ABSTRACT

SZAKACS, ALEXANDRIA DIANE. Using Multiple Approaches to Explore the Past and Present of “Piedmont Prairie” Vegetation. (Under the direction of Dr. Alexander Krings and Dr. William Hoffmann).

Historical records and paleontological evidence suggest the eastern Piedmont of North America, a currently heavily developed and otherwise forested region, once had areas of grassland, savanna, and/or woodland that were characterized by shade-intolerant native heliophytes. Naturally open areas of the landscape were almost entirely lost following European settlement of the region due to changes in land use and disruption of historical fire regimes. Because some of the remnant heliophytes are midwestern prairie disjuncts (e.g., *Silphium terebinthinaceum*), or southeastern endemic congeners of prairie-affinity genera (e.g., *Echinacea laevigata*), the term “Piedmont prairie” has become a popular name for this vegetation type. Remnant prairie-affinity flora now largely persist in human-maintained open areas, such as roadsides and utility right-of-ways. Such marginal existence of a once-common ecosystem is cause for concern, so conservation and restoration of Piedmont prairie vegetation are now receiving much attention. Several impediments to successful conservation and restoration exist. For example, the historical distribution and composition of this vegetation type(s) is uncertain, and so few high-quality remnants remain that it is difficult to formulate clear goals for conservation and restoration. This work uses multiple approaches to better understand Piedmont prairie vegetation. We explored the potential utility for historical vegetation reconstruction in the Southeast using phytoliths, silica plant microfossils. To this end, we created the first comprehensive reference collection of phytoliths produced by 28 species of eastern North American conifers (Chapter 1). While we did not find clear distinctions between species or between most genera we sampled, we did document at least one phytolith type that was characteristic of Pinaceae; future studies using higher magnification to study phytolith surface features seem promising. We then compiled a carefully selected 1300-plot dataset from the Carolina Vegetation Survey database, the largest database of regional vegetation plots, to assess the shade-tolerance of regional herbaceous species by proxy of their association with open, semi-open, and closed habitats (Chapter 2). We identified 141 (17% of herbaceous species in our dataset) heliophytes associated with very open habitats (canopy cover <25%), and only 81 (10%) very shade-tolerant species associated with closed habitats (canopy cover >75%). We examined a series of vegetation surveys that took place over 25 years in a putative Piedmont prairie remnant (Picture Creek Diabase Barrens located in Granville County, North Carolina) in order to assess how rare heliophytes, such as *Echinacea laevigata*, and associated vegetation are responding to differences in management (Chapter 3). We found that vegetation in the monitoring plots has been very forest-like during the last 25 years (most of this time under fire suppression), but recent (2017) prescribed fire is shifting vegetation toward a more open, pine-woodland structure with increasing herbaceous understory. Finally, we used a 195-plot subset of the 1300-plot Carolina Vegetation Survey dataset to characterize and better define the major types of Piedmont heliophilic vegetation through multivariate analyses (Chapter 4). Using hierarchical clustering, partition optimization, and nonmetric multidimensional scaling ordination, we identified and characterized 12 major types of Piedmont heliophilic vegetation, which we organized into five larger groupings: Piedmont Oak-Hickory and Red Cedar Woodlands, Piedmont Glades, Piedmont Pine Woodlands, Piedmont Savannas and Grasslands, and Piedmont River Terrace Glades. We found plots traditionally refered to as “Piedmont prairie” formed a compositionally distinctive cluster characterized by the abundance of heliophytes such as *Oenothera fruticosa*, and *Silphium terebinthinaceum*.

Using Multiple Approaches to Explore the Past and Present of “Piedmont Prairie” Vegetation.

by
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BIOGRAPHY

Alexandria Szakacs grew up in Warren, Ohio. She developed a love and appreciation of nature at a young age, and her parents encouraged her interest in science. She attended Youngstown State University (YSU) where she met Professor Carl Chuey, who invited her to work in the Youngstown State University Herbarium and inspired her to pursue the study of Plant Systematics and Field Botany. After earning a Bachelor's in Biology at YSU, she moved to Raleigh, North Carolina and joined the Plant Biology Graduate Program at North Carolina State University to pursue a Doctorate studying the ecology of native prairie plants.

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TABLE OF CONTENTS

LIST OF TABLES v
LIST OF FIGURES vi

CHAPTER 1: Phytoliths Produced by Eastern North American Conifers and Their Potential for Reconstructing Historical Vegetation of the Southeast 1
- Introduction 2
- Methods 4
- Results 5
- Discussion 7
- References 10
- Tables 14
- Figures 22

CHAPTER 2: Shade-tolerance Classification of the Upland Herbaceous Flora of the Carolina and Virginia Piedmont 35
- Introduction 36
- Methods 37
- Results 40
- Discussion 42
- References 44
- Tables 48
- Figures 76

CHAPTER 3: Long-term Monitoring of Vegetation Plots and *Echinacea laevigata* at Picture Creek Diabase Barrens (Granville Co., NC) 77
- Introduction 78
- Methods 79
- Results 85
- Discussion 92
- References 99
- Tables 102
- Figures 108

CHAPTER 4: In Search of the "Piedmont Prairies": Multivariate Analyses of Heliophilic Plant Communities of the Eastern Piedmont of North America 118
- Introduction 119
- Methods 120
- Results 123
- Discussion 134
- References 140
- Tables 143
- Figures 160

APPENDICES 168
APPENDIX A 169
APPENDIX B 174
APPENDIX C 183

LIST OF TABLES

Table 1.1 Overview of the 28 species of conifers sampled for phytoliths. 14

Table 1.2 Details of the 140 herbarium specimens sampled for phytoliths. 15

Table 1.3 Summary of the total number of phytoliths and the different phytolith morphotypes found in each species 19

Table 1.4 Mean length (µm) and standard deviation for phytolith morphotypes measured in 27 species of eastern conifers 21

Table 2.1 Overview of the vascular plant taxa present in the 1300-plot final dataset following quality control and taxonomic homogenization steps.............................. 48

Table 2.2 Number of vegetation plots assigned to each habitat shade class as determined from estimated total tree cover of each plot 49

Table 2.3 Various assessments of the 892 herbaceous species in the dataset 50

Table 2.4 Herbaceous species and their habitat shade class associations as determined by point biserial correlation coefficients 51

Table 3.1 Counts for Echinacea laevigata individuals and reproductive stems 102

Table 3.2 Summary of rare species found in the monitoring plots at PCDB 103

Table 3.3 Summary of exotic species found in the monitoring plots at PCDB...................... 104

Table 3.4 Overstory summary statistics based on measurements of all living trees reaching at least 9.5cm DBH in each plot 105

Table 3.5 Visual cover estimates of environmental data by subplot..................................... 106

Table 3.6 Full taxonomy and species codes used for the study of Picture Creek Diabase Barrens Echinacea laevigata monitoring plots 174

Table 4.1 Frequency and average cover of species by cluster 143

Table 4.2 Species indicator values (IndVals) 151

Table 4.3 Mean (and range) species richness and estimated tree cover for the 12 clusters representing Piedmont heliophilic vegetation 159

Table 4.4 Confusion matrix of USNVC Groups and clusters 183

LIST OF FIGURES

Figure 1.1 Representative elongate entire phytoliths from selected conifer species 22

Figure 1.2 Elongate sinuate phytolith morphotype found in *Pinus rigida* 23

Figure 1.3 Representative spheroid ornate phytoliths from selected conifer species 24

Figure 1.4 Spheroid ornate (white arrows) and fusiform ornate (black arrows) phytoliths seen together in partially combusted tissue sheets 25

Figure 1.5 Representative fusiform ornate phytoliths from selected conifer species 26

Figure 1.6 Representative blocky phytoliths from selected conifer species............................. 27

Figure 1.7 Representative prismatic psilate phytoliths from selected conifer species 28

Figure 1.8 Length of elongate entire phytolith morphotype by species 29

Figure 1.9 Length of spheroid ornate phytolith morphotype by species 30

Figure 1.10 Length of fusiform ornate phytolith morphotype by species 31

Figure 1.11 Length of prismatic psilates phytolith morphotype by species 32

Figure 1.12 Length of blocky phytolith morphotype by species 33

Figure 1.13 Length of elongate entire phytolith morphotype by genus...................................... 34

Figure 2.1 Location of the 1300 plots in the Virginia, North Carolina, and South Carolina Piedmont... 76

Figure 3.1 Locations of the five Picture Creek Glade (PCG) plots at Picture Creek Diabase Barrens.. 108

Figure 3.2 Figure from Lunsford (2002) showing layout of 0.1 ha plots with nested modules 109

Figure 3.3 Plot species richness by growth habit over time 110

Figure 3.4 NMDS ordination of plot-level species presence over three survey years............ 111

Figure 3.5 Trends in Piedmont prairie indicator species richness 112

Figure 3.6 Trends in habitat shade class associations of the herbaceous species found in PCDB monitoring plots.. 113

Figure 3.7 NMDS ordination of 1 m2 nested modules 114

Figure 3.8 NMDS ordination of 1 m2 nested modules for 2001 and 2018 suveys 115

Figure 3.9 Overstory summary statistics based on measurements of all living trees reaching at least 9.5cm DBH in each plot 116

Figure 3.10 Average total herbaceous cover of subplots 117

Figure 3.11 Photograph of PCG05 taken during the 2018 survey 182

Figure 4.1 NMDS Ordination 160

Figure 4.2 Stride for Flexbeta showing a peak in both measurements corresponding to 12 clusters 161

