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Contents

Special feature: Vegetation survey: a new focus for Applied Vegetation Science
Edited by Milan Chytrý, Joop H.J. Schaminée & Angelika Schwabe

Original Articles

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Applied Vegetation Science Volume 14 Issue 4 435 – 606 October 2011

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APPLIED VEGETATION SCIENCE

Official organ of the International Association for Vegetation Science (www.iavs.org)

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Cover photograph: Rocky Shoals Spider Lily (*Hymenocallis coronaria*) in peak bloom on the Catawba River at Landsford Canal State Park, South Carolina, USA. Photo depicts *Hymenocallis coronaria - Justicia americana* herbaceous vegetation (Type Vb.) in the foreground. Photo taken May 2007 by Liz Matthews. See Matthews et al., 'Classification and description of alluvial plant communities of the Piedmont region, North Carolina, USA', *Applied Vegetation Science*, 14: 485–505.

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SPECIAL FEATURE: VEGETATION SURVEY

Classification and description of alluvial plant communities of the Piedmont region, North Carolina, USA

Elizabeth R. Matthews, Robert K. Peet, & Alan S. Weakley

Keywords
Cluster analysis; Fluvial geomorphology; Ordination; Random forests; US National Vegetation Classification; Wetlands.

Abbreviations
CCA = canonical correspondence analysis; NVC = United States National Vegetation Classification; GIS = geographic information system

Nomenclature:
Weakley (2010)

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Abstract

Questions: What are the alluvial vegetation types of the North Carolina Piedmont? How is species composition related to site conditions?

Location: Catawba, Yadkin-PeeDee, Cape Fear, Neuse and Tar-Pamlico River Basins, North Carolina Piedmont region, southeast USA.

Methods: We recorded 194 alluvial vegetation plots. Vegetation types were derived using flexible β-hierarchical cluster analysis and random forests classifiers to reassign misclassified plots. We used canonical correspondence analysis to show the relationship between species composition and key environmental variables.

Results: Twelve forested vegetation types and two herbaceous types were distinguished, nested within a hierarchical classification structure of five higher-level groups. The five mega groups describe broad geomorphic–floristic conditions, whereas the narrower vegetation types characterize finer-scale floristic variation. Floristic variation is related to stream order and soil chemistry (pH and Ca:Mg ratio), as well as soil texture variables (percentage sand and percentage clay). We present a summary of floristic composition and structure, environmental setting and geographic distribution for each of the 14 vegetation types.

Conclusions: We suggest recognition of 14 alluvial vegetation types in the North Carolina Piedmont. In comparing our vegetation types with the community concepts currently recognized in the US National Vegetation Classification, some of our types fit well within recognized NVC associations, whereas others deviate sharply from established types, suggesting the need for reworking the currently recognized NVC alluvial type concepts.

Introduction

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

Due to the ecological significance of floodplain ecosystems and their current imperiled status, there is significant interest in conservation and restoration of these habitats, and North Carolina, in particular, is a hotspot for riparian restoration in the southeastern United States (Sudduth et al. 2007). However, informed management decisions and restoration project design and evaluation require detailed information regarding the composition and structure of natural alluvial plant communities, in addition to an understanding of the environmental

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drivers associated with compositional variation. Plant community classifications and descriptions can provide the detailed vegetation information necessary for many applications, including facilitation of communication between conservation and land management agencies, advancing basic scientific understanding of vegetation patterns, and providing reference information for planning and assessing the success of restoration activities (Harris 1999; Faber-Langendoen et al. 2007; Jennings et al. 2009; Lane & Texler 2009).

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

Alluvial vegetation patterns of the southeastern United States have been studied by many plant ecologists (e.g. Wharton et al. 1982; Hupp & Osterkamp 1985; Hupp 1986, 2000; Hodges 1997; Kellison et al. 1998; Townsend 2001), but most of these studies have focused on the larger rivers of the Coastal Plain region, rather than the relatively smaller streams of the topographically more complex inland Piedmont (except see Hupp & Osterkamp 1985; Hupp 1986). These previous Coastal Plain studies of southeastern alluvial vegetation found a strong relationship between bottomland vegetation and fluvial geomorphic processes and land forms. Wharton et al. (1982) emphasized the anaerobic gradient generated by hydroperiod on floodplains as the dominant driver of vegetation patterns in bottomland hardwood swamps, with soil pH and nutrient availability as secondary drivers. Hodges (1997) presented hydrologic events and the resulting patterns of deposition across the floodplain as the primary drivers of floristic composition and successional patterns in Coastal Plain bottomland hardwoods. He also noted that patterns of deposition across floodplains are closely related to topographic features and result in a predictable distribution of soil texture and nutrient content. Hupp (2000) also emphasized the importance of hydrologic events in controlling the development of fluvial land forms and sediment deposition, which then determine vegetation patterns. In contrast to Coastal Plain rivers, however, Piedmont rivers are restricted by resistant bedrock, constraining the width of the floodplain and the development of topographic features and fluvial land forms. This may result in less species sorting than has been found along the strong hydrogeomorphic gradient evident in many Coastal Plain systems. As Hodges (1997) points out, in the narrower floodplains of the upper Coastal Plain there is less variation in soil texture and drainage class than one finds in the larger-order rivers of the outer Coastal Plain.

Although alluvial vegetation patterns of Coastal Plain rivers have been well studied, the relationship between alluvial vegetation and the Piedmont floodplain landscape remains poorly understood and described. Our goal was to document the remaining high-quality floodplain vegetation of the North Carolina Piedmont and to collect the quantitative vegetation data necessary to define and characterize the patterns in alluvial vegetation of this region. Here we present a classification and description of the alluvial plant communities of the North Carolina Piedmont based on 194 vegetation plots sampled in the Catawba, Yadkin-PeeDee, Cape Fear, Neuse and Tar-Pamlico River Basins (Fig. 1). We also describe the geographic distribution, geomorphic and hydrologic setting and edaphic characteristics associated with each vegetation type to clarify the relationship between the Piedmont floodplain landscape and alluvial vegetation. We expect our results will provide the information necessary to inform revisions of the NVC, guide management decisions and generate appropriate restoration targets in the NC Piedmont region.

Methods

Study area

Our study area included five contiguous North Carolina river basins: the Catawba, Yadkin, Cape Fear, Neuse and Tar-Pamlico. The study area also includes the northern section of the Catawba River basin in South Carolina (Fig. 1). We restricted our study sites to the Piedmont portion of each river basin, as defined by mapped geologic and soil units. The Piedmont is one of three physiographic regions in North Carolina. It is underlain by metamorphic and igneous bedrock and bounded on the northwest by the Southern Appalachian Mountains and on the southeast where crystalline Piedmont bedrock meets the softer sedimentary bedrock of the southeastern Coastal Plain. Although Piedmont bedrock is largely composed of erosion-resistant metamorphic and intrusive igneous rocks, a large southwest–northeast trending rift basin composed of Triassic sedimentary rock is a prominent geologic feature of the lower Piedmont (Benedetti et al. 2006). Where Piedmont rivers cross the more resistant igneous and metamorphic bedrock, the resulting river valleys are relatively narrow and incised, whereas in the Triassic

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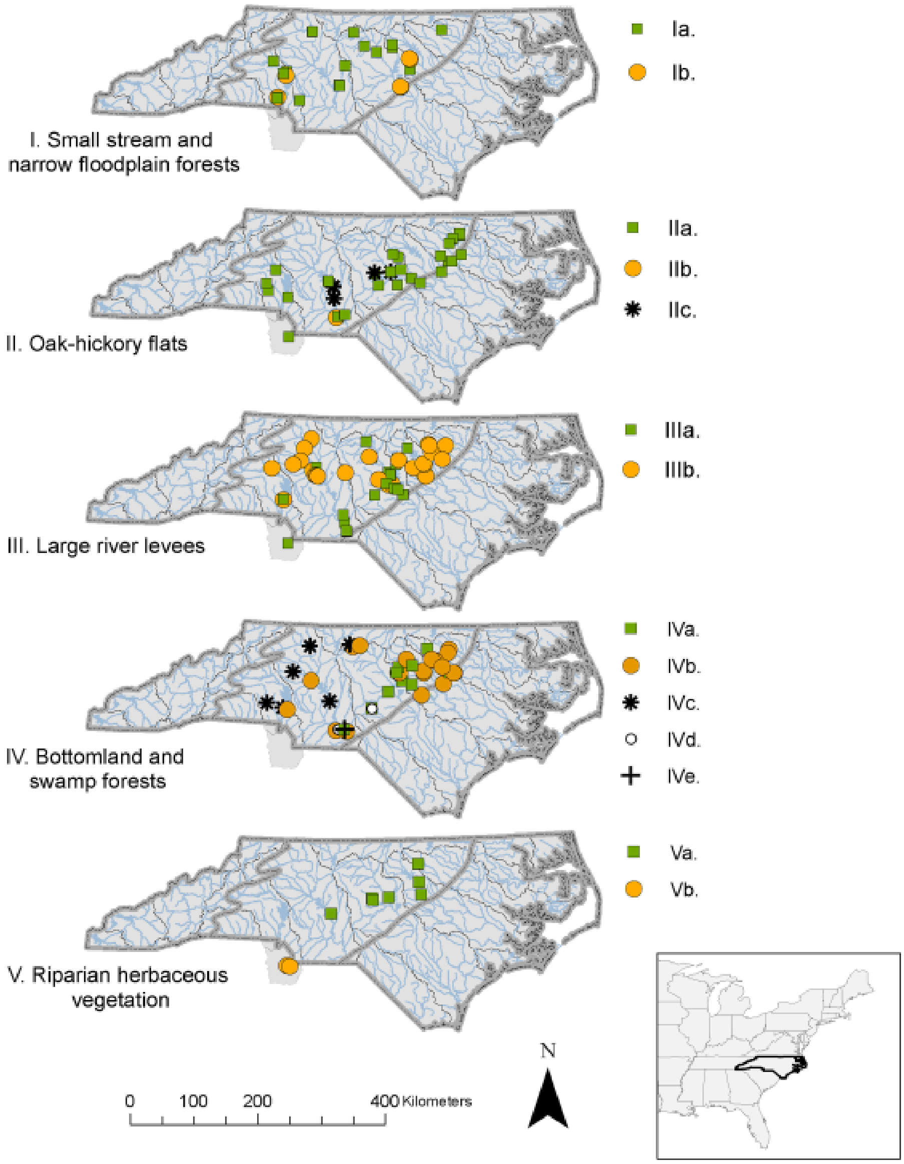

Fig. 1. Distribution of 194 vegetation plots for the five mega vegetation groups. The inset map identifies the location of North Carolina in the USA. In the North Carolina state maps, the wide grey lines delineate the three broad physiographic regions of North Carolina (left Mountains, centre Piedmont, right Coastal Plain). The narrow grey lines delineate river basin boundaries; moving from west to east: Catawba, Yadkin- PeeDee, Cape Fear, Neuse and Tar-Pamlico River Basins. The narrow blue lines indicate river courses.

