the NVC associations are recognized as community subtypes (Michael Schafale, pers. comm). Current Fourth Approximation community types for seepage wetlands strongly overlap with the NVC associations discussed above, so the recommendations for NVC associations would apply to the North Carolina community concepts as well.

The Fourth Approximation concept of Piedmont Boggy Streamhead, which corresponds to the NVC association *Acer rubrum* var. *trilobum - Liriodendron tulipifera / Ilex opaca var. opaca / Osmunda cinnamomea* Forest (CEGL004551) is included in the Streamhead Seeps community type identified here. It is recommended that Piedmont Boggy Streamheads be likewise expanded to include seepage wetlands in other headwater settings. The Fourth Approximation concept of Hillside Seepage Bog corresponds to the NVC association *Acer rubrum* var. *trilobum / Morella caroliniensis - Gaylussacia frondosa / Andropogon glomeratus - (Sarracenia flava)* Woodland (CEGL004781), which is approximately equivalent to the Headwater Boggy Seeps community type. The Hillside Seepage Bog concept is supported by the results of this study and the only recommendation is the minimal refinement of its compositional description suggested for the NVC association. The Fourth Approximation concept of Low Elevation Seep is somewhat broad like the NVC association *Acer rubrum* var. *trilobum / Viburnum nudum var. nudum / Osmunda cinnamomea - Saururus cernuus - Impatiens capensis* Forest (CEGL004426). Low Elevation Seep includes most of the variation in Infertile Swampy Seeps, Rich Foot-slope

Seeps, and Floodplain Seeps community types. It is recommended that each of these community types be recognized in the Fourth Approximation, possibly as subtypes of Low Elevation Seeps. A graphical overview of the relationships between community types of this study and Fourth Approximation concepts is presented in Table 2.4.

Table 2.1. Synoptic vegetation table of identified seepage wetland community types. Constancy (% Const.), average cover, fidelity (% Fid), and diagnostic value (% DV) are given for prevalent taxa within the five identified community types. Taxa are sorted alphabetically and must be prevalent in at least one community type to be included in the table. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Headwater Boggy Seeps				Streamhead Seeps				Infertile Swampy Seeps				Rich Footslope Seeps				Floodplain Seeps			
Group Plot Count	4				19				16				20				12			
Group Avg Plot Spp Richness	57				53				54				56				45			
taxon name	% Const	Cover	% Fid	% DV	% Const	Cover	% Fid	% DV	% Const	Cover	% Fid	% DV	% Const	Cover	% Fid	% DV	% Const	Cover	% Fid	% DV
Acer rubrum	100	4	9.3	9.3	100	7	9.3	9.3	100	7	9.3	9.3	100	7	9.3	9.3	83	7	0	0
Alnus serrulata	100	4	40.8	40.8	42	3	0	0	75	2	15.2	11.4	25	2	0	0	58	7	0	0
Amelanchier [arborea + canadensis]	50	3	15.4	7.7	42	2	7.2	3.02	63	2	28.5	18	5	2	0	0	17	1	0	0
Amphicarpaea bracteata	--	--	0	--	11	2	0	0	13	1	0	0	40	2	29.4	11.8	25	2	9.7	2.43
Andropogon sp	100	4	89.5	89.5	11	2	0	0	--	--	--	--	--	--	--	--	8	2	0	0
Arisaema triphyllum	--	--	--	--	68	2	23.2	15.8	50	2	4.7	2.35	100	4	54.9	54.9	8	2	0	0
Aronia arbutifolia	75	2	24.5	18.4	58	2	7.4	4.29	81	2	30.8	24.9	30	2	0	0	8	2	0	0
Arundinaria [gigantea + tecta]	--	--	--	--	42	4	27.9	11.7	19	2	0	0	30	4	12.7	3.81	8	2	0	0
Asclepias sp	75	2	80.3	60.2	5	1	0	0	--	--	--	--	--	--	--	--	--	--	--	--
Athyrium asplenioides	--	--	--	--	47	2	11.2	5.26	44	3	7.5	3.3	75	3	39.9	29.9	17	1	0	0

Bignonia capreolata	--	--	--	--	26	2	11.2	2.91	13	1	0	0	50	2	42.2	21.1	--	--	--	--
Boehmeria cylindrica	--	--	--	--	5	2	0	0	19	2	0	0	65	2	32.1	20.9	83	2	51.4	42.7
Calamovilfa brevipilis	25	6	45.9	11.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Campsis radicans	--	--	--	--	5	2	0	0	6	2	0	0	45	2	43	19.4	17	2	2.9	0.49
Carex [*atlantica + howei*]	--	--	--	--	26	2	0	0	50	3	15	7.5	35	3	0	0	67	2	32.4	21.7
Carex [*radiata + rosea*]	--	--	--	--	--	--	--	--	6	2	0	0	--	--	--	--	33	2	47.1	15.5
Carex allegheniensis	--	--	--	--	--	--	--	--	56	2	60.1	33.7	15	2	1.1	0.17	--	--	--	--
Carex crinita	--	--	--	--	26	2	2.2	0.57	13	3	0	0	25	2	0.7	0.18	58	2	39.5	22.9
Carex debilis	25	2	0	0	53	2	15	7.95	31	2	0	0	65	2	27.7	18	17	2	0	0
Carex laevivaginata	--	--	--	--	--	--	--	--	25	2	0	0	35	2	11.1	3.89	67	2	47.5	31.8
Carex leptalea var. leptalea	25	2	0	0	42	2	14.9	6.26	56	2	30.5	17.1	20	2	0	0	--	--	--	--
Carex lurida	25	2	0	0	5	2	0	0	44	2	9.4	4.14	25	2	0	0	75	2	42.2	31.7
Carex tribuloides	--	--	--	--	5	2	0	0	6	2	0	0	5	2	0	0	42	2	46.8	19.7
Carpinus caroliniana	--	--	--	--	21	3	0	0	--	--	--	--	70	5	58.9	41.2	17	2	0	0
Chasmanthium laxum	25	2	0	0	84	2	46.1	38.7	25	2	0	0	45	2	6	2.7	17	1	0	0
Chelone [glabra + obliqua]	--	--	--	--	16	2	0	0	50	2	25.2	12.6	55	2	30.8	16.9	17	2	0	0
Chrysopsis mariana	50	1	66.7	33.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Cinna arundinacea	--	--	--	--	11	3	0	0	--	--	--	--	25	2	3.5	0.88	75	2	63.7	47.8
Danthonia sericea	50	3	66.7	33.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Danthonia spicata	50	3	51.4	25.7	16	1	2.3	0.37	--	--	--	--	5	2	0	0	--	--	--	--
Decumaria barbara	--	--	--	--	--	--	--	--	38	4	37.8	14.4	25	2	18.9	4.73	--	--	--	--

Dichanthelium [chamaelonche + ensifolium]	25	7	39.7	9.93	5	2	0	0	--	--	--	--	--	--	--	--	--	--	--	--
Dichanthelium dichotomum var. ramulosum	--	--	--	--	42	2	8.2	3.44	31	2	0	0	65	2	32.3	21	33	2	0	0
Dichanthelium lucidum	25	7	8.1	2.03	21	2	3	0.63	38	2	24.1	9.16	10	2	0	0	--	--	--	--
Dichanthelium scoparium	75	2	78.3	58.7	--	--	--	--	--	--	--	--	--	--	--	--	8	1	0	0
Dioscorea [quaternata + villosa]	--	--	--	--	42	2	32.5	13.7	--	--	--	--	45	2	36.4	16.4	--	--	--	--
Diospyros virginiana	50	2	14.1	7.05	47	2	11.4	5.36	31	2	0	0	20	3	0	0	33	3	0	0
Drosera brevifolia	50	2	66.7	33.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Eubotrys racemosa	--	--	--	--	74	3	62.4	46.2	6	3	0	0	30	3	9.7	2.91	--	--	--	--
Euonymus americanus	--	--	--	--	79	2	27.4	21.6	69	2	17.2	11.9	85	2	33.5	28.5	25	1	0	0
Eupatorium [pubescens + rotundifolium]	100	2	100	100	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Eupatorium hyssopifolium	25	5	45.9	11.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Eupatorium leucolepis	50	2	66.7	33.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Eupatorium pilosum	75	2	84	63	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Eutrochium fistulosum	25	2	0	0	58	2	22.2	12.9	56	2	20.5	11.5	35	2	0	0	8	2	0	0
Fagus grandifolia	--	--	--	--	5	2	0	0	6	6	0	0	40	4	34.3	13.7	25	2	13.5	3.38
Fraxinus pennsylvanica	--	--	--	--	21	5	0	0	63	4	16.5	10.4	80	5	34.1	27.3	67	5	20.7	13.9
Galium tinctorium	--	--	--	--	--	--	--	--	13	2	0	0	5	2	0	0	50	2	53.4	26.7
Gaylussacia frondosa	75	4	49.6	37.2	68	3	42.4	28.8	--	--	--	--	5	2	0	0	--	--	--	--
Glyceria striata var. striata	--	--	--	--	11	3	0	0	50	2	6.6	3.3	65	2	21.7	14.1	92	3	48.6	44.7
Hexastylis sp	--	--	--	--	37	2	22.1	8.18	25	2	7.1	1.78	35	2	19.8	6.93	--	--	--	--

Hypericum mutilum var. mutilum	--	--	--	--	11	2	0.8	0.09	6	2	0	0	--	--	--	--	33	2	38.8	12.8
Hypericum setosum	50	2	66.7	33.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Ilex opaca var. opaca	50	2	0	0	84	3	26.5	22.3	88	2	29.9	26.3	60	2	2	1.2	8	2	0	0
Ilex verticillata	--	--	--	--	53	2	0.9	0.48	88	2	35.8	31.5	85	2	33.3	28.3	33	5	0	0
Impatiens [*capensis + pallida*]	--	--	--	--	--	--	--	--	31	2	1.8	0.56	25	2	0	0	92	2	68	62.6
Itea virginica	--	--	--	--	53	2	20.4	10.8	63	2	30.9	19.5	35	2	1.7	0.6	17	4	0	0
Juncus [*effusus + pylaei*]	--	--	--	--	11	1	0	0	38	2	16.8	6.38	35	2	13.9	4.87	33	2	11.9	3.93
Juncus coriaceus	50	2	28.9	14.5	21	2	0	0	19	2	0	0	10	2	0	0	25	2	0	0
Kalmia latifolia	--	--	--	--	16	2	8.3	1.33	38	3	43.5	16.5	--	--	--	--	--	--	--	--
Leersia oryzoides	--	--	--	--	--	--	--	--	25	2	10.1	2.53	20	2	3.5	0.7	42	2	32.1	13.5
Leersia virginica	--	--	--	--	32	2	0	0	56	2	17.4	9.74	75	2	36.6	27.5	33	2	0	0
Leucobryum sp	--	--	--	--	37	2	24.5	9.07	25	2	9.1	2.28	20	2	2.6	0.52	8	2	0	0
*Ligustrum sinense**	--	--	--	--	21	2	0	0	69	2	26	17.9	75	2	32.4	24.3	50	2	7.1	3.55
Lindera benzoin	--	--	--	--	11	2	0	0	25	5	0	0	55	5	29.9	16.4	50	4	24.4	12.2
Liquidambar styraciflua	100	4	23.7	23.7	95	5	16.9	16.1	69	2	0	0	95	5	17.2	16.3	50	5	0	0
Liriodendron tulipifera	75	2	0	0	100	6	22	22	88	6	5	4.4	90	6	8.4	7.56	67	1	0	0
*Lonicera japonica**	25	2	0	0	26	2	0	0	94	2	34.4	32.3	80	2	20.4	16.3	75	2	15.3	11.5
Lycopus virginicus	25	2	0	0	68	2	3.2	2.18	75	2	10.1	7.58	75	2	10.1	7.58	83	2	18.9	15.7
Lyonia ligustrina	25	6	34.3	8.58	--	--	--	--	11	2	7.5	0.83	--	--	--	--	--	--	--	--
Magnolia virginiana	--	--	--	--	53	5	39.3	20.8	6	5	0	0	45	5	29.9	13.5	--	--	--	--
Marchantiophyta sp	--	--	--	--	16	2	0	0	63	2	37.9	23.9	30	2	1.9	0.57	33	2	5.6	1.85
Medeola virginiana	--	--	--	--	53	2	47.4	25.1	13	2	0	0	20	2	4	0.8	--	--	--	--

*Microstegium vimineum**	--	--	--	--	--	--	--	--	75	2	29.8	22.4	60	2	14.7	8.82	92	6	46.5	42.8
Mitchella repens	--	--	--	--	68	2	27.8	18.9	69	2	28.1	19.4	60	2	19.2	11.5	8	2	0	0
Mnium sp	--	--	--	--	11	2	0	0	31	2	0	0	40	2	9.3	3.72	75	2	47	35.3
Morella caroliniensis	50	3	30.3	15.2	42	2	21.1	8.86	--	--	--	--	20	2	0	0	8	7	0	0
*Murdannia keisak**	--	--	--	--	--	--	--	--	19	2	7.8	1.48	15	2	2.3	0.35	33	6	29.2	9.64
Nyssa [*biflora + sylvatica swamp variety*]	50	2	12.7	6.35	32	4	0	0	69	8	32	22.1	30	7	0	0	8	6	0	0
Nyssa sylvatica	100	3	52.7	52.7	68	5	21.1	14.3	25	4	0	0	35	3	0	0	8	2	0	0
Osmunda regalis var. spectabilis	25	2	0	0	95	4	56	53.2	31	2	0	0	40	3	0.1	0.04	8	3	0	0
Osmundastrum cinnamomeum	75	4	11.3	8.48	95	4	31.9	30.3	56	3	0	0	70	3	6.1	4.27	25	3	0	0
Oxydendrum arboreum	75	2	30.5	22.9	79	4	34.4	27.2	31	4	0	0	30	4	0	0	8	2	0	0
Panicum virgatum	50	3	66.7	33.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Parthenocissus quinquefolia	25	2	0	0	63	2	0	0	88	2	24.1	21.2	80	2	16.2	13	67	2	2.3	1.54
Peltandra virginica	--	--	--	--	--	--	--	--	19	2	7.8	1.48	15	2	2.3	0.35	33	3	29.2	9.64
*Persicaria longiseta**	--	--	--	--	--	--	--	--	13	1	3.9	0.51	5	2	0	0	33	2	38.3	12.6
Persicaria sagittata	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	50	2	66.7	33.4
Pinus palustris	75	3	80.3	60.2	5	3	0	0	--	--	--	--	--	--	--	--	--	--	--	--
Pinus taeda	50	2	19.2	9.6	53	2	22	11.7	6	1	0	0	35	2	3.1	1.09	17	3	0	0
Platanthera sp	--	--	--	--	37	1	0.1	0.04	69	2	33.1	22.8	70	2	34.4	24.1	8	1	0	0
Pogonia ophioglossoides	50	1	66.7	33.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Polygala lutea	50	2	66.7	33.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Polystichum acrostichoides	--	--	--	--	5	1	0	0	13	2	0	0	35	2	20.6	7.21	42	2	29.1	12.2

Prunus serotina var. serotina	25	3	0	0	32	2	0	0	63	2	26.2	16.5	25	2	0	0	42	2	4.7	1.97
Pteridium aquilinum	50	2	54.5	27.3	16	2	3.9	0.62	--	--	--	--	--	--	--	--	--	--	--	--
Pycnanthemum tenuifolium	25	5	45.9	11.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Quercus alba	100	1	47.6	47.6	95	5	42.3	40.2	38	2	0	0	30	2	0	0	--	--	--	--
Quercus phellos	50	1	11.8	5.9	32	2	0	0	38	2	0	0	40	2	1.6	0.64	33	2	0	0
Quercus rubra	--	--	--	--	37	2	35.8	13.2	13	2	0	0	15	1	3.2	0.48	--	--	--	--
Quercus stellata	75	2	77	57.8	5	3	0	0	--	--	--	--	5	1	0	0	--	--	--	--
Quercus velutina	25	1	1.9	0.48	42	1	22.1	9.28	25	2	1.9	0.48	25	2	1.9	0.48	--	--	--	--
Rhexia mariana	75	2	78.3	58.7	--	--	--	--	--	--	--	--	--	--	--	--	8	2	0	0
Rhododendron sp	25	1	0	0	63	2	32.9	20.7	44	2	12.1	5.32	30	2	0	0	--	--	--	--
*Rosa multiflora**	--	--	--	--	--	--	--	--	44	2	40.9	18	5	2	0	0	25	2	14.5	3.63
Rosa palustris	--	--	--	--	--	--	--	--	31	2	19.7	6.11	10	1	0	0	42	2	33.7	14.2
Rubus pensilvanicus	50	2	10.4	5.2	11	1	0	0	44	2	4	1.76	45	2	5.3	2.39	50	2	10.4	5.2
Saccharum sp	50	4	66.7	33.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sagittaria latifolia	--	--	--	--	--	--	--	--	--	--	--	--	10	1	0	0	67	2	71.2	47.7
Sambucus canadensis	--	--	--	--	5	1	0	0	44	2	19.6	8.62	50	2	26.7	13.4	33	2	7.8	2.57
Sanicula sp	--	--	--	--	11	2	0	0	19	2	6	1.14	35	2	29.1	10.2	8	2	0	0
Sarracenia purpurea var. venosa	25	6	34	8.5	5	2	0	0	6	3	0	0	--	--	--	--	--	--	--	--
Saururus cernuus	--	--	--	--	--	--	--	--	--	--	--	--	70	3	60.9	42.6	33	7	15.6	5.15
Scleria [*nitida + triglomerata*]	75	2	84	63	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Scleria ciliata	25	5	45.9	11.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--

Scutellaria integrifolia	50	2	28.5	14.3	58	2	37.6	21.8	--	--	--	--	10	1	0	0	8	2	0	0
Smilax glauca	25	2	0	0	79	2	35.4	28	50	2	6.3	3.15	40	2	0	0	25	2	0	0
Smilax laurifolia	75	2	27	20.3	58	2	9.9	5.74	69	3	20.8	14.4	30	2	0	0	8	2	0	0
Smilax rotundifolia	25	2	0	0	74	2	5.2	3.85	88	2	20.1	17.7	100	3	33.6	33.6	58	2	0	0
Smilax walteri	--	--	--	--	16	2	0	0	56	2	51.2	28.7	15	2	0	0	--	--	--	--
Solidago caesia	--	--	--	--	42	2	3.4	1.43	50	2	11.5	5.75	60	2	21.8	13.1	42	2	3	1.26
Solidago rugosa	25	4	0.3	0.08	21	2	0	0	13	2	0	0	40	2	17.7	7.08	25	2	0.3	0.08
Solidago stricta	50	2	62.1	1.24	5	2	0	0	--	--	--	--	--	--	--	--	--	--	--	--
Sophronanthe pilosa	50	2	66.7	33.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sphagnum sp	25	2	0	0	47	2	9.3	4.37	38	2	0	0	40	3	1.7	0.68	42	4	3.5	1.47
Symphyotrichum dumosum	100	2	100	100	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Symphyotrichum puniceum var. puniceum	--	--	--	--	--	--	--	--	6	2	0	0	--	--	--	--	42	2	54.5	22.9
Thuidium sp	--	--	--	--	53	2	0	0	81	2	23.8	19.3	80	2	22.5	18	75	2	17.4	13.1
Toxicodendron radicans	50	2	0	0	84	2	2.4	2.02	88	2	6.8	5.98	90	2	10	9	100	2	23.2	23.2
Toxicodendron vernix	--	--	--	--	--	--	--	--	38	2	52	19.8	5	2	0	0	--	--	--	--
Ulmus alata	50	1	32.6	16.3	--	--	--	--	--	--	--	--	30	2	8.8	2.64	33	3	12.7	4.19
Uvularia [*puberula + sessilifolia*]	--	--	--	--	42	2	38.8	16.3	6	2	0	0	25	2	14.6	3.65	--	--	--	--
Vaccinium [corymbosum + fuscatum + formosum]	75	2	14.4	10.8	100	4	40	40	75	4	14.4	10.8	55	4	0	0	--	--	--	--
Viburnum dentatum	25	3	0	0	16	3	0	0	38	3	13.1	4.98	35	2	10.3	3.61	17	3	0	0
Viburnum nudum	25	2	0	0	89	3	35.6	31.7	94	5	39.9	37.5	45	4	0	0	17	4	0	0

Viola primulifolia	50	2	15.8	7.9	53	2	18.5	9.81	44	2	9.2	4.05	20	2	0	0	8	3	0	0
Viola sp	25	2	0	0	26	2	0	0	50	2	12.1	6.05	40	2	1.8	0.72	50	2	12.1	6.05
Vitis rotundifolia var. rotundifolia	25	1	0	0	95	2	34.9	33.2	75	2	14.7	11	75	2	14.7	11	33	1	0	0
Vitis subgenus Vitis	50	2	17.4	8.7	47	2	14.6	6.86	19	2	0	0	35	2	1.5	0.53	17	5	0	0
Woodwardia areolata	50	2	1.5	0.75	58	3	9.4	5.45	56	4	7.8	4.37	70	4	21.5	15.1	8	4	0	0
Xanthorhiza simplicissima	--	--	--	--	26	2	12	3.12	50	2	43.3	21.7	10	1	0	0	--	--	--	--
Xyris sp	75	2	76.9	57.7	11	2	0	0	--	--	--	--	--	--	--	--	--	--	--	--

Table 2.2. Means and standard errors of measured environmental and compositional variables by seepage wetland community type.