Figure 4.3 Hierarchical cluster (Flexible-beta, beta = -0.25) of the 12 clusters. 162

Figure 4.4 Geographic locations of the plots and their cluster membership 163

Figure 4.5 Shade class occurrences by cluster 164

Figure 4.6 Prairie indicator occurrences by cluster 165

Figure 4.7 Soil reaction classes of plots in each cluster 166

Figure 4.8 Elevation of plots in each cluster 167

CHAPTER 1: Phytoliths Produced by Eastern North American Conifers and Their Potential for Reconstructing Historical Vegetation of the Southeast

ABSTRACT

Paleoecological evidence and historical records suggest the southeastern Piedmont of North America once held a mosaic of open and forested vegetation. Pollen has typically been employed to examine deeper-time vegetation history, but this technique has had limited success in the eastern Piedmont region due to a general scarcity of suitable sites of pollen deposition and preservation. Other approaches are needed to corroborate existing interpretations of past regional vegetation history, to reveal the deeper-time history and extent of Piedmont open vegetation, and to examine past vegetation patterns at smaller scales. The chemical stability and generally autochthonous deposition of phytoliths, silica bodies produced in plant tissues and deposited into soil during decomposition, make them an ideal tool for examining vegetation history at local scales and in acidic upland soils such as those found in the southeastern Piedmont. We focus here on conifer phytoliths because conifers are important dominants of regional vegetation (current and past), and phytoliths have only been examined in about half of the conifers of eastern North America, including none of the southeastern species such as *Pinus palustris*. Our objectives were to 1) identify the different phytolith morphotypes produced by regional conifers (current and past), and 2) look for potential size differences for any phytolith morphotypes that are produced by multiple species. We sampled leaf material from 140 herbarium specimens representing 28 of the 32 species of conifers found in eastern North America, and extracted phytoliths through dry ashing. Over four thousand (n = 4004) phytoliths were imaged, measured, and assigned to morphotypes that follow ICPN v 2.0 naming conventions. We identified six different morphotypes present in our samples: elongate entire, elongate sinuate, spheroid ornate, fusiform ornate, blocky, and prismatic psilate. One common morphotype, elongate entire, was found to be unique to Pinaceae, among the conifers we analyzed. Elongate sinuate was only found in our samples of *Pinus rigida*, but it was very rare (n = 7). Simple length measurements of phytoliths were highly variable, overlapping in range, and generally unable to clearly differentiate morphotypes produced in multiple species. Probabilistic approaches and more detailed studies of surface morphology may be promising avenues of future study for differentiating conifer phytoliths of the region.

INTRODUCTION

Paleoecological evidence and historical records suggest the southeastern Piedmont of North America once held a mosaic of open and forested vegetation (Lederer 1670; De L'Isle 1718; Rostlund 1957; Juras 1997; Barone 2005). The name "Piedmont prairie" has become a popular term used to describe the occurrence of remnant flora with a Midwest prairie affinity found in the region (Barden 1997; Davis et al. 2002), although other types of open native vegetation, such as glades and savannas, are also recognized (Schafale 2012, Fleming and Patterson 2017). Most remnant Piedmont prairie sites presently occur in areas of high human impact, such as utility corridors and roadsides (Davis et al. 2002; Schmidt and Barnwell 2002; Benson 2011; Adams 2012; Stanley et al. 2019;). Given this relict distribution, the history of native prairie flora in the region is of great interest for understanding if these assemblages represent "ancient" grassland/woodland vegetation (Rackham 2008; Veldman et al. 2015) or more recent assemblages resulting from factors such as human-mediated dispersal (e.g., through the movement of soil for construction projects or propagules via mowers). Areas that could be shown to presently host or have once hosted ancient open vegetation would be priority targets for conservation, restoration, and paleoecological studies to understand landscape history. While approaches such as dendrochronology (Sigmon-Chatham 2015) are helping to reconstruct the more recent landscape history of specific Piedmont prairie remnant sites (past ~100 years), deeper-time vegetation history is still a challenge, and many questions remain about the historical extent, biogeographic history, and ecological dynamics of Piedmont open vegetation.

Pollen has been employed successfully to examine deeper-time vegetation history in the mountain and Coastal Plain provinces of the southeastern United States (Delcourt and Delcourt 1987), but there is no direct empirical pollen evidence regarding the historical character of the Piedmont flora for lack of natural lakes in the region. In fact, the sites used to reconstruct southeastern vegetation completely skirt the Piedmont east of the Appalachians (Delcourt and Delcourt 1987; Prentice 2001; Harrison 2017). Given the stark contrast of today's Piedmont vegetation from that of adjoining Coastal Plain and mountain physiographic regions, not to mention their differential geologic character (US EPA 2018), it is highly unlikely that the vegetation of all these regions, at any point since the last glaciation, would have been uniform. Then as today, given its complex geology, dissected nature, and topography, it is much more likely that the Piedmont exhibited vegetation types distinct from the adjoining physiographic provinces, vegetation whose signature could not possibly be captured through extra-provincial sampling. Because of these limitations, other approaches are needed to corroborate existing interpretations of past regional vegetation history and to reveal the deeper-time history and extent of Piedmont open vegetation, which was likely distributed at smaller scales and in areas unfavorable to pollen preservation.

Phytoliths—silica bodies produced in plant tissues and deposited into soil upon plant decomposition—have become an increasingly popular tool for reconstructing vegetation history of forest-grassland systems (e.g., Alexandré et al. 1997; Blinnikov et al. 2002; McCune et al. 2015). Although some phytoliths have been shown to be deposited far from their source, most phytoliths are not associated with plant reproduction and their deposition is thought to be more autochthonous than would be expected of a wind dispersed structure such as pollen (Piperno 2006). Their chemical resistance to acidic soil conditions and generally autochthonous deposition make them an ideal tool for examining vegetation history at local scales and in acidic upland soils, such as those found in the southeastern Piedmont.

We focus here on conifer phytoliths because conifers (especially *Pinus* spp.) are important components of the past (see Delcourt and Delcourt 1987) and present Piedmont landscape (see Schafale 2012), and at least some diagnostic phytoliths are already known to be produced in some conifers. For example, *Pseudotsuga* is known for its production of distinctive "asterosclereid" phytoliths that have proven informative in the studies of vegetation history of other regions (McCune and Pellatt 2013). Given the varied life history of conifers (various levels of shade intolerance, cold adaptation, fire adaptation, and soil moisture limitations; Burns and Honkala 1990), they are potentially useful in reconstructing vegetation patterns. For instance, *Pinus echinata* Mill. is an important component of remnant prairie-like and savanna-like plant communities in the Piedmont (Davis et al. 2002; Schafale 2012; Fleming and Patterson 2017). Its seeds require open conditions to germinate and the species is unable to recruit in closed canopy conditions (Burns and Honkala 1990). Being able to recognize this species in material recovered from soil cores would provide evidence of open conditions at the time corresponding to the sampled soil depth. The same would hold true for fire adapted *Pinus palustris* Mill., a foundation species of eastern Coastal Plain savannas (Peet and Allard 1993; Peet 2007), but whose distribution also includes some portions of the Piedmont (Parker 1998; Schafale 2012). Several species of pines (e.g., *P. banksiana* Lam.), as well as hemlocks (e.g., *Tsuga canadensis* (L.)

Carrière, *T. caroliniana* Engelm.), firs (e.g., *Abies balsamea* (L.) Mill., *A. fraseri* (Pursh) Poir.), and spruces (e.g., *Picea rubens* Sarg.) are currently restricted to colder climates (i.e., higher altitudes in the Southeast or higher latitudes in eastern North America; Adams 1993; Chambers 1993; Hunt 1993; Kral 1993; Michener 1993; Parker 1993; Taylor 1993a, b; Watson 1993). Being able to distinguish among these taxa in the Piedmont would provide empirical evidence of the timing and pattern of vegetation shifts in the province, currently an extrapolation from extra-provincial data. Given the persistence of geographically isolated populations of typically cooler climate taxa like *T. canadensis* in the far eastern Piedmont in North Carolina (Taylor 1993), the timing and pattern of shifts was likely much more complex than currently understood.

At present, there have been no comprehensive studies to assess the utility of phytoliths of eastern North American conifers in reconstructing vegetation history. Phytoliths have only been investigated in around half of the native eastern conifer species (Rovner 1971; Klein and Geis 1978; Kondo et al. 2002), with no sampling of regionally important species such as *Pinus echinata*, *P. palustris*, or *P. serotina*. We addressed this gap by extracting and analyzing the phytoliths of all southern pines (with the exception of *P. densa*), as well as northern conifers suspected to have been in the area based on inferences from the pollen record of adjoining regions. Our objectives were to 1) identify the different phytolith morphotypes produced by regional conifers; 2) quantitatively assess size differences for any phytolith morphotypes produced by multiple species; and 3) evaluate the potential utility of conifer phytoliths for distinguishing ecologically characteristic groups and species.