Basins Piedmont rivers are better able to erode the softer sedimentary rock, resulting in wider floodplains (though still somewhat more constrained than in the unconsolidated sediments of the Coastal Plain).

There has been a long history of human disturbance in the North Carolina Piedmont, with the most extensive alteration of native forest vegetation occurring after European colonization. Although fertile, arable lands were most affected, even vegetation on land unfavourable for cultivation has been altered by selective tree harvesting (Peet & Christensen 1980). Bottomland habitat in the Piedmont that was not converted to agriculture during European settlement was subject to this selective harvesting.

Site selection

Because we anticipate this classification will be used as a reference for the development of restoration targets, we aimed to sample high-quality alluvial vegetation, which we defined as stands with minimal recent natural disturbance (e.g. treefall gaps), minimal anthropogenic disturbance (e.g. ≥50 years since harvest) and minimal cover contributed by exotic species. However riparian areas are known to be highly invaded (DeFerrari & Naiman 1994; Brown & Peet 2003; Williams & Wiser 2004), and many stands included in our data set had high exotic species cover. Since large extents of the natural riparian vegetation in the Piedmont region have been subject to anthropogenic disturbances, one of the most important steps in collecting data for this project was the identification of remaining patches of high-quality floodplain vegetation. This was accomplished with assistance from state agencies and non-profit, conservation organizations, which track natural areas of the state.

After we identified areas of remaining high-quality natural vegetation, we selected sample sites to ensure representation from a broad geographic area within each of five river basins. We also selected sites to provide a broad representation of various geologic features, stream order, watershed area and geomorphic setting. However, because high-quality alluvial vegetation is rare in the highly fragmented and disturbed North Carolina Piedmont, we sampled the majority of high-quality sites that were identified. At sample sites, plots were located subjectively in representative homogenous vegetation, with the intent of capturing high-quality vegetation and a single geomorphic setting. In total, we established and recorded 194 vegetation plots (Fig. 1).

Field methods

We surveyed vegetation in May–August, 2006-2008, following the Carolina Vegetation Survey (CVS) protocol (Peet et al. 1998). Six alluvial plots surveyed by CVS prior to the 2006-2008 field seasons were exported from the archived CVS database and included in this data set. Forested plots ranged in size from 400 m^2 (typically 20 m × 20 m) to 1000 m^2 (typically 20 m × 50 m), depending upon the width of the floodplain. The 14 strictly herbaceous vegetation plots were 100 m^2. Within each plot, cover was estimated for all vascular plant taxa in intensive subplots (100 m^2) following the CVS cover class scale (1 = trace, 2 = 0-1%, 3 = 1-2%, 4 = 2-5%, 5 = 5-10%, 6 = 10-25%, 7 = 25-50%, 8 = 50-75%, 9 = 75-95%, 10 = > 95%); all forested plots included four 100-m^2 intensive subplots. Cover by strata was also estimated for each taxon at the scale of the whole plot; strata include tree (> 5 m to canopy height), shrub (0.5 to 5.0 m), and herb (0 to 0.5 m) strata, although the height ranges of strata could be adjusted in the field to reflect local vegetation structure. Cover by strata better reflects the size and structure of the vegetation than a single cover value. Woody species reaching breast height were tallied by CVS size classes.

Plots were oriented with the long axis parallel to the longitudinal axis of the river in an effort to maintain a constant geomorphic setting. Sample sites on first- and second-order streams, where geomorphology is poorly developed and there are not clear distinctions between geomorphic positions, were identified as *small stream floodplains*. Sites on larger streams were identified to one of five geomorphic positions: *rocky bar and shore* (within the river channel inside any levee structure); *levee* (the area of the floodplain closest to the river, running parallel to the flow direction, and often slightly raised); *backswamp* (further from the river channel, beyond the levee, and flooded for longer periods of time when compared to other geomorphic settings); *flat* (typically parallel to a levee or the actual levee in smaller rivers in place of a true raised levee, generally intermediate to or intergrading with the levee and backswamp, where geomorphology is poorly developed); and *bottomland* (primarily restricted to the Triassic Basins, on very wide floodplains with poorly defined and generally low-lying geomorphic settings).

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

Plant taxa were identified to the finest taxonomic resolution possible. Taxonomy follows Weakley (2010). Taxa that were difficult to identify to species without fruit or flower due to the timing of field sampling were grouped into lower resolution complexes (examples: *Viola* spp., *Oxalis* spp., *Solidago* spp., *Carex grisea* group). All finer-scale taxa were included in the lower resolution complexes. Additionally, taxonomy was reviewed and

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standardized prior to analysis to account for differences due to plant identifications by a variety of individuals, both in the field and in the lab. The final analysis data-set contained 606 consistently recorded taxonomic units.

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

Analytical methods

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

We adjusted the number and composition of vegetation types using discriminant analyses with the random forests method (as implemented in the 'randomForest' 4.5-35 package in R 2.11.1; R Development Core Team 2010). Random forest classifiers have many of the same benefits as classification and regression tree (CART) models, including the ability to account for interactions among predictor variables and no underlying assumptions of normally distributed data. Random forests, however, improve on traditional CART models by producing more robust results that do not over-fit data, yet still have very high classification accuracy; this is accomplished by repeatedly creating individual trees using a random subset of the data and then combining the predictions from all trees (Breiman 2001; Liaw & Wiener 2002; Cutler et al. 2007). To identify misclassified plots, we classified our clusters with random forests using the floristic matrix as predictor variables; this analysis identified plots that could not be assigned to the correct group based on the floristic data and identified a more appropriate group assignment. Random forest classifiers also allow the researcher to identify predictors that were most important in driving the splits in the classification; we classified our clusters using the environmental matrix to identify the most useful environmental variables in discriminating between vegetation types. Following random forest analyses, we used ordination analyses to clarify how variation in vegetation relates to key environmental variables identified in the second random forests analysis. For this purpose, we used canonical correspondence analysis (CCA; as implemented in the 'vegan' 1.17-3 package in R) to constrain our ordination to a subset of environmental drivers of vegetation patterns. Vegetation plots used for this study have been archived in VegBank (http://vegbank.org) and are available to the public for re-analysis.

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

Finally, we developed a community characterization for each vegetation type. Vegetation type names are consistent with the naming system used in the US National Vegetation Classification (U.S. FGDC 2008; Jennings et al. 2009). Names reflect species with high constancy, high cover and/or high indicator value.

A '-' separates species within the same vertical strata, while a '/' separates strata. For each group, we determined average cover and constancy of each pseudo-species. Average cover class was calculated using only plots where the species was present. Constancy was calculated as the percentage of plots within a group in which a given species occurred. Only prevalent species (*sensu* Curtis 1959) in each group are reported in the floristic tables, where prevalent species were identified by ranking species by constancy and selecting the most common species such that the total number of prevalent species equals average species richness per 400 m^2 within the group. Prevalence was calculated separately for each stratum. Cover and constancy for woody vines were calculated separately with slightly altered methodology in the two synoptic tables. Since many woody vines cross stratum boundaries, we limited reported species to a single stratum. Vine cover and constancy in these tables were calculated based on the geometric mean cover in the four intensive subplots (cover in the subplots is not recorded in separate strata). Woody vine species summarized by these methods include *Bignonia capreolata, Campsis radicans, Lonicera japonica, Parthenocissus quinquefolia, Smilax* spp., *Toxicodendron radicans* and *Vitis* spp. Homotoneity (Peet 1981), or mean constancy of the prevalent species, was calculated for each group. Homotoneity is an indicator of the degree of compositional variability among plots belonging to a described community type. Non-native species are identified in the floristic tables based on Weakley (2010). Digital appendices include floristic tables for each group, including diagnostic and indicator values, in addition to summarized basal area, average values of soil variables and mapped geographic distribution (Appendices S1-S8).

Results

Cluster analysis, indicator species analysis and discriminant analysis together suggested recognition of 12 forested vegetation types and two herbaceous types, nested within five broad vegetation groups, which we refer to hereafter as 'mega groups' (Fig. 2). Cluster analyses consistently indicated that herbaceous vegetation plots formed a unique cluster, and these plots were removed and analysed separately from further analyses of forested communities. Indicator species analyses suggested recognition of 14 forested types, based on a dip in average *P*-value and peak in the total number of significant *P*-values. The random forests analysis indicated four problematic groups in the classification because no plots in these groups were classified correctly by the random forests algorithm. Two of these groups were small and non-cohesive; plots in these groups were reassigned based

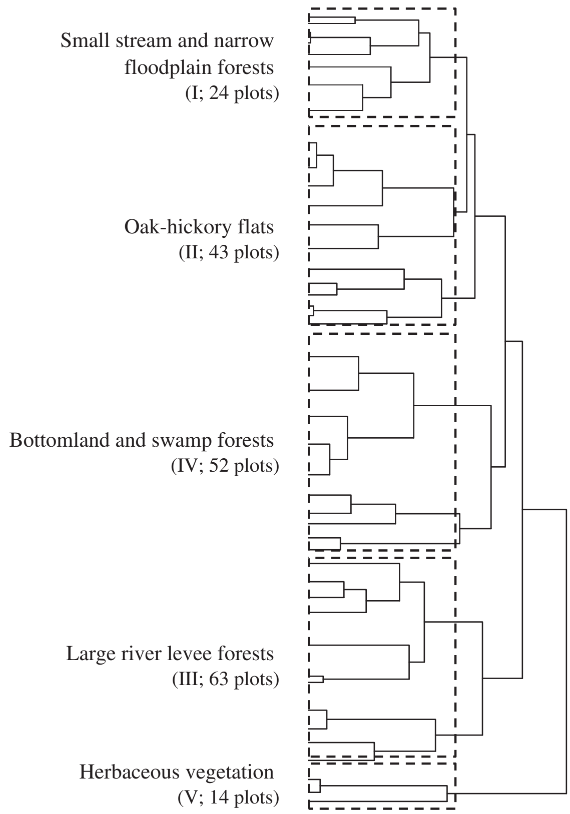

Fig. 2. Dendrogram produced by flexible β cluster analysis (β = 0.25) of 194 vegetation plots. Five broader vegetation groups denoted by dashed boxes; Roman numerals correspond with notation in the text.

on random forests output. We recognize the additional two problematic groups as separate vegetation types here, despite the random forests output, based on high cover of species not normally present in the Piedmont of North Carolina. Random forests indicated that both the *Quercus lyrata – Fraxinus pennsylvanica/Saururus cernuus* and the *Carya aquatic – Nyssa aquatica* swamp types (IVd and IVe in the notation below) should be relocated into the *Fraxinus pennsylvanica – Acer rubrum – Ulmus americana/Ilex decidua/ Saururus cernuus* (IVb) type, likely due to all three of these types having very high *Acer rubrum* and *Fraxinus pennsylvanica* cover. However, we elected to recognize these types as different due to the high cover of *Quercus lyrata* in the first type and *Carya aquatica* and *Nyssa aquatica* in the second (see further discussion below in the sections describing these vegetation types). Twenty-five additional plots were reassigned to different vegetation types based on the random forests output.