Community Type	% Org Mean	% Org ±SE	% Sand Mean	% Sand ±SE	% Silt Mean	% Silt ±SE	% Clay Mean	% Clay ±SE	pH Mean	pH ±SE
Streamhead Seeps	8.66	3.38	42.63	5.24	48.06	3.90	9.31	1.81	4.57	0.12
Headwater Boggy Seeps	5.52	0.66	11.74	8.44	72.13	4.82	16.13	4.32	4.23	0.35
Infertile Swampy Seeps	7.46	1.27	78.56	3.40	17.33	3.17	4.12	0.53	5.03	0.06
Rich Foot-slope Seeps	10.99	2.34	65.81	3.89	29.53	3.89	4.66	0.98	4.99	0.09
Floodplain Seeps	9.17	0.85	38.09	5.65	46.45	4.45	15.45	2.80	4.99	0.09

	CEC Mean	CEC ±SE	BaseSat Mean	BaseSat ±SE	N Mean	N ±SE	S Mean	S ±SE	P Mean	P ±SE
Streamhead Seeps	7.80	1.00	37.02	3.20	50.03	1.69	26.17	4.98	22.07	2.64
Headwater Boggy Seeps	4.53	0.60	31.55	7.09	50.83	2.13	35.58	15.09	13.42	4.88
Infertile Swampy Seeps	5.32	0.72	49.46	1.76	51.20	2.79	13.83	0.97	18.89	3.59
Rich Foot-slope Seeps	8.79	0.89	49.03	2.27	52.18	3.08	18.61	3.00	19.00	2.92
Floodplain Seeps	10.62	1.33	48.70	2.31	58.38	1.84	24.17	2.46	30.92	7.20

	Ca ppm Mean	Ca ppm ±SE	Mg ppm Mean	Mg ppm ±SE	K ppm Mean	K ppm ±SE	Na ppm Mean	Na ppm ±SE	% Ca Mean	% Ca ±SE
Streamhead Seeps	355.75	51.58	73.82	10.40	55.47	10.99	29.71	2.29	24.72	2.79
Headwater Boggy Seeps	169.92	19.17	40.50	2.36	27.33	4.48	19.17	4.69	20.12	5.23
Infertile Swampy Seeps	371.75	57.83	66.09	10.80	44.03	6.83	23.56	1.27	34.64	1.61
Rich Foot-slope Seeps	574.66	61.42	126.45	21.24	50.45	5.61	41.93	5.04	33.57	2.04
Floodplain Seeps	747.33	110.45	147.17	35.22	61.08	7.48	34.17	6.94	34.99	1.87

	% Mg Mean	% Mg ±SE	% K Mean	% K ±SE	% Na Mean	% Na ±SE	% Othr Mean	% Othr ±SE	% H Mean	% H ±SE
Streamhead Seeps	8.34	0.70	1.96	0.23	2.00	0.22	8.56	0.31	55.59	3.32
Headwater Boggy Seeps	7.67	0.61	1.70	0.52	2.07	0.78	8.95	0.71	59.50	6.38
Infertile Swampy Seeps	10.29	0.57	2.20	0.21	2.33	0.24	7.33	0.13	43.20	1.63
Rich Foot-slope Seeps	11.57	1.04	1.63	0.18	2.25	0.20	7.41	0.17	43.56	2.11
Floodplain Seeps	10.50	1.14	1.55	0.14	1.66	0.36	7.43	0.17	44.46	1.91

	B ppm Mean	B ppm ±SE	Fe ppm Mean	Fe ppm ±SE	Mn ppm Mean	Mn ppm ±SE	Cu ppm Mean	Cu ppm ±SE	Zn ppm Mean	Zn ppm ±SE
Streamhead Seeps	0.28	0.05	296.33	32.44	16.09	3.65	0.58	0.07	1.93	0.23
Headwater Boggy Seeps	0.42	0.10	402.17	106.18	7.42	2.90	0.35	0.07	0.99	0.08
Infertile Swampy Seeps	0.25	0.04	423.13	44.68	10.27	2.44	1.17	0.11	2.33	0.29
Rich Foot-slope Seeps	0.26	0.02	448.61	29.58	27.48	4.94	1.31	0.17	4.63	1.01
Floodplain Seeps	0.37	0.06	546.08	62.06	50.17	18.84	2.26	0.28	3.10	0.59

	Al ppm		Ca/Mg ppm		StrmVel		StrmVol		StrmSlope	
	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**
Streamhead Seeps	456.12	33.43	5.31	0.70	0.84	0.02	1.81	0.23	15.74	2.20
Headwater Boggy Seeps	546.67	72.07	4.31	0.75	0.77	0.06	1.00	0.67	24.61	2.47
Infertile Swampy Seeps	654.64	51.19	5.94	0.51	0.80	0.04	2.07	0.78	16.63	5.82
Rich Foot-slope Seeps	514.31	30.08	5.62	0.57	1.00	0.07	1.75	0.35	5.33	1.45
Floodplain Seeps	738.17	59.07	6.34	0.91	1.06	0.11	3.16	1.11	3.76	0.75

	DistStrm (m)		DistFld (m)		HydInd		StrmOrder		CanHt (m)	
	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**
Streamhead Seeps	133.06	24.52	2092.57	246.35	3.38	0.04	1.26	0.15	25.47	1.69
Headwater Boggy Seeps	290.71	80.98	1378.43	378.31	3.33	0.12	1.00	0.00	8.33	3.33
Infertile Swampy Seeps	150.00	41.42	977.04	246.04	3.60	0.05	1.38	0.13	25.94	1.60
Rich Foot-slope Seeps	295.31	48.38	154.18	49.53	3.53	0.05	2.80	0.38	29.20	1.13
Floodplain Seeps	109.75	22.87	-1.05	23.68	3.78	0.08	3.00	0.44	19.75	1.42

	Elev (m)		Slope (°)		Stems/m^2	
	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**
Streamhead Seeps	183.93	16.17	2.79	0.39	0.85	0.13
Headwater Boggy Seeps	224.77	1.23	5.33	2.40	0.14	0.06
Infertile Swampy Seeps	321.08	15.31	1.81	0.26	1.26	0.18
Rich Foot-slope Seeps	97.13	13.04	1.88	0.25	0.81	0.09
Floodplain Seeps	227.88	23.91	1.17	0.11	0.72	0.17

Table 2.3. Relationship of the identified seepage wetland community types to recognized NVC associations. Relationships are depicted in the table by four symbols: < indicates the community type is included in the NVC concept, > indicates the community type includes the NVC concept, >< indicates that the two concepts overlap, ~ indicates the community type is approximately equivalent to the NVC concept.

Community	Seep Vegetation Type	Relationship	CEGL	NVC Association (Alliance)
		Headwater Seeps		
Streamhead Seeps	*Acer rubrum / Vaccinium fuscatum - Eubotrys racemosa / Osmundastrum cinnamomeum - Osmunda regalis var. spectabilis - Chasmanthium laxum Forest*	>	4551	*Acer rubrum var. trilobum - Liriodendron tulipifera / Ilex opaca var. opaca / Osmunda cinnamomea* Forest (Acer rubrum - Nyssa sylvatica Saturated Forest Alliance)
Headwater Boggy Seeps	*Acer rubrum / Gaylussacia frondosa / Andropogon spp (A. glomeratus) - Osmundastrum cinnamomeum - Eupatorium rotundifolium Woodland*	~	4781	*Acer rubrum var. trilobum / Morella caroliniensis - Gaylussacia frondosa / Andropogon glomeratus - (Sarracenia flava)* Woodland (*Acer rubrum* Saturated Woodland Alliance)
		Lowland Seeps		
Infertile Swampy Seeps	*Acer rubrum - Nyssa sylvatica swamp variety (Nyssa biflora) / Viburnum nudum – Aronia arbutifolia / Smilax laurifolia / Carex allegheniensis Forest*	><	4426	*Acer rubrum var. trilobum / Viburnum nudum var. nudum / Osmunda cinnamomea - Saururus cernuus - Impatiens capensis Forest* (*Acer rubrum - Nyssa sylvatica* Saturated Forest Alliance)
		><		No Association but within (*Nyssa biflora - Acer rubrum - (Liriodendron tulipifera)* Saturated Forest Alliance)
Rich Foot-slope Seeps	*Acer rubrum / Ilex verticillata / Arisaema triphyllum - Saururus cernuus – Platanthera sp. Forest*	<	4426	*Acer rubrum var. trilobum / Viburnum nudum var. nudum / Osmunda cinnamomea - Saururus cernuus - Impatiens capensis* Forest (*Acer rubrum - Nyssa sylvatica* Saturated Forest Alliance)
		Floodplain Seeps		
Floodplain Seeps	*Acer rubrum / Alnus serrulata - Lindera benzoin / Glyceria striata - Impatiens capensis – Carex atlantica Forest*	<	4426	*Acer rubrum var. trilobum / Viburnum nudum var. nudum / Osmunda cinnamomea - Saururus cernuus - Impatiens capensis* Forest (*Acer rubrum - Nyssa sylvatica* Saturated Forest Alliance)

Table 2.4. Relationship of the identified seepage wetland community types to established community concepts from the North Carolina state classification. Community types are compared to North Carolina's *Classification of the natural communities of North Carolina: fourth approximation* (Schafale 2003). Relationships are depicted in the table by four symbols: < indicates the community type is included in the concept, > indicates the community type includes the concept, >< indicates that the two concepts overlap, ~ indicates the community type is approximately equivalent to the concept.

Community	Seep Vegetation Type	Relationship	NC State Classification Community Type
Headwater Seeps			
Streamhead Seeps	*Acer rubrum / Vaccinium fuscatum - Eubotrys racemosa / Osmundastrum cinnamomeum - Osmunda regalis var. spectabilis - Chasmanthium laxum Forest*	>	Piedmont Boggy Streamhead
Headwater Boggy Seeps	*Acer rubrum / Gaylussacia frondosa / Andropogon spp (A. glomeratus) - Osmundastrum cinnamomeum - Eupatorium rotundifolium Woodland*	<	Hillside Seepage Bog
Lowland Seeps			
Infertile Swampy Seeps	*Acer rubrum - Nyssa sylvatica swamp variety (Nyssa biflora) / Viburnum nudum – Aronia arbutifolia / Smilax laurifolia / Carex allegheniensis Forest*	<	Low Elevation Seep
Rich Foot/Backslope Seeps	*Acer rubrum / Ilex verticillata / Arisaema triphyllum - Saururus cernuus- Platanthera sp. Forest*	<	Low Elevation Seep
Floodplain Seeps			
Floodplain Seeps	*Acer rubrum / Alnus serrulata - Lindera benzoin / Glyceria striata - Impatiens capensis – Carex atlantica Forest*	<	Low Elevation Seep

Table 2.5. Plot assignment to community types derived from cluster analysis of seepage wetlands. The source of plot data, from the Carolina Vegetation Survey (CVS) or the Virginia Natural Heritage Program (VANHP), is indicated in the table. Plots that well-represent the core concept of the community type, are indicated by an asterisk (*).

Plot	Source	Assigned Community Type
004-01-0146	CVS	Streamhead Seep
004-01-0147	CVS	Streamhead Seep*
004-02-0158	CVS	Headwater Boggy Seep
004-04-0147	CVS	Streamhead Seep
004-06-0153	CVS	Headwater Boggy Seep*
004-05-0153	CVS	Streamhead Seep
042-01-0628	CVS	Infertile Swampy Seep
089-01-1228	CVS	Streamhead Seep
089-03-1226	CVS	Rich Foot-slope Seep
089-03-1227	CVS	Rich Foot-slope Seep
114-01-0001	CVS	Floodplain Seep*
114-01-0002	CVS	Floodplain Seep
114-01-0003	CVS	Rich Foot-slope Seep
114-01-0004	CVS	Rich Foot-slope Seep
114-01-0005	CVS	Floodplain Seep
114-01-0006	CVS	Infertile Swampy Seep
114-01-0007	CVS	Infertile Swampy Seep
114-01-0008	CVS	Infertile Swampy Seep
114-01-0009	CVS	Infertile Swampy Seep
114-01-0010	CVS	Floodplain Seep
114-01-0011	CVS	Infertile Swampy Seep
114-01-0018	CVS	Streamhead Seep
114-01-0020	CVS	Streamhead Seep
114-01-0021	CVS	Streamhead Seep
114-01-0022	CVS	Streamhead Seep
114-01-0025	CVS	Rich Foot-slope Seep
114-01-0026	CVS	Rich Foot-slope Seep
114-01-0028	CVS	Rich Foot-slope Seep
114-01-0029	CVS	Rich Foot-slope Seep
114-01-0030	CVS	Streamhead Seep
114-01-0031	CVS	Streamhead Seep

114-01-0033	CVS	Streamhead Seep
114-01-0034	CVS	Headwater Boggy Seep
114-01-0035	CVS	Streamhead Seep
114-01-0036	CVS	Streamhead Seep
114-01-0040	CVS	Floodplain Seep
114-01-0041	CVS	Infertile Swampy Seep
114-01-0042	CVS	Floodplain Seep
114-01-0043	CVS	Infertile Swampy Seep
114-01-0044	CVS	Infertile Swampy Seep
114-01-0045	CVS	Infertile Swampy Seep
114-01-0046	CVS	Infertile Swampy Seep*
114-01-0047	CVS	Infertile Swampy Seep
114-01-0048	CVS	Streamhead Seep
114-01-0049	CVS	Infertile Swampy Seep
114-01-0050	CVS	Infertile Swampy Seep
114-01-0051	CVS	Floodplain Seep
114-01-0052	CVS	Floodplain Seep
114-01-0053	CVS	Infertile Swampy Seep
114-01-0054	CVS	Floodplain Seep
114-01-0055	CVS	Infertile Swampy Seep
114-01-0058	CVS	Rich Foot-slope Seep*
114-01-0059	CVS	Rich Foot-slope Seep
114-01-0060	CVS	Rich Foot-slope Seep
114-01-0061	CVS	Rich Foot-slope Seep
114-01-0062	CVS	Rich Foot-slope Seep
114-01-0063	CVS	Streamhead Seep
114-01-0064	CVS	Rich Foot-slope Seep
114-01-0065	CVS	Rich Foot-slope Seep
114-01-0066	CVS	Rich Foot-slope Seep
114-01-0067	CVS	Rich Foot-slope Seep
114-01-0071	CVS	Rich Foot-slope Seep
114-01-0072	CVS	Floodplain Seep
114-01-0074	CVS	Streamhead Seep
114-01-0075	CVS	Floodplain Seep
114-06-0076	CVS	Rich Foot-slope Seep
120-07-1434	CVS	Rich Foot-slope Seep
APCO008	VANHP	Floodplain Seep
FPMR002	VANHP	Headwater Boggy Seep
PNBP004	VANHP	Streamhead Seep
PNBP008	VANHP	Streamhead Seep

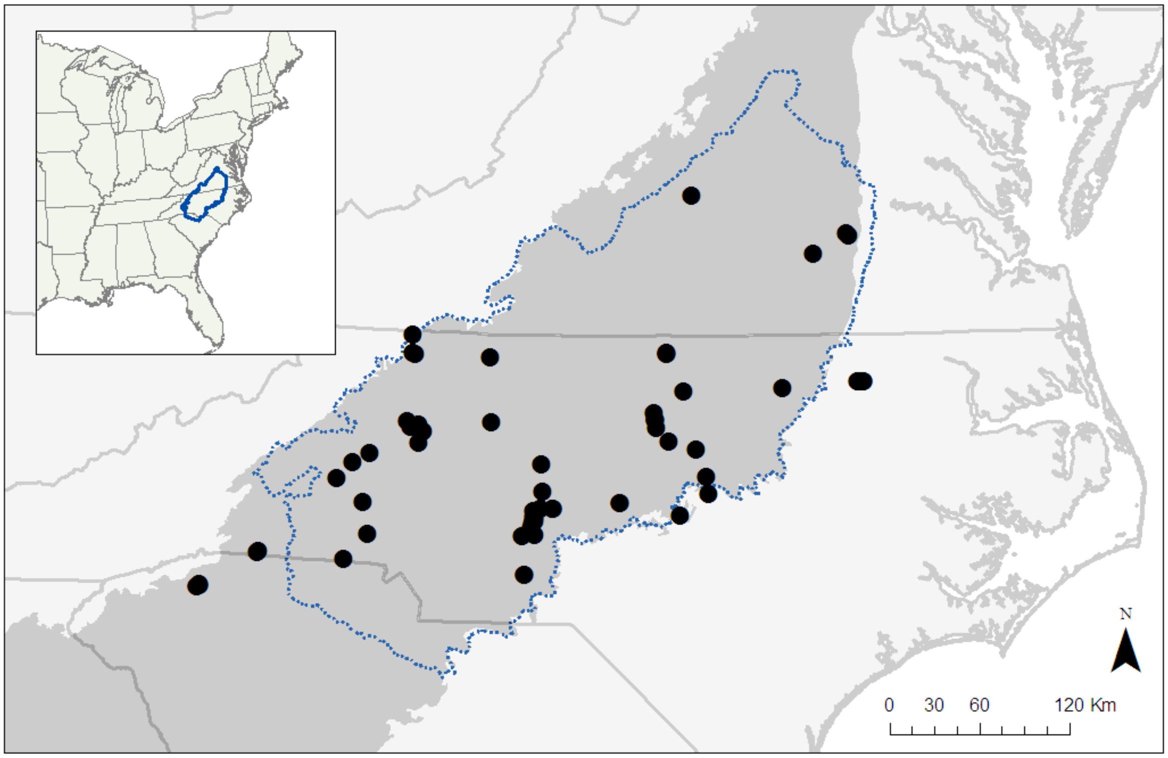

Figure 2.1. Map of study area and locations of 71 seepage wetland vegetation plots. Plots are marked by black circles and the Piedmont physiographic province is shaded in gray. The dashed blue line represents the "northern Piedmont" MRLC map zone recognized by NatureServe (NatureServe 2010).

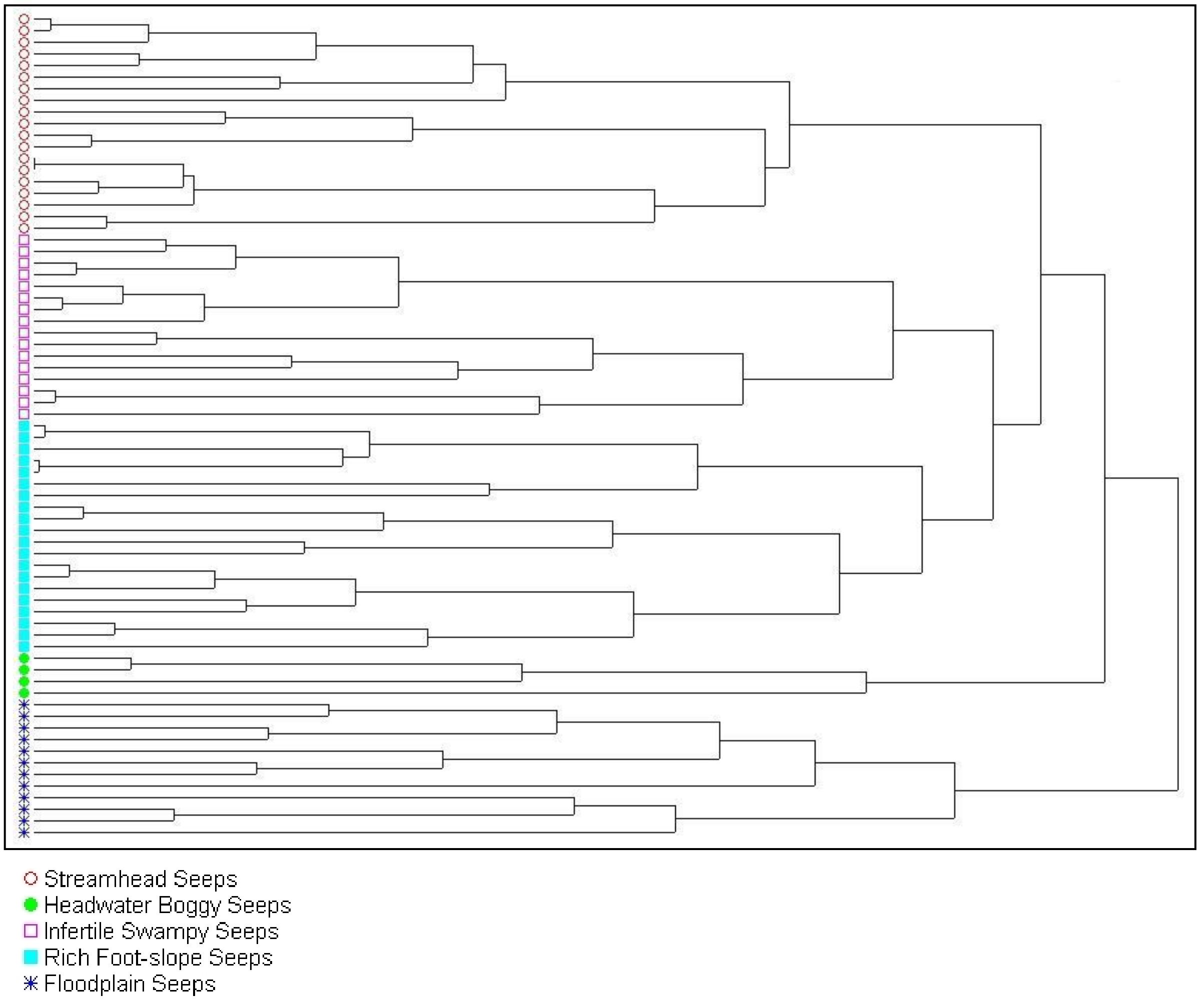

Figure 2.2. Dendrogram from a hierarchical cluster analysis with flexible β linkage (β = -0.25) used to identify seepage wetland community types. Color coded symbols correspond to community types identified from the cluster analysis.

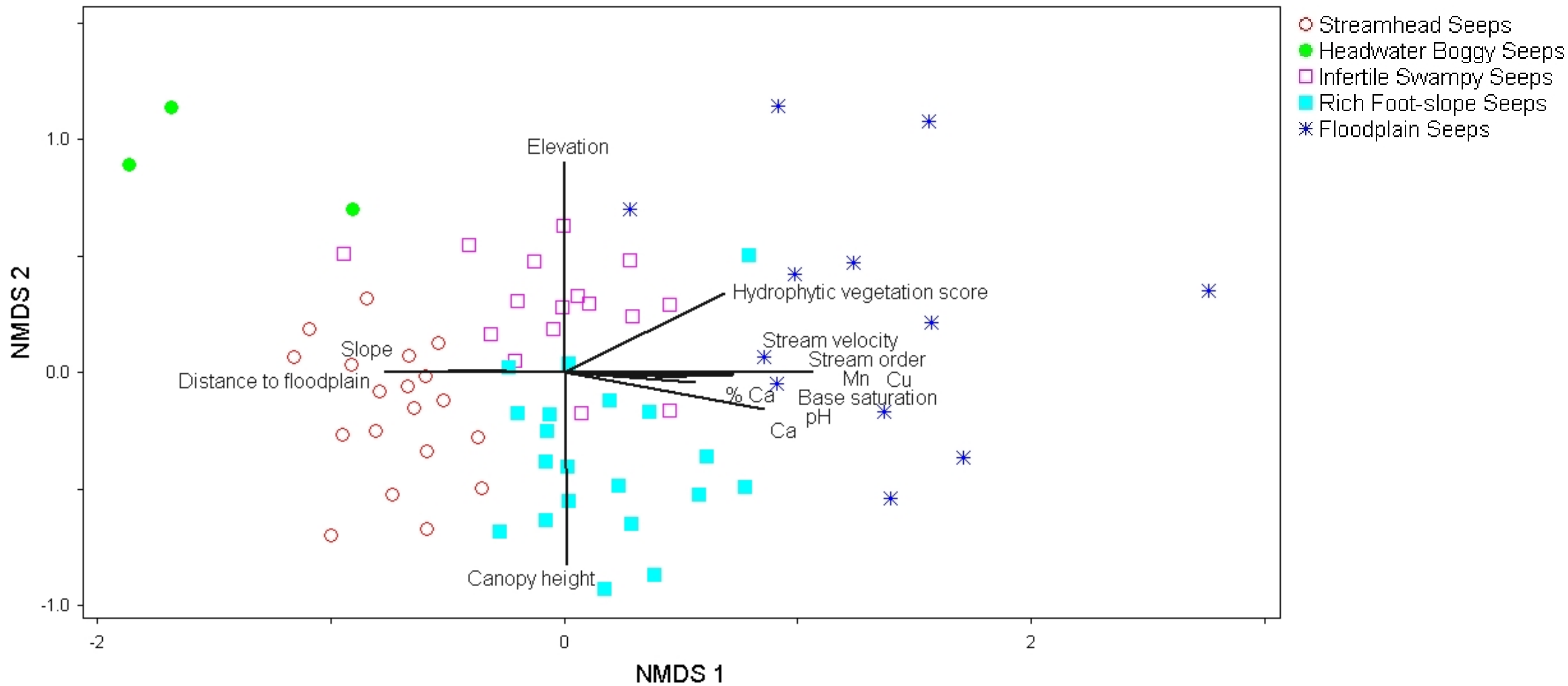

Figure 2.3. Two-dimensional non-metric multidimensional scaling (NMS) ordination of seepage wetland vegetation with joint-plot overlay. Correlation of environmental variables with ordination axes (cutoff r = 0.4) are displayed with joint-plot overlay vectors, where the length and direction of the vector represent the strength and the direction of correlation with the axes, respectively. Color coded symbols correspond to community types identified from the cluster analysis.