METHODS

We collected leaf samples from herbarium specimens of 28 different conifer species (Table 1.1), with five individuals sampled per species (140 total specimens sampled). These species either presently occur in southeastern North America or are believed to have once occurred in the region based on fossil pollen records (Delcourt and Delcourt 1987). Among native eastern conifers, only four species are not represented in our study: *Pinus densa* (Little and K.W. Dorman) Silba, *Taxus canadensis* Marshall, *T. floridana* Nutt. ex Chapm., and *Torreya taxifolia* Torrey. Mature leaf samples were harvested from herbarium specimens (Table 1.2) at the North Carolina State University Vascular Plant Herbarium (NCSC; Raleigh, North Carolina), or the University of North Carolina at Chapel Hill Herbarium (NCU; Chapel Hill, North

Carolina). Leaf samples were rinsed with DI water, dried, and combusted in a muffle furnace at 375°C for eight hours. We chose 375°C as the combustion temperature following tests at variable temperatures with dried material of well-documented phytolith-producing species (*Musa* L. sp. and *Zea mays* L.) and found this to be an ideal temperature for combustion of material without potential distortion of phytoliths. The resulting ashes were moved to storage vials and samples of the ashes were mounted on microscope slides with Permount (Fisher Scientific, Waltham, MA, USA). Slides were examined using an Olympus CX41 microscope and images were captured using a Lumenera INFINITY 2-2 camera. These images were captured in a transect starting from just off center of the slide and moving from left to right across the densest area of material. Photos were captured of each microscope view (400x) that contained recognizable phytoliths or phytolith-like objects, leading to approximately 5–30 images captured per sample. For slides with no recognizable phytolith objects, at least one representative image was still captured. Storage vials, slides, and images were deposited in the North Carolina State University Vascular Plant Herbarium (NCSC; Raleigh, North Carolina).

Measurements were taken using ImageJ version 1.52d (Abràmoff et al. 2004). Phytoliths were measured using a straight-line tool by tracing the longest axis of the morphotype. Each morphotype was named according to the International Code for Phytolith Nomenclature (ICPN) version 2.0 (Neumann et al. 2019). Statistical comparisons of morphotype measurements were conducted to assess potential differences between the same morphotypes produced in different species. The Shapiro-Wilk test was employed to assess the normality of the data and Levene's test was employed to assess if variance was equal for each morphotype dataset. Based on the results of these tests, we employed Welch's ANOVA followed by the Games-Howell test to assess significant difference in morphotype sizes between species. All statistical analyses were performed in JMP Pro 14.0.0 (SAS Institute Inc., Cary, NC). The Games-Howell test was performed using a community add-in (https://community.jmp.com/t5/JMP-Add-Ins/Games-Howell-Test-Tukey-HSD-with-Welch-s-correction-for-Unequal/ta-p/213771#).

RESULTS

We identified phytoliths in 27 of the 28 conifer species. No recognizable phytoliths were recovered from any specimens of *Taxodium ascendens* Brongn. We measured 4004 phytolith objects and identified six distinct morphotypes among them (Table 1.2). The most common morphotype encountered was elongate entire (ELO_ENT), which composed 40% (1604/4004) of all phytoliths. Spheroid Ornate (SPH_ORN) was the second most common morphotype, comprising 39% (1559/4004) of the total. Uncommon and rare morphotypes were fusiform ornate (FUS_ORN; 14%; 577/4004), prismatic psilate (PRI_PSI; 4%; 169/4004), blocky (BLO; 2%; 88/4004), and elongate sinuate (ELO_SIN; <1%; 7/4004).

ELO_ENT are longer than wide (usually more than 2x longer) with generally straight sides (in profile) and resemble a long tube or thin rectangle (Figure 1.1). One or both ends are often angled or tapered. This type was found in all members of Pinaceae and is exclusive to that family among the conifers we examined (22 species total; Table 1.3). ELO_SIN is similar in appearance to elongate entire but has a sinuate (wavy) margin (Figure 1.2). This type was only recovered from *Pinus rigida* Mill. and was very rare (only seven encountered). SPH_ORN phytoliths are spherical in shape with some surface ornamentation, usually rounded protuberances (Figure 1.3). Phytoliths of this morphotype were sometimes found as part of partially combusted sheets of tissue, where they usually occurred in a matrix with FUS_ORN (Figure 1.4). The SPH_ORN morphotype was found in all species examined except *Pinus banksiana*. The FUS_ORN morphotype is a cylindrical or spherical shape that tapers toward a point at one or (usually) both ends, and it often has variable surface protuberances similar to those seen on SPH_ORN phytoliths (Figure 1.5). The FUS_ORN morphotype was restricted to members of Pinaceae in our study, where it was primarily found in species of *Pinus*, although rarely also in *Larix laricina* (Du Roi) K. Koch, *Picea* A. Dietr., and *Tsuga canadensis*. The BLO morphotype has angular sides and resembles a polyhedron (Figure 1.6). It can be nearly cubic or highly multi-faceted and was found in *Abies* Mill., *Larix laricina*, *Picea*, six species of *Pinus*, and both species of *Tsuga* (Endl.) Carrière. It was most frequent in species of *Picea* and generally rare in other genera. The PRI_PSI morphotype resembles a cubic crystal and is square to slightly rectangular in profile (Figure 1.7). Despite their crystalline appearance (a character atypical of silica phytoliths), PRI_PSI phytoliths clearly originate from within plant tissues and are resistant to the application of HCl (suggesting they are not calcium oxalate crystals). They were especially notable in *Pinus strobus* L., where they were found in masses of only partially combusted tissue (Figure 1.7). Statistical analyses showed overlap in the measured lengths of phytolith morphotypes produced by multiple species and no clear distinction between species (Table 1.4 and Figures 1.8–1.12).

DISCUSSION

Morphotypes

ELO_ENT and ELO_SIN are known and accepted morphotypes in ICPN v2.0. The ELO_ENT morphotype we found in our conifer specimens is likely synonymous with the "tabular elongate unsculpted" morphotype identified in An (2016). In general, the elongate morphotypes are common among land plants and generally thought to have little diagnostic potential (Neumann et al. 2019). However, An (2016) was able to distinguish among some common elongate morphotypes found in both conifers and grasses by careful study of features such as surface morphology and cross-section shape. It is also possible that some of the elongate morphotypes encountered in this study are actually casts of tracheary elements, and they may be more appropriately named as such (Klein and Geis 1978; Neumann et al. 2019). ICPN v2.0 recognizes multiple types of tracheary morphotypes, of which the TRACHEARY BORDERED morphotype is thought to be diagnostic of conifers and Gnetales (Neumann et al. 2019). The tracheary morphotypes are distinguished from the more general elongate morphotypes by the presence of surface ridges or pits indicative of their origin as silica casts of tracheary elements (Neumann et al. 2019). Studies of these samples with higher magnification, such as available in SEM, could allow for this possibility to be explored.

BLO is another morphotype recognized in ICPN v2.0 and is well-known to occur in conifers, although it also occurs in other plant groups (Neumann et al. 2019). The current concept of the BLO morphotype is quite broad and encompasses both many-faceted polyhedral morphotypes as well as cubic morphotypes. Klein and Geis (1978) described them as "epidermal cells" and found them to be the most abundant morphotype observed in their study. They state "[s]everal distinct morphologies are present," and describe a variety of sizes, dimensions, and surface features (e.g., undulating and smooth). An (2016) described a "blocky and cubic" morphotype and indicated it was synonymous with the Klein and Geis (1978) epidermal cell. We frequently encountered cubic BLO phytoliths that were highly regular and square in profile. These cubic morphotypes were especially abundant in *P. strobus,* and we chose to recognize them as a unique type, PRI_PSI, instead of lumping them into the heterogeneous BLO. The BLO we recognize are all relatively large (11–98 µm, mean = 37 µm) and polyhedral, with a non-square profile. The PRI_PSI we recognize are smaller (2–16 µm, mean = 7 µm) and cubic, with a square or slightly rectangular profile.

SPH_ORN is also an accepted morphotype in ICPN v 2.0 known to occur in a variety of plant groups (Neumann et al. 2019) but does not seem to be well documented as occurring within conifers. The SPH_ORN we recognize are likely synonymous with the “globules” described in Rovner (1977). We frequently found this morphotype in association with FUS_ORN, a morphotype that is possibly synonymous with the “cylindric echinate” form described by An (2016). While An (2016) only encountered cylindric echinates in *Larix kaempferi* (Lamb.) Carr. among the Asian conifer species studied, we encountered FUS_ORN more broadly in eastern North American Pinaceae. Our observations of the close association of SPH_ORN and FUS_ORN in partially combusted sheets of tissue suggest they share an anatomical origin (Figure 1.4). Additional studies of fresh material could give insight into the anatomical origins of the SPH_ORN and FUS_ORN morphotypes.

Prospects for historical reconstruction

While we found ELO_SIN to be apparently restricted to *Pinus rigida* among the species we sampled, this morphotype was very rare, and it is not clear how variable it is or how useful it would be for historical reconstruction. ELO_ENT, a far more common morphotype that was restricted to Pinaceae, shows some promise for paleoecological studies in the region. For example, the appearance of ELO_ENT in conjunction with grass phytoliths in ancient soil samples could be used to explore the past distribution of pine savannas in the southeastern Piedmont. The next step would be to sample other vegetation in the region to confirm if the ELO_ENT morphotype is unique to regional Pinaceae. As An (2016) demonstrated with Asian taxa, careful study of surface and cross-sectional features can be used to differentiate morphotypes produced in both conifers and grasses, so this is a promising avenue of future study. Unique phytolith morphotypes to distinguish important prairie/savanna species such as *Pinus echinata* from other eastern North American conifers were lacking, but additional studies of the FUS_ORN morphotype may be worthwhile. The FUS_ORN morphotype was common among southeastern *Pinus* spp. and may have variability in surface projections. We recommend further examination of this morphotype with higher magnification.