The 12 forested types are nested within four broader mega groups, where compositional variation among the groups is strongly related to geomorphology and edaphic variables. CCA ordination illustrates the relationship of

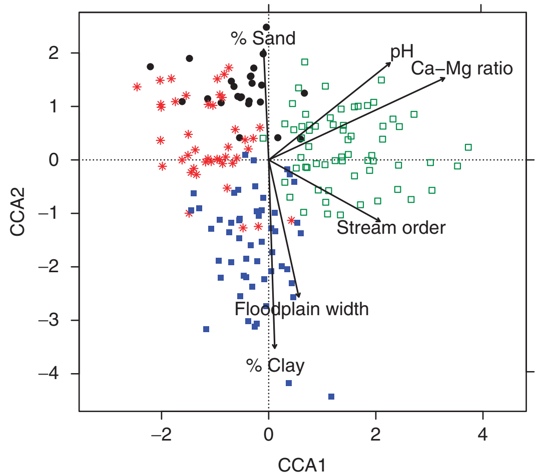

Fig. 3. Canonical correspondence analysis (CCA) of 182 forest vegetation plots**.** The four broader geomorphic–floristic groups are indicated, where small stream and narrow floodplain forests (I) are indicated by filled circles, oak–hickory flats (II) are by asterisks, large river levees (III) by open squares, and bottomland and swamp forests (IV) by filled squares.

floristic variation among the four mega groups to five key environmental variables: percentage clay, percentage sand, pH, Ca:Mg ratio and 100-year floodplain width (Fig. 3). Stream order is a strong differentiating factor among the mega groups. Two mega groups are plotted on the upper left portion of the ordination diagram, associated with low to mid-order rivers, narrow floodplains and sandy soils; these groups most commonly occur along small streams and alluvial flats. Alternatively, the large river levees are plotted on the right side of the ordination space and are related to higher pH, Ca:Mg ratio and stream order. The second axis is mainly related to soil texture and floodplain width, and the bottomland and swamp forests are plotted in the lower portion of the ordination diagram, associated with decreasing sand and increasing clay content and floodplain width.

Additional floristic differences within both the high stream order mega groups (i.e. large river levees and bottomland swamps) and the low stream order mega groups (i.e. small streams and narrow floodplains, oak–hickory flats) can be attributed primarily to soil chemistry and texture (Appendix S1). In the set of types associated with smaller floodplains, chemistry is the strongest gradient differentiating the two mega groups, with *Quercus–Carya* dominated flats occurring in the more nutrient-poor sites and small stream alluvial forests occurring in the sites where soils have a higher average pH and percentage base saturation. Within the larger floodplain forests, there is substantial variation in soil texture. The texture gradient is related to variation in flooding dynamics and hydroperiod. High sand content is associated with the levee land form and high clay content is associated with backswamps, where longer periods of standing water result in fine sediment deposition. Levee vegetation types are also differentiated from other larger floodplain forests by more nutrient-rich soils. The 12 forested vegetation types are presented below by their mega group, reflecting four geomorphic settings: small streams and narrow floodplains (I), alluvial flats (II), large river levees (III) and wide floodplain bottoms and swamps (IV). The two herbaceous vegetation types are presented in a fifth group (V).

Small streams and narrow floodplain forests

The two vegetation types of this group are associated with narrow floodplains. The narrow floodplains of the Piedmont occur for two reasons: low-order rivers or geologic formations that restrict floodplain development, typically metamorphic and igneous bedrock. The narrow floodplain restricts geomorphic development and results in communities where species are not well sorted along a hydrologic gradient and are more strongly influenced by the surrounding upland flora than are the alluvial types found on larger rivers This group is associated with higher elevations of the North Carolina Piedmont, occurring in areas further removed from the fall-line. The soils are very sandy (both types recognized having higher average percentage sand in both the A and B horizons than any of the other ten forested types recognized; Appendix S1) and are associated with high pH and base saturation when compared with other types occurring along low-order streams.

Ia. Liriodendron tulipifera – Liquidambar styraciflua/Lindera benzoin/Amphicarpaea bracteata forest (18 plots): This small stream, narrow floodplain community type occurs on sandy soils, with high cation exchange capacity, high Ca and Mg content, and high pH (Appendix S1) and is distributed across all five river basins (Fig. 1). It is found across a variety of stream orders, but all occurrences are associated with narrow floodplains ($\bar{x} = 171.5$ m, SE = 26.1 m).

The type is typically species-rich, with an average of 79 species/400 m^2 and includes plots having some of the highest richness values observed in this study (Table 2). The tree stratum is dominated by the nominal species (*Liriodendron* and *Liquidambar*) in addition to *Betula nigra, Fagus grandifolia* and *Acer rubrum*, with substantial subcanopy cover contributed by *Cornus florida* and *Carpinus caroliniana* (Appendices S2, S3). Both nominals are common successional species in Piedmont forests and may be somewhat transient dominants in this type; *Quercus* and *Carya* species, presently found at low constancy and cover, may become more dominant with succession. The shrub stratum is dense, with smaller individuals from the sub-

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canopy in addition to abundant *Lindera benzoin* and frequent *Viburnum prunifolium*. *Corylus americana* has a high diagnostic value for this group and may also contribute substantial shrub cover. The diverse herb stratum is dominated by a mix of alluvial and mesic slope species and frequently includes *Botrypus virginianus*, *Galium triflorum* and *Phryma leptostachya* (which is also an indicator for this group). The exotic grass *Microstegium vimineum* often has high cover.

Ib. Liriodendron tulipifera – Betula nigra/Cornus florida/Sanicula canadensis var. canadensis forest (six plots): This type is found on first- and second-order streams in three river basins: the Catawba, Cape Fear and Neuse (Fig. 1). This type is floristically similar to group Ia, but it is associated with lower cation exchange capacity and extremely sandy soils in comparison to the other narrow floodplain forest type (Appendix S1).

These sites are infrequently flooded, resulting in the presence of more species commonly associated with both mesic slopes and upland forests. The canopy is dominated by the nominal species, in addition to species more typical of well-drained upland forests, such as *Oxydendrum arboreum* and *Quercus alba* (Table 2; Appendix S3). *Ilex opaca* and the indicator species *Ostrya virginiana* are also frequent sub-canopy species. The shrub layer is relatively open and primarily composed of small individuals of the tree stratum. In contrast to Ia, where *Lindera benzoin* contributes a large percentage of shrub cover, *Lindera benzoin* was not observed in any plots assigned to this group.

Oak–hickory flats

The vegetation types in this group occur on levees and flats along mid-sized rivers, primarily third to fifth order, although IIb occurs on larger-order rivers (IIb was treated in this section due to its floristic affinity with the other *Quercus*–*Carya*-dominated vegetation types of group II). In general, the soils of oak–hickory flats are relatively infertile with low base saturation, Ca:Mg ratios and cation exchange capacities (Appendix S1). The three vegetation types recognized are dominated by a mix of *Quercus* species and other common bottomland tree species, in addition to high *Carya* cover in some types (Table 1). Within this group, there is a strong gradient of floodplain width, with IIb occurring on the widest floodplains and consequently the finest textured soils and IIc on the narrowest floodplains (Table 2). IIa is associated with intermediate-width floodplains, but with the sandiest soils (Appendix S1).

IIa. Liquidambar styraciflua – Quercus nigra/Carpinus caroliniana/Mitchella repens Forest (32 plots): These forests are found on levees and flats along third- to fifth-order streams in all five river basins (Fig. 1). The geomorphic position of this type intergrades between the levee concept of larger-order rivers and alluvial flats of smaller-order rivers; these sites are often located directly adjacent to the river channel, yet may not be identifiable as a classic levee where floodplain geomorphology is not well developed. In contrast to IVa, which may also have high *Quercus* cover and is associated with wet areas of wide floodplains, this type is associated with relatively dry, flat landscape positions. The soils tend to be sandy, approaching the percentage sand that characterized the low-order, narrow floodplain forests mega group (Appendix S1).

This community is dominated by the nominal tree species, especially *Quercus* species, and including *Q. nigra*, *Q. phellos* and *Q. pagoda*, in addition to *Fagus grandifolia* (in contrast to all other oak-dominated groups) and a mix of *Carya* species, including *C. ovata* and *C. alba* (Table 2; Appendix S2). The high sand content and abundance of *Fagus* suggests affinities with type Ia, but IIa has less affinity with the upland sites and is characteristic of higher-order streams. *Fagus grandifolia* and *Ilex opaca* are known to be intolerant to extended flooding, further suggesting a drier setting with a short hydroperiod (Townsend 2001). In contrast to IVa, *Quercus nigra* more consistently contributes a large percentage of the tree cover in this type (Table 2). The dense shrub/understorey stratum is dominated by *Carpinus caroliniana*, while a diverse set of grass species contribute significant cover to the herb stratum, including especially *Chasmanthium latifolium*, *Elymus virgincus* s.l., *Poa autumnalis* and *Melica mutica* (Appendix S4).