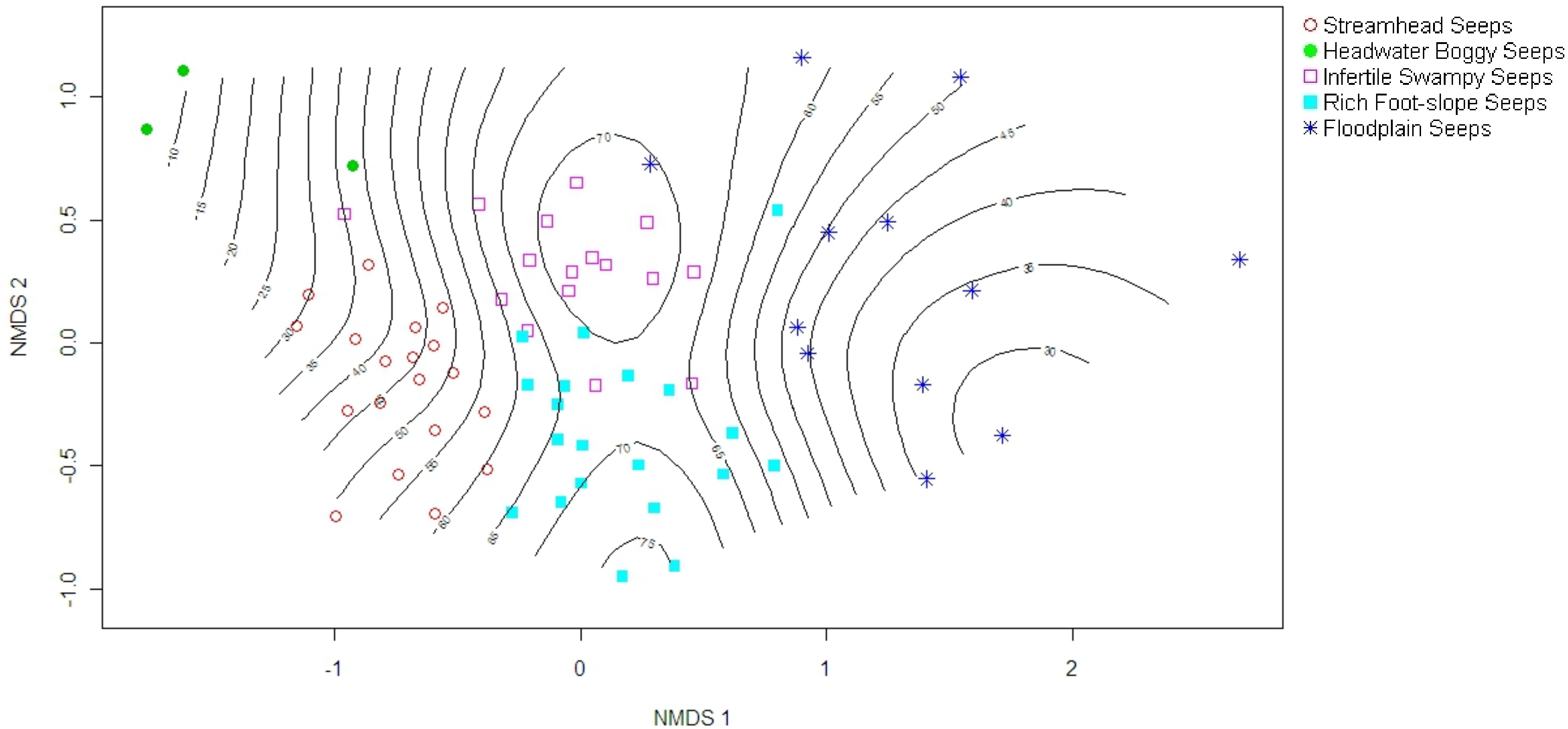

Figure 2.4. Two-dimensional non-metric multidimensional scaling (NMS) ordination of seepage wetland vegetation with surface overlay. Overlaid contour map is a fitted surface of plot percent sand content ($D^2 = 0.5385$). The surface overlay displays the non-linear relationship between % sand content and the ordination axes that is not visible from a joint plot overlay. Color coded symbols correspond to community types identified from the cluster analysis.

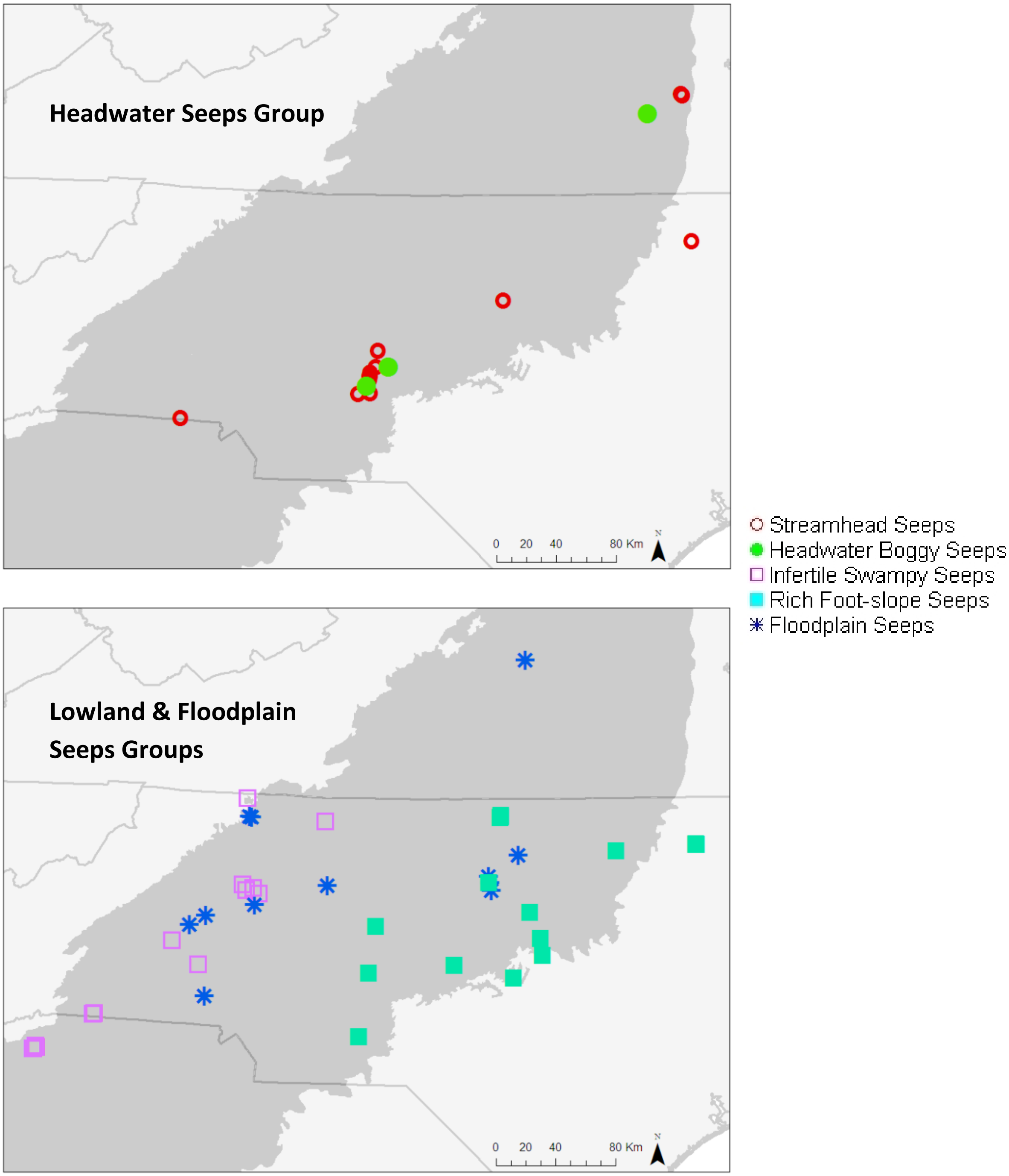

Figure 2.5. Geographic distribution of plots within identified seepage wetland community types. Community types are mapped by higher-level groups. Color coded symbols correspond to community types identified from the cluster analysis. The boundaries of the Piedmont are show in gray.

Chapter 3. Classification and Description of Piedmont Upland Depression Swamp Plant Communities

Introduction

Wetlands that form in topographic depressions are often called vernal pools, temporary ponds, or ephemeral wetlands. These depressional wetlands typically occur as small, closed topographic concavities underlain by low-permeability substrates that impede drainage. In climates with seasonal rainfall, they are characterized by a seasonal wet-dry cycle driven by precipitation. These depressions fill with seasonal rains that produce saturated conditions, followed by period of a gradual drying as conditions in the wetland begin to mirror those in neighboring terrestrial habitats (Zedler 2003; Kirkman et al. 2000). Many depressional wetlands are isolated from other aquatic systems and lack permanent connections to surface waters. Such isolated depressions, surrounded by upland habitat, form wetland inclusions in a terrestrial landscape (Sharitz 2003; Tiner 2003a; Hérault & Thoren 2009). Some commonly studied forms of depressional wetlands in the U.S. are the Mediterranean-climate driven “vernal pools” of California, “vernal pools” formed in glaciated landscapes of the Northeast, and “Carolina bays” of the Mid-Atlantic and southeastern Atlantic Coastal Plain (Sharitz & Gibbons 1982; Keeley & Zedler 1998; Sharitz 2003; Colburn 2004; Barbour et al. 2005).

However, depressional wetlands in some regions have received limited research attention. Upland depressional wetlands in the Piedmont of the southeastern U.S. have been broadly ignored in studies of both biological communities and wetland function. In this unglaciated region of the U.S., depressional wetlands are commonly formed as subtle low-points on poorly drained upland flats that may be closed basins or drainage headwaters of very low relief. Most examples are found over low-permeability substrates weathered from mafic rock, resulting in heavy montmorillonitic clays with a high shrink-swell capacity or in the presence of an impermeable hardpan below the surface (Schafale & Weakley 1990; Fleming et al. 2010; NatureServe 2010). The terrestrial setting and impermeable substrate act to isolate upland depressions from widespread groundwater systems. Water inputs are from rainfall and localized surface runoff, while water losses are primarily through evapotranspiration. In the Southeast's humid temperate climate, depressions usually fill in winter and early spring, drying progressively through the summer as plants draw on water for evapotranspiration. On slopes or flats without seasonal ponding of water, the soils characteristic of depressions support dry to xeric oak-hickory forests (Schafale & Weakley 1990). Depressions in this region have brief to long periods of inundation followed by dry, or even quite xeric, conditions as the growing season advances.

North Carolina and Virginia state classifications of natural communities have termed such wetlands "Upland Depression Swamps" or "Upland Pools" (Schafale and Weakley 1990; Fleming et al. 2010). Both terms are used in North Carolina, where the distinction between the two types is based on hydroperiod, which is the length and frequency of inundation or saturation. Upland Pools are considered to be a deeper class of depressions that can support pools of water with a longer hydroperiod. Long-standing ponded water limits tree growth in the deepest parts of the basin, creating zones of vegetation and an open canopy. Upland Depression Swamps, in contrast, have a closed canopy and are believed to have a shorter hydroperiod (Schafale and Weakley 1990). In studies of depressional wetlands in other regions, hydroperiod appears to be one of the most important abiotic factors driving assembly of their biological communities (Semlitsch et al. 1996; Williams 1997; Barbour et al. 2005; Pinto-Cruz et al. 2009).

Although depressional wetlands tend to be small, they play an important ecological role for many species. DeMaynadier and Hunter (1997) have used the term "keystone ecosystem" to refer to ecosystems that have a greater effect on the surrounding landscape than would be expected based on their size. Depressional wetlands could be considered keystone ecosystems because they serve as nurseries for many species of amphibians and invertebrates, where animals congregate during breeding season and from which new adults emerge to colonize the surrounding landscape (Hunter 2008). Depressional wetlands such as Carolina bays and vernal pools have been well documented to be important for many species that require both aquatic and terrestrial phases for their life cycle (Semlitsch et al. 1996; Sharitz 2003). One study of the reproductive potential for amphibians in a Carolina bay wetland found 24 species of breeding amphibians and more than 1,400 kg of amphibian biomass produced there in a single breeding season (Gibbons et al. 2006). Such isolated temporary wetlands may be important areas of allopatric speciation and endemism for some taxa. These endemic taxa and specialists require depressions as their primary habitat or as habitat for a crucial life stage (Keeley & Zedler 1998; Deil 2005; Hunter 2008). It has been estimated that more than one-third of the rare species of the southeastern Coastal Plain are found in non-alluvial wetlands, including depressions (Sutter & Kral 1994). As upland depressions of the southeastern Piedmont have been little studied, their ecological role is unclear. There is evidence from a study of Mississippi forested pools that Piedmont depressional wetlands provide important habitat for a diverse assemblage of amphibians, invertebrates, and zooplankton (Bonner et al. 1997). In this region, salamanders of the genus *Ambystoma* (mole salamanders) in particular, rely on temporary pools (Semlitsch et al. 1988; Bonner et al. 1997). Depressional wetlands in the southeastern Piedmont are not known to have obligate plant species, but they do support uncommon and distinctive plant communities (Schafale and Weakley 1990; Fleming et al. 2010; NatureServe 2010).

In order to conserve and restore these valuable wetlands, it is important to document their natural communities and understand their dynamics. A national classification of natural communities, the U.S. National Vegetation Classification (NVC), has been developed using vegetation as a basis for community concepts (Jennings et al. 2009). Community classification systems can provide a framework for understanding patterns in relationships among species and between species and the environment. Community descriptions and detailed summary data of plant composition can be used to guide targets for restoration as well as land management initiatives. However, the vegetation of upland depression wetlands in the southeastern Piedmont has not been systematically studied and many community concepts are based on localized or qualitative information. The purpose of this study is to develop a quantitative, plot-based classification and description of upland depression plant communities from the southeastern Piedmont. This classification will provide documentation for, and may be used to support and refine, existing community concepts for upland depressional wetlands. In an effort to understand the ecological dynamics of upland depressions, the environmental factors associated with compositional variation will also be explored as a means for determining important environmental gradients driving community assembly.

Methods

Study area

Vegetation was surveyed in the eastern Piedmont physiographic province of the southeastern U.S., spanning a zone from the southern Piedmont of Virginia to the northern Piedmont of South Carolina. This area represents the northern half of the Piedmont Upland Depression Swamp Ecological System (CES202.336) recognized by NatureServe (2010). The eastern Piedmont is an ancient peneplain characterized by erosional forces (Oosting 1942; Markewich et al. 1990). It is geologically complex and consists of broad regions of igneous or metamorphic rock with areas of volcanic intrusion as well as several basins of Triassic sedimentary rock. There are occasional inselbergs, formed from erosion resistant rock or from ancient weathered mountain chains that contribute areas of sharp topographic relief (Stuckey 1965). Landform and topographic relief are controlled primarily by differences in the weathering and resistance to erosion of bedrock types (Markewich et al. 1990; Woodruff & Parizek 1956). The variation in bedrock also creates a variety of soil types. Soils of the southeastern Piedmont are dominated by ultisols, accompanied by aflisols derived from pockets of more mafic bedrock. There are four major soil landscapes in this region of the Piedmont: felsic crystalline terrains, underlain by granite, gneiss, and schist; the Carolina Slate belt, comprised of agrilites, fine-grained schists, and felsic and mafic volcanic rock; the sedimentary Triassic basins; and a mixed mafic and felsic unit that is composed of a closely associated complex of different rock types (Daniels 1984). Known locations of upland depressions occur primarily in the Carolina Slate belt and in mafic zones of the mixed mafic and felsic unit, although there are also a few examples from the Triassic basins.

Climate is humid subtropical, but there is considerable variation in both temperature and precipitation across the relatively large study area (Markewich et al. 1990). Mean annual temperature of study sites ranges from 12-16 degrees C. Mean annual temperature is lower in the northern and western reaches of the study area and higher in the southern and eastern reaches. Mean annual precipitation of study sites ranges from 1074-1475 mm/year. Precipitation rates are highest near the southern Blue Ridge and decline to the north and towards the Coastal Plain. The Piedmont has a long history of disturbance in the form of urban development, agriculture, and silviculture. Beginning with the settlement of Europeans, most locations in the Piedmont that are suitable for agriculture were cleared. Early agricultural practices resulted in substantial topsoil erosion throughout the Piedmont (Trimble 1974). Land cover is currently a mix of developed land, agriculture, and forest used for silviculture or natural areas (Markewich et al. 1990). Remaining natural forests are second growth and often exist within a patchwork of other land uses (Oosting 1942).

Site selection

Sampling locations were selected in an attempt to capture a large proportion of the remaining examples of high-quality, natural upland depression vegetation in the study area. Upland depressions were defined as locations with a visible topographic depression in an upland setting that supported wetland vegetation and had evidence ponded water. Depressions were recognizable during the dry season due to the presence of a physical topographic depression, evidence of water staining on leaf litter and trees, as well as a marked change in plant species composition from the surrounding uplands. Depressions on floodplains were not included in the scope of this study because of their association with alluvial wetland vegetation. Because much of the Piedmont has been subject to anthropogenic disturbance, sites were sought that showed signs of minimal disturbance and that were large enough to be sampled by our standard protocol. Sites were chosen in an attempt to cover a broad geographic area and a range of geologic types. Many of the upland depressions included in this study were recognized as element occurrences of high-quality "Upland Depression Swamp" or "Upland Pool" communities by the North Carolina Natural Heritage Program. Additional high-quality wetlands were located through consultation with regional agencies, biologists, and conservation organizations. Plots included from South Carolina are from an area known as Camassia Flat, which supports the Midwestern prairie disjunct, *Camassia scilloides*. Depressions from Virginia were not sampled directly for this project but were included from an archive database of plots sampled by the Virginia Natural Heritage Program (VANHP) (Fleming et al. 2010). Plots from sites described as upland depression swamps from Virginia's "Southern Piedmont" ecoregion were selected for inclusion from the database. A total of 52 plots from Piedmont upland depressional wetlands were compiled: 40 from North Carolina, 10 from Virginia, and 2 from South Carolina (Figure 3.1).

Field methods

The primary fieldwork for this study was conducted May-September 2009-2010. During this time, 31 permanent vegetation plots were established in upland depressional wetlands using the Carolina Vegetation Survey (CVS) protocol (Peet et al. 1998). Data from 9 additional CVS-style plots were obtained from the CVS archive database. Plots from the archive database were sampled in July 1989, June 1994, and August 2003. Plots from the VANHP database were established following Virginia's DCR-DNH plot data collection protocol (Virginia Department of Conservation and Recreation 2011) and were sampled in May-September from 1998-2006.

The CVS protocol allows plots to range in size from 100 m^2 to 1000 m^2, comprised of between one and ten 100 m^2 modules, in order to accommodate stands of different size and configuration. Plots included in the analysis range in size from 100 m^2 to 1000 m^2 (frequently 200-600 m^2). Plot sizes less than 1000 m^2 often indicate that the depression sampled was smaller than 1000 m^2. Plots from Virginia are 400 m^2, the standard DCR-DNH plot size for forest/woodland vegetation. Plots were placed in stands of relatively homogenous vegetation and an attempt was made to establish the plot within the wetland boundaries. In some plots, either due to the shape of the wetland or to internal heterogeneity caused by mosaic microtopography, patches of upland vegetation were incidentally captured. Depressions encountered in this study were typically small enough for one plot to capture the majority of the site's compositional variation but in occasional circumstances, when the wetland was very large and included large swaths of distinct vegetation, multiple plots were established.

Within each plot, all vascular plant taxa were recorded and the aerial cover of each taxon was estimated using cover classes. Several low-resolution bryophyte taxa were also recognized in many plots, including *Sphagnum* spp., *Mnium* spp., *Climacium* spp., *Thuidium* spp., *Leucobryum* spp., and *Marchantiophyta* spp. Aerial cover was estimated for each taxon as total plot cover and cover by strata. The CVS protocol uses the following cover class scale: 1 = trace (<0.1%), 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%. Virginia DCR-DNH protocol follows the same cover class scale, except the scale ranges from 1-9, with 9 representing 75-100%. There were no examples of taxa occurrences given cover class 10 from the CVS plots, so for this dataset the two scales are functionally equivalent. For each stratum, the height and percent aerial cover were estimated. The diameter at breast height (dbh) of woody stems was tallied by taxa in the following diameter classes: 0-1 cm, 1-2.5 cm, 2.5-5 cm, 5-10 cm, 10-15 cm, 15-20 cm, 20-25 cm, 25-30 cm, 30-35 cm, and 35-40 cm (Virginia plots do not have tallies for stems <2.5 cm). Diameters of trees larger than 40 cm were recorded to the nearest 1 cm.

Plants were identified to the finest taxonomic resolution possible, most frequently to species or variety. However, due to the vegetative condition of most specimens, the difficulty of distinguishing some species in the field, the need to standardize taxonomic concepts across several data sources, and some identifications that were treated as species complexes in archived plots, some occurrences were treated as lower resolution taxonomic complexes for analyses (*Bidens* spp., *Vaccinium [corymbosum + fuscatum + formosum]* and *Carex [albolutescens + festucacea]*). For example, *Carex festuceacea* and *C. albolutescens* are difficult to distinguish, particularly when fruiting specimens have not reached optimal maturity. Most specimens encountered were past optimal maturity and could not be distinguished between the two species definitively. Several *Vaccinium* species were lumped into a highbush blueberry complex due to the difficulty identifying the species vegetatively, their frequent hybridization, as well as concern about inconsistent use of the taxonomic concepts across many different surveyors because this taxonomic group has been subject to revision by several authorities (Weakley 2010). Plots are archived in VegBank along with a full index of lower resolution taxonomic concepts used in analyses that links these concepts to species listed in the plots. Nomenclature follows Weakley (2010).

Additional descriptive and environmental data were collected for each plot including geographic coordinates, slope, aspect, hydrologic regime class, soil drainage class, estimated stand size, landform, and topographic position. Field soil samples were collected and analyzed for nutrients and texture. For CVS plots, a soil sample was collected from the A horizon (top 10 cm of mineral soil) of each intensive module (number of intensive modules ranged from 1-4, depending on plot size). One sample from the B horizon (approximately 50 cm below the surface) was also collected from the center of each plot. Soil samples from Virginia plots were collected in multiple locations from the A horizon and combined. All soil samples were analyzed by Brookside Laboratories, Inc. in New Knoxville, Ohio. Total cation exchange capacity (CEC) (meq/100 g), pH, exchangeable cations (Ca, Mg, K, Na ppm), percent base saturation, estimated nitrogen release, easily extractable P, soluble sulfur, extractable micronutrients (B, Fe, Mn, Cu, Zn, Al ppm), percent organic matter, and bulk density values were determined for each sample. Extractions were carried out using the Mehlich III method (Mehlich 1984) and percent organic matter was determined by loss on ignition. Soil texture was determined as percentage sand (2 mm – 63 μm), silt (63 μm – 2 μm), and clay (<2 μm). Values from the A horizon samples were used in the analysis because B horizon data were not available for all plots. If multiple A horizon samples were collected, the values were averaged to provide a single set of soil data from each plot prior to analysis. In addition to the data collected on site, some environmental data were derived remotely using a Geographic Information System (ArcGIS 9.3: ESRI 2008). Bedrock geology was obtained from USGS state digital geology maps for Virginia, North Carolina, and South Carolina (U.S. Department of the Interior, U.S. Geological Survey: http://tin.er.usgs.gov/geology/state/). Soil series and soil taxonomic classification were determined using digital SSURGO soil maps from USDA Natural Resource Conservation Service (http://soils.usda.gov/survey/geography/ssurgo/).