Although we were unable to clearly differentiate morphotypes produced by multiple conifer species based on simple size measurements, other approaches still have potential to solve this issue. One possibility could be to analyze the measurements through a probabilistic approach such as a Bayesian classifier (Tyrrell 2019), which may be better able to differentiate measurements otherwise found to be not significantly different through other statistical approaches. It is also possible overall morphotype size is simply too variable to be a discriminating measurement. Kondo et al. (2002) saw some success differentiating *Pinus*, *Picea*, and *Abies* based on measurements of bordered pits on the surfaces of tracheid phytoliths, so an approach using higher magnification and examining more specific morphotype features is warranted.

Conclusions

This work provides a robust sampling of phytoliths produced by eastern conifer species, the first to include nearly all (28/32) species found in the region. These samples will serve as a phytolith reference collection for future work to reconstruct vegetation history of the Piedmont. While we were unable to clearly differentiate redundant morphotypes produced by multiple conifer species based on overall size measurements, more detailed study of surface features using approaches beyond light microscopy is a promising avenue for future study.

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TABLES

Table 1.1: Overview of the 28 species of conifers sampled for phytoliths. All presently occur in southeastern North America or are thought to have occurred in the region in the past based on paleobotanical evidence.

Family	**Species**	**Present Range**
Cupressaceae	*Chamaecyparis thyoides* (L.) Britton, Sterns & Poggenb.	Atlantic Coast
Cupressaceae	*Juniperus communis* Thunb.	Circumboreal
Cupressaceae	*Juniperus virginiana* L.	E NA
Cupressaceae	*Taxodium ascendens* Brongn.	SE NA
Cupressaceae	*Taxodium distichum* (L.) Rich.	SE NA
Cupressaceae	*Thuja occidentalis* L.	N & NE NA, Canada
Pinaceae	*Abies balsamea* (L.) Mill.	N NA, Canada
Pinaceae	*Abies fraseri* (Pursh) Poir.	SE, Appalachian Mtns endemic
Pinaceae	*Larix laricina* (Du Roi) K. Koch	N NA, Canada
Pinaceae	*Picea glauca* (Moench) Voss	N NA, Canada
Pinaceae	*Picea mariana* (Mill.) Britton, Sterns & Poggenb.	N NA, Canada
Pinaceae	*Picea pungens* Engelm.	W & N NA
Pinaceae	*Picea rubens* Sarg.	NE NA, Appalachian Mtns
Pinaceae	*Pinus banksiana* Lamb.	N NA (mostly Canada)
Pinaceae	*Pinus clausa* (Chapm. ex Engelm.) Sarg.	SE endemic, primarily Florida
Pinaceae	*Pinus echinata* Mill.	E-SE NA
Pinaceae	*Pinus elliottii* Engelm.	SE NA
Pinaceae	*Pinus glabra* Walter	SE-S NA
Pinaceae	*Pinus palustris* Mill.	SE NA
Pinaceae	*Pinus pungens* Lamb.	Appalachian Mtns
Pinaceae	*Pinus resinosa* Aiton	N NA (mostly Canada)
Pinaceae	*Pinus rigida* Mill.	NE NA, Appalachian Mtns
Pinaceae	*Pinus serotina* Michx.	Atlantic Coastal Plain
Pinaceae	*Pinus strobus* L.	N & NE NA, Appalachian Mtns
Pinaceae	*Pinus taeda* L.	SE NA
Pinaceae	*Pinus virginiana* Mill.	E NA, mostly Appalachian Mtns
Pinaceae	*Tsuga canadensis* (L.) Carrière	N & NE NA, Canada
Pinaceae	*Tsuga caroliniana* Engelm.	SE, Appalachian Mtns endemic

Table 1.2: Details of the 140 herbarium specimens sampled for phytoliths.

Species	Herbarium	Collector(s)	Collector #	State/Province
Abies balsamea	NCSC	H E Ahles	86452	Massachusetts
Abies balsamea	NCSC	J W Moore	10736	Minnesota
Abies balsamea	NCSC	M F Buell	1800	Minnesota
Abies balsamea	NCSC	R M Downs	2308	Maine
Abies balsamea	NCSC	W Deane	s.n.	Maine
Abies fraseri	NCSC	A B Russell	2291	North Carolina
Abies fraseri	NCSC	J W Hardin	13922	North Carolina
Abies fraseri	NCSC	R M Downs	11286	North Carolina
Abies fraseri	NCSC	W B Fox	818	North Carolina
Abies fraseri	NCSC	W B Fox	998	North Carolina
Chamaecyparis thyoides	NCSC	C D Ware	18	Virginia
Chamaecyparis thyoides	NCSC	G L Nesom	941	South Carolina
Chamaecyparis thyoides	NCSC	J M Lynch	62	South Carolina
Chamaecyparis thyoides	NCSC	L J Musselman	s.n.	Virginia
Chamaecyparis thyoides	NCSC	V C Matthews	s.n.	South Carolina
Juniperus communis	NCSC	A P Anderson	1948	North Carolina
Juniperus communis	NCSC	J M Lynch	154	North Carolina
Juniperus communis	NCSC	J W Hardin	996	North Carolina
Juniperus communis	NCSC	W B Fox	1234	North Carolina
Juniperus communis	NCSC	W B Fox	666	North Carolina
Juniperus virginiana	NCSC	A Herford	s.n.	North Carolina
Juniperus virginiana	NCSC	V Cooper, M Lee, & E M Croom, Jr.	360	North Carolina
Juniperus virginiana	NCSC	F R Fosberg	17903	North Carolina
Juniperus virginiana	NCSC	O Veerhoff	352	North Carolina
Juniperus virginiana	NCSC	S W Bowers	71628	North Carolina
Larix laricina	NCSC	H E Ahles	82364	Massachusetts
Larix laricina	NCSC	J W Moore	11226	Minnesota
Larix laricina	NCSC	M F Buell	1798	Minnesota
Larix laricina	NCSC	M F Buell	656	Minnesota
Larix laricina	NCSC	R M Downs	2309	Maine
Picea glauca	NCSC	H F Buell	1725	Montana
Picea glauca	NCSC	J W Moore	10731	Minnesota
Picea glauca	NCU	L Jenkins	8224	Quebec
Picea glauca	NCU	S R Hill	17230	Maine
Picea glauca	NCSC	W Deane	s.n.	Maine
Picea mariana	NCSC	J W Moore	11219	Minnesota
Picea mariana	NCSC	J W Moore	18323	Minnesota
Picea mariana	NCU	L Jenkins	5455	Ontario

Table 1.2: (Continued).

Picea mariana	NCSC	M F Buell	1677	Minnesota
Picea mariana	NCSC	C A Weatherby	2609	Connecticut
Picea pungens	NCU	C S Johnson	138	Ohio
Picea pungens	NCU	Halverson	184	Arizona
Picea pungens	NCU	Thieret & Brandenburg	55223	Colorado
Picea pungens	NCSC	W A Weber	s.n.	Colorado
Picea pungens	NCU	W Hess	2389	New Mexico
Picea rubens	NCSC	A B Russell	1239	North Carolina
Picea rubens	NCSC	A B Russell	1915	North Carolina
Picea rubens	NCSC	J W Hardin	13208	North Carolina
Picea rubens	NCSC	R M Downs	11435	North Carolina
Picea rubens	NCSC	R M Downs	2313	Maine
Pinus banksiana	NCSC	A S Pease	19637	Nova Scotia
Pinus banksiana	NCSC	H E Ahles	86430A	Massachusetts
Pinus banksiana	NCSC	F H Sargent	s.n.	Quebec
Pinus banksiana	NCSC	M L Peterson	3821	New Hampshire
Pinus banksiana	NCSC	R Kral	3359	Indiana
Pinus clausa	NCSC	A S Rhoads	s.n.	Florida
Pinus clausa	NCSC	C C Deam	63939	Florida
Pinus clausa	NCSC	C C Deam	64374	Florida
Pinus clausa	NCSC	T Shuff	s.n.	Florida
Pinus clausa	NCSC	X M Gaines	291	Alabama
Pinus echinata	NCSC	A W Cooper	2816	North Carolina
Pinus echinata	NCSC	E C Swab	642	North Carolina
Pinus echinata	NCSC	G S Hartshorn	354	North Carolina
Pinus echinata	NCSC	J Slapcinsky	700	North Carolina
Pinus echinata	NCSC	S L Corda	143	North Carolina
Pinus elliottii	NCU	D Demaree	34143	Mississippi
Pinus elliottii	NCSC	X M Gaines	300	Alabama
Pinus elliottii	NCSC	H M Curran	s.n.	North Carolina
Pinus elliottii	NCSC	T Shuff	s.n.	Florida
Pinus elliottii	NCSC	W B Fox	5711	Florida
Pinus glabra	NCSC	J C Barber	s.n.	South Carolina
Pinus glabra	NCSC	J H Beaman	345	Florida
Pinus glabra	NCSC	R Kral	1779	Florida
Pinus glabra	NCSC	R K Godfrey	52864	Florida
Pinus glabra	NCSC	S B Jones	16332	Mississippi
Pinus palustris	NCSC	A E Blair	851	North Carolina
Pinus palustris	NCSC	D M DuMond	450	North Carolina

Table 1.2: (Continued).