IIb. Liquidambar styraciflua – Quercus pagoda – Carya cordiformis/Asimina triloba/Arundinaria tecta forest (three plots): In contrast to the other oak–hickory flats, this type is found on wide flats along high-order rivers (all ≥fourth order). The soils are characterized by a high clay content and are associated with very high Ca content and cation exchange capacity (Appendix S1). The three plots documenting this vegetation type occur in the Yadkin River Basin in the Triassic Basins close to the fall line (Appendix S2). As a result of its location in the Triassic Basins, this type is associated with very wide floodplains and has the widest average floodplain width of any group recognized here (> 1 km). In the CCA ordination, these three plots appear in the cloud of bottomland and swamp forest plots, reflecting the wide floodplains of this group (Fig. 3). However, the abundance of species rarely present in the wetter types, including *Arundinaria tecta* and *Asimina triloba*, floristically distinguishes this type from the bottomland and swamp forests of group IV (Table 2).

The dominant trees of this type include the nominal species as well as *Quercus michauxii*, *Q. nigra* and *Nyssa*

Applied Vegetation Science
Doi: 10.1111/j.1654-109X.2011.01150.x

Table 1. Trees, vines, shrubs and herbs with high constancy and high average cover where present in each of the four mega groups. Only prevalent species with constancy > 25% and average cover > 3 for trees, shrubs and herbs and > 2 for vines are shown (see text for description of prevalence and calculation of constancy and cover). Groups are identified by the Roman numerals used in the text. Constancy and cover are shaded in mega groups where species have a significant Dufrêne and Legendre indicator value ($P < 0.05$). Constancy is bolded in mega groups where a species is prevalent. Species only appear in one stratum (i.e. the stratum where the adult life form is found). Non-native species are identified with an asterisk.

Groups	I		II		III		IV	
Plot count	24		43		63		52	
Avg plot spp. richness (400 m^2)	77.1		72.6		55.2		52.6	
Avg plot spp. richness (100 m^2)	42.8		42.8		32.6		31.4	
Avg plot spp. richness (10 m^2)	23.8		23.2		17.1		15.6	
Avg plot spp. richness (1 m^2)	10.4		10.0		8.0		6.6	
Homotoneity	58%		57%		57%		56%	
	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Tree taxon name								
Betula nigra	**58**	7	14	6	33	5	**38**	6
Cornus florida	**92**	6	**42**	5	29	4	4	3
Fagus grandifolia	**50**	6	**40**	6	5	6	4	3
Liriodendron tulipifera	**92**	6	**53**	5	**43**	6	10	6
Ostrya virginiana	**33**	6	23	6	11	5	–	–
Oxydendrum arboreum	**42**	5	14	4	–	–	–	–
Quercus shumardii	**33**	6	26	6	10	5	12	5
Carpinus caroliniana	**75**	7	**86**	7	**48**	6	**44**	6
Carya ovata	25	6	**40**	6	10	6	21	5
Ilex opaca var. *opaca*	**29**	6	**42**	6	24	5	12	4
Liquidambar styraciflua	**75**	6	**98**	6	**68**	6	**88**	6
Nyssa sylvatica	17	5	**58**	5	8	4	27	4
Quercus alba	25	5	**44**	6	8	4	13	5
Quercus nigra	13	6	**58**	6	11	7	19	5
Quercus pagoda	8	6	**40**	6	6	6	**33**	6
Ulmus alata	**29**	5	**63**	6	29	6	**48**	6
Acer negundo var. *negundo*	8	5	2	2	**79**	7	4	4
Carya cordiformis	**38**	6	28	6	**49**	6	6	5
Celtis laevigata	4	6	5	5	**67**	6	12	5
Juglans nigra	**33**	5	9	4	**35**	6	–	–
Platanus occidentalis	**29**	6	14	6	**73**	6	**31**	5
Acer rubrum	**88**	6	**72**	6	19	6	**96**	7
Fraxinus pennsylvanica	**42**	4	**56**	5	**73**	6	**87**	7
Quercus phellos	–	–	**49**	6	5	4	**56**	6
Ulmus [americana+rubra]	**42**	5	**42**	5	**79**	6	**87**	6
Acer floridanum	**29**	7	**33**	7	**41**	7	13	6
Quercus michauxii	8	6	26	6	21	7	**29**	6
Vine taxon name								
Campsis radicans	**75**	2	**58**	2	**60**	2	**90**	2
Bignonia capreolata	**54**	2	**95**	3	**84**	3	**79**	3
*Lonicera japonica**	**100**	4	**91**	3	**95**	4	**85**	3
Parthenocissus quinquefolia	**100**	3	**100**	3	**100**	2	**94**	2
Smilax rotundifolia	**63**	2	**93**	2	**73**	3	**98**	3
Toxicodendron radicans	**100**	3	**98**	4	**100**	4	**100**	5
Vitis [cinerea+vulpina]	**38**	3	12	2	22	4	**8**	2
Vitis rotundifolia	**100**	3	**95**	3	**67**	3	**67**	2
Shrub taxon name								
Viburnum prunifolium	**38**	4	**51**	4	21	3	**40**	4
*Ligustrum sinense**	17	2	19	2	**68**	5	**37**	3
Lindera benzoin	**42**	7	14	3	**56**	6	12	5
Ilex decidua	13	2	**70**	4	**37**	4	**71**	5
Herb taxon name								
Festuca subverticillata	**71**	2	**40**	2	**49**	4	21	3
Polystichum acrostichoides	**100**	4	**65**	3	**44**	2	19	2

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Table 1. Continued

	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Danthonia spicata	4	2	**28**	4	–	–	–	–
Carex grayi	4	1	16	2	**51**	4	23	5
Elymus virginicus s.l.	**38**	2	**42**	4	**65**	6	**44**	2
Galium aparine	**29**	2	12	2	**67**	4	23	2
Laportea canadensis	4	1	–	–	**54**	5	10	2
Verbesina occidentalis	**46**	4	**30**	2	**68**	2	8	2
Boehmeria cylindrica	**63**	2	**47**	2	**73**	3	**87**	4
Carex crinita	13	2	12	2	3	2	**38**	4
Carex lupulina	4	1	–	–	10	2	**46**	4
Carex tribuloides	29	2	23	2	**51**	4	**81**	4
Carex typhina	8	2	16	2	16	3	**63**	4
Saururus cernuus	13	2	16	2	19	3	**56**	6
Carex [amphibola+grisea+corrugata]	**58**	3	**65**	4	**73**	4	**42**	4

sylvatica, and high sub-canopy cover of *Carpinus caroliniana* (Table 2; Appendix S2). The shrub stratum is sparse and frequently dominated by *Asimina triloba*, whereas the herb layer is dominated by *Arundinaria tecta*, which floristically distinguishes this type from IIa (Appendix S4). IIIa occasionally includes significant *Asimina* and *Arundinaria* cover, but lacks the frequent and abundant *Quercus* cover observed in this type.

IIc. Carya carolinae-septentrionalis – Acer floridanum/Aesculus sylvatica/Zizia aurea Forest (eight plots): This community is found across a variety of stream orders, but primarily mid-sized, second- to fourth-order streams. Even when found on higher-order rivers, it is always associated with narrow floodplains, similar to the forested vegetation group presented above (I). However, it is grouped with the oak–hickory flats because of its floristic affinity with these types. This type is also associated with higher percentage slope values, suggesting sites influenced by the slope forests surrounding the floodplain. It is only found in the Cape Fear and Yadkin River Basins, on soils with high silt content (Fig. 1; Appendix S1).

These forests are the most diverse among those documented here, with an average of 84.9 species observed in 400 m^2 (Table 2). The diverse tree stratum is dominated by the nominals, in addition to a mix of other *Quercus* and *Carya* species and a dense sub-canopy of *Carpinus caroliniana* (Table 2; Appendix S4). The sparse shrub stratum is primarily composed of smaller individuals of the tree stratum species. The herb stratum is dominated by grasses, many of which are significant indicators for this group, including *Elymus hystrix, Dichanthelium boscii* and *Danthonia spicata* (Appendix S4).

Large river levee forests

This group is associated with levees on mid- to large-order rivers (third- to seventh-order streams). In contrast to other types associated with higher-order streams, the soils are sandy, with high pH and Ca:Mg ratios (Fig. 3). Compositional variation within this group may reflect disturbance history. The canopy of IIIb is more frequently dominated by fast-growing, often early successional species, including *Platanus occidentalis, Fraxinus pennsylvanica* and *Acer negundo*, which are typical dominants of young, newly accreted pointbar forests in southeastern riparian zones (Meitzen 2009; Romano 2010). These dominants may also reflect a history of human disturbance, as they are known to increase following tree harvesting. Abundant species in IIIa, on the other hand, more frequently include long-lived successional species (*Liriodendron tulipifera* and *Liquidambar styraciflua*) and shade-tolerant species typically associated with older natural levee forests (*Celtis laevigata* and *Ulmus americana*). Additional compositional variation within this group reflects geographic distribution of the types, as well as river size.

IIIa. Ulmus americana – Celtis laevigata/Lindera benzoin/Osmorhiza longistylis levee forest (33 plots): This levee community occurs on large fourth- to seventh-order rivers in the Catawba, Yadkin, Cape Fear and Neuse River Basins (Fig. 1). This type is associated with relatively wide floodplains of large watersheds (i.e. rivers that drain larger areas and more sub-watersheds) and tends to occur at lower elevation and further downstream than the other levee type (Table 2), though the stream order range for the two types broadly overlaps. The soils associated with this type are some of the most fertile alluvial soils, with average pH, Mg content and base saturation values higher than any other type described, although there is considerable overlap in the range of these measures with the other levee vegetation type (Appendix S1).

The dominant tree species include the nominals, with *Celtis* often contributing a large proportion of the cover (Table 2). Additional tree cover may be contributed by a variety of species commonly associated with nutrient-rich

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Table 2. Prevalant species in each vegetation type, by stratum. Species shown are prevalent in at least one type and also have > 50% constancy and an average cover class > 2 in at least one type (see text for description of prevalence and calculation of constancy and cover). Constancy and cover are shaded in types where species have a significant Dufrêne and Legendre indicator value ($P < 0.05$). Constancy is bolded in types where a species is prevalent. Species are only listed in the stratum in which the adult life form is present (only one stratum per species). Non-native species are identified with an asterisk.