An estimate of depression wetness was generated using a hydrophytic vegetation index. The index was developed with data from region 2 (Southeast) of the U.S. Fish and Wildlife's wetland indicator lists (U.S. Fish and Wildlife Service 1988). The wetland indicator lists place plant species in one of five wetland indicator categories according to frequency of occurrence in wetland habitat (estimated probability of occurring in wetland habitat: UPL = <1%, FACU = 1%-33%, FAC = 34%-66%, FACW = 67%-99%, OBL = >99%). The wetland indicator categories were converted to a hydrophytic scale as follows: OBL = 5, FACW+ = 4.25, FACW = 4, FACW- = 3.75, FAC+ = 3.25, FAC = 3, FAC- = 2.75, FACU+ = 2.25, FACU = 2, FACU- = 1.75, UPL = 1. Hydrophytic scale values for each species were weighted by cover class and averaged by plot to generate a hydrophytic vegetation score for each plot (Wentworth et al 1988).

Numerical Analyses

A community classification was developed using a hierarchical agglomerative cluster analysis. A hierarchical approach was employed because it has been widely used in community classification and provides a flexible framework for creating hierarchical clusters (McCune et al. 2002). Rare taxa (those in two plots or fewer, which represents 5% of all plots) were removed from the analysis because rare taxa create noise in calculations of inter-plot similarity and can obscure relationships between composition and the environment (McCune et al. 2002). However, rare taxa that may be important to stand composition, here defined as taxa with aerial cover greater than 5-10% or with a restricted habitat (those that are found in 6 or fewer community types in the CVS archive database), were included in the analysis. A distance matrix, using Sørensen distance, was created for 52 plots x 161 taxa, representing inter-plot similarity in taxa composition and abundance. Several different measures of taxa abundance were employed in the calculation of the distance matrix, including cover classes, percentage cover mid-points, percentage cover mid-points relativized by species maximum, and presence-absence. The final distance matrix was calculated using cover classes, which represent a log scale of percentage cover estimates, because cover classes provided a means of de-emphasizing the dominant aspect of tree and shrub growth-forms, which has been found to be useful in other community classifications (McCune et al. 2002) and produced the most ecologically interpretable results.

A clustering dendrogram was created using the distance matrix with flexible beta linkage method ($\beta = 0.25$) in PC-ORD 5.31 (McCune and Mefford 2006). Flexible beta linkage ($\beta = 0.25$) is compatible with Sørensen distance and is a space conserving approach (McCune et al. 2002). Dufrêne-Legendre (DL) indicator species analysis (calculated in PC-ORD 5.31) was used in conjunction with cluster analysis to determine the optimal number of clusters to recognize based on maximization of the number and representation of significant indicator species ($p < 0.05$) in each group (Dufrêne & Legendre 1997; McCune et al. 2002). Higher-level groups were also recognized from the hierarchical dendrogram structure. A hierarchical framework of vegetation concepts allows for flexibility in the resolution with which vegetation patterns in depressional wetlands may be viewed, ideally providing broader utility for various classification, conservation, or restoration projects that may have different scopes and goals.

Two plots (004-07-0151 and 004-05-0155) were identified as outliers based on a high minimum dissimilarity as well as high average dissimilarity. The outliers were included in the cluster analysis but they were found to cluster together and were the last cluster to join the remainder of the dataset in the dendrogram (Figure 3.2). These depressions have historically been termed “bogs” and appear to be quite distinct from the main dataset. Each outlier also represents a unique association recognized by the NVC. Plot 004-07-0151 represents the location that was used to describe the *Leucothoe racemosa - Vaccinium fuscatum - Smilax walteri* Shrubland association (CEGL004533) recognized by the NVC. Plot 004-05-0155 represents the location that was used to describe the NVC’s *Nyssa biflora / Cephalanthus occidentalis - Leucothoe racemosa* Forest association (CEGL004550). Because the depression bogs are outliers and vegetation from each depression has been well-documented in independent associations of the NVC, they were not included as community types derived from the cluster analysis. However, the features of each wetland are briefly described in the results. The outlier plots were also removed from further analyses, which facilitated the detection of compositional patterns and environmental relationships within the main dataset that would have been obscured by the strong signals introduced by the outliers.

The relationship of vegetation composition to environmental variables was explored with non-metric multidimensional scaling (NMS) ordination using varimax rotation and Sørensen distance of taxa cover classes with rare species removed. One plot (114-01-0016) included in other analyses was removed from the final ordination as it occupied an outlier position in compositional space. The ordination was implemented in PCORD 5.31 using all defaults, for both two and three-dimensional solutions. Each resulting ordination represents the solution with the lowest stress from 20 random starting configurations. The two-dimensional ordination was selected for its graphical clarity and because the three-dimensional solution provided very little additional information. Joint-plot overlays were created using Pearson correlation values of environmental variables with ordination axes.

Synoptic vegetation tables were created for each cluster using JUICE 7.0, which provided an efficient means for compiling synoptic information and was used to calculate fidelity using the phi-coefficient method (Tichý 2002). Synoptic tables provide the constancy, average cover, fidelity, diagnostic value, and DL indicator species value for prevalent taxa in each cluster. Constancy was calculated as the percent frequency of taxa occurrence within a cluster. Fidelity is a measure of cluster faithfulness and was calculated using phi-coefficient, which accounts for differences in cluster size. Values greater than zero indicate taxon-cluster co-occurrence is more frequent than expected by chance (Chytrý et al. 2002). Diagnostic value (DV = constancy * fidelity/100) and DL indicator species value (IndVal) both highlight taxa that are characteristic of a cluster, where values increase as a given taxon is both increasingly common and faithful to a cluster. Prevalent taxa (*sensu* Curtis 1959) were identified by ranking cluster taxa by constancy and selecting the N most common taxa, where N is the cluster average species richness. Average cover, followed by diagnostic value, was used as a secondary selection criterion in the case of ties in constancy. Cluster homoteneity, calculated as mean constancy of prevalent taxa, is a measure of cluster compositional similarity. Community types were named following standards used by NVC. Names are composed of species found from numerical analyses to have high constancy in the community and that also have high cover and diagnostic value when possible. Species are listed by growth form, with hyphens ("-") separating species within the same stratum and slashes ("/") distinguishing species of different strata (NatureServe 2010).

Results

The results of the cluster analysis combined with indicator species analysis indicated five distinct clusters, or community types, within the main dataset. The cluster dendrogram can be seen in Figure 3.2 and a summary synoptic table for all five community types is provided in Table 3.1. A list of plots included in the analysis and their assignment to community type is included in 3.5. The five identified community types will be described individually, but they can also be understood within a hierarchical framework that corresponds to higher-order divisions of the dendrogram. The first division of the dendrogram represents a distinction in relative swamp wetness. One branch of the dendrogram is composed of relatively wet examples of upland depression communities while the other branch is composed of drier examples. Within the broad group of wet swamps, three separate community types were identified. The most distinct is a community of *Carex joorii* Pools, which appear to be the wettest type. *Carex joorii* Pools are typically small, deep depressions that have an open canopy and very few species. The division that forms the remaining two community types of wet depressions is related to a difference in soil composition. Wet Felsic Depression Swamps have very low nutrient availability and low pH, while Wet Mafic Depression Swamps have more clay and somewhat higher values for most soil nutrients and pH. For the other primary branch of the dendrogram, which is a broad group of dry depressional swamps, the division between the two community types found in this group also appears to reflect differences in soil composition. Dry Mafic Depression Swamps have higher values for most soil nutrients and more clay than the silty Dry Felsic Depression Swamps.

The NMS ordination results also indicate that the community types can be distinguished by swamp wetness and soil fertility. Swamp wetness, as estimated by plot hydrophytic vegetation score, as well as several edaphic variables, are correlated with compositional variation (Figure 3.3). The cumulative R^2 of the NMS ordination was 0.720. Hydrophytic vegetation score, along with Percent H and Al, are positively correlated with the first axis, while pH, base saturation, Mn, and Ca are negatively correlated with the first axis. The second axis is positively correlated with Zn, K, and somewhat more weakly with percent clay, while it is negatively correlated with percent silt. Copper and percent Mg are correlated with both axes, increasing along the second axis with percent clay and decreasing along the first axis in contrast to estimated wetness. The results of the ordination, combined with mean environmental values by community type, suggest that beyond the distinctive *Carex joorii* Pool type, patterns in compositional variation of upland depressions can be considered in a two gradient framework, creating four community combinations across a wetness dichotomy and a soil composition dichotomy.

Wet and Dry Depression Swamps

Wet depressions have higher hydrophytic vegetation scores (community type means = 3.31-3.55) than dry depression types (community type means = 3.05-3.22). Table 3.2 provides summary environmental data for each community type. When comparing wet and dry groups edaphically, dry depression swamps have higher average pH, base saturation, and values for Ca, Mn, Cu, and Fe. Wet depressions are characterized by an abundance of species such as *Acer rubrum*, *Smilax rotundifolia*, *Vaccinium [corymbosum + fuscatum + formosum]*, and *Carex joorii*, some of which may be present incidentally in dry depressions but are do not have high cover. Species richness is notably higher in both dry communities as they are able to support many additional upland species not commonly found in wet depressions. The drier community types are characterized by a greater abundance of species such as *Fraxinus [americana + pennsylvanica]*, *Ulmus alata*, *Juniperus virginiana* var. *virginiana*, *Danthonia spicata*, and *Scutellaria integrifolia*. Some pairs of depressions from the same area have one member in the Wet Felsic Depression Swamps type and the other in the Dry Felsic Depression Swamps type. This suggests that the local soil characteristics have an influence on plant composition but this driver is superseded by site wetness, which can vary locally with the size and depth of individual depressions.

Mafic and Felsic Depressions

When considering the two broad groups that reflect differences in substrate fertility, both mafic types have higher percent clay content, while the two felsic types have comparatively silty soils. Mafic types also have higher average values for most nutrients than felsic types; Mg, K, Na, B, Zn show this signal in particular. Higher cation exchange capacity and a higher proportion of Mg to Ca seem to be particularly characteristic of the mafic types. An abundance of *Nyssa sylvatica* and *Liquidambar styraciflua* as well as presence of *Vitis rotundifolia* var. *rotundifolia* and *Quercus alba* seedlings in the herb stratum are indicative of the felsic community types. In contrast, *Quercus lyrata* and *Ulmus americana* var. *americana* occur primarily in the mafic community types along with incidental diagnostic species such as *Trachelospermum difforme*, *Campsis radicans*, and *Celtis sp.* seedlings. There appears to be an interaction between the two primary sorting gradients of wetness and soil fertility, where the wet community types have lower pH and lower values for soil nutrients than do dry community types. A number of edaphic variables show this interaction, displaying consistently higher values in dry depressions than in the wet depressions, but within wetness groups, the mafic type has higher soil fertility values than the corresponding felsic type. Variables that show this interaction pattern include: pH, base saturation, Ca, % Ca, Fe, Mn and Cu. With this interaction in mind, is possible that if sites are very wet it may obscure the soil fertility signal of the primary substrate.

***Carex joorii* Pools**: (6 plots)

Quercus phellos - Liquidambar styraciflua / Cephalanthus occidentalis / Carex joorii Woodland

Environmental Setting:

Carex joorii Pools have the highest estimated wetness (mean = 3.55) of the five described community types. Deep standing water could be observed in examples of this type and several salamander egg masses were encountered during field sampling. While there are no direct measures of depression size or depth, most members of this type appeared to be small but also with sharp relief creating relatively deep depressions. *Carex joorii* Pools have substantially higher clay (mean = 36.0%), organic matter (mean = 20.5%), and soil nitrogen (mean = 66.1 lbs/acre) content than the other community types. Soil fertility is mixed and does not fit well into the fertility dichotomy pattern seen in the other four community types. The pools are acidic (mean pH = 4.17) and have particularly high K and low Mg. Four of the six plots included in this type are found in depressions at the summit of monadnocks in the Uwharries region of North Carolina (Figure 3.5). Monadnock summits are an atypical landscape setting for upland depressions in the southeastern Piedmont. It is possible that the formation of depressions that have the size and shape particular to *Carex joorii* Pools may be more likely to occur from the weathering of monadnocks than from weathering of upland flats, which are a more common setting for upland depressions in this region.

Vegetation:

Carex joorii Pools have somewhat open canopies with low stem densities (mean = 0.17 stems/m^2), which is consistent with the concept that depressions with frequent or prolonged inundation have limited tree growth (Weakley and Schafale 1990). Canopy trees are the nominals *Quercus phellos* and *Liquidambar styraciflua* and rarely *Quercus lyrata*. *Acer rubrum* and *Nyssa sylvatica* are also occasionally present, often in the shrub stratum. Trees are often more abundant in peripheral positions in the depression. Depressions of this type have a very limited shrub layer. Within the depression, *Cephalanthus occidentalis* may occur as a small and scattered shrub. Some examples of this type also have a ring of shrubs along the outer edge composed of *Smilax rotundifolia*, *Vaccinium [corymbosum + fuscatum + formosum]*, or *Eubotrys racemosa*. This type is most distinctly characterized by very low species richness and by dominance by the sedge *Carex joorii*, which is a significant indicator. *Carex joorii* typically forms a dense cover, approaching a monoculture, in the herb stratum and is only accompanied by occasional scattered tree seedlings, one of several *Carex* spp., or mosses, such as *Climacium* spp. The striking absence of other members of the herb stratum is perhaps more characteristic of this community than is the presence of *Carex joorii* itself. A synoptic vegetation table for *Carex joorii* Pools is provided in Appendix 3A.

Classification:

The *Carex joorii* Pools community type is approximately equivalent to the NVC association *Cephalanthus occidentalis - (Leucothoe racemosa) / Carex joorii* Shrubland (CEGL004075). See the Discussion for additional details.

Wet Felsic Depression Swamps: (8 plots)

Quercus phellos - Acer rubrum - Nyssa sylvatica / Vaccinium fuscatum / Scirpus cyperinus - Sphagnum spp. Forest

Environmental Setting:

Wet Felsic Depression Swamps range in shape from broad, shallow depressions to somewhat small, steep-sided pools. This community has the second highest average wetland indicator score (mean = 3.42). As such, it shares an environmental affinity with *Carex joorii* Pools and there may be examples transitional between the two types. Wet Felsic Depression Swamps are characterized by having a more complex assemblage of plants than *Carex joorii* Pools, with a well-developed shrub stratum as well as a more diverse herb layer. Wet Felsic Depression Swamps are also distinct from the other community types edaphically. In contrast to *Carex joorii* Pools and Wet Mafic Depression Swamps, Wet Felsic Depression Swamps have relatively silty soils (mean = 52.9 %) with low clay (mean = 23.7 %) and low organic matter (mean 10.6%). This community type has the lowest values for most measures of soil fertility, including pH (mean = 4.14), CEC, base saturation, and most measured soil nutrients.

Vegetation:

The canopy is somewhat diverse compared to other types and consists of *Quercus phellos*, *Liquidambar styraciflua*, *Acer rubrum*, and *Nyssa sylvatica*; the latter two, while typically having only moderate cover, are both significant indicators. These four tree species are constant in all examples of the community but there are no other prevalent canopy species. The shrub stratum is well-developed and this community type has the highest average stem density (mean = 0.45 stems/m^2). The highbush blueberry complex (*Vaccinium [corymbosum + fuscatum + formosum]*) and *Smilax rotundifolia* are constant constituents, often with a dense cover that forms the dominant aspect of the community. Other common constituents of the shrub stratum include *Ilex verticillata*, *Vitis rotundifolia* var. *rotundifolia*, and *Cephalanthus occidentalis*. Dominant members of the herb layer include the indicator species *Scirpus cyperinus*, *Sphagnum* spp., *Bidens* spp, and *Erechtites hieracifolia*. More occasional species include *Chasmanthium laxum* and several *Carex* spp. (*C. joorii*, *C. albolutescens, C. lupulina*, and *C. complanata*). *Carex joorii* and *Sphagnum* spp., when present, can have high cover. Wet Felsic Depressions may display zonation of all three strata, depending on the extent of the hydrological gradient created by topographic relief in the depression. A synoptic vegetation table for Wet Felsic Depression Swamps is provided in Appendix 3B.

Classification:

The Wet Felsic Depression Swamps community type overlaps the NVC association *Quercus phellos / Carex (albolutescens, intumescens, joorii) / Climacium americanum* Forest (CEGL007403), but it is narrower and more constant in composition and environmental setting. See the Discussion for additional details.

Wet Mafic Depression Swamps: (10 plots)

Quercus phellos - Quercus lyrata - Acer rubrum / Smilax rotundifolia / Carex albolutescens - Carex louisianica Forest

Environmental Setting:

Wet Mafic Depression Swamps typically occur on broad flats and most examples are underlain by Iredell soils, which are strongly mafic with high shrink-swell capacity, and found in landscapes with limited relief. The hydrophytic vegetation score (mean = 3.31) is somewhat lower than the score for the Wet Felsic Depression Swamps. Wet Mafic Depression Swamps have clayey soils (mean = 31.8 %) with relatively low silt (mean = 40.8 %). Soil fertility is intermediate for the dataset as a whole, but higher than that found in the other two wet community types. Soil nutrients and pH (mean = 4.36) are notably higher in this type than in Felsic Wet Depression Swamps; Na and Mg are particularly high. Species richness is comparable to that of Wet Felsic Depression Swamps but much greater than that of *Carex joorii* Pools. The shrub stratum is moderately well-developed but not as dominant a feature as it is in the Wet Felsic Depression Swamps.

Vegetation:

This community type often has *Quercus lyrata* in the canopy and, when it is present, it is usually the canopy dominant. *Quercus phellos* is present in all examples of this community type but when *Quercus lyrata* is present it is typically subdominant. *Acer rubrum* and *Liquidambar styraciflua* occur frequently in the subcanopy. Very few shrub species are common in this community type and the shrub stratum is dominated by the vine *Smilax* *rotundifolia*, which can range from a few scattered individuals to dense stands or rings of shrub-height thickets. Other possible constituents of the shrub stratum include scattered individuals of *Campsis radicans*, *Diospyros virginiana*, *Fraxinus [americana + pennsylvanica]*, *Toxicodendron radicans*, and *Trachelospermum difforme*. The herb stratum is typically a mosaic of graminoid-dominated patches and areas of sparse cover that contain scattered forbs and seedlings of woody species. *Carex [albolutescens + festuceacea]* is the most common member of the herb layer and a significant indicator of this community type. *Carex louisianica* as well as *C. typhina*, while somewhat less common, are also diagnostic. A synoptic vegetation table for Wet Mafic Depression Swamps is provided in Appendix 3C.

Classification:

The Wet Mafic Depression Swamps community type overlaps with the NVC association *Quercus phellos / Carex (albolutescens, intumescens, joorii) / Climacium americanum* Forest (CEGL007403) but is narrower and more constant in composition and environmental setting. See the Discussion for additional details.

Dry Mafic Depression Swamps: (10 plots)

Quercus phellos - Ulmus alata / Campsis radicans - Smilax bona-nox / Leersia virginica Forest

Environmental Setting:

Dry Mafic Depression Swamps are also commonly found on Iredell soils, in similar locations to Wet Mafic Depression Swamps, but also occur on soils of Triassic basins and on the Armenia mollisols of northern South Carolina. They have intermediate soil texture in that they have more clay (mean = 27.6 %) than the silty Dry Felsic Depression Swamps, but still have a lower clay content than the Wet Mafic Depression Swamps or *Carex joorii* Pools. This type has the highest average pH (mean = 4.62) and CEC, with soils rich in most nutrients: values for Ca, Mg, Cu, and Mn are particularly high. This group is characterized by a mix of upland and wetland species. Examples are typically shallow with a low grade basin floor and do not show the pronounced zonation often found in wet depressions.

Vegetation:

Quercus phellos is co-dominated in the canopy by *Ulmus alata*, which are both found in all examples of this type. *Fraxinus [americana + pennsylvanica]* and *Ulmus americana* var. *americana* are common species that may occur in the canopy or subcanopy. *Acer rubrum*, *Nyssa sylvatica,* and *Liquidambar styraciflua* are conspicuously absent as canopy species. The shrub stratum is typically sparse and the most common constituents are shrub-height vines such as *Smilax bona-nox* and *Campsis radicans*, which are both significant indicators. Other members of the shrub stratum include *Rubus pensilvanicus*, *Juniperus virginiana* var. *virginiana*, and *Smilax rotundifolia*. The exotic vine, *Lonicera japonica*, is also common constituent and a significant indicator. The herb stratum is less sedge-dominated than the wet variants but has a greater diversity of grasses. *Scutellaria integrifolia*, *Leersia virginica*, the moss *Climacium* spp., *Danthonia spicata*, *Cinna arundinacea*, *Panicum anceps*, and *Asplenium platyneuron* are all common species. A number of woody species also occur in the herb layer as scattered seedlings including *Celtis* sp. (a significant indicator), *Toxicodendron radicans*, *Trachelospermum difforme*, *Parthenocissus quinquefolia*, and *Gleditsia triacanthos* (a significant indicator). A synoptic vegetation table for Dry Mafic Depression Swamps is provided in Appendix 3D.

Classification:

The Dry Mafic Depression Swamps community type partially overlaps the NVC association *Quercus phellos / Carex (albolutescens, intumescens, joorii) / Climacium americanum* Forest (CEGL007403), but some of its unique compositional and environmental features are not represented in the NVC association. See the Discussion for additional details.

Dry Felsic Depression Swamps*:* (16 plots)

Quercus phellos / Vitis rotundifolia var. rotundifolia / Danthonia spicata - Juncus coriaceus Forest

Environmental Setting:

This community type is the largest and occurs over a diverse set of substrates that are derived from mafic rock, mixed mafic/felsic rock, or felsic rock. As a whole, depressions of this type are less characteristic of broad flats and often occur in landscapes of moderate relief, such as in the Uwarrie Mountains region of North Carolina (Figure 3.5). Soils are silty (mean = 53.7 %) and low in clay (mean = 23.1 %) compared to other types. Soils are intermediate in fertility and have lower values for most soil nutrients than Dry Mafic Depression Swamps. Dry Felsic Depression Swamps have the lowest hydrophytic vegetation score (mean = 3.05) and the highest species richness (mean = 46 species/plot).

Vegetation:

The canopy in Dry Felsic Depression Swamps is strongly *Quercus phellos* dominated. No other canopy species typically have high cover except for *Liquidambar styraciflua*. Species such as *Acer rubrum*, *Fraxinus [americana + pennsylvanica]*, and *Ulmus alata* are common but not abundant. As with Dry Mafic Depression Swamps, this type has a very limited shrub stratum that consists primarily of the low-cover trees listed above or mounded lianas. *Smilax glauca* (a significant indicator), *Smilax rotundifolia*, and *Vitis rotundifolia* var. *rotundifolia* are common lianas that may occur in the shrub stratum. The herb layer is quite diverse relative to the wet community types and is characterized by a mix of wetland and upland species. *Juncus coriaceus, Carex [flaccosperma + glaucodea + pigra], Danthonia spicata*, and *Hypericum hypericoides* are all common and significant indicators. *Quercus alba* and *Pinus [echinata + virginiana]* seedlings are common and diagnostic of this type. These species occur only as seedlings, or occasionally as overhanging trees, and are likely reflective of the matrix forest characteristic of this type. A synoptic vegetation table for Dry Felsic Depression Swamps is provided in Appendix 3E.

Classification:

The Dry Felsic Depression Swamps community type partially overlaps with the NVC association *Quercus phellos / Carex (albolutescens, intumescens, joorii) / Climacium americanum* Forest (CEGL007403), but some of its unique compositional and environmental features are not represented in the NVC association. See the Discussion for additional details.