Pinus palustris	NCSC	V Cooper & E M Croom, Jr.	76	North Carolina
Pinus palustris	NCSC	L J Musselman	4837	North Carolina
Pinus palustris	NCSC	R M Downs	11941	North Carolina
Pinus pungens	NCSC	W M Brewster	s.n.	North Carolina
Pinus pungens	NCSC	D M DuMond	1725	North Carolina
Pinus pungens	NCSC	J W Hardin	13935	North Carolina
Pinus pungens	NCSC	M A Mulkey	s.n.	North Carolina
Pinus pungens	NCSC	W B Fox	713	North Carolina
Pinus resinosa	NCSC	J W Moore	10725	Minnesota
Pinus resinosa	NCSC	J W Moore	19008	Minnesota
Pinus resinosa	NCSC	J W Moore	10725	Minnesota
Pinus resinosa	NCSC	M A Berdine	83-3	West Virginia
Pinus resinosa	NCSC	W Deane	s.n.	New Hampshire
Pinus rigida	NCSC	A P Anderson	1887	North Carolina
Pinus rigida	NCSC	D M DuMond	1726	North Carolina
Pinus rigida	NCSC	J W Hardin	13925	North Carolina
Pinus rigida	NCSC	W B Fox	1245	North Carolina
Pinus rigida	NCSC	W B Fox	871	North Carolina
Pinus serotina	NCSC	A E Blair	1035	North Carolina
Pinus serotina	NCSC	N Howell	SILA-37	North Carolina
Pinus serotina	NCSC	P Smouse	201	North Carolina
Pinus serotina	NCSC	R L Wilbur	3968	North Carolina
Pinus serotina	NCSC	W B Fox	383	North Carolina
Pinus strobus	NCSC	D M DuMond	747	North Carolina
Pinus strobus	NCSC	L Smith	396	North Carolina
Pinus strobus	NCSC	R M Downs	12017	North Carolina
Pinus strobus	NCSC	W B Fox	894	North Carolina
Pinus strobus	NCSC	R M Downs	12663	North Carolina
Pinus taeda	NCSC	E Scherrer	99-096	North Carolina
Pinus taeda	NCSC	N Howell	SILA-12	North Carolina
Pinus taeda	NCSC	R M Downs	11743	North Carolina
Pinus taeda	NCSC	R R Hill, Jr	s.n.	North Carolina
Pinus taeda	NCSC	S L Corda	6	North Carolina
Pinus virginiana	NCSC	D M DuMond	1170	South Carolina
Pinus virginiana	NCSC	G P Johnson	994	Kentucky
Pinus virginiana	NCSC	L Smith	394	North Carolina
Pinus virginiana	NCSC	R L Wilbur	3631	North Carolina
Pinus virginiana	NCSC	W H Duncan	3874	Georgia
Taxodium ascendens	NCSC	B W Wells	s.n.	North Carolina

Table 1.2: (Continued).

Taxodium ascendens	NCSC	N Howell	LAWA-13	North Carolina
Taxodium ascendens	NCSC	N Howell	LISI-4	North Carolina
Taxodium ascendens	NCSC	N Howell	SALA-8	North Carolina
Taxodium ascendens	NCSC	B W Wells	s.n.	North Carolina
Taxodium districhum	NCSC	E O Beal	1772	North Carolina
Taxodium districhum	NCSC	F D Watson	1238	North Carolina
Taxodium districhum	NCSC	F D Watson	1303	North Carolina
Taxodium districhum	NCSC	L A Whitford	1956	North Carolina
Taxodium districhum	NCSC	S L Corda	38	North Carolina
Thuja occidentalis	NCSC	A T Hotchkiss	78-10-28-1	Kentucky
Thuja occidentalis	NCSC	D W Suiter	95	West Virginia
Thuja occidentalis	NCSC	J K Small	s.n.	West Virginia
Thuja occidentalis	NCSC	J W Hardin	13656	North Carolina
Thuja occidentalis	NCSC	W B Fox	2476	Virginia
Tsuga canadensis	NCSC	D M DuMond	843	North Carolina
Tsuga canadensis	NCSC	J B Taggart	33	North Carolina
Tsuga canadensis	NCSC	J W Hardin	13904	North Carolina
Tsuga canadensis	NCSC	R M Downs	11342	North Carolina
Tsuga canadensis	NCSC	R M Downs	12585	North Carolina
Tsuga caroliniana	NCSC	D M DuMond	903	North Carolina
Tsuga caroliniana	NCSC	E T Wherry	s.n.	North Carolina
Tsuga caroliniana	NCSC	J W Hardin	13896	North Carolina
Tsuga caroliniana	NCSC	R M Downs	11341	North Carolina
Tsuga caroliniana	NCSC	R M Downs	407	North Carolina

Table 1.3: Summary of the total number of phytoliths and the different phytolith morphotypes found in each species. The Morphotypes column lists the different phytolith morphotypes found in each species. The Phytoliths column indicates the total number of phytolith objects measured per species.

Species	**Morphotype #**	**Phytoliths**	**Morphotypes**
Abies balsamea	4	154	Blocky (BLO) Elongate Entire (ELO_ENT) Prismatic Psilate (PRI_PSI) Spheroid Ornate (SPH_ORN)
Abies fraseri	3	222	Blocky (BLO) Elongate Entire (ELO_ENT) Spheroid Ornate (SPH_ORN)
Chamaecyparis thyoides	1	16	Spheroid Ornate (SPH_ORN)
Juniperus communis	1	23	Spheroid Ornate (SPH_ORN)
Juniperus virginiana	1	167	Spheroid Ornate (SPH_ORN)
Larix laricina	5	110	Blocky (BLO) Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Prismatic Psilate (PRI_PSI) Spheroid Ornate (SPH_ORN)
Picea glauca	4	163	Blocky (BLO) Elongate Entire (ELO_ENT) Prismatic Psilate (PRI_PSI) Spheroid Ornate (SPH_ORN)
Picea mariana	4	107	Blocky (BLO) Elongate Entire (ELO_ENT) Prismatic Psilate (PRI_PSI) Spheroid Ornate (SPH_ORN)
Picea pungens	5	186	Blocky (BLO) Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Prismatic Psilate (PRI_PSI) Spheroid Ornate (SPH_ORN)
Picea rubens	4	65	Blocky (BLO) Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)
Pinus banksiana	4	71	Blocky (BLO) Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Prismatic Psilate (PRI_PSI)
Pinus clausa	3	57	Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)
Pinus echinata	4	521	Blocky (BLO) Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)
Pinus elliottii	3	213	Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)
Pinus glabra	3	319	Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)

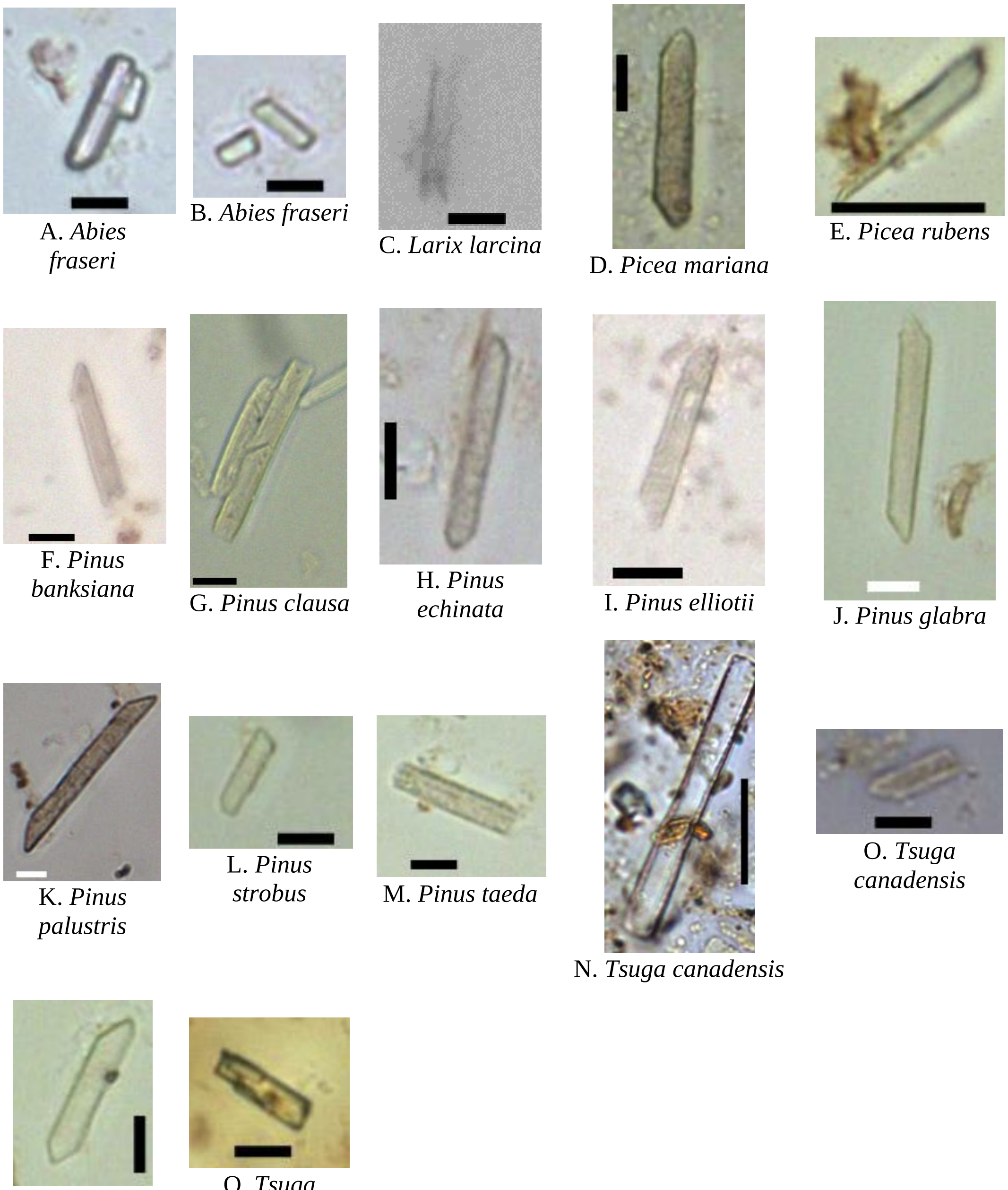
Table 1.3: (Continued).