Groups	I. Small streams and narrow floodplain forests						II. Oak–hickory flats				III. Large river levees				IV. Bottomland and swamp forests									
Types	Ia.		Ib.		IIa.		IIb.		IIc.		IIIa.		IIIb.		IVa.		IVb.		IVc.		IVd.		IVe.	
Plot count	18		6		32		3		8		33		30		17		24		6		3		2	
Avg plot spp. richness (400 m²)	79.3		70.5		70.7		53.0		84.9		58.2		51.9		56.2		53.5		54.8		33.3		35.0	
Avg plot spp. richness (100 m²)	43.0		42.5		42.3		33.9		48.2		36.3		28.5		36.1		31.8		27.6		18.7		16.6	
Avg plot spp. richness (10 m²)	24.4		22.1		22.4		17.8		28.6		18.9		15.2		17.6		15,7		17.3		7.8		5.9	
Avg plot spp. richness (1 m²)	10.6		9.6		9.6		8.1		12.7		8.7		7.1		7.4		6.6		7.4		3.5		2.1	
Homotoneity	61%		60%		59%		78%		65%		61%		58%		58%		62%		59%		63%		62%	
Average floodplain width (m)	172		119		420		1150		142		489		370		624		639		471		603		1100	
Average pH	5.11		5.08		4.87		4.93		4.91		5.36		5.16		4.74		4.82		4.63		4.76		4.81	
Average Ca:Mg ratio (ppm)	5.54		5.34		3.91		2.77		3.39		6.15		6.11		3.83		4.52		4.38		4.03		3.95	
Average % Ca	38.32		36.30		28.89		28.36		28.69		45.10		39.71		26.77		29.72		25.59		27.02		27.59	
% Clay	14.55		11.40		18.40		43.82		17.49		20.37		21.94		27.45		35.58		30.91		35.65		44.25	
% Sand	47.04		70.18		45.36		17.23		37.02		34.18		44.02		22.76		27.87		30.96		13.88		15.50	
	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Tree taxon name																								
Liriodendron tulipifera	**100**	6	**67**	6	**66**	5	–	–	**25**	6	**58**	6	27	6	24	6	–	–	17	6	–	–	–	–
Cornus florida	**89**	6	**100**	6	**44**	5	–	–	**50**	4	**42**	5	13	4	6	3	4	3	–	–	–	–	–	–
Ostrya virginiana	22	5	**67**	6	22	6	–	–	**38**	7	15	5	7	5	–	–	–	–	–	–	–	–	–	–
Acer floridanum	**33**	8	17	2	19	7	–	–	**100**	7	**55**	7	27	6	**35**	6	4	5	–	–	–	–	–	–
Carya carolinae-septentrionalis	–	–	–	–	–	–	–	–	**100**	7	3	6	–	–	6	5	–	–	–	–	–	–	–	–
Ulmus alata	**39**	5	–	–	**56**	6	**33**	3	**100**	5	36	6	20	6	**76**	6	**46**	6	17	5	–	–	–	–
Celtis laevigata	6	6	–	–	–	–	**67**	5	–	–	**73**	7	**60**	6	18	6	13	4	–	–	–	–	–	–
Acer negundo var. *negundo*	11	5	–	–	–	–	**33**	2	–	–	**64**	6	**97**	7	6	5	–	–	17	3	–	–	–	–
Platanus occidentalis	22	7	**50**	5	16	6	–	–	13	7	**58**	6	**90**	6	24	4	25	6	**67**	6	**33**	4	**50**	2
Fraxinus pennsylvanica	**44**	5	**33**	3	**53**	5	**67**	3	**63**	6	**58**	6	**90**	7	**71**	6	**96**	7	**100**	8	**100**	6	**50**	4
Quercus lyrata	–	–	–	–	13	5	–	–	–	–	6	4	–	–	12	7	17	6	–	–	**100**	6	**100**	6
Quercus phellos	–	–	–	–	**56**	6	–	–	**38**	6	6	4	3	4	**76**	7	**54**	6	–	–	**100**	6	–	–
Carya aquatica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**100**	6
Nyssa aquatica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**100**	8
Acer rubrum	**83**	6	**100**	7	**78**	7	**100**	6	**38**	5	18	5	20	6	**88**	6	**100**	8	**100**	7	**100**	7	**100**	6
Betula nigra	**56**	6	**67**	8	19	6	–	–	–	–	24	4	**43**	6	**41**	6	29	6	**83**	6	–	–	**50**	4
Carpinus caroliniana	**78**	7	**67**	7	**88**	7	**100**	7	**75**	7	**52**	6	**43**	6	**71**	6	**33**	7	17	6	**33**	3	**50**	6
Carya cordiformis	**39**	6	**33**	4	25	6	**67**	7	25	5	**76**	6	20	6	12	6	4	3	–	–	–	–	–	–
Carya ovata	**33**	6	–	–	**38**	6	**67**	5	**38**	4	18	6	–	–	**41**	6	17	5	–	–	–	–	–	–
Fagus grandifolia	**56**	6	**33**	3	**50**	6	–	–	13	3	9	6	–	–	6	3	4	2	–	–	–	–	–	–
Ilex opaca var. *opaca*	17	6	**67**	6	**53**	6	–	–	13	4	36	5	10	4	29	4	4	4	–	–	–	–	–	–
Liquidambar styraciflua	**78**	6	**67**	6	**97**	6	**100**	5	**100**	6	**94**	6	**40**	6	**100**	7	**88**	6	**67**	6	**67**	5	**100**	5

Table 2. Continued

	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Nyssa sylvatica	6	5	**50**	5	**56**	5	**33**	7	**75**	5	15	4	–	–	**35**	5	29	4	–	–	**33**	5	–	–
Quercus alba	22	5	**33**	5	**41**	6	**33**	6	**63**	5	12	4	3	3	**41**	5	–	–	–	–	–	–	–	–
Quercus michauxii	6	4	17	7	**28**	6	**67**	6	–	–	36	7	3	6	**41**	6	**33**	6	–	–	–	–	–	–
Quercus nigra	6	7	**33**	5	**69**	6	**67**	6	13	5	15	7	7	6	**35**	5	8	4	**33**	6	–	–	–	–
Quercus pagoda	6	5	17	6	**47**	6	**67**	7	–	–	9	6	3	5	**53**	6	**33**	5	–	–	–	–	–	–
Ulmus [americana+rubra]	**44**	5	**33**	4	**44**	5	**33**	4	**38**	6	**82**	6	**77**	6	**94**	6	**88**	6	**67**	5	**67**	5	**100**	4
Vine taxon name																								
Bignonia capreolata	**56**	2	**50**	2	**94**	3	**100**	5	**100**	2	**97**	3	**70**	2	**100**	3	**79**	3	**67**	2	–	–	**50**	2
*Lonicera japonica**	**100**	5	**100**	2	**97**	3	**33**	2	**88**	2	**100**	4	**90**	4	**100**	2	**79**	2	**100**	4	**33**	1	**50**	1
Parthenocissus quinquefolia	**100**	3	**100**	2	**100**	3	**100**	3	**100**	2	**100**	2	**100**	2	**100**	3	**96**	2	**100**	3	**33**	1	**100**	2
Smilax rotundifolia	**67**	2	**50**	2	**94**	2	**100**	2	**88**	2	**76**	2	**70**	4	**94**	4	**100**	3	**100**	3	**100**	2	**100**	2
Smilax walteri	6	2	**33**	2	13	2	–	–	25	5	12	3	–	–	18	3	21	2	17	2	–	–	**50**	3
Toxicodendron radicans	**100**	4	100	3	97	4	**100**	5	**100**	3	100	3	**100**	4	100	5	8	5	**83**	5	**100**	2	**100**	2
Vitis [cinerea + vulpina]	**78**	3	–	–	38	2	–	–	25	3	27	4	**70**	3	35	2	46	2	**33**	2	–	–	–	–
Vitis rotundifolia	**100**	3	100	4	100	4	**100**	2	75	2	85	3	**47**	3	88	2	58	2	**67**	3	–	–	**100**	2
Shrub taxon name																								
Asimina triloba	17	5	17	1	19	4	**100**	5	–	–	**45**	6	7	4	29	6	13	3	–	–	–	–	–	–
Alnus serrulata	11	3	–	–	–	–	–	–	–	–	3	4	3	4	–	–	–	–	**67**	5	–	–	–	–
Aesculus sylvatica	11	4	–	–	9	2	–	–	**63**	4	**42**	4	17	4	24	4	4	3	–	–	**33**	2	–	–
Carpinus caroliniana	**78**	6	**67**	4	**91**	6	**67**	4	**75**	6	**64**	5	**37**	4	**88**	5	**71**	4	**50**	6	**67**	4	–	–
Cornus florida	**61**	4	**50**	4	28	3	–	–	13	2	27	4	13	3	18	3	–	–	–	–	–	–	–	–
Ilex decidua	17	2	–	–	**72**	4	**67**	3	**63**	4	**52**	4	20	4	**88**	5	**71**	5	–	–	**100**	3	**100**	4
*Ligustrum sinense**	22	2	–	–	22	2	**33**	3	–	–	**64**	5	**73**	4	**47**	4	**33**	2	**50**	4	–	–	–	–
Lindera benzoin	**56**	7	–	–	19	3	–	–	–	–	**67**	6	**43**	6	18	4	8	4	17	7	–	–	–	–
Viburnum prunifolium	**50**	4	–	–	**50**	4	**67**	4	**50**	4	27	3	13	3	**65**	4	**38**	4	17	2	–	–	–	–
Herb taxon name																								
Botrypus virginianus	**83**	2	**33**	2	**34**	2	–	–	25	2	**45**	2	17	2	12	2	4	1	17	1	–	–	–	–
Galium circaezans	**78**	2	17	1	**50**	2	–	–	**63**	2	6	1	3	1	–	–	4	1	–	–	–	–	–	–
Galium triflorum	**89**	2	**83**	2	**44**	2	–	–	**50**	2	27	2	13	1	18	2	8	2	–	–	–	–	–	–
Phryma leptostachya	**72**	2	–	–	6	1	–	–	–	–	6	2	3	1	–	–	4	2	–	–	–	–	–	–
Polystichum acrostichoides	**100**	4	**100**	3	**63**	3	–	–	**100**	2	**52**	2	**37**	2	**35**	2	13	2	17	1	–	–	–	–
Euonymus americanus	**100**	2	**100**	2	**100**	2	**100**	2	**100**	2	**58**	2	**30**	2	**76**	2	**71**	2	**33**	2	–	–	–	–
Melica mutica	22	3	–	–	**56**	2	–	–	25	2	12	3	–	–	18	1	8	2	–	–	–	–	–	–
Mitchella repens	22	2	**67**	2	**91**	2	**67**	2	38	2	3	2	–	–	24	2	21	2	–	–	–	–	–	–
Arisaema dracontium	11	2	–	–	3	1	**67**	2	13	1	**42**	2	17	2	24	2	4	1	17	1	–	–	–	–
Arundinaria tecta	17	2	17	4	28	6	**100**	5	25	2	**39**	5	13	6	24	5	17	4	17	5	–	–	50	1
Asarum canadense	17	4	–	–	16	2	**100**	2	–	–	21	5	17	2	**29**	2	–	–	17	1	–	–	–	–
Carex intumescens	**6**	2	**33**	1	**41**	2	**100**	2	–	–	3	2	**10**	2	**47**	3	29	5	–	–	**67**	2	–	–
Elephantopus carolinianus	–	–	–	–	6	2	**67**	2	–	–	–	–	–	–	–	–	4	2	–	–	–	–	–	–
Ranunculus abortivus	**44**	2	17	1	6	1	**100**	2	**50**	1	39	2	**33**	2	**41**	2	17	2	**50**	1	–	–	**50**	2
Bromus [nottowayanus+pubescens]	**39**	2	–	–	9	2	–	–	**75**	2	30	2	3	2	6	2	–	–	–	–	**33**	2	–	–
Carex laxiculmis	17	3	**33**	2	9	2	–	–	**63**	3	6	2	–	–	–	–	–	–	–	–	–	–	–	–