Outlier Depression Bogs

Both outlier depression wetlands are found in the Uwharrie Mountains region of North Carolina. In contrast to the other depressional wetlands in the study area, these two wetlands are embedded in a matrix that includes longleaf pine forest, which may indicate that there are differences in substrate or fire regime that have affected these communities. Both depressions are underlain by the Biscoe-Secrest Complex soil series, which is a silty, felsic soil series not found in other Piedmont depressional wetlands. Both wetlands occur as large, deep depressions with substantial standing water for much of the growing season, which creates an open canopy in the center of the depression. Vegetation is notably zoned in both examples, although the vegetation composition is distinctive in each wetland.

Pleasant Grove Bog: *Nyssa biflora / Cephalanthus occidentalis - Leucothoe racemosa* Forest (CEGL004550). This depression supports an outer ring of trees dominated by *Nyssa biflora* along with *Acer rubrum var. rubrum*, *Nyssa sylvatica*, and *Liquidambar styraciflua*. A second, more interior zone of vegetation is dominated by *Cephalanthus occidentalis* and *Eubotrys racemosa*, mixed with *Vaccinium fuscatum*, *Viburnum nudum*, *Juncus repens*, *Smilax laurifolia*, *Alnus serrulata*, *Ilex verticillata*, and *Itea virginica*. The innermost zone of the depression often contains standing water with little vegetation.

Roberdo Bog: *Leucothoe racemosa - Vaccinium fuscatum - Smilax walteri* Shrubland (CEGL004533). This depression contains scattered *Liquidambar styraciflua* and *Acer rubrum* but is predominately treeless. The outer portion of the depression is occupied by a ring of abundant *Smilax walteri* and *Eubotrys racemosa*, with *Vaccinium fuscatum* and *V. formosum.* Several sedge species also occur in this zone, including *Carex crinita*, *C. glaucescens*, *Rhynchospora* sp. *Scleria* sp., and *Eleocharis* sp. The center of the depression supports deep standing water with the aquatic, carnivorous species *Utricularia gibba.*

Discussion

Hydroperiod

Swamp wetness appears to be a primary driver of compositional variation in upland depression swamps of the southeastern Piedmont. This is consistent with other studies that have found depressional wetland vegetation to be strongly driven by inundation and wetland hydroperiod (Crowe et al. 1994; Kirkman et al. 2000; De Steven & Toner 2004; Barbour et al

2005; Battaglia & Collins 2006; Casey & Ewel 2006; Pinto-Cruz et al. 2009). Hydroperiod in this study was estimated using a hydrophytic vegetation index, which reflects the proportions of wetland vs. upland-adapted species present in the depression. Plants in vernal pools of the Northeast have been found to be reliable indicators of hydroperiod classes (Mitchell 2005), but vegetation is likely to be a relatively coarse proxy for hydrological data. The terms "wet" and "dry" used in community names reflect relative positions along this hydrophytic gradient. While dry depression swamps may have a shorter hydroperiod and support more upland-adapted species than wet depressions, the use of the term "dry" depressions is not meant to imply that these communities are fully terrestrial and are not wetlands, as they also support many wetland-adapted species.

Unfortunately, direct measures of swamp hydrology are not available for our study sites, so a complete understanding of the relationship between wetland hydrology and compositional variation remains unresolved. Wetness is most likely not one-dimensional gradient in this ecosystem because wetland hydroperiod can vary both in duration and frequency of saturation as well as depth of inundation (De Steven & Toner 2004). Hydrological dynamics in other types of depressional wetlands have been found to be driven by depression area, depth, and basin profile as well as by permeability of the substrate. Hydroperiod is strongly related to depression volume, where the largest and deepest pools have the greatest water storage capacity and dry down very slowly. However, depressions spanning a large area may be deep or shallow, so hydroperiod is not directly determined by depression area. Small, deep pools would be more likely to fill quickly and frequently but also dry out more quickly than a much larger depression of similar depth, which due to its greater volume would fill and dry down more slowly. Basin profile also plays a role in hydrology and wetland zonation. Steep sided basins create a greater storage volume than basins with gentle grade but similar area and maximum depth because gentle grade depressions have a greater proportion of shallow inundation (Collins & Battaglia 2001; Brooks and Hayashi 2002; Brooks 2005). *Carex joorii* Pools are typically small and steep-sided compared to the other community types, which could impart different hydrodynamics. Such a configuration could perhaps create a "flashier" hydrology that is more responsive to individual precipitation events and able to create deep inundation quickly (Collins & Battaglia 2001). Permeability of the substrate interacts with basin morphology to influence hydroperiod (Bonner et al. 1997; Keeley & Zedler 1998). Basins with higher soil silt content, such as was seen in the two felsic communities, are likely to be better drained than basins with very low-permeability clay. This could indicate that felsic depressions may require a deeper basin or greater water input to maintain a similar hydroperiod to a mafic depression underlain by dense clay. These different facets of wetness make the vegetation response to such a driver complex to interpret.

Soil Composition

In general, Piedmont upland depressions are found on soil series that poorly drained. Such soils are typically higher in clay and more mafic in composition, than the widespread felsic soil series characteristic of this Piedmont. As with the terms "wet" and "dry", "mafic" and "felsic" refer to relative positions along a felsic-mafic gradient, where "mafic" types are strongly mafic and "felsic" types may have a mixed, mafic-felsic influence. Depressions in the mafic types are found on alfisols or on the few examples of mollisols encountered in this study. The depressions in the felsic types form on both alfisols and ultisols. When considering patterns in soil series across community types, there is a trend toward soil series derived from solely mafic rock, with higher estimated pH and shrink-swell capacity to be found in the mafic types, while the felsic types tend to have soils series weathered from a mix of felsic and mafic rock, with lower estimated pH. There are exceptions to this trend and there are some examples of depressions in the felsic group that occur on strongly mafic soil series. However, soil series are somewhat coarsely defined and may not be adequate to capture inclusions and finer-scale variation in soils relevant for communities of such limited extent. Several of the depressions in the felsic types that are underlain by strongly mafic soil series are closer in compositional space of the NMS ordination to mafic depressions. Because soil texture and soil fertility vary fairly continuously along a mafic-felsic gradient, many of the depressions may be transitional between types.

Edaphic features appear to be secondary to hydroperiod as a driver of vegetation patterns in this region. Edaphic qualities have been found to be related to plant composition in other classifications of depressional wetlands (Holland 1986; De Steven & Toner 2004; Cutko & Rawinski 2008). In a study of depressions in Europe, Hérault and Thoren (2009), found plant composition to be driven by soil productivity, particularly for non-aquatic plant species. They also found that depressions with nutrient-rich soils supported more annuals and fewer large-seeded perennials and graminoids. The composition of vernal pools in Pennsylvania was also found to be influenced by substrate characteristics, where acid-loving heath shrubs and *Sphagnum* spp. occurred in depressions of acidic, peaty settings (Cutko & Rawinski 2008). The interaction observed here between wetness and soil fertility may be caused by a combination of nutrient transformations, slowed decomposition, or buildup of organic matter that accompanies anaerobic conditions in waterlogged soils (Bonner et al. 1997; Mitch & Gosselink 2007). It is interesting to note that while upland depressions in this region occur primarily on mafic substrates with high pH (estimated pH is of soil series is most commonly 4.5-6.5 or 5.1- 7.3) relative to most soils in the region, the measured pH from soil samples in depressions (mean pH = 4.3) is consistently lower than that predicted for the underlying soil series. In depressional wetlands in Europe, the accumulation of organic matter that accompanies long hydroperiods creates acidic conditions that favor the colonization of *Sphagnum* spp. (Hérault & Thoren 2008). It has been proposed that a gradient from high fertility to low fertility can represent a successional trend caused by the buildup of peat over time (Casey & Ewel 2006; Hérault & Thoren 2008). While substantial buildup of peat does not appear to occur in southeastern Piedmont depressions, these findings point to the possibility that a smaller-scale interaction between hydrology and substrate conditions may be occurring.

Compositional Variation

In a summary of vernal pool vegetation in the Northeast, Cutko and Rawinski (2008) note that several studies have found vernal pools difficult to classify based on vegetation, due in part to a high degree of heterogeneity among pools. A number of processes could be occurring to create high beta-diversity and apparently stochastic composition among depressional wetlands (Lopez et al. 2002; Colburn 2004; Pinto-Cruz et al. 2009). Two of the main mechanisms that have been considered are habitat isolation and the temporal abiotic variation that characterize depressional wetlands. Upland depressions in the Southeast are surrounded by terrestrial forest and may function as habitat islands with limited opportunities for dispersal among wetlands. Studies on regional processes in depressional wetlands from several different regions (Europe, California, and Ohio) all found plant composition to be dispersal limited (Lopez et al. 2002; Collinge & Ray 2009; Hérault & Thoren 2009). This was found to be particularly true for depressions in forested landscapes and for species with low mobility or large seeds. The terrestrial matrix that surrounds isolated wetlands can exert a strong influence on wetland composition by interacting with dispersal processes of wetland species, influencing the abiotic conditions of the wetland, and providing potential seed source for colonization (Hérault & Thoren 2009). Dispersal limitation can lead to priority or founder effects, where species that colonize first affect the establishment or growth of subsequent colonizers. Priority effects could account for some of the apparent stochasticity of upland depressions; early colonizers were found to be more successful than later-arriving species in one study of vernal pool vegetation in California (Collinge and Ray 2009).

A defining feature of depressional wetlands is their temporary hydrology. Wet conditions in upland depressions of the southeastern Piedmont are driven by precipitation, which can be highly variable over both monthly and yearly scales. In drought years with very little precipitation, depressions have been seen to support different species than those found in wet years. In general, depressional wetlands tend to have substantial yearly variation in plant composition (Deil 2005; Mitchell 2005). Observable plant composition can also change through the course of the growing season as wet-adapted ephemeral species give way to upland species that may flourish as the pools dry down. It has been proposed that some temporary wetlands undergo a seasonal succession and in reality support not just one, but a series, of plant communities. This is particularly true for depressions where ephemerals constitute a large proportion of community composition, such as in California's vernal pools or in pools of flackrock outcrops in the Southeast (Deil 2005; Barbour et al. 2005). Such a seasonal change is not pronounced in this region, where upland depressions are dominated by perennial and woody vegetation, however some seasonal change is likely to occur. In this study each wetland was sampled only once, most during mid-summer, which may have created a systematic undersampling of both wet-adapted spring ephemeral species and late-season upland herbs and grasses.

It is interesting to note that plot species richness varies inversely with estimated wetness. This is perhaps an indication of the relatively few species that are well adapted to the extremes between aquatic and xeric conditions (Zedler 2003) that seem to characterize the wet variants of upland depressions in this region. This pattern of low species richness has also been found in Mediterranean-climate vernal pools of both California and Europe, which have a xeric phase (Barbour et al. 2005; Pinto-Cruz et al. 2009). Bliss & Zedler (1998) found hydroperiod affected seed bank germination through long-term inundation effectively suppressing germination of non-pool species. Upland depressions as a group are relatively species poor (mean = 33.7 species/plot), which may be due in part to their isolation and dispersal limitation (Lopez et al. 2002). Considering the specialized nature of the habitat and the depressional wetland specialists known from other regions, it is perhaps surprising that relatively few rare species were encountered in this study. The rare species that were found are regionally, rather than globally, rare and not of sufficient concern to be subject to state protection. They also are not depressional wetland specialists but are either plants characteristic of fertile, mafic soils or wetland species at the edge of their range (examples: *Quercus bicolor*, *Veronica anagallis-aquatica*, *Solidago gracillima*, *Packera paupercula* var. *paupercula*, and *Ilex longipes*). However, some of these rare species, as well as somewhat more common species like *Carex joorii* and *Isoetes melanopoda*, seem to rely on upland depressions as their primary habitat in the southeastern Piedmont, despite being found in a broader range of mafic or wetland habitats elsewhere. It is possible that Piedmont depressional wetlands are too infrequent on the landscape or too heterogeneous to support a specialized flora of their own. In forested wetlands it has been observed that species-poor communities do not tend to support rare species and this pattern seems to hold true for upland depressions of the southeastern Piedmont (Bedford et al. 1999).

Conservation

In general, patchy, isolated habitats such as depressional wetlands have a higher chance for local extinction events and reduced opportunity for dispersal and re-colonization. The dispersal limitation and matrix influence found for depressional wetlands in other regions suggests that conservation of these communities may require protection of surrounding matrix habitat as well as networks of nearby depressions (Zedler 2003; Hérault & Thoren 2009). Lopez et al. (2002) found a strong correlation between percent native species in depressional wetlands of Ohio and the proportion of surrounding land that was maintained as forest. More exotic species were found when the surrounding landscape was dominated by agriculture. The results of this study also showed that with increasing isolation, depressional wetlands became increasingly species poor and homogeneous. The surrounding forest is also likely to play an important role in maintaining the hydrodynamics of forested depressional wetlands.

Classification

Patterns in vegetation and environmental distinctions among community types could be useful in providing a framework for understanding variation in this poorly studied ecosystem. The classification presented here may be useful in supplementing and informing established community concepts for depressional wetlands recognized by the U.S. National

Vegetation Classification and state classifications. The five upland depression community types recognized here have been developed to be compatible with NVC associations (Jennings et al. 2009), although they represent a somewhat finer resolution than current NVC upland depression concepts. NVC associations for Piedmont upland depressional wetlands are rated as having weak or moderate confidence, so plot data and the systematic classification over a large geographic area from this study could be used to refine or increase the confidence of association concepts. In an effort to facilitate the refinement of NVC concepts, a summary of the relationships between the community types found in this study and recognized NVC concepts has been developed, along with recommendations for the revision of several NVC associations. A comparison of the relationships between the community types described here and NVC associations is also summarized in Table 3.3.

Cephalanthus occidentalis - (Leucothoe racemosa) / Carex joorii Shrubland (CEGL004075) is an association described from the Piedmont of North Carolina, with potential to occur in the adjacent Piedmont of South Carolina. The classification confidence of this association is not rated and it is not tied to plot data. The composition and physical setting of this association are approximately equivalent to the *Carex joorii* Pool community type identified in this study. Compositional and environmental data obtained from the *Carex joorii* Pools type is expected to be valuable in providing quantitative support for this association. It is recommended that the association be slightly refined to also include *Quercus phellos* as a canopy species in the association name. *Quercus phellos* is less dominant in *Carex joorii* Pools than it is in other upland depressions of the Piedmont, due to the open-canopied nature of *Carex joorii* Pools, but *Quercus phellos* does comprise a significant portion of the community and should be represented. It is also recommended that this association be shifted from the *Cephalanthus occidentalis* Semipermanently Flooded Shrubland Alliance, in which it is currently placed, and moved to the *Quercus phellos* Seasonally Flooded Forest Alliance that contains the other Piedmont depressional wetland associations. This transition would reflect the compositional affinity this association shares with other Piedmont depressional wetland associations as well as the greater importance of *Quercus phellos* as compared to *Cephalanthus occidentalis*, which is not always present.

Quercus phellos / Carex (albolutescens, intumescens, joorii) / Climacium americanum Forest (CEGL007403) is a broad upland depressional wetland association found in the Piedmont of the Carolinas, Virginia, and a portion of Maryland. The association is rated as having moderate confidence and was developed from eight Virginia plots and one Maryland plot. This association is also attributed to three plots from the Congaree Swamp National Monument, a location on a large river floodplain in the Coastal Plain of South Carolina. The composition and physical setting of this association are rather generally defined and the association represents a complex of most *Quercus phellos*-dominated upland depression wetlands of the Piedmont. The understory is particularly broadly defined and described as having limited diagnostic value. This association overlaps with Dry Mafic Depression Swamps, Dry Felsic Depression Swamps, Wet Mafic Depression Swamps, and Wet Felsic Depression Swamps community types identified in this study. The Wet Mafic Depression Swamps and Wet Felsic Depression Swamps community types could be considered to be mostly contained within this association. It is recommended that the broad *Quercus phellos / Carex (albolutescens, intumescens, joorii) / Climacium americanum* Forest association be subdivided into two associations that reflect Wet Mafic Depression Swamps and Wet Felsic Depression Swamps. This would allow the new associations to have more constant environmental settings and compositional patterns, along with diagnostic understory species. These two new associations derived from *Quercus phellos / Carex (albolutescens, intumescens, joorii) / Climacium americanum* Forest, should also be somewhat expanded to include a number of important species such as *Nyssa sylvatica*, *Vaccinium fuscatum*, and *Eubotrys racemosa* that are not currently included in the description.

For both of the dry depression swamp community types, the *Quercus phellos / Carex (albolutescens, intumescens, joorii) / Climacium americanum* Forest association does not describe their environmental dynamics and many of their important species, such as *Ulmus alata*, *Fraxinus americana*, *Scutellaria integrifolia* and *Danthonia spicata*. The importance of the mixed composition of upland and wetland species that characterize these short-hydroperiod wetlands is notably absent in the description of this association. It is also recommended that two new associations be developed for each of the dry community types identified in this study, particularly because these drier Piedmont upland depressional wetlands with short hydroperiods have limited represented in current NVC associations.

The three plots from the Congaree Swamp National Monument attributed to the *Quercus phellos / Carex (albolutescens, intumescens, joorii) / Climacium americanum* Forest association occur outside of the study area but were included in a preliminary cluster analysis. These three plots were found to cluster together and distinctly from all other depressional wetlands in the dataset. Because these plots appear to be substantially different from the depressional wetlands in the study area, and they occur in a different physiographic province and landscape setting, it is recommended that the Congaree plots be removed from this association or its segregates and possibly placed into a new association for Coastal Plain floodplain depressions.

Leucothoe racemosa - Vaccinium fuscatum - Smilax walteri Shrubland (CEGL004533*)* and *Nyssa biflora / Cephalanthus occidentalis - Leucothoe racemosa* Forest (CEGL004550) are two Piedmont upland depression associations, each is described from one plot and rated as having moderate confidence. Each association is also known from only one location and both locations occur in the Uwharrie Mountains region of North Carolina. These associations were defined from plots 004-07-0151 and 004-05-0155, which were also included in this study. As was mentioned in the Methods section, these two plots were identified as outliers. In the cluster analysis, the two plots formed a distinct cluster that was the last cluster to join the main dataset. The two plots also joined together at a relatively high point in the dendrogram, suggesting that they are fairly dissimilar. The results from the outlier and cluster analyses support the current position that each of these depressional wetlands represents a highly distinctive assemblage relative to other Piedmont upland depressional wetlands and that they warrant recognition as unique associations.

There are several other depressional wetland associations recognized by the NVC reported from the Piedmont of Virginia, North Carolina, or South Carolina. However, these associations occur predominately in other geographic regions and have some floristic differences that help to distinguish the concepts of this study from associations in adjacent areas. *Quercus phellos - Quercus (michauxii, shumardii) - Fraxinus americana / (Quercus oglethorpensis) / Zephyranthes atamasca* Gabbro Upland Depression Forest (CEGL008484) is an association described for depressions on gabbro flats of the Georgia Piedmont and a disjunct region in the Piedmont of northern South Carolina. The classification confidence for this association is not rated and it is represented by plots from the Oconee National Forest of Georgia. The floristic description of the association is rather heterogeneous and there appear to be compositional differences between the two geographic locals. This association is attributed to the depressions at the Camassia Flat site of northern South Carolina that were included in this study (plots 059-03-0855 and 059-04-0855) and were classified as Dry Mafic Depression Swamps. The Camassia Flat depressions are geographically disjunct from the Georgia plots tied to this association. The Camassia Flat depressions also appear to be floristically distinct from the description of this association and lack many species of importance such as *Quercus shumardii*, *Quercus michauxii*, *Quercus oglethorpensis*, and *Zephyranthes atamasca*. It is recommended that the Camassia Flat depressions, and possibly other similar depressions from northern South Carolina, be reassigned to the new association proposed for Dry Mafic Depression Swamps.

Liquidambar styraciflua - *Acer rubrum / Carex* spp. - *Sphagnum* spp. Forest (CEGL007388) is an association described for upland depressions in the Mountains of North Carolina and Tennessee as well as from several locations in the Piedmont of Georgia and Alabama. This association is rated as having weak classification confidence. There is a notation in the description that this association may also occur in the Piedmont of North Carolina. However, the examples from the North Carolina Piedmont attributed to this association are young, successional stands, and in one case the wetland is not a depression (Michael Schafale, pers. comm). The composition described for this association is quite distinct from that found in Piedmont depressional wetlands. Species characteristic of this association, such as *Cornus amomum, Cornus foemina, Alnus serrulata, Berchemia scandens, Decumaria barbara*, and *Smilax laurifolia* are notably absent from virtually all depressional wetlands encountered in this study. It is recommended that the North Carolina Piedmont examples be removed from this association's circumscription.

Cephalanthus occidentalis / Carex spp. - *Lemna* spp. Southern Shrubland (CEGL002191) is also an association that has been attributed to upland depressional wetlands in the Piedmont. This association is very broad and covers *Cephalanthus occidentalis*-dominated wetlands in a wide variety of hydrologic settings throughout the southeastern U.S. This association may have served as a "catch-all" for a many different natural communities that share the common feature of supporting *Cephalanthus occidentalis*. The *Cephalanthus occidentalis - (Leucothoe racemosa) / Carex joorii* Shrubland (CEGL004075) association seems to be a more refined variant of this association that is described specifically for upland depressional wetlands. The compositional description of *Cephalanthus occidentalis / Carex* spp. - *Lemna* spp. Southern Shrubland appears to be more consistent with alluvial settings and is markedly different from the composition found in Piedmont upland depressions. Important species of this association, such as *Cornus stricta, C. amomum, Salix* spp., *Carex stricta, C. stipata, Hibiscus* spp., and *Lemna* spp., were not encountered in this study. It is recommended that this association be revised to exclude upland depressional wetlands of the Piedmont.

State specific classifications often recognize somewhat broader community concepts and may incorporate a hierarchical format for community types, depending on the scale of resolution that is most appropriate for the state. This study provides fairly comprehensive coverage of the North Carolina Piedmont, but contains relatively limited geographic coverage of South Carolina and Virginia. While the results of this study will likely be informative for state classifications in Virginia and South Carolina, specific recommendations for refinement of state upland depression wetland community concepts would have limited utility without more complete geographic coverage of the state. The results of this study are most directly comparable to the North Carolina state classification. The Classification of the Natural Communities of North Carolina: Fourth Approximation (Fourth Approximation; Schafale 2003) describes community concepts for North Carolina. Fourth Approximation community concepts have been developed to be congruent with NVC associations, although some NVC associations are recognized as community subtypes (Michael Schafale, pers. comm).

Current Fourth Approximation community types for upland depression wetlands strongly overlap with the NVC associations discussed above, so the recommendations for NVC associations would apply to the North Carolina community concepts as well. The Fourth Approximation concept of Upland Pool (Typic Piedmont Subtype) corresponds to the NVC association *Cephalanthus occidentalis - (Leucothoe racemosa) / Carex joorii* Shrubland (CEGL004075) and is approximately equivalent to the *Carex joorii* Pool community type identified in this study. This Fourth Approximation Upland Pool (Typic Piedmont Subtype) concept is supported by the results of this study. The Upland Pool (Roberdo Subtype) and Upland Pool (Pleasant Grove Subtype) of the Fourth Approximation are equal to the NVC associations *Leucothoe racemosa - Vaccinium fuscatum - Smilax walteri* Shrubland (CEGL004533*)* and *Nyssa biflora / Cephalanthus occidentalis - Leucothoe racemosa* Forest (CEGL004550), and both of these community concepts are also supported by the results of this study. The Upland Depression Swamp community concept of the Fourth Approximation is equivalent to *Quercus phellos / Carex (albolutescens, intumescens, joorii) / Climacium americanum* Forest (CEGL007403). The Upland Depression Swamp concept overlaps with the Dry Mafic Depression Swamps, Dry Felsic Depression Swamps, Wet Mafic Depression Swamps, and Wet Felsic Depression Swamps community types identified in this study. It is recommended that each of these community types be recognized in the Fourth Approximation, possibly as Upland Depression Swamp subtypes. A graphical overview of the relationships between community types of this study and Fourth Approximation concepts is presented in Table 3.4.