Pinus palustris	3	414	Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)
Pinus pungens	3	56	Elongate Entire (ELO_ENT) Prismatic Psilate (PRI_PSI) Spheroid Ornate (SPH_ORN)
Pinus resinosa	4	121	Blocky (BLO) Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)
Pinus rigida	3	168	Elongate Entire (ELO_ENT) Elongate Sinuate (ELO_SIN) Spheroid Ornate (SPH_ORN)
Pinus serotina	4	62	Blocky (BLO) Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)
Pinus strobus	5	103	Blocky (BLO) Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Prismatic Psilate (PRI_PSI) Spheroid Ornate (SPH_ORN)
Pinus taeda	3	506	Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)
Pinus virginiana	4	88	Blocky (BLO) Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)
Taxodium ascendens	0	0	None
Taxodium distichum	2	14	Prismatic Psilate (PRI_PSI) Spheroid Ornate (SPH_ORN)
Thuja occidentalis	1	11	Spheroid Ornate (SPH_ORN)
Tsuga canadensis	4	47	Blocky (BLO) Elongate Entire (ELO_ENT) Fusiform Ornate (FUS_ORN) Spheroid Ornate (SPH_ORN)
Tsuga caroliniana	3	20	Blocky (BLO) Elongate Entire (ELO_ENT) Spheroid Ornate (SPH_ORN)
Totals	6 unique	4004	

Table 1.4: Mean length (µm) and standard deviation for phytolith morphotypes measured in 27 species of eastern conifers. The ELO_SIN morphotype was only found in *Pinus rigida* and is excluded from this table.

Species	**BLO**		**ELO_ENT**		**FUS_ORN**		**PRI_PSI**		**SPH_ORN**	
	x̄	*s*	x̄	*s*	x̄	*s*	x̄	*s*	x̄	*s*
Abies balsamea	20.3	n<2	12.5	8.3	.	.	5.9	0.9	8.3	3.2
Abies fraseri	27.1	n<2	12.9	6.5	.	.	.	.	7.4	2.6
Chamaecyparis thyoides	.	.	.	.	.	.	.	.	4.8	2.2
Juniperus communis	.	.	.	.	.	.	.	.	3.8	1.3
Juniperus virginiana	.	.	.	.	.	.	.	.	5.9	2.7
Larix laricina	44.2	19.0	16.1	6.7	19.9	n<2	6.3	1.8	7.0	2.3
Picea glauca	31.4	12.8	45.9	30.1	.	.	7.3	1.3	5.8	1.7
Picea mariana	36.1	12.5	16.9	7.8	.	.	7.5	1.7	5.5	1.9
Picea pungens	32.5	76.0	12.9	4.5	15.2	19.0	8.8	1.6	5.7	2.0
Picea rubens	35.8	18.9	14.0	5.9	12.3	37.0	.	.	8.5	3.9
Pinus banksiana	50.9	30.7	19.9	6.8	21.6	41.0	13.5	n<2	.	.
Pinus clausa	.	.	21.8	8.2	23.3	31.0	.	.	11.0	3.0
Pinus echinata	29.2	n<2	21.0	7.3	27.7	68.0	.	.	10.1	2.1
Pinus elliottii	.	.	19.3	6.6	19.2	33.0	.	.	11.2	4.8
Pinus glabra	.	.	25.5	9.2	26.5	69.0	.	.	10.7	2.1
Pinus palustris	.	.	24.6	12.7	22.0	56.0	.	.	10.5	2.6
Pinus pungens	.	.	25.3	9.8	.	.	9.3	.	9.7	2.8
Pinus resinosa	43.8	21.2	23.8	8.7	12.8	35.0	.	.	11.1	1.8
Pinus rigida	.	.	23.3	7.0	.	.	.	.	11.4	2.1
Pinus serotina	53.4	13.9	20.2	11.4	15.0	36.0	.	.	9.3	1.5
Pinus strobus	44.0	55.0	13.9	3.4	14.2	15.0	8.0	2.5	12.0	3.6
Pinus taeda	.	.	21.1	9.0	25.1	60.0	.	.	9.9	2.3
Pinus virginiana	48.4	27.5	16.2	5.2	19.7	30.0	.	.	15.0	7.4
Taxodium distichum	.	.	.	.	.	.	10.3	n<2	6.8	2.1
Thuja occidentalis	.	.	.	.	.	.	.	.	7.0	2.1
Tsuga canadensis	20.8	n<2	29.0	16.6	30.0	13.8	.	.	7.5	2.4
Tsuga caroliniana	21.6	10.1	18.3	5.4	.	.	.	.	6.9	2.5

FIGURES



A. *Abies fraseri*

B. *Abies fraseri*

C. *Larix larcina*

D. *Picea mariana*

E. *Picea rubens*

F. *Pinus banksiana*

G. *Pinus clausa*

H. *Pinus echinata*

I. *Pinus elliotii*

J. *Pinus glabra*

K. *Pinus palustris*

L. *Pinus strobus*

M. *Pinus taeda*

N. *Tsuga canadensis*

O. *Tsuga canadensis*

P. *Tsuga caroliniana*

Q. *Tsuga caroliniana*

Figure 1.1: Representative elongate entire (ELO_ENT) phytoliths from selected conifer species. Scale bars in E and N indicate 30 µm; all other scale bars indicate 10 µm. Photo C captured by Athena Giavasis.