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Danthonia spicata	–	–	17	2	22	3	–	–	**63**	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dichanthelium boscii	22	2	**33**	4	16	2	–	–	**63**	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dichanthelium laxiflorum	28	2	**33**	2	**34**	2	–	–	**75**	2	3	1	–	–	12	2	–	–	–	–	–	–	–	–
Elymus hystrix	**33**	4	**33**	3	9	2	–	–	**100**	3	15	3	23	4	–	–	–	–	–	–	–	–	–	–
Hexastylis arifolia	28	2	**67**	2	22	2	**33**	1	**100**	2	6	2	–	–	–	–	–	–	–	–	–	–	–	–
Hypericum hypericoides	6	1	**33**	2	**59**	2	–	–	**88**	2	–	–	–	–	6	1	8	1	–	–	–	–	–	–
Potentilla [simplex+canadensis]	17	2	**33**	1	**34**	2	–	–	**75**	2	6	2	–	–	6	1	8	2	–	–	–	–	–	–
Ruellia caroliniensis	**33**	2	17	1	**31**	2	–	–	**75**	2	3	2	–	–	18	1	21	2	–	–	–	–	–	–
Salvia lyrata	**50**	2	**50**	2	22	2	–	–	**88**	2	3	1	3	2	–	–	–	–	–	–	–	–	–	–
Symphoricarpos orbiculatus	17	2	–	–	13	2	–	–	**63**	2	36	3	10	2	–	–	–	–	–	–	–	–	–	–
Zizia aurea	–	–	–	–	–	–	–	–	**75**	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Laportea canadensis	6	1	–	–	–	–	–	–	–	–	**52**	5	**57**	4	24	2	**4**	1	–	–	–	–	–	–
Carex typhina	6	1	17	2	13	2	**100**	2	–	–	12	2	20	3	**47**	2	**88**	4	**33**	4	**67**	2	–	–
Boehmeria cylindrica	**67**	2	**50**	2	**47**	2	**100**	2	25	2	**64**	2	**83**	3	**76**	2	**92**	3	**100**	6	**100**	2	50	1
Carex crinita	11	2	17	3	16	2	–	–	–	–	3	2	3	2	29	2	**33**	3	**83**	6	**67**	2	–	–
Carex tribuloides	**33**	2	17	1	25	2	**33**	1	13	1	**42**	2	**60**	4	**76**	3	**88**	4	**100**	4	**33**	2	**50**	2
Peltandra virginica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	29	2	**83**	4	–	–	–	–
Persicaria spp.	11	1	17	2	–	–	**33**	1	–	–	6	2	**40**	2	12	2	**46**	3	**83**	3	**33**	1	**50**	2
Ludwigia palustris	–	–	17	1	–	–	–	–	–	–	–	–	3	1	6	1	21	2	–	–	**100**	2	**50**	2
Saururus cernuus	6	2	**33**	2	19	2	–	–	13	2	15	2	23	3	29	2	**71**	6	**33**	6	**100**	7	**100**	2
Amphicarpaea bracteata	**89**	3	**50**	2	**44**	2	–	–	**63**	2	**39**	2	27	2	6	1	8	2	17	3	–	–	–	–
Arisaema triphyllum	**78**	2	**50**	2	19	2	–	–	**75**	2	**39**	2	**37**	2	**88**	2	17	2	**33**	1	–	–	–	–
Bidens frondosa	11	1	17	2	13	2	**33**	1	25	1	6	3	27	2	24	2	29	2	**50**	3	**67**	2	**100**	2
Carex [amphibola+grisea+corrugata]	**72**	3	17	2	**66**	5	**100**	3	**50**	3	**73**	4	**73**	4	**59**	4	**38**	4	**33**	1	–	–	**50**	3
Carex [radiata+rosea]	**89**	3	**83**	2	**66**	3	**67**	2	**63**	2	**67**	5	**33**	4	**53**	2	**42**	2	17	1	–	–	–	–
Carex blanda	**61**	3	**50**	2	**41**	3	–	–	**63**	3	**67**	3	**33**	3	**35**	2	29	2	–	–	–	–	50	1
Carex caroliniana	22	2	–	–	**41**	3	–	–	25	2	12	2	13	2	**41**	2	25	2	–	–	–	–	–	–
Carex debilis	**39**	3	**50**	2	**66**	3	**67**	2	–	–	9	2	3	2	**41**	3	**50**	4	–	–	–	–	–	–
Carex grayi	6	1	–	–	13	2	–	–	**38**	2	**61**	3	**40**	5	12	3	**33**	5	17	3	–	–	**50**	2
Carex lupulina	6	1	–	–	–	–	–	–	–	–	3	1	17	2	29	2	**58**	4	**67**	4	**33**	5	–	–
Carex oxylepis	**39**	3	**50**	2	22	3	–	–	**75**	3	18	2	10	2	24	4	4	8	–	–	–	–	–	–
Chasmanthium latifolium	**50**	3	–	–	**69**	4	**100**	5	**75**	6	**45**	5	**77**	6	**47**	2	**54**	4	**67**	4	–	–	50	1
Commelina virginica	11	1	–	–	6	2	**33**	1	25	2	27	2	**57**	2	24	1	**54**	2	**67**	6	**33**	3	–	–
Dichanthelium commutatum	**72**	2	**83**	2	**84**	3	**100**	2	**100**	3	**45**	3	23	2	29	2	**46**	2	**33**	2	**33**	1	**50**	2
Dioscorea [quaternata+villosa]	28	2	–	–	**56**	2	**33**	2	**63**	2	27	2	13	2	6	2	8	2	17	2	–	–	–	–
Elymus virginicus s.l.	**33**	2	**50**	2	**47**	4	–	–	38	2	**67**	5	**63**	6	**65**	3	**42**	2	**33**	1	–	–	–	–
Erechtites hieracifolia	22	2	**33**	1	16	1	**100**	2	13	1	30	2	**37**	2	**59**	2	**63**	1	17	1	**33**	1	**100**	1
Festuca subverticillata	**78**	2	**50**	2	**44**	3	–	–	38	2	**39**	5	**60**	3	**35**	2	17	4	–	–	**33**	2	–	–
Galium aparine	**39**	2	–	–	3	1	–	–	**50**	2	**64**	2	**70**	4	18	2	17	2	**67**	2	**33**	1	–	–
Galium tinctorium	17	2	17	1	**38**	2	–	–	38	2	–	–	3	1	**65**	2	**42**	2	–	–	–	–	50	1
Gelsemium sempervirens	–	–	17	2	**47**	2	–	–	–	–	–	–	–	–	12	2	4	1	17	1	**67**	2	–	–
Geum canadense	**84**	2	**50**	2	**34**	2	–	–	**50**	1	**48**	2	**43**	2	29	2	**50**	2	**50**	2	–	–	–	–
Glyceria striata	**39**	2	**50**	2	16	2	–	–	13	1	15	2	**37**	2	**65**	2	**50**	4	**83**	4	**67**	2	–	–
[Gonolobus+Matelea]	**33**	2	**33**	1	**34**	2	**67**	2	25	2	**73**	2	**60**	2	18	2	8	2	–	–	–	–	–	–
Impatiens capensis	**33**	2	17	1	3	1	**67**	2	38	1	27	5	23	2	29	4	**38**	2	**33**	2	**67**	2	50	1