Table 3.1. Synoptic vegetation table of identified upland depression wetland community types. Constancy (% Const.), average cover, fidelity (% Fid), and diagnostic value (% DV) are given for prevalent taxa within the five identified community types. Taxa are sorted alphabetically and must be prevalent in at least one community type to be included in the table. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Dry Felsic Depressions				*Carex joorii* Pools				Dry Mafic Depressions				Wet Mafic Depressions				Wet Felsic Depressions			
Group Plot Count	16				6				10				10				8			
Group Avg Plot Spp Richness	46				12				42				25				26			
Group homoteneity	56.5				63.9				55.7				59.2				58.5			
taxon name	% Const	Cover	% Fid	% DV	% Const	Cover	% Fid	% DV	% Const	Cover	% Fid	% DV	% Const	Cover	% Fid	% DV	% Const	Cover	% Fid	% DV
Acer rubrum	94	3	17.1	16.1	67	3	0	0	40	2	0	0	100	5	24.9	24.9	100	5	24.9	24.9
Andropogon sp	31	2	18.5	5.74	--	--	--	--	20	2	3.6	0.72	10	2	0	0	25	2	10.3	2.58
Asplenium platyneuron	31	1	7.5	2.33	--	--	--	--	50	2	29.3	14.7	30	2	6.1	1.83	13	1	0	0
Bidens sp	--	--	--	--	--	--	--	--	--	--	--	--	10	1	0.9	0.09	38	2	47.7	18.1
Campsis radicans	75	2	11.5	8.63	50	2	0	0	100	2	37.5	37.5	70	2	6.3	4.41	25	1	0	0
Carex [*albolutescens* + *festucacea*]	25	5	0	0	--	--	--	--	20	2	0	0	80	2	50.7	40.6	38	3	5.3	2.01
Carex [*caroliniana* + *complanata*]	63	2	35.5	22.4	--	--	--	--	30	2	0	0	20	1	0	0	38	2	8.2	3.12

Carex [*flaccosperma* + *glaucodea* + *pigra*]	75	2	66.3	49.7	--	--	--	--	30	2	11	3.3	--	--	--	--	--	--	--	--
Carex typhina	13	2	0	0	--	--	--	--	20	6	7.8	1.56	40	2	36.2	14.5	--	--	--	--
Carex joorii	19	5	0	0	100	6	56.7	56.7	--	--	--	--	50	5	6.3	3.15	50	6	6.3	3.15
Carex louisianica	6	2	0	0	--	--	--	--	--	--	--	--	30	4	43.9	13.2	--	--	--	--
Carex lupulina	13	1	0	0	--	--	--	--	20	3	5.5	1.1	10	2	0	0	38	2	29.3	11.1
Carex section Laxiflorae	25	2	17.8	4.45	--	--	--	--	40	2	40.1	16	--	--	--	--	--	--	--	--
Carpinus caroliniana	31	2	23.3	7.22	--	--	--	--	10	4	0	0	20	2	7.4	1.48	13	2	0	0
Carya carolinae-septentrionalis	38	2	21.9	8.32	--	--	--	--	40	2	25	10	10	1	0	0	13	1	0	0
Carya glabra	44	2	27.5	12.1	--	--	--	--	40	1	22.9	9.16	10	3	0	0	13	3	0	0
Celtis sp	19	1	0	0	--	--	--	--	80	1	62	49.6	30	1	4.9	1.47	--	--	--	--
Cephalanthus occidentalis	--	--	--	--	50	2	25.2	12.6	10	4	0	0	40	1	14	5.6	38	2	11.2	4.26
Chasmanthium laxum	44	2	29.2	12.8	--	--	--	--	10	1	0	0	10	2	0	0	38	2	21.5	8.17
Cinna arundinacea	25	2	10.6	2.65	--	--	--	--	50	2	43.9	22	10	1	0	0	--	--	--	--
Climacium sp	31	2	0	0	50	2	16	8	60	3	26.5	15.9	20	2	0	0	13	2	0	0
Cornus florida	38	1	39.2	14.9	--	--	--	--	10	2	0	0	--	--	--	--	13	2	0.8	0.1
Danthonia spicata	81	2	43.4	35.2	33	1	0	0	60	2	21.6	13	20	1	0	0	--	--	--	--
Dichanthelium acuminatum	6	2	0	0	--	--	--	--	40	2	53.1	21.2	--	--	--	--	--	--	--	--
Dichanthelium laxiflorum	25	1	13.1	3.28	--	--	--	--	40	2	33.8	13.5	--	--	--	--	13	2	0	0
Diospyros virginiana	63	2	0	0	50	2	0	0	90	2	27.1	24.4	80	2	16.7	13.4	38	2	0	0

Eleocharis [*acicularis* + *tenuis*]	31	2	51.6	16	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Elymus sp	--	--	--	--	--	--	--	--	40	1	59	23.6	--	--	--	--	--	--	--	--
Erechtites hieraciifolius	19	1	0	0	--	--	--	--	40	1	18.4	7.36	--	--	--	--	63	2	44.6	28.1
Erigeron sp	--	--	--	--	--	--	--	--	10	2	0	0	30	1	31.8	9.54	13	1	3.3	0.43
Euonymus americanus	50	1	35.6	17.8	--	--	--	--	20	2	0	0	10	2	0	0	25	1	4.9	1.23
Eupatorium serotinum	--	--	--	--	--	--	--	--	40	1	59	23.6	--	--	--	--	--	--	--	--
Fraxinus [*americana* + *pennsylvanica*]	94	3	38.7	36.4	--	--	--	--	80	5	24.9	19.9	90	2	34.9	31.4	13	1	0	0
Galium circaezans	25	1	45.9	11.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Gleditsia triacanthos	6	1	0	0	--	--	--	--	50	2	47	23.5	10	1	0	0	13	1	0	0
Hypericum hypericoides	63	2	42.4	26.7	--	--	--	--	30	2	5.2	1.56	10	2	0	0	25	1	0	0
Ilex decidua	13	3	0	0	--	--	--	--	40	2	41.6	16.6	10	3	0	0	--	--	--	--
Ilex opaca var. opaca	38	1	47.7	18.1	--	--	--	--	--	--	--	--	10	1	0.9	0.09	--	--	--	--
Ilex verticillata	25	2	11.4	2.85	--	--	--	--	--	--	--	--	20	1	4.7	0.94	38	2	28.3	10.8
Juncus coriaceus	63	2	68.2	43	--	--	--	--	10	4	0	0	--	--	--	--	--	--	--	--
Juniperus virginiana var. virginiana	75	2	28.1	21.1	--	--	--	--	70	3	23	16.1	40	2	0	0	50	1	3	1.5
Leersia virginica	31	2	16.8	5.21	--	--	--	--	60	2	54	32.4	--	--	--	--	--	--	--	--
Leucobryum sp	38	2	8.6	3.27	33	2	4	1.32	30	2	0.4	0.12	10	2	0	0	38	2	8.6	3.27
*Ligustrum sinense**	--	--	--	--	--	--	--	--	40	2	59	23.6	--	--	--	--	--	--	--	--
Liquidambar styraciflua	88	6	5.4	4.75	100	6	22.2	22.2	40	3	0	0	90	4	8.8	7.92	100	6	22.2	22.2
Liriodendron tulipifera	56	1	50.4	28.2	--	--	--	--	10	1	0	0	10	1	0	0	13	1	0	0

*Lonicera japonica**	56	2	26.3	14.7	--	--	--	--	70	4	41.1	28.8	20	1	0	0	13	1	0	0
Nyssa sylvatica	75	3	14.4	10.8	50	2	0	0	20	1	0	0	60	1	0	0	100	4	40	40
Oxalis sp	31	2	34.6	10.7	--	--	--	--	20	1	16.1	3.22	--	--	--	--	--	--	--	--
Panicum anceps	6	2	0	0	--	--	--	--	40	3	45.5	18.2	10	2	0	0	--	--	--	--
Parthenocissus quinquefolia	56	2	18.5	10.4	--	--	--	--	60	1	22.4	13.4	50	2	12.1	6.05	25	2	0	0
Persicaria hydropiperoides	--	--	--	--	--	--	--	--	30	3	30.4	9.12	--	--	--	--	25	2	22.4	5.6
Phytolacca americana	6	1	0	0	17	1	0	0	30	2	11.6	3.48	--	--	--	--	50	1	36.4	18.2
Pinus [*echinata* + *virginiana*]	56	2	39.4	22.1	17	1	0	0	10	1	0	0	20	1	0	0	13	2	0	0
Pinus taeda	13	4	0	0	--	--	--	--	20	1	0	0	20	2	0	0	63	2	46.9	29.5
Poa sp	31	2	51.6	16	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Prunus serotina var. serotina	56	1	33.3	18.6	--	--	--	--	30	1	3.7	1.11	10	1	0	0	38	1	12.1	4.6
Quercus alba	81	2	67.6	54.8	--	--	--	--	--	--	--	--	--	--	--	--	38	2	16.2	6.16
Quercus bicolor	--	--	--	--	--	--	--	--	30	6	50.5	15.2	--	--	--	--	--	--	--	--
Quercus lyrata	6	1	0	0	17	7	0	0	10	6	0	0	60	7	47.7	28.6	13	6	0	0
Quercus phellos	100	7	0	0	100	6	0	0	100	7	0	0	100	6	0	0	100	6	0	0
Quercus stellata	56	2	40.9	22.9	--	--	--	--	30	5	9.3	2.79	--	--	--	--	25	2	3.3	0.83
Rubus pensilvanicus	25	1	0	0	33	1	0	0	70	2	34	23.8	20	1	0	0	38	2	0.3	0.11
Ruellia caroliniensis	13	1	3.3	0.43	--	--	--	--	40	2	48.1	19.2	--	--	--	--	--	--	--	--
Sanicula sp	13	1	0	0	--	--	--	--	40	1	41.6	16.6	10	2	0	0	--	--	--	--
Scirpus cyperinus	--	--	--	--	--	--	--	--	--	--	--	--	10	2	0	0	63	2	68.2	43
Scirpus georgianus	38	2	26.3	9.99	--	--	--	--	40	3	29.6	11.8	10	2	0	0	--	--	--	--

Scutellaria integrifolia	63	1	28.2	17.8	--	--	--	--	70	1	36	25.2	20	1	0	0	25	1	0	0
Smilax bona-nox	44	1	11.9	5.24	17	3	0	0	80	2	50.6	40.5	10	1	0	0	13	2	0	0
Smilax glauca	63	2	36.2	22.8	--	--	--	--	30	1	0.5	0.15	30	1	0.5	0.15	25	1	0	0
Smilax rotundifolia	88	2	9.9	8.71	50	4	0	0	70	2	0	0	90	5	13	11.7	100	3	25.4	25.4
Sphagnum sp	19	2	0	0	17	4	0	0	--	--	--	--	10	2	0	0	50	6	39.3	19.7
Toxicodendron radicans	56	2	3	1.68	--	--	--	--	70	2	16.8	11.8	90	1	36.8	33.1	50	2	0	0
Trachelospermum difforme	50	2	13.1	6.55	17	2	0	0	60	2	23.4	14	60	1	23.4	14	--	--	--	--
Ulmus alata	81	3	21	17	50	1	0	0	100	6	40.2	40.2	60	2	0	0	13	3	0	0
Ulmus americana var. americana	13	5	0	0	--	--	--	--	60	4	58.6	35.2	10	1	0	0	--	--	--	--
Vaccinium arboreum	31	2	34.6	10.7	--	--	--	--	20	3	16.1	3.22	--	--	--	--	--	--	--	--
Vaccinium [corymbosum + fuscatum + formosum]	31	2	0	0	50	2	5.8	2.9	--	--	--	--	40	4	0	0	100	4	56.1	56.1
Vaccinium stamineum	31	2	39.8	12.3	--	--	--	--	--	--	--	--	--	--	--	--	13	2	6.6	0.86
Viburnum prunifolium	31	2	34.6	10.7	--	--	--	--	20	1	16.1	3.22	--	--	--	--	--	--	--	--
Vitis rotundifolia var. rotundifolia	88	2	36.2	31.9	17	2	0	0	50	2	0	0	40	2	0	0	63	2	11.2	7.06

Table 3.2. Means and standard errors of measured environmental and compositional variables by upland depression wetland community type.

	% Org		% Sand		% Silt		% Clay		pH	
Community Type	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**
Dry Felsic Depressions	12.39	2.36	23.10	2.91	53.77	2.76	23.12	2.25	4.41	0.09
Dry Mafic Depressions	8.13	1.14	26.33	3.28	46.07	2.64	27.59	3.91	4.62	0.18
Wet Mafic Depressions	12.37	2.82	27.44	1.80	40.82	1.65	31.75	2.31	4.36	0.10
Wet Felsic Depressions	10.64	1.97	23.37	0.91	52.92	2.01	23.72	1.46	4.14	0.08
C. joorii Pools	20.51	3.60	26.33	3.89	37.70	7.35	35.96	5.26	4.17	0.07

	CEC		BaseSat		N		S		P	
	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**
Dry Felsic Depressions	14.93	2.17	35.58	2.52	57.36	1.92	38.91	6.48	19.30	3.13
Dry Mafic Depressions	19.95	3.35	40.44	4.60	55.41	2.38	41.30	4.57	24.00	4.43
Wet Mafic Depressions	18.18	2.50	30.10	3.11	59.43	2.09	41.18	5.88	27.50	3.92
Wet Felsic Depressions	14.61	2.23	20.82	3.96	59.38	2.24	48.38	7.17	48.75	12.54
C. joorii Pools	16.16	3.51	29.48	1.44	66.06	1.27	47.96	13.77	37.79	4.18

	Ca ppm		Mg ppm		K ppm		Na ppm		% Ca	
	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**
Dry Felsic Depressions	631.2	91.10	205.30	35.14	70.92	7.04	32.65	1.91	21.58	2.09
Dry Mafic Depressions	963.0	230.67	325.08	65.25	86.25	15.72	40.33	5.49	23.30	3.33
Wet Mafic Depressions	536.4	91.96	305.80	93.86	91.53	19.24	44.95	7.48	15.03	1.49
Wet Felsic Depressions	352.8	84.30	72.38	10.82	47.38	5.96	29.50	4.05	13.82	2.98
C. joorii Pools	591.5	127.70	159.17	44.39	99.71	9.90	35.54	2.73	18.36	1.04

	% Mg		% K		% Na		% Othr		% H	
	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**
Dry Felsic Depressions	11.21	0.80	1.49	0.16	1.29	0.16	8.67	0.28	56.93	2.41
Dry Mafic Depressions	14.62	1.89	1.27	0.21	1.25	0.31	8.15	0.35	51.41	4.25
Wet Mafic Depressions	12.31	2.19	1.54	0.39	1.23	0.26	9.61	0.57	64.84	4.29
Wet Felsic Depressions	4.80	0.82	1.08	0.24	1.12	0.26	10.94	0.76	74.68	5.52
C. joorii Pools	7.95	0.93	1.98	0.44	1.19	0.26	9.07	0.14	61.46	1.30

	B ppm		Fe ppm		Mn ppm		Cu ppm		Zn ppm	
	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**
Dry Felsic Depressions	0.35	0.06	397.63	21.69	46.79	21.40	1.31	0.16	2.71	0.35
Dry Mafic Depressions	0.42	0.07	401.05	36.93	104.85	38.97	2.28	0.47	4.06	0.87
Wet Mafic Depressions	0.38	0.06	388.25	28.24	6.08	1.46	1.03	0.13	3.23	0.48
Wet Felsic Depressions	0.22	0.06	282.38	55.26	7.63	1.83	1.05	0.16	2.21	0.32
C. joorii Pools	0.24	0.07	313.92	25.51	11.50	0.76	1.60	0.31	4.58	1.51

	Al ppm		Ca/Mg ppm		Stems/m^2		Elev		CanHt (m)	
	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**	Mean	**±SE**
Dry Felsic Depressions	842.7	52.01	3.50	0.39	0.20	0.03	185.24	12.29	29.56	1.28
Dry Mafic Depressions	839.0	53.90	2.91	0.36	0.26	0.06	194.65	7.08	24.40	1.21
Wet Mafic Depressions	1117.	73.82	2.65	0.46	0.34	0.14	177.64	19.85	29.60	0.82
Wet Felsic Depressions	1133.	76.45	4.72	0.63	0.45	0.11	171.99	20.24	26.88	1.37
C. joorii Pools	1149.	90.76	4.10	0.51	0.17	0.09	225.74	4.52	24.83	2.52

	HydInd	
	Mean	**±SE**
Dry Felsic Depressions	3.05	0.06
Dry Mafic Depressions	3.22	0.09
Wet Mafic Depressions	3.31	0.03
Wet Felsic Depressions	3.42	0.10
C. joorii Pools	3.55	0.10

Table 3.3. Relationship of the identified upland depression wetland community types to recognized NVC associations. Relationships are depicted in the table by four symbols: < indicates the community type is included in the NVC concept, > indicates the community type includes the NVC concept, >< indicates that the two concepts overlap, ~ indicates the community type is approximately equivalent to the NVC concept.

Community	Seep Vegetation Type	Relationship	CEGL	NVC Association (Alliance)
Wet Depression Swamps				
***Carex joorii* Pools**	*Quercus phellos - Liquidambar styraciflua / Cephalanthus occidentalis / Carex joorii Woodland*	~	4075	Cephalanthus occidentalis - (Leucothoe racemosa) / Carex joorii Shrubland (Cephalanthus occidentalis Semipermanently Flooded Shrubland Alliance)
Wet Mafic Depression Swamps	*Quercus phellos - Quercus lyrata - Acer rubrum / Smilax rotundifolia / Carex albolutescens - Carex louisianca Forest*	<	7403	Quercus phellos / Carex (albolutescens, intumescens, joorii) - Chasmanthium laxum / Sphagnum lescurii Forest (Quercus phellos Seasonally Flooded Forest Alliance)
Wet Felsic Depression Swamps	*Quercus phellos - Acer rubrum - Nyssa sylvatica / Vaccinium fuscatum / Scirpus cyperinus -Spagnum spp Forest*	<	7403	Quercus phellos / Carex (albolutescens, intumescens, joorii) - Chasmanthium laxum / Sphagnum lescurii Forest (Quercus phellos Seasonally Flooded Forest Alliance)
Dry Depression Swamps				
Dry Mafic Depression Swamps	*Quercus phellos - Ulmus alata / Campsis radicans - Smilax bona-nox / Leersia virginica Forest*	><	7403	Quercus phellos / Carex (albolutescens, intumescens, joorii) - Chasmanthium laxum / Sphagnum lescurii Forest (Quercus phellos Seasonally Flooded Forest Alliance)
Dry Felsic Depression Swamps	*Quercus phellos / Vitis rotundifolia var. rotundifolia / Danthonia spicata - Juncus coriaceus Forest*	><	7403	Quercus phellos / Carex (albolutescens, intumescens, joorii) - Chasmanthium laxum / Sphagnum lescurii Forest (Quercus phellos Seasonally Flooded Forest Alliance)

Table 3.4. Relationship of the identified upland depression wetland community types to established community concepts from the North Carolina state classification. Community types are compared to North Carolina's *Classification of the natural communities of North Carolina: fourth approximation* (Schafale 2003). Relationships are depicted in the table by four symbols: < indicates the community type is included in the concept, > indicates the community type includes the concept, >< indicates that the two concepts overlap, ~ indicates the community type is approximately equivalent to the concept.

Community	Upland Depression Vegetation Type	Relationship	NC State Classification Community Type
	Wet Depression Swamps		
***Carex joorii* Pools**	*Quercus phellos - Liquidambar styraciflua / Cephalanthus occidentalis / Carex joorii Woodland*	~	Upland Pool (typic Piedmont subtype)
Wet Mafic Depression Swamps	*Quercus phellos - Quercus lyrata - Acer rubrum / Smilax rotundifolia / Carex albolutescens - Carex louisianca Forest*	<	Upland Depression Swamp Forest (typic subtype)
Wet Felsic Depression Swamps	*Quercus phellos - Acer rubrum - Nyssa sylvatica / Vaccinium fuscatum / Scirpus cyperinus -Spagnum spp Forest*	<	Upland Depression Swamp Forest (typic subtype)
	Dry Depression Swamps		
Dry Mafic Depression Swamps	*Quercus phellos - Ulmus alata / Campsis radicans - Smilax bona-nox / Leersia virginica Forest*	><	Upland Depression Swamp Forest (typic subtype)
Dry Felsic Depression Swamps	*Quercus phellos / Vitis rotundifolia var. rotundifolia / Danthonia spicata - Juncus coriaceus Forest*	><	Upland Depression Swamp Forest (typic subtype)

Table 3.5. Plot assignment to community types derived from cluster analysis of upland depression wetlands. The source of plot data, from the Carolina Vegetation Survey (CVS) or the Virginia Natural Heritage Program (VANHP), is indicated in the table. Plots that well-represent the core concept of the community type, are indicated by an asterisk (*).