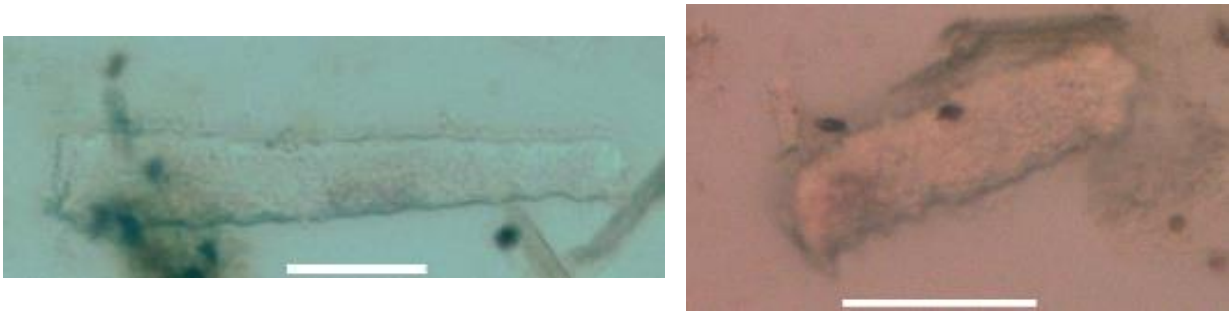
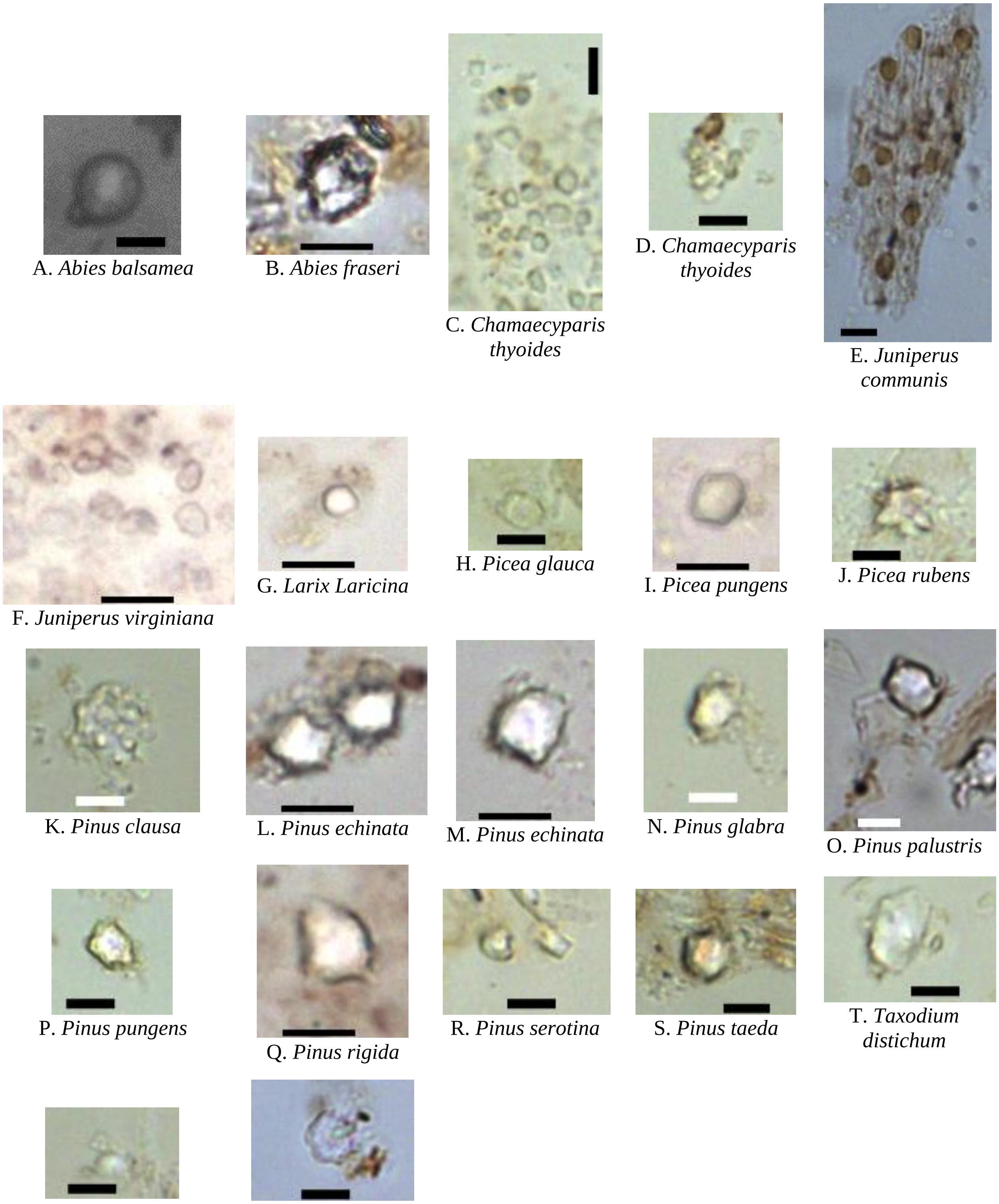
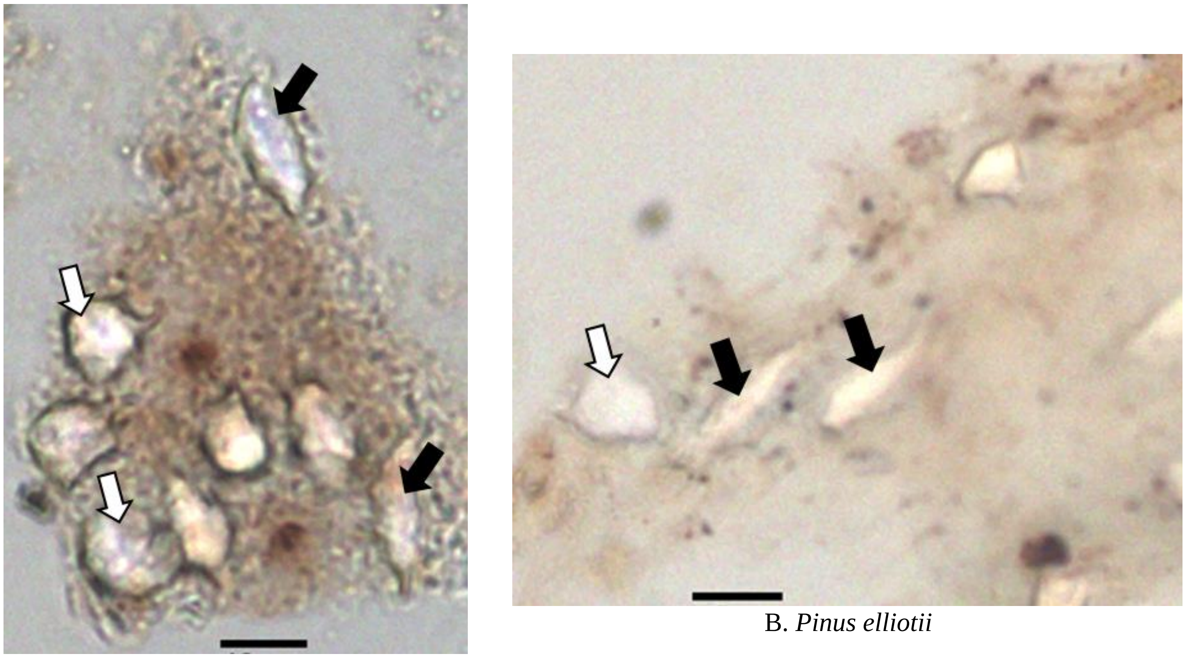


Figure 1.2: Elongate sinuate (ELO_SIN) phytolith morphotype found in *Pinus rigida*. Scale bars indicate 30 µm. Photos captured by Athena Giavasis.



A. *Abies balsamea*
B. *Abies fraseri*
C. *Chamaecyparis thyoides*
D. *Chamaecyparis thyoides*
E. *Juniperus communis*
F. *Juniperus virginiana*
G. *Larix Laricina*
H. *Picea glauca*
I. *Picea pungens*
J. *Picea rubens*
K. *Pinus clausa*
L. *Pinus echinata*
M. *Pinus echinata*
N. *Pinus glabra*
O. *Pinus palustris*
P. *Pinus pungens*
Q. *Pinus rigida*
R. *Pinus serotina*
S. *Pinus taeda*
T. *Taxodium distichum*
U. *Thuja occidentalis*
V. *Tsuga canadensis*

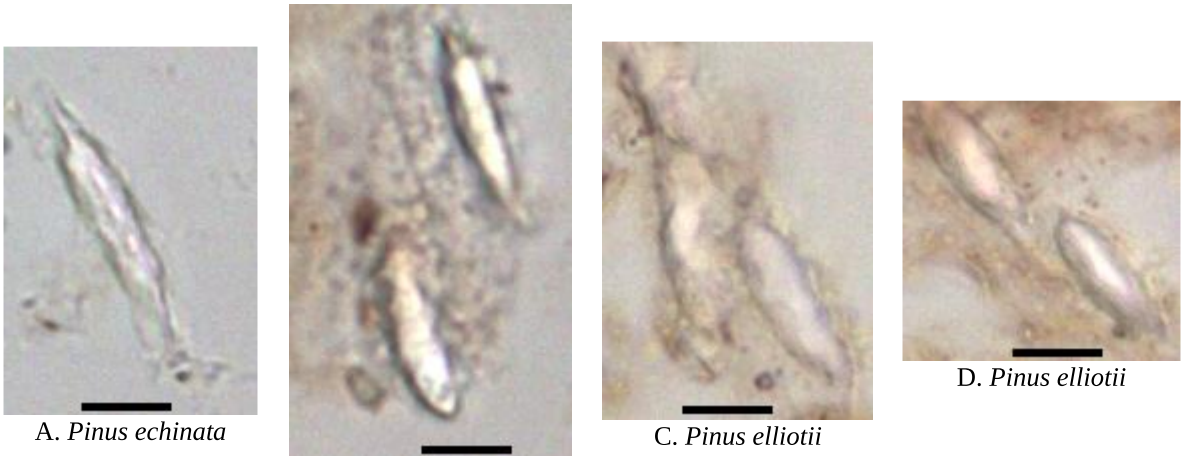
Figure 1.3: Representative spheroid ornate (SPH_ORN) phytoliths from selected conifer species. All scale bars indicate 10 µm. Photo A captured by Athena Giavasis.



B. *Pinus elliotii*

A. *Pinus echinata*

Figure 1.4: Spheroid ornate (white arrows) and fusiform ornate (black arrows) phytoliths seen together in partially combusted tissue sheets. Scale bars indicate 10 µm.