Table 2. Continued

	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.	con.	cov.
Juncus coriaceus	28	2	**83**	2	**28**	2	–	–	**88**	2	6	2	10	2	**35**	2	**33**	3	**33**	2	**33**	2	–	–
Juncus effusus	22	2	**50**	2	**19**	2	–	–	13	1	3	2	23	2	24	2	**54**	3	**33**	4	–	–	–	–
Leersia virginica	17	2	**33**	2	**31**	2	–	–	**63**	4	9	3	**53**	2	18	2	**50**	3	**50**	3	–	–	–	–
Lobelia cardinalis	6	2	**–**	–	3	1	–	–	–	–	–	–	7	1	12	1	13	2	**67**	2	**33**	2	–	–
*Lonicera japonica**	**100**	4	**100**	2	**97**	4	**33**	2	**88**	2	**100**	4	**90**	4	**100**	2	**79**	2	**100**	3	**33**	1	50	1
Lycopus virginicus	28	2	**50**	2	**19**	2	**67**	2	25	1	9	2	23	2	24	2	**54**	2	**100**	3	**100**	2	**100**	2
*Microstegium vimineum**	**94**	6	**83**	6	**66**	2	–	–	**100**	3	**85**	6	**93**	7	**82**	4	**67**	4	**83**	7	**33**	2	50	1
Oxalis spp.	**61**	2	**100**	2	**31**	2	–	–	**88**	2	**48**	2	**60**	2	12	1	13	1	–	–	–	–	–	–
Parthenocissus quinquefolia	**100**	3	**100**	2	**100**	3	**100**	3	**100**	2	**100**	2	**100**	2	**100**	3	**96**	2	**100**	2	**33**	1	**100**	2
Passiflora lutea	**39**	2	**67**	2	**38**	2	**67**	1	**50**	2	39	2	27	2	6	1	4	1	–	–	–	–	–	–
Persicaria virginiana	**50**	2	**50**	2	19	2	**33**	2	25	1	**76**	2	**87**	2	**53**	2	**42**	2	**67**	2	**33**	2	–	–
Phytolacca americana	6	2	–	–	–	–	**67**	2	–	–	21	2	**53**	2	6	1	17	1	**50**	2	–	–	–	–
Pilea pumila	17	2	–	–	–	–	–	–	13	1	27	2	**63**	2	29	2	**38**	2	**33**	3	**33**	2	**100**	2
Poa [autumnalis+cuspidata]	**50**	5	**50**	2	**78**	4	–	–	**63**	3	**45**	3	27	2	**82**	3	**42**	3	**50**	2	–	–	**50**	2
Polygonatum biflorum	**56**	2	**67**	2	**53**	2	**33**	2	**50**	2	**39**	2	17	1	–	–	4	1	–	–	–	–	–	–
Rosa spp.	**50**	2	–	–	**34**	2	**33**	2	13	1	**39**	2	**30**	2	**35**	2	25	2	**67**	2	–	–	–	–
Rubus spp.	**94**	2	**50**	2	**94**	2	**100**	2	38	1	**55**	2	**40**	2	**71**	3	**79**	2	**100**	2	**67**	2	**50**	2
Sanicula canadensis	**89**	2	**100**	2	**72**	2	**67**	2	**88**	2	**70**	2	**37**	2	**47**	2	**33**	2	**67**	1	–	–	**100**	1
Sceptridium [biternatum+dissectum]	**67**	2	**50**	2	**78**	2	**33**	1	**50**	2	39	2	17	2	**53**	2	**54**	2	17	2	–	–	**50**	1
Solidago spp.	**89**	2	**100**	2	**91**	2	**100**	2	**100**	2	**52**	2	**77**	2	**88**	2	**96**	3	**83**	4	**67**	2	**100**	2
Trachelospermum difforme	6	2	–	–	**50**	2	–	–	38	2	6	2	10	2	**59**	2	29	2	17	1	–	–	–	–
Verbesina alternifolia	**39**	2	**33**	2	**38**	2	–	–	**100**	2	**70**	3	**80**	3	12	1	8	1	17	2	–	–	–	–
Verbesina occidentalis	**50**	2	**33**	5	28	2	–	–	**50**	3	**70**	2	**67**	2	12	2	8	2	–	–	–	–	–	–
Viola spp.	**94**	2	**100**	2	**81**	2	**100**	2	**88**	2	**88**	2	**73**	3	**100**	2	**67**	2	**50**	2	–	–	**100**	2

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habitats, including *Carya cordiformis, Acer floridanum* and *Juglans nigra* (Appendix S5). *Acer negundo* is prominent in the sub-canopy. The shrub layer is relatively dense and diverse, with additional cover contributed by *Asimina triloba, Aesculus sylvatica* and the exotic *Ligustrum sinense*. The herb stratum is composed of a mix of graminoid species, occasionally including substantial cover of *Arundinaria tecta*, and various forb species, commonly including *Laportea canadensis*. The exotic species *Microstegium vimineum, Glechoma hederacea* and *Lonicera japonica*, may also contribute high cover in the herb stratum (Appendix S5).

IIIb. Fraxinus pennsylvanica – Platanus occidentalis/Acer negundo/Chasmanthium latifolium levee forest (30 plots): This levee community primarily occurs on third- to sixth-order rivers across all five river basins and is associated with slightly narrower floodplains than the other levee type. In comparison to IIIa, it is associated with higher elevations and longer river course distances from the river mouth, reflecting locations more towards the interior Piedmont, although there is considerable spatial overlap (Fig. 1). The soils are also quite fertile, with high pH and base saturation; in comparison to the other levee group, these soils have a higher percentage of sand, expected of interior types (Appendix S1).

The nominal species dominate the canopy of this levee type, in addition to *Ulmus americana, Betula nigra* and *Liquidambar styraciflua. Acer negundo* consistently contributes very high cover in the sub-canopy. In comparison to the other levee vegetation type, this type tends to have a less diverse tree stratum with higher cover and constancy of *Fraxinus pennsylvanica* and *Platanus occidentalis* (Table 2). The shrub layer is moderately diverse and primarily composed of smaller individuals from the tree stratum, in addition to *Lindera benzoin* and the exotic *Ligustrum sinense*. Graminoid species commonly dominate the herb stratum, particularly *Chasmanthium latifolium*, *Elymus virginicus* s.l. and *Carex grayi*. As with IIIa, exotic species may be prominent in this group; *Microstegium vimineum* often contributes substantial cover in the herb stratum (Appendix S5).

Bottomland and swamp forests

The bottomland and swamp forest group occurs on the widest floodplains and mid- to high-order rivers (primarily third order and higher). These types are found on low areas of the floodplain where standing water remains for a longer period of the year and growing season. The soils have a high concentration of silt, clay and organic matter; they are relatively acidic and infertile, with low base saturation and Ca:Mg ratios. In ordination space, soil texture separates the drier oak–hickory flats (II) from the wetter, more commonly flooded oak bottomlands, which have much higher clay content (Fig. 3). Soil variables suggest that floristic variation within this group is largely driven by hydroperiod, with types IVd and IVe occurring in the wettest sites, types IVa and IVb occurring in intermediate sites, and IVc occurring in the narrower floodplains of the inner Piedmont where the hydroperiod is shorter (Table 2). The two intermediate groups (IVa and IVb) are also separated by hydroperiod, with IVa being drier than IVb; the soils of IVa are characterized by high silt levels, while IVb is characterized by high clay content (Appendix S1).

IVa. Quercus (phellos – pagoda – michauxii) – Ulmus americana/Ilex decidua/Arisaema triphyllum bottomland forest (17 plots): This bottomland forest community is found in wide floodplains on larger rivers in the Triassic Basins; six plots were classified to this group that do not map directly over Triassic Basin bedrock, but they were all located directly adjacent to this region. This type is associated with bottomland geomorphology, on low, broad Piedmont floodplains, often without obvious relief or geomorphologic development (in contrast to levees, which are often raised, or backswamps, which are often obvious depressions on the floodplain). This type is documented in every river basin except the Catawba, likely due to the North Carolina section of the Catawba basin lacking Triassic Basin bedrock (Fig. 1). In addition, many of the larger-order rivers of the Catawba basin are heavily dammed, resulting in very little remaining bottomland forest habitat. The soils of this type have moderately high clay content, although not as high as the other swamp groups described below; this likely reflects the shorter flooding duration at these sites (Appendix S1).

The nominal *Quercus* spp. dominate the tree stratum, along with common canopy co-dominants of wet Piedmont forests, such as *Acer rubrum* and *Fraxinus pennsylvanica*. Climbing vines may also contribute substantial cover in the tree stratum, especially *Toxicodendron radicans* (Table 2). The considerable cover contributed by *A. rubrum* and *F. pennsylvanica* floristically differentiates this type from other vegetation types with high *Quercus* cover (IIa and IIb). Also in contrast to group II, *Quercus nigra* is much less common in the wetter vegetation types of group IV. As expected in these wetter sites, *Fagus grandifolia* is extremely rare, also differentiating this type from IIa. *Carpinus caroliniana* and *Ulmus alata* frequently contribute cover to the sub-canopy and shrub strata. The herb stratum tends to be more open when compared to the other mega groups, with most cover contributed by patches of *Carex* spp. (Appendix S6).

IVb. Fraxinus pennsylvanica – Acer rubrum – Ulmus americana/Ilex decidua/Saururus cernuus swamp forest (24 plots): This swamp forest type is associated with medium- to large-sized rivers (all ≥third order). Approximately a quarter of the plots in this group were located in the Triassic Basins, where Piedmont rivers have broader floodplains with better-developed geomorphology. Even where plots included in this type were found outside of the Triassic Basins, they were located on wider Piedmont floodplains. This type occurs in the back-swamp geomorphic position, with relatively acidic soils characterized by high clay content and frequent flooding (Appendix S1).

The dominant tree stratum species of this type include the nominal species in addition to *Liquidambar styraciflua* and *Quercus phellos*. There is some degree of overlap, both in floristics and environmental setting, of this type and the more oak-dominated types in this group, IVa and IVd. This type may be an earlier successional stage of the bottomland forests (IVa) and is found in slightly wetter sites with longer periods of flooding. Alternatively, in comparison to group IVd, this group represents slightly shorter hydroperiods, with *Quercus lyrata* occasionally present in small, very wet inclusions (Appendix S6). The shrub layer tends to be moderately open, while the herb stratum is heavily dominated by *Carex* spp. and wetland forbs.

IVc. Fraxinus pennsylvanica – Betula nigra – Platanus occidentalis/Alnus serrulata/Boehmaria cylindrica swamp forest (six plots): This forested type is found along the larger-order rivers at high regional elevations in the river basin, further from the fall line and mouth of the river (Fig. 1). This type occurs on wet areas of the floodplain, but in contrast to the other bottomland and swamp forests, these floodplains are restricted by resistant granitic bedrock and tend to be narrower than those found closer to the fall line in the Triassic Basins. The wet areas of these narrower floodplains may be the result of ponding due to dams, natural or human, or seepage areas at the edge of the floodplain. Soils at these sites are sandier than the other swamp types, perhaps as a result of erratic, short-duration flooding events common in the narrow valleys of the upper Piedmont (Appendix S1).

The tree canopy of this type is more open than other swamp types and is dominated by the nominal species, with additional cover from *Ulmus americana, Liquidambar styraciflua* and *Salix nigra*. The open canopy and dominance of many early successional species may be a result of flooding disturbance. The shrub stratum is composed of small individuals of the tree stratum, in addition to *Alnus serrulata, Carpinus caroliniana, Cornus amomum* and *Viburnum dentatum*. The herb stratum is well developed and dominated by a mix of sedges and grasses (Appendix S6).

IVd. Quercus lyrata – Fraxinus pennsylvanica/Saururus cernuus swamp forest (three plots): This type is found in the wide floodplains of the Triassic Basins. While there is some floristic overlap with other swamp types, these forests dominate in sites where there is prolonged flooding over a larger area, and therefore they are not included in other vegetation types (such as IVb, where *Quercus lyrata* is present in small-scale floodplain depressions). While random forests analysis indicated that these plots should be lumped with IVb, we chose to recognize this as a distinct type due to the high *Quercus lyrata* cover in these plots, which is not common in the Piedmont (Weakley 2010), and is generally associated with very wet conditions. The soils of this type are very acidic, with a very high clay content (Appendix S1).

This type is dominated by high *Quercus lyrata* cover, in addition to the other common swamp co-dominants. The shrub stratum is very sparse and mostly composed of young tree species. The herb layer is heavily dominated by *Saururus cernuus*, with additional herb cover contributed by common wetland species such as *Impatiens capensis, Bidens frondosa* and *Carex* spp. (Appendix S6).