Plot	Source	Assigned Community Type
004-01-0156	CVS	Dry Felsic Depression Swamps
004-04-0151	CVS	Dry Felsic Depression Swamps
004-05-0150	CVS	Dry Felsic Depression Swamps
004-05-0151	CVS	*Carex joorii* Pools
004-05-0155	CVS	Outlier (CEGL004550)
004-07-0151	CVS	Outlier (CEGL004533)
019-01-0018	CVS	Dry Felsic Depression Swamps
059-02-0852	CVS	Dry Mafic Depression Swamps
059-02-0853	CVS	Wet Mafic Depression Swamps*
059-03-0855	CVS	Dry Mafic Depression Swamps
059-04-0855	CVS	Dry Mafic Depression Swamps*
111-01-1353	CVS	Dry Felsic Depression Swamps
111-01-1355	CVS	Dry Mafic Depression Swamps
111-03-1351	CVS	Wet Mafic Depression Swamps
111-06-1353	CVS	Dry Felsic Depression Swamps
111-06-1359	CVS	Dry Felsic Depression Swamps
114-01-0012	CVS	*Carex joorii* Pools
114-01-0013	CVS	Wet Felsic Depression Swamps*
114-01-0014	CVS	*Carex joorii* Pools
114-01-0015	CVS	*Carex joorii* Pools
114-01-0016	CVS	Dry Mafic Depression Swamps
114-01-0017	CVS	Dry Mafic Depression Swamps
114-01-0019	CVS	Wet Mafic Depression Swamps
114-01-0023	CVS	Dry Felsic Depression Swamps*
114-01-0024	CVS	Dry Felsic Depression Swamps
114-01-0027	CVS	Wet Felsic Depression Swamps
114-01-0032	CVS	Dry Felsic Depression Swamps
114-01-0037	CVS	Dry Mafic Depression Swamps
114-01-0038	CVS	*Carex joorii* Pools
114-01-0039	CVS	Dry Mafic Depression Swamps
114-01-0056	CVS	Wet Mafic Depression Swamps

114-01-0057	CVS	Dry Felsic Depression Swamps
114-01-0068	CVS	Wet Felsic Depression Swamps
114-01-0069	CVS	Wet Felsic Depression Swamps
114-01-0070	CVS	Dry Felsic Depression Swamps
114-01-0073	CVS	*Carex joorii* Pools*
114-01-0076	CVS	Dry Mafic Depression Swamps
114-01-0077	CVS	Dry Mafic Depression Swamps
120-01-1438	CVS	Wet Mafic Depression Swamps
120-04-1431	CVS	Dry Felsic Depression Swamps
120-04-1436	CVS	Dry Felsic Depression Swamps
120-07-1431	CVS	Wet Mafic Depression Swamps
APCO003	VANHP	Wet Mafic Depression Swamps
APCO014	VANHP	Dry Felsic Depression Swamps
BESP001	VANHP	Wet Felsic Depression Swamps
CUSF003	VANHP	Wet Mafic Depression Swamps
CUSF018	VANHP	Dry Felsic Depression Swamps
CUSF029	VANHP	Wet Felsic Depression Swamps
KERR025	VANHP	Wet Mafic Depression Swamps
LUNE003	VANHP	Wet Mafic Depression Swamps
LUNE004	VANHP	Wet Felsic Depression Swamps
PITT005	VANHP	Wet Felsic Depression Swamps

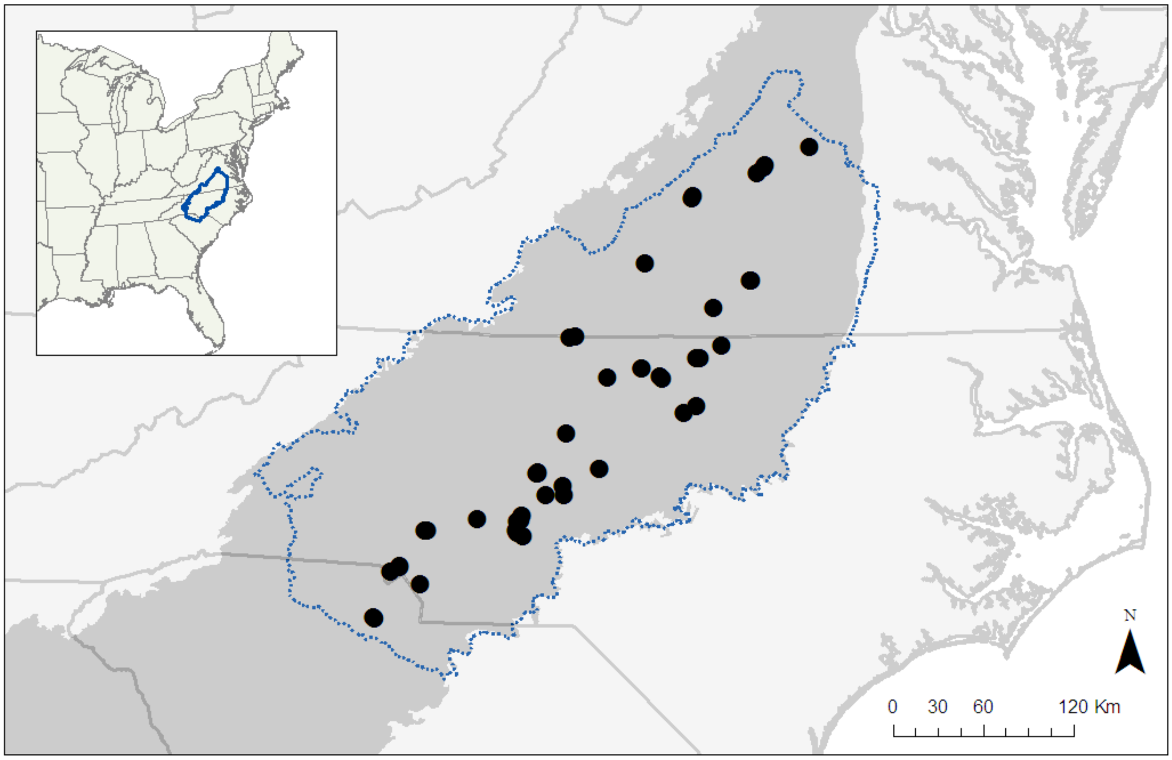

Figure 3.1. Map of study area and locations of 52 upland depression wetland vegetation plots. Plots are marked by black circles and the Piedmont physiographic province is shaded in gray. The dashed blue line represents the “northern Piedmont” MRLC map zone recognized by NatureServe (NatureServe 2010).

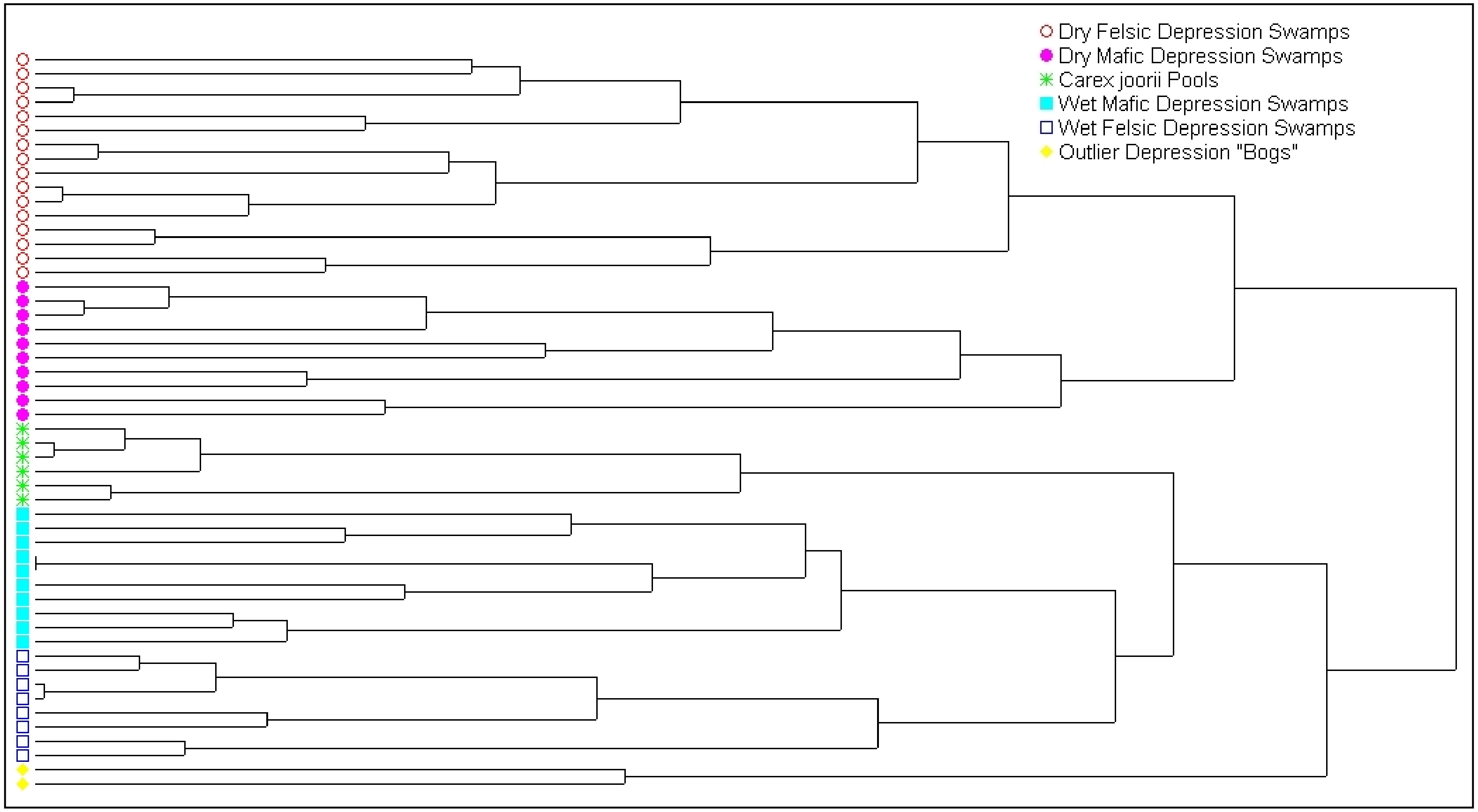

Figure 3.2. Dendrogram from hierarchical cluster analysis with flexible β linkage (β = -0.25) used to identify upland depression wetland community types and higher level groups. Color coded symbols correspond to community types identified from the cluster analysis.

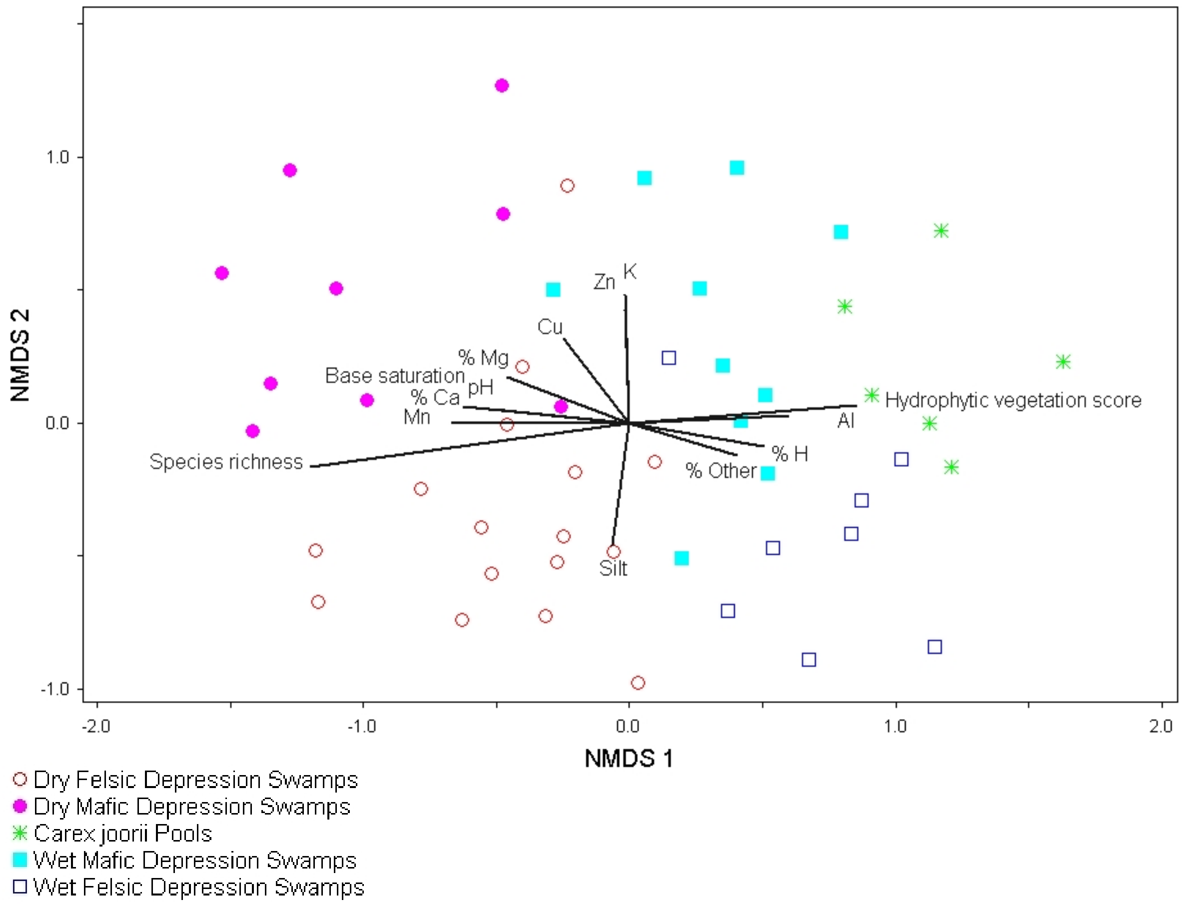

Figure 3.3. Two-dimensional non-metric multidimensional scaling (NMS) ordination of upland depression vegetation with joint-plot overlay. Correlation of environmental variables with ordination axes (cutoff r = 0.4) are displayed by joint-plot overlays, where the length and direction of the vector represent the strength and the direction of correlation with the axes, respectively. Color coded symbols correspond to community types identified from the cluster analysis.

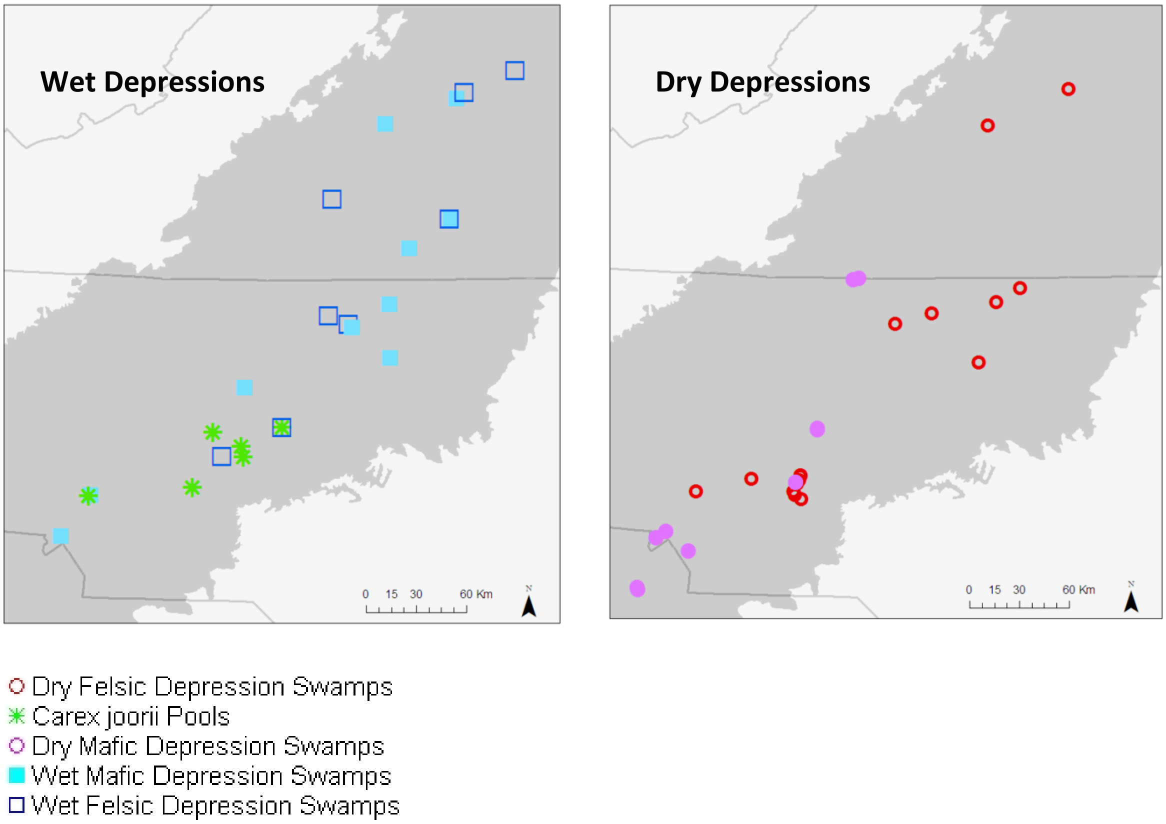

Figure 3.4. Geographic distribution of plots within identified upland depression wetland community types. Community types are mapped by higher-level groups. Color coded symbols correspond to community types identified from the cluster analysis. The boundaries of the Piedmont are shown in gray.

Appendix 2A

Synoptic vegetation table of Headwater Boggy Seeps. Constancy (% Const.), average cover, fidelity (% Fid), diagnostic value (% DV), and DL indicator species value (IndVal) of prevalent taxa in Headwater Boggy Seeps. Only DL indicator species values that are significant ($p < 0.5$) are shown. Taxa are sorted in order of decreasing constancy, then cover, then fidelity. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Headwater Boggy Seeps				
Group Plot Count	4				
Group Avg Plot Spp Richness	57				
Group homoteneity	61.0				
taxon name	% Const	Cover	% Fid	% DV	IndVal
Andropogon sp	100	4	89.5	89.5	92.3
Alnus serrulata	100	4	40.8	40.8	34.8
Liquidambar styraciflua	100	4	23.7	23.7	--
Acer rubrum	100	4	9.3	9.3	--
Nyssa sylvatica	100	3	52.7	52.7	36.2
Eupatorium [*pubescens* + *rotundifolium*]	100	2	100	100	100
Symphyotrichum dumosum	100	2	100	100	100
Quercus alba	100	1	47.6	47.6	--
Gaylussacia frondosa	75	4	49.6	37.2	46
Osmundastrum cinnamomeum	75	4	11.3	8.475	--
Pinus palustris	75	3	80.3	60.225	70.9
Eupatorium pilosum	75	2	84	63	--
Scleria [*nitida* + *triglomerata*]	75	2	84	63	75
Asclepias sp	75	2	80.3	60.225	72.5
Dichanthelium scoparium	75	2	78.3	58.725	71.6
Rhexia mariana	75	2	78.3	58.725	68.5
Quercus stellata	75	2	77	57.75	65.9
Xyris sp	75	2	76.9	57.675	64.2
Oxydendrum arboreum	75	2	30.5	22.875	--
Smilax laurifolia	75	2	27	20.25	--
Aronia arbutifolia	75	2	24.5	18.375	--
Vaccinium [*corymbosum* + *fuscatum* + *formosum*]	75	2	14.4	10.8	--
Liriodendron tulipifera	75	2	0	0	--
Saccharum sp	50	4	66.7	33.35	50
Danthonia sericea	50	3	66.7	33.35	50
Panicum virgatum	50	3	66.7	33.35	--
Danthonia spicata	50	3	51.4	25.7	41.4
Morella caroliniensis	50	3	30.3	15.15	--

Amelanchier [*arborea* + *canadensis*]	50	3	15.4	7.7	--
Drosera brevifolia	50	2	66.7	33.35	--
Eupatorium leucolepis	50	2	66.7	33.35	--
Hypericum setosum	50	2	66.7	33.35	--
Polygala lutea	50	2	66.7	33.35	--
Sophronanthe pilosa	50	2	66.7	33.35	--
Solidago stricta	50	2	62.1	31.05	--
Pteridium aquilinum	50	2	54.5	27.25	39.6
Juncus coriaceus	50	2	28.9	14.45	--
Scutellaria integrifolia	50	2	28.5	14.25	--
Pinus taeda	50	2	19.2	9.6	--
Vitis subgenus Vitis	50	2	17.4	8.7	--
Viola primulifolia	50	2	15.8	7.9	--
Diospyros virginiana	50	2	14.1	7.05	--
Nyssa [*biflora* + *sylvatica swamp variety*]	50	2	12.7	6.35	--
Rubus pensilvanicus	50	2	10.4	5.2	--
Woodwardia areolata	50	2	1.5	0.75	--
Ilex opaca var. opaca	50	2	0	0	--
Toxicodendron radicans	50	2	0	0	--
Chrysopsis mariana	50	1	66.7	33.35	--
Pogonia ophioglossoides	50	1	66.7	33.35	--
Ulmus alata	50	1	32.6	16.3	--
Quercus phellos	50	1	11.8	5.9	--
Dichanthelium [*chamaelonche* + *ensifolium*]	25	7	39.7	9.925	23.6
Dichanthelium lucidum	25	7	8.1	2.025	--
Calamovilfa brevipilis	25	6	45.9	11.475	--
Lyonia ligustrina	25	6	34.3	8.575	--
Sarracenia purpurea var. venosa	25	6	34	8.5	20.9
Eupatorium hyssopifolium	25	5	45.9	11.475	--
Pycnanthemum tenuifolium	25	5	45.9	11.475	--
Scleria ciliata	25	5	45.9	11.475	--

Appendix 2B

Synoptic vegetation table of Streamhead Seeps. Constancy (% Const.), average cover, fidelity (% Fid), diagnostic value (% DV), and DL indicator species value (IndVal) of prevalent taxa in Streamhead Seeps. Only DL indicator species values that are significant (p < 0.5) are shown. Taxa are sorted in order of decreasing constancy, then cover, then fidelity. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Streamhead Seeps				
Group Plot Count	19				
Group Avg Plot Spp Richness	53				
Group homoteneity	64.0				
taxon name	% Const	Cover	% Fid	% DV	IndVal
Acer rubrum	100	7	9.3	9.3	--
Liriodendron tulipifera	100	6	22	22	--
Vaccinium [*corymbosum* + *fuscatum* + *formosum*]	100	4	40	40	39.3
Quercus alba	95	5	42.3	40.185	49
Liquidambar styraciflua	95	5	16.9	16.055	--
Osmunda regalis var. spectabilis	95	4	56	53.2	51.4
Osmundastrum cinnamomeum	95	4	31.9	30.305	31.4
Vitis rotundifolia var. rotundifolia	95	2	34.9	33.155	32.1
Viburnum nudum	89	3	35.6	31.684	--
Ilex opaca var. opaca	84	3	26.5	22.26	--
Chasmanthium laxum	84	2	46.1	38.724	38.9
Toxicodendron radicans	84	2	2.4	2.016	--
Oxydendrum arboreum	79	4	34.4	27.176	35.3
Smilax glauca	79	2	35.4	27.966	--
Euonymus americanus	79	2	27.4	21.646	--
Eubotrys racemosa	74	3	62.4	46.176	50.8
Smilax rotundifolia	74	2	5.2	3.848	--
Nyssa sylvatica	68	5	21.1	14.348	--
Gaylussacia frondosa	68	3	42.4	28.832	--
Mitchella repens	68	2	27.8	18.904	--
Arisaema triphyllum	68	2	23.2	15.776	--
Lycopus virginicus	68	2	3.2	2.176	--
Rhododendron sp	63	2	32.9	20.727	--
Parthenocissus quinquefolia	63	2	0	0	--
Woodwardia areolata	58	3	9.4	5.452	--
Scutellaria integrifolia	58	2	37.6	21.808	25
Eutrochium fistulosum	58	2	22.2	12.876	--
Smilax laurifolia	58	2	9.9	5.742	--
Aronia arbutifolia	58	2	7.4	4.292	--
Magnolia virginiana	53	5	39.3	20.829	--
Medeola virginiana	53	2	47.4	25.122	29

Pinus taeda	53	2	22	11.66	--
Itea virginica	53	2	20.4	10.812	--
Viola primulifolia	53	2	18.5	9.805	--
Carex debilis	53	2	15	7.95	--
Ilex verticillata	53	2	0.9	0.477	--
Thuidium sp	53	2	0	0	--
Vitis subgenus Vitis	47	2	14.6	6.862	--
Diospyros virginiana	47	2	11.4	5.358	--
Athyrium asplenioides	47	2	11.2	5.264	--
Sphagnum sp	47	2	9.3	4.371	--
Arundinaria [*gigantea* + *tecta*]	42	4	27.9	11.718	--
Alnus serrulata	42	3	0	0	--
Uvularia [*puberula* + *sessilifolia*]	42	2	38.8	16.296	24.4
Dioscorea [*quaternata* + *villosa*]	42	2	32.5	13.65	--
Morella caroliniensis	42	2	21.1	8.862	--
Carex leptalea var. leptalea	42	2	14.9	6.258	--
Dichanthelium dichotomum var. ramulosum	42	2	8.2	3.444	--
Amelanchier [*arborea* + *canadensis*]	42	2	7.2	3.024	--
Solidago caesia	42	2	3.4	1.428	--
Quercus velutina	42	1	22.1	9.282	--
Quercus rubra	37	2	35.8	13.246	--
Leucobryum sp	37	2	24.5	9.065	--