IVe. Carya aquatic – Nyssa aquatica swamp forest (two plots): The two plots of this swamp forest type occur in very wide floodplains of the lower Triassic Basins, close to the fall line in the Yadkin River Basin. Soils at these sites are acidic, with very high clay content, which are indications of long flooding periods (Appendix S1).

The tree stratum is dominated by the two nominal species, both of which are more typical dominants of swamp vegetation on the Coastal Plain of North Carolina. *Carya aquatica* and *Nyssa aquatica* are rare in the Piedmont region of North Carolina (Weakley 2010). Random forests analysis also indicated that these plots should be lumped with IVb, but we chose to recognize this type due to the rarity of the dominant tree species. If the analysis had included Coastal Plain plots, this type would likely have been seen to have higher affinities to the Coastal Plain plots than to IVb. Other canopy trees include species commonly associated with the wettest sites in the floodplain, including *Quercus lyrata, Acer rubrum* and *Fraxinus pennsylvanica*. The shrub and herb layer of this community type is very sparse as the plots are frequently inundated for extended periods (Appendix S6).

Riparian herbaceous vegetation

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

Va. Justicia americana herbaceous vegetation (ten plots): This type is found in rocky-bottomed rivers in all basins except the Catawba. The vegetation is heavily

Applied Vegetation Science
Doi: 10.1111/j.1654-109X.2011.01150.x

dominated by herbaceous cover from *Justicia americana* (Appendix S7). Other herbs that commonly contribute cover include *Boehmeria cylindrica* and the exotic *Murdannia keisak*. Occasional tree cover is contributed by overhanging bottomland species that may include *Platanus occidentalis, Fraxinus pennslyvanica* and *Betula nigra*.

Vb. Hymenocallis coronaria – Justicia americana herbaceous vegetation (two plots): The two plots documenting this type are located in the Catawba River in South Carolina, where *Hymenocallis coronaria* is a state-listed rare species (South Carolina Department of Natural Resources; https://www.dnr.sc.gov/pls/heritage/county_species.list?pcounty=all). This vegetation type is heavily dominated by herbaceous cover of both nominal species (Appendix S7).

Discussion

Piedmont alluvial vegetation is driven in large part by geomorphology, which is strongly related to stream order, floodplain width and soil texture and chemistry. The floodplains of the lower-order Piedmont rivers are often narrow and the geomorphic landscape is poorly developed, primarily as a result of the prevalence of resistant metamorphic and granitic bedrock. Where distinct fluvial land forms are not easily identifiable in these narrow floodplain rivers, compositional variation is strongly correlated with soil texture and chemistry. Vegetation group I (small streams and narrow floodplain forests) and group II (oak–hickory flats) generally occur in such settings: group I is associated with fertile, sandy soils and group II is associated with less fertile, loamy soils. In contrast, the higher-order rivers with wider floodplains have a better-developed geomorphic landscape, with distinct geomorphic settings and more variation in substrate. Vegetation group III (large river levee forests) and group IV (bottomland and swamp forests) are dominant in the higher-order rivers, where vegetation types are sorted along a hydrologic gradient and are associated with distinct fluvial land forms. The levee forests are associated with higher and drier regions of the floodplain, located close to the river channel, where flooding events are short in duration and soils are sandy and very fertile. The bottomland and swamp forests are often further removed from the river channel, in the low topographic areas of floodplains where longer hydroperiods result in deposition of fine sediment and soils with high clay content. However, in contrast to the very wide floodplains of the Coastal Plain, where fluvial geomorphologic settings and their associated vegetation are distinct, the geomorphic features of the narrower Piedmont floodplains intergrade over smaller spatial distances. Our results suggest less species sorting in the narrower Piedmont floodplains and stronger species sorting in the more Coastal Plain-like settings of groups III and IV; however, we are unable to directly compare the degree of species sorting in the Piedmont versus the Coastal Plain because previous studies of Coastal Plain vegetation are primarily qualitative, descriptive studies and lack plot data.

Our classification describes remnant alluvial plant communities in a highly fragmented landscape, representing only a portion of the original diversity of these systems (Peet & Christensen 1980). In addition, the natural hydrologic regime of Piedmont rivers has been altered by anthropogenic activities since the beginning of European colonization (Walter & Merritts 2008). Although we attempted to locate and sample the most natural, high-quality vegetation possible, it is important to realize the implications of the highly altered Piedmont landscape. A long history of selective tree harvesting may have resulted in certain species being under-represented in vegetation types where they historically may have been prominent (Peet & Christensen 1980). The presence of non-native invasive species in many of our samples suggests the structural and compositional differences between the pre-European native vegetation and the vegetation on the landscape today; 7% of the riparian flora sampled was exotic, and only three plots (2%) did not contain an exotic species. These values are similar to those documented in a previous study of southeastern US riparian vegetation, which found 11.5% of the riparian flora was exotic and only 7% of plots were exotic-free (Brown & Peet 2003). Finally, extensive sediment deposition following European agriculture on the uplands during the period 1700-1940 homogenized the hydrogeomorphic landscape of many Piedmont rivers, decreasing floodplain habitat complexity and likely resulting in floristic changes to pre-European riparian vegetation (Trimble 1974).

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

The classification presented here complements and can be expected to inform future revision of floodplain associations in the southeastern United States recognized in the US National Vegetation Classification (NVC; U.S. FGDC 2008; Jennings et al. 2009). The vegetation types we describe are comparable to NVC associations in terms of compositional variation and consistency, although NVC community concepts may reflect the broader geographic scope of the NVC. The current NVC floodplain associations of the Piedmont region are considered provisional and ranked as having low confidence, for although the current NVC floodplain associations are based on a synthesis of available literature and qualitative field surveys of variation across their range, plot data are usually lacking. The current NVC set of alluvial vegetation associations occurring in the Piedmont includes a mixture of broadly defined 'placeholders' (provisional type concepts), types with uncertain conceptual boundaries and types based on limited, unavailable or non-existent plot data. In contrast, the descriptions of most of our types are based on a large number of plots distributed across a wide geographic area and capture compositional variation within the groups across this area. These plots are archived in VegBank and thus are available for re-analysis and integration into larger data sets that can better test the full range of variation expressed by current NVC types across their geographic extent. The specific plots for each type are shown in Appendix S8.

Although a few of our types (five out of 14) fit well within currently recognized NVC community concepts, others deviate sharply from established types and may point to the need for re-working currently recognized NVC alluvial type concepts. To facilitate comparison of our types and existing NVC associations, we have matched each of our 14 types to the closest recognized NVC association, as well as any other NVC associations that appear to overlap our own, and placed each of our types within the current NVC hierarchy (Table 3; Appendix S9). Table 3 illustrates the complexity of interrelationships between the quantitatively derived types presented

Table 3. Relationship of the 14 recognized vegetation types to established USNVC associations (http://www.natureserve.org/explorer/, September 1, 2010). Relationships are depicted in the table by four symbols: < indicating our type is included in the NVC concept, > indicating our type includes the NVC concept, > < indicating that the two concepts overlap, ~ indicating our type is approximately equivalent to NVC concept, and = indicating the two concepts are equal to each other.

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

Applied Vegetation Science
Doi: 10.1111/j.1654-109X.2011.01150.x

Table 3. Continued

Type	N	Alluvial vegetation type name	Relationship	NVC community type (with CEGL code)	
			> <	4419	*Liriodendron tulipifera/Asimina triloba/ Arundinaria gigantea* ssp. *gigantea* forest
IIIb.	30	*Fraxinus pennsylvanica- Platanus occidentalis/ Acer negundo/ Chasmanthium latifolium* levee forest	<	7340	*Platanus occidentalis – Liquidambar styraciflua/ Carpinus caroliniana – Asimina triloba* forest
IV. Bottomland and swamp forests					
IVa.	17	*Quercus (phellos-pagoda-michauxii) – Ulmus americana/Ilex decidua/Arisaema triphyllum* bottomland forest	<	7356	*Quercus pagoda – Quercus phellos – Quercus lyrata – Quercus michauxii/Chasmanthium latifolium* forest
IVb.	24	*Fraxinus pennsylvanica -Acer rubrum-Ulmus americana/ Ilex decidua/Saururus cernuus* swamp forest	∼	6548	*Acer (rubrum, saccharinum) – Fraxinus pennsylvanica – Ulmus americana/Boehmeria cylindrica* forest
IVc.	6	*Fraxinus pennsylvanica –Betula nigra –Platanus occidentalis/ Alnus serrulata/Boehmaria cylindrica* swamp forest	∼	7312	*Betula nigra – Platanus occidentalis/Alnus serrulata/Boehmeria cylindrica* forest
IVd.	3	*Quercus lyrata Fraxinus pennsylvanica/ Saururus cernuus* swamp forest	<	7356	*Quercus pagoda – Quercus phellos – Quercus lyrata – Quercus michauxii/Chasmanthium latifolium* forest
IVe.	2	*Carya aquatica- Nyssa aquatica* swamp forest	∼	7397	*Quercus lyrata – Carya aquatica* forest
V. Riparian herbaceous vegetation					
Va.	10	*Justicia americana* herbaceous vegetation	=	4286	*Justicia americana* herbaceous vegetation
Vb.	2	*Hymenocallis coronaria – Justicia americana* herbaceous vegetation	=	4285	*Hymenocallis coronaria – Justicia americana* herbaceous vegetation

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

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

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Means and standard errors (±SE) of soil variables by vegetation type.

Appendix S2. Average constancy and basal area of woody vegetation in each type.

Appendix S3. Floristic table for the small stream and narrow floodplain forests (I), including average cover by strata, constancy, fidelity, diagnostic value (DV) and indicator value (IV) of prevalent species.

Appendix S4. Floristic table for the three oak–hickory flat types (II).

Appendix S5. Floristic table for the two large river levee forest types (III).

Appendix S6. Floristic table for the five bottomland and swamp forest types (IV).

Appendix S7. Floristic table for the two herbaceous vegetation types (V).

Appendix S8. The 192 vegetation plots archived in Vegbank, with assignment to the 14 vegetation types (VegBank accession code: http://vegbank.org/cite/VB.ds.199019.MATTHEWS).

Appendix S9. Relationship of the 14 vegetation types to the NVC hierarchy. The placement of NVC associations within the hierarchy is in draft status as of March 2011; this table will be updated to reflect the final position of associations within the hierarchy.

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