Appendix 2C

Synoptic vegetation table of Infertile Swampy Seeps. Constancy (% Const.), average cover, fidelity (% Fid), diagnostic value (% DV), and DL indicator species value (IndVal) of prevalent taxa in Infertile Swampy Seeps. Only DL indicator species values that are significant ($p < 0.5$) are shown. Taxa are sorted in order of decreasing constancy, then cover, then fidelity. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Infertile Swampy Seeps				
Group Plot Count	16				
Group Avg Plot Spp Richness	54				
Group homoteneity	63.0				
taxon name	% Const	Cover	% Fid	% DV	IndVal
Acer rubrum	100	7	9.3	9.3	--
Viburnum nudum	94	5	39.9	37.506	39
*Lonicera japonica**	94	2	34.4	32.336	--
Liriodendron tulipifera	88	6	5	4.4	--
Ilex verticillata	88	2	35.8	31.504	--
Ilex opaca var. opaca	88	2	29.9	26.312	--
Parthenocissus quinquefolia	88	2	24.1	21.208	--
Smilax rotundifolia	88	2	20.1	17.688	--
Toxicodendron radicans	88	2	6.8	5.984	--
Aronia arbutifolia	81	2	30.8	24.948	31.1
Thuidium sp	81	2	23.8	19.278	--
Vaccinium [*corymbosum + fuscatum + formosum*]	75	4	14.4	10.8	--
*Microstegium vimineum**	75	2	29.8	22.35	--
Alnus serrulata	75	2	15.2	11.4	--
Vitis rotundifolia var. rotundifolia	75	2	14.7	11.025	--
Lycopus virginicus	75	2	10.1	7.575	--
Nyssa [*biflora + sylvatica swamp variety*]	69	8	32	22.08	35.9
Smilax laurifolia	69	3	20.8	14.352	--
Platanthera sp	69	2	33.1	22.839	--
Mitchella repens	69	2	28.1	19.389	--
*Ligustrum sinense**	69	2	26	17.94	--
Euonymus americanus	69	2	17.2	11.868	--
Liquidambar styraciflua	69	2	0	0	--
Fraxinus pennsylvanica	63	4	16.5	10.395	--
Marchantiophyta sp	63	2	37.9	23.877	--
Itea virginica	63	2	30.9	19.467	--
Amelanchier [*arborea + canadensis*]	63	2	28.5	17.955	--
Prunus serotina var. serotina	63	2	26.2	16.506	--
Woodwardia areolata	56	4	7.8	4.368	--
Osmundastrum cinnamomeum	56	3	0	0	--
Carex allegheniensis	56	2	60.1	33.656	44.9
Smilax walteri	56	2	51.2	28.672	37.7

Carex leptalea var. leptalea	56	2	30.5	17.08	--
Eutrochium fistulosum	56	2	20.5	11.48	--
Leersia virginica	56	2	17.4	9.744	--
Carex [*atlantica* + *howei*]	50	3	15	7.5	--
Xanthorhiza simplicissima	50	2	43.3	21.65	33.5
Chelone [*glabra* + *obliqua*]	50	2	25.2	12.6	--
Viola sp	50	2	12.1	6.05	--
Solidago caesia	50	2	11.5	5.75	--
Glyceria striata var. striata	50	2	6.6	3.3	--
Smilax glauca	50	2	6.3	3.15	--
Arisaema triphyllum	50	2	4.7	2.35	--
Athyrium asplenioides	44	3	7.5	3.3	--
*Rosa multiflora**	44	2	40.9	17.996	--
Sambucus canadensis	44	2	19.6	8.624	--
Rhododendron sp	44	2	12.1	5.324	--
Carex lurida	44	2	9.4	4.136	--
Viola primulifolia	44	2	9.2	4.048	--
Rubus pensilvanicus	44	2	4	1.76	--
Decumaria barbara	38	4	37.8	14.364	--
Kalmia latifolia	38	3	43.5	16.53	26.4
Viburnum dentatum	38	3	13.1	4.978	--
Toxicodendron vernix	38	2	52	19.76	34.7

Appendix 2D

Synoptic vegetation table of Rich Foot-slope Seeps. Constancy (% Const.), average cover, fidelity (% Fid), diagnostic value (% DV), and DL indicator species value (IndVal) of prevalent taxa in Rich Foot-slope Seeps. Only DL indicator species values that are significant ($p < 0.5$) are shown. Taxa are sorted in order of decreasing constancy, then cover, then fidelity. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Rich Foot-slope Seeps				
Group Plot Count	20				
Group Avg Plot Spp Richness	56				
Group homoteneity	60.6				
taxon name	% Const	Cover	% Fid	% DV	IndVal
Acer rubrum	100	7	9.3	9.3	--
Arisaema triphyllum	100	4	54.9	54.9	54.1
Smilax rotundifolia	100	3	33.6	33.6	34.1
Liquidambar styraciflua	95	5	17.2	16.34	--
Liriodendron tulipifera	90	6	8.4	7.56	--
Toxicodendron radicans	90	2	10	9	--
Euonymus americanus	85	2	33.5	28.475	--
Ilex verticillata	85	2	33.3	28.305	--
Fraxinus pennsylvanica	80	5	34.1	27.28	--
Thuidium sp	80	2	22.5	18	--
*Lonicera japonica**	80	2	20.4	16.32	--
Parthenocissus quinquefolia	80	2	16.2	12.96	--
Athyrium asplenioides	75	3	39.9	29.925	34.4
Leersia virginica	75	2	36.6	27.45	30.9
*Ligustrum sinense**	75	2	32.4	24.3	--
Vitis rotundifolia var. rotundifolia	75	2	14.7	11.025	--
Lycopus virginicus	75	2	10.1	7.575	--
Carpinus caroliniana	70	5	58.9	41.23	51.6
Woodwardia areolata	70	4	21.5	15.05	--
Saururus cernuus	70	3	60.9	42.63	36.8
Osmundastrum cinnamomeum	70	3	6.1	4.27	--
Platanthera sp	70	2	34.4	24.08	29.4
Dichanthelium dichotomum var. ramulosum	65	2	32.3	20.995	--
Boehmeria cylindrica	65	2	32.1	20.865	--
Carex debilis	65	2	27.7	18.005	--
Glyceria striata var. striata	65	2	21.7	14.105	--
Solidago caesia	60	2	21.8	13.08	--
Mitchella repens	60	2	19.2	11.52	--

*Microstegium vimineum**	60	2	14.7	8.82	--
Ilex opaca var. opaca	60	2	2	1.2	--
Lindera benzoin	55	5	29.9	16.445	--
Vaccinium [*corymbosum* + *fuscatum* + *formosum*]	55	4	0	0	--
Chelone [*glabra* + *obliqua*]	55	2	30.8	16.94	--
Bignonia capreolata	50	2	42.2	21.1	30.5
Sambucus canadensis	50	2	26.7	13.35	--
Magnolia virginiana	45	5	29.9	13.455	--
Viburnum nudum	45	4	0	0	--
Campsis radicans	45	2	43	19.35	24.9
Dioscorea [*quaternata* + *villosa*]	45	2	36.4	16.38	--
Chasmanthium laxum	45	2	6	2.7	--
Rubus pensilvanicus	45	2	5.3	2.385	--
Fagus grandifolia	40	4	34.3	13.72	--
Sphagnum sp	40	3	1.7	0.68	--
Osmunda regalis var. spectabilis	40	3	0.1	0.04	--
Amphicarpaea bracteata	40	2	29.4	11.76	--
Solidago rugosa	40	2	17.7	7.08	--
Mnium sp	40	2	9.3	3.72	--
Viola sp	40	2	1.8	0.72	--
Quercus phellos	40	2	1.6	0.64	--
Smilax glauca	40	2	0	0	--
Carex [*atlantica* + *howei*]	35	3	0	0	--
Nyssa sylvatica	35	3	0	0	--
Sanicula sp	35	2	29.1	10.185	--
Polystichum acrostichoides	35	2	20.6	7.21	--
Hexastylis sp	35	2	19.8	6.93	--
Juncus [*effusus* + *pylaei*]	35	2	13.9	4.865	--

Appendix 2E

Synoptic vegetation table of Floodplain Seeps. Constancy (% Const.), average cover, fidelity (% Fid), diagnostic value (% DV), and DL indicator species value (IndVal) of prevalent taxa in Floodplain Seeps. Only DL indicator species values that are significant (p < 0.5) are shown. Taxa are sorted in order of decreasing constancy, then cover, then fidelity. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Floodplain Seeps				
Group Plot Count	12				
Group Avg Plot Spp Richness	45				
Group homoteneity	56.9				
taxon name	% Const	Cover	% Fid	% DV	IndVal
Toxicodendron radicans	100	2	23.2	23.2	--
*Microstegium vimineum**	92	6	46.5	42.78	55.2
Glyceria striata var. striata	92	3	48.6	44.712	50.4
Impatiens [*capensis* + *pallida*]	92	2	68	62.56	66.4
Acer rubrum	83	7	0	0	--
Boehmeria cylindrica	83	2	51.4	42.662	47.3
Lycopus virginicus	83	2	18.9	15.687	--
Cinna arundinacea	75	2	63.7	47.775	53
Mnium sp	75	2	47	35.25	38
Carex lurida	75	2	42.2	31.65	33.6
Thuidium sp	75	2	17.4	13.05	--
*Lonicera japonica**	75	2	15.3	11.475	--
Fraxinus pennsylvanica	67	5	20.7	13.869	--
Sagittaria latifolia	67	2	71.2	47.704	61.2
Carex laevivaginata	67	2	47.5	31.825	39.5
Carex [*atlantica* + *howei*]	67	2	32.4	21.708	--
Parthenocissus quinquefolia	67	2	2.3	1.541	--
Liriodendron tulipifera	67	1	0	0	--
Alnus serrulata	58	7	0	0	--
Carex crinita	58	2	39.5	22.91	30.4
Smilax rotundifolia	58	2	0	0	--
Liquidambar styraciflua	50	5	0	0	--
Lindera benzoin	50	4	24.4	12.2	--
Persicaria sagittata	50	2	66.7	33.35	50
Galium tinctorium	50	2	53.4	26.7	37
Viola sp	50	2	12.1	6.05	--
Rubus pensilvanicus	50	2	10.4	5.2	--
*Ligustrum sinense**	50	2	7.1	3.55	--

Sphagnum sp	42	4	3.5	1.47	--
Symphyotrichum puniceum var. puniceum	42	2	54.5	22.89	36.2
Carex tribuloides	42	2	46.8	19.656	32.5
Rosa palustris	42	2	33.7	14.154	24.3
Leersia oryzoides	42	2	32.1	13.482	--
Polystichum acrostichoides	42	2	29.1	12.222	--
Prunus serotina var. serotina	42	2	4.7	1.974	--
Solidago caesia	42	2	3	1.26	--
Saururus cernuus	33	7	15.6	5.148	--
*Murdannia keisak**	33	6	29.2	9.636	--
Ilex verticillata	33	5	0	0	--
Peltandra virginica	33	3	29.2	9.636	--
Ulmus alata	33	3	12.7	4.191	--
Diospyros virginiana	33	3	0	0	--
Carex [*radiata + rosea*]	33	2	47.1	15.543	28.1
Hypericum mutilum var. mutilum	33	2	38.8	12.804	--
*Persicaria longiseta**	33	2	38.3	12.639	--

Appendix 3A

Synoptic vegetation table of *Carex joorii* Pools. Constancy (% Const.), average cover, fidelity (% Fid), diagnostic value (% DV), and DL indicator species value (IndVal) of prevalent taxa in *Carex joorii* Pools. Only DL indicator species values that are significant (p < 0.5) are shown. Taxa are sorted in order of decreasing constancy, then cover, then fidelity. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	*Carex joorii* Pools				
Group Plot Count	6				
Group Avg Plot Spp Richness	12				
Group homoteneity	63.9				
taxon name	% Const	Cover	% Fid	% DV	IndVal
Quercus phellos	100	6	0	0	--
Liquidambar styraciflua	100	6	22.2	22.2	--
Carex joorii	100	6	56.7	56.7	48.9
Acer rubrum	67	3	0	0	--
Cephalanthus occidentalis	50	2	25.2	12.6	--
Smilax rotundifolia	50	4	0	0	--
Ulmus alata	50	1	0	0	--
Campsis radicans	50	2	0	0	--
Nyssa sylvatica	50	2	0	0	--
Diospyros virginiana	50	2	0	0	--
Climacium sp	50	2	16	8	--
Vaccinium [*corymbosum* + *fuscatum* + *formosum*]	50	2	5.8	2.9	--

Appendix 3B

Synoptic vegetation table of Wet Felsic Depression Swamps. Constancy (% Const.), average cover, fidelity (% Fid), diagnostic value (% DV), and DL indicator species value (IndVal) of prevalent taxa in Wet Felsic Depression Swamps. Only DL indicator species values that are significant ($p < 0.5$) are shown. Taxa are sorted in order of decreasing constancy, then cover, then fidelity. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Wet Felsic Depression Swamps				
Group Plot Count	8				
Group Avg Plot Spp Richness	26				
Group homoteneity	58.5				
taxon name	% Const	Cover	% Fid	% DV	IndVal
Quercus phellos	100	6	0	0	--
Liquidambar styraciflua	100	6	22.2	22.2	--
Acer rubrum	100	5	24.9	24.9	30.1
Nyssa sylvatica	100	4	40	40	39.5
Vaccinium [*corymbosum* + *fuscatum* + *formosum*]	100	4	56.1	56.1	57.9
Smilax rotundifolia	100	3	25.4	25.4	--
Erechtites hieraciifolius	63	2	44.6	28.098	35.6
Vitis rotundifolia var. rotundifolia	63	2	11.2	7.056	--
Pinus taeda	63	2	46.9	29.547	30.2
Scirpus cyperinus	63	2	68.2	42.966	55.1
Carex joorii	50	6	6.3	3.15	--
Sphagnum sp	50	6	39.3	19.65	34.4
Toxicodendron radicans	50	2	0	0	--
Phytolacca americana	50	1	36.4	18.2	--
Juniperus virginiana var. virginiana	50	1	3	1.5	--
Carex [*albolutescens* + *festucacea*]	38	3	5.3	2.014	--
Quercus alba	38	2	16.2	6.156	--
Diospyros virginiana	38	2	0	0	--
Cephalanthus occidentalis	38	2	11.2	4.256	--
Ilex verticillata	38	2	28.3	10.754	--
Rubus pensilvanicus	38	2	0.3	0.114	--
Carex [*caroliniana* + *complanata*]	38	2	8.2	3.116	--
Bidens sp	38	2	47.7	18.126	33.7
Leucobryum sp	38	2	8.6	3.268	--
Carex lupulina	38	2	29.3	11.134	--
Chasmanthium laxum	38	2	21.5	8.17	--

Appendix 3C

Synoptic vegetation table of Wet Mafic Depression Swamps. Constancy (% Const.), average cover, fidelity (% Fid), diagnostic value (% DV), and DL indicator species value (IndVal) of prevalent taxa in Wet Mafic Depression Swamps. Only DL indicator species values that are significant (p < 0.5) are shown. Taxa are sorted in order of decreasing constancy, then cover, then fidelity. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Wet Mafic Depression Swamps				
Group Plot Count	10				
Group Avg Plot Spp Richness	25				
Group homoteneity	59.2				
taxon name	% Const	Cover	% Fid	% DV	IndVal
Quercus phellos	100	6	0	0	--
Acer rubrum	100	5	24.9	24.9	--
Smilax rotundifolia	90	5	13	11.7	--
Liquidambar styraciflua	90	4	8.8	7.92	--
Fraxinus [*americana* + *pennsylvanica*]	90	2	34.9	31.41	--
Toxicodendron radicans	90	1	36.8	33.12	--
Carex [*albolutescens* + *festucacea*]	80	2	50.7	40.56	33.5
Diospyros virginiana	80	2	16.7	13.36	--
Campsis radicans	70	2	6.3	4.41	--
Quercus lyrata	60	7	47.7	28.62	38.4
Ulmus alata	60	2	0	0	--
Trachelospermum difforme	60	1	23.4	14.04	--
Nyssa sylvatica	60	1	0	0	--
Carex joorii	50	5	6.3	3.15	--
Parthenocissus quinquefolia	50	2	12.1	6.05	--
Vaccinium [*corymbosum* + *fuscatum* + *formosum*]	40	4	0	0	--
Carex typhina	40	2	36.2	14.48	--
Juniperus virginiana var. virginiana	40	2	0	0	--
Vitis rotundifolia var. rotundifolia	40	2	0	0	--
Cephalanthus occidentalis	40	1	14	5.6	--
Carex louisianica	30	4	43.9	13.17	26.9
Asplenium platyneuron	30	2	6.1	1.83	--
Erigeron sp	30	1	31.8	9.54	--
Celtis sp	30	1	4.9	1.47	--
Smilax glauca	30	1	0.5	0.15	--

Appendix 3D

Synoptic vegetation table of Dry Mafic Depression Swamps. Constancy (% Const.), average cover, fidelity (% Fid), diagnostic value (% DV), and DL indicator species value (IndVal) of prevalent taxa in Dry Mafic Depression Swamps. Only DL indicator species values that are significant ($p < 0.5$) are shown. Taxa are sorted in order of decreasing constancy, then cover, then fidelity. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Dry Mafic Depression Swamps				
Group Plot Count	10				
Group Avg Plot Spp Richness	42				
Group homoteneity	55.7				
taxon name	% Const	Cover	% Fid	% DV	IndVal
Quercus phellos	100	7	0	0	--
Ulmus alata	100	6	40.2	40.2	--
Campsis radicans	100	2	37.5	37.5	40.1
Diospyros virginiana	90	2	27.1	24.39	--
Fraxinus [*americana + pennsylvanica*]	80	5	24.9	19.92	31.8
Smilax bona-nox	80	2	50.6	40.48	39
Celtis sp	80	1	62	49.6	57.4
*Lonicera japonica**	70	4	41.1	28.77	38.3
Juniperus virginiana var. virginiana	70	3	23	16.1	--
Rubus pensilvanicus	70	2	34	23.8	--
Toxicodendron radicans	70	2	16.8	11.76	--
Smilax rotundifolia	70	2	0	0	--
Scutellaria integrifolia	70	1	36	25.2	--
Ulmus americana var. americana	60	4	58.6	35.16	47.2
Climacium sp	60	3	26.5	15.9	--
Leersia virginica	60	2	54	32.4	42.7
Trachelospermum difforme	60	2	23.4	14.04	--
Danthonia spicata	60	2	21.6	12.96	--
Parthenocissus quinquefolia	60	1	22.4	13.44	--
Gleditsia triacanthos	50	2	47	23.5	38.8
Cinna arundinacea	50	2	43.9	21.95	29.9
Asplenium platyneuron	50	2	29.3	14.65	--
Vitis rotundifolia var. rotundifolia	50	2	0	0	--
Panicum anceps	40	3	45.5	18.2	31.5
Scirpus georgianus	40	3	29.6	11.84	--
Liquidambar styraciflua	40	3	0	0	--
*Ligustrum sinense**	40	2	59	23.6	40
Dichanthelium acuminatum	40	2	53.1	21.24	33.9
Ruellia caroliniensis	40	2	48.1	19.24	31.5

Ilex decidua	40	2	41.6	16.64	--
Carex section Laxiflorae	40	2	40.1	16.04	--
Dichanthelium laxiflorum	40	2	33.8	13.52	--
Carya carolinae-septentrionalis	40	2	25	10	--
Acer rubrum	40	2	0	0	--
Elymus sp	40	1	59	23.6	40
Eupatorium serotinum	40	1	59	23.6	40
Sanicula sp	40	1	41.6	16.64	--
Carya glabra	40	1	22.9	9.16	--
Erechtites hieraciifolius	40	1	18.4	7.36	--
Quercus bicolor	30	6	50.5	15.15	30
Quercus stellata	30	5	9.3	2.79	--
Persicaria hydropiperoides	30	3	30.4	9.12	--

Appendix 3E

Synoptic vegetation table of Dry Felsic Depression Swamps. Constancy (% Const.), average cover, fidelity (% Fid), diagnostic value (% DV), and DL indicator species value (IndVal) of prevalent taxa in Dry Felsic Depression Swamps. Only DL indicator species values that are significant ($p < 0.5$) are shown. Taxa are sorted in order of decreasing constancy, then cover, then fidelity. See text for definition of terms and calculations of metrics. * Indicates non-native taxa.

Community Type	Dry Felsic Depression Swamps				
Group Plot Count	16				
Group Avg Plot Spp Richness	46				
Group homoteneity	56.5				
taxon name	% Const	Cover	% Fid	% DV	IndVal
Quercus phellos	100	7		0.0	--
Fraxinus [*americana* + *pennsylvanica*]	94	3	38.7	36.4	--
Acer rubrum	94	3	17.1	16.1	--
Liquidambar styraciflua	88	6	5.4	4.8	--
Vitis rotundifolia var. rotundifolia	88	2	36.2	31.9	--
Smilax rotundifolia	88	2	9.9	8.7	--
Ulmus alata	81	3	21	17.0	--
Quercus alba	81	2	67.6	54.8	65
Danthonia spicata	81	2	43.4	35.2	37.1
Nyssa sylvatica	75	3	14.4	10.8	--
Carex [*flaccosperma* + *glaucodea* + *pigra*]	75	2	66.3	49.7	56.8
Juniperus virginiana var. virginiana	75	2	28.1	21.1	--
Campsis radicans	75	2	11.5	8.6	--
Diospyros virginiana	63	2	0	0.0	--
Juncus coriaceus	63	2	68.2	43.0	48.9
Hypericum hypericoides	63	2	42.4	26.7	30.6
Smilax glauca	63	2	36.2	22.8	34.7
Carex [*caroliniana* + *complanata*]	63	2	35.5	22.4	31.4
Scutellaria integrifolia	63	1	28.2	17.8	--
Quercus stellata	56	2	40.9	22.9	28.9
Pinus [*echinata* + *virginiana*]	56	2	39.4	22.1	35.1
*Lonicera japonica**	56	2	26.3	14.7	--
Parthenocissus quinquefolia	56	2	18.5	10.4	--
Toxicodendron radicans	56	2	3	1.7	--
Liriodendron tulipifera	56	1	50.4	28.2	42.5
Prunus serotina var. serotina	56	1	33.3	18.6	--
Trachelospermum difforme	50	2	13.1	6.6	--
Euonymus americanus	50	1	35.6	17.8	--

Chasmanthium laxum	44	2	29.2	12.8	--
Carya glabra	44	2	27.5	12.1	--
Smilax bona-nox	44	1	11.9	5.2	--
Scirpus georgianus	38	2	26.3	10.0	--
Carya carolinae-septentrionalis	38	2	21.9	8.3	--
Leucobryum sp	38	2	8.6	3.3	--
Ilex opaca var. opaca	38	1	47.7	18.1	31.8
Cornus florida	38	1	39.2	14.9	--
Climacium sp	31	2	0	0.0	--
Vaccinium [*corymbosum* + *fuscatum* + *formosum*]	31	2	0	0.0	--
Eleocharis [*acicularis* + *tenuis*]	31	2	51.6	16.0	31.2
Poa sp	31	2	51.6	16.0	31.2
Vaccinium stamineum	31	2	39.8	12.3	--
Oxalis sp	31	2	34.6	10.7	--
Vaccinium arboreum	31	2	34.6	10.7	--
Viburnum prunifolium	31	2	34.6	10.7	--
Carpinus caroliniana	31	2	23.3	7.2	--
Andropogon sp	31	2	18.5	5.7	--
Leersia virginica	31	2	16.8	5.2	--

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