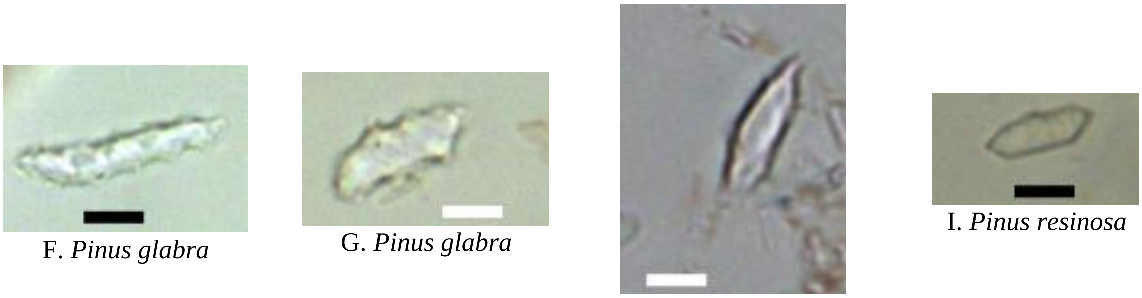


A. *Pinus echinata*

B. *Pinus echinata*

C. *Pinus elliotii*

D. *Pinus elliotii*



F. *Pinus glabra*

G. *Pinus glabra*

H. *Pinus palustris*

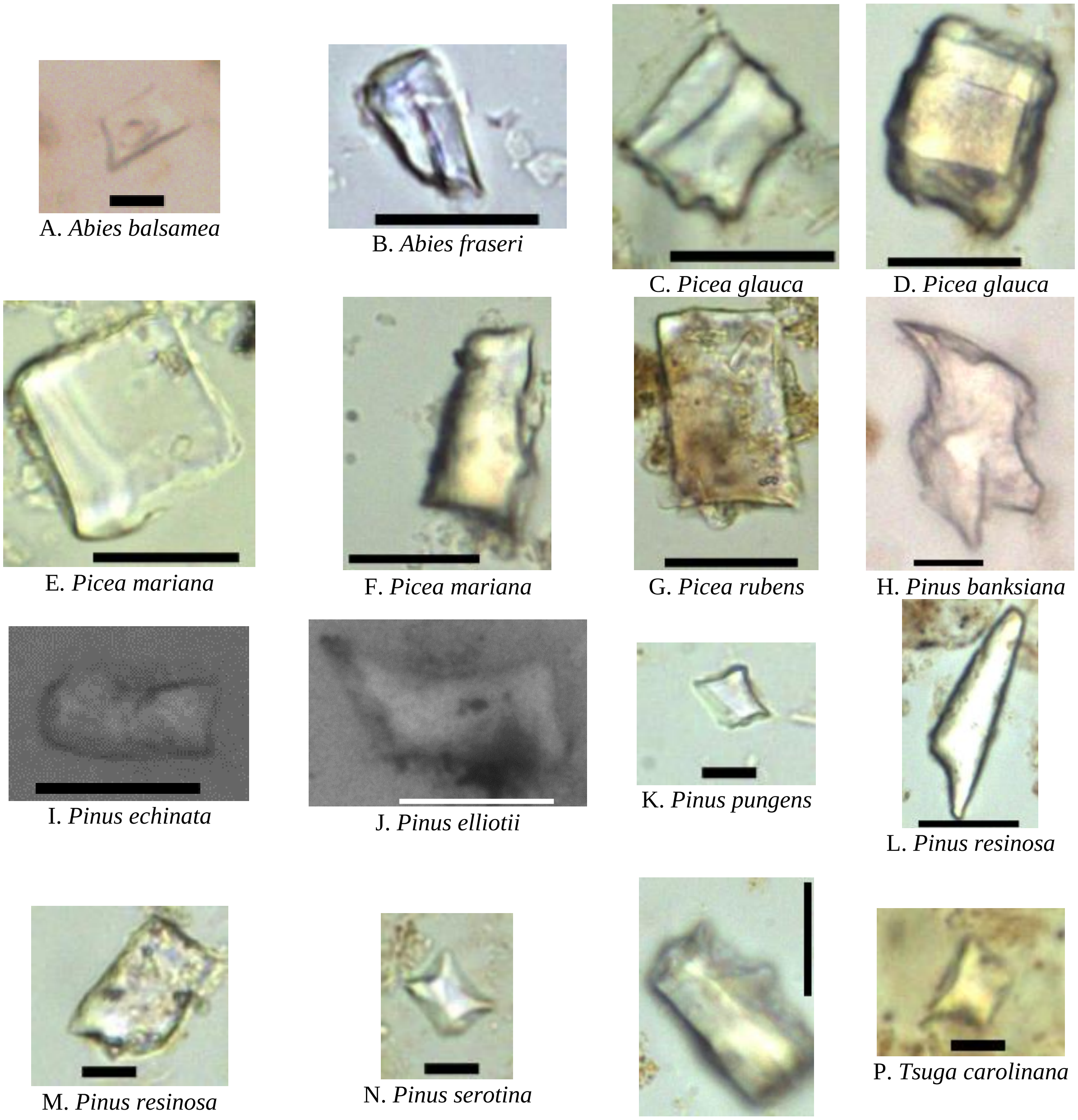
I. *Pinus resinosa*

J. *Pinus taeda*

K. *Pinus virginiana*

L. *Tsuga canadensis*

Figure 1.5: Representative fusiform ornate phytoliths from selected conifer species. All scale bars indicate 10 µm.



A. *Abies balsamea*

B. *Abies fraseri*

C. *Picea glauca*

D. *Picea glauca*

E. *Picea mariana*

F. *Picea mariana*

G. *Picea rubens*

H. *Pinus banksiana*

I. *Pinus echinata*

J. *Pinus elliotii*

K. *Pinus pungens*

L. *Pinus resinosa*

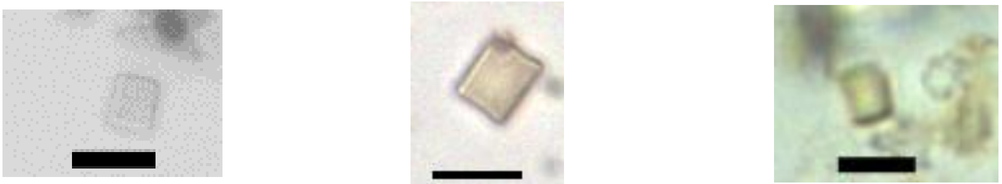
M. *Pinus resinosa*

N. *Pinus serotina*

O. *Pinus strobus*

P. *Tsuga carolinana*

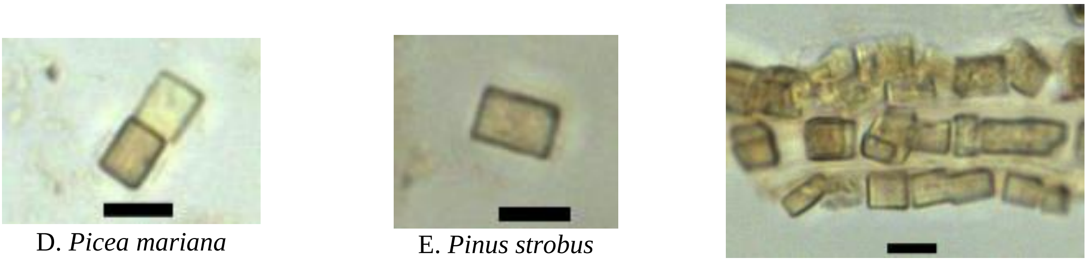
Figure 1.6: Representative blocky (BLO) phytoliths from selected conifer species. Scale bars in A, H, K, M, N, and P indicate 10 µm. All other scale bars indicate 30 µm. Photos A, I, and J captured by Athena Giavasis.



A. *Abies balsamea* (A)

B. *Larix laricina*

C. *Picea glauca*



D. *Picea mariana*

E. *Pinus strobus*

F. *Pinus strobus*

Figure 1.7: Representative prismatic psilate (PRI_PSI) phytoliths from selected conifer species. All scale bars indicate 10 µm.

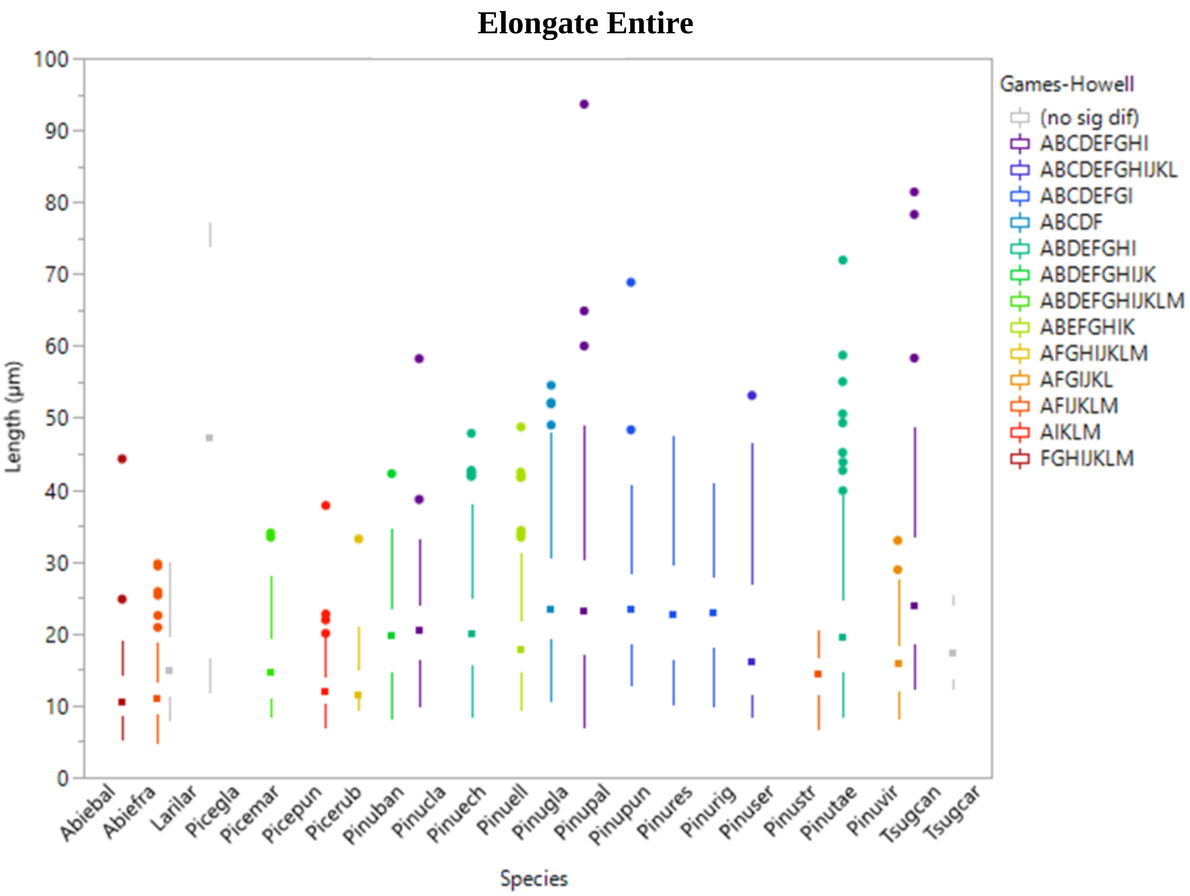


Figure 1.8: Length of elongate entire phytolith morphotype by species. Whiskers indicate +/- 1.5*(interquartile range). Squares indicate means. Dots indicate outliers (beyond 1.5*interquartile range). Colors indicate significant difference as determined by Welch's ANOVA followed by Games-Howell HSD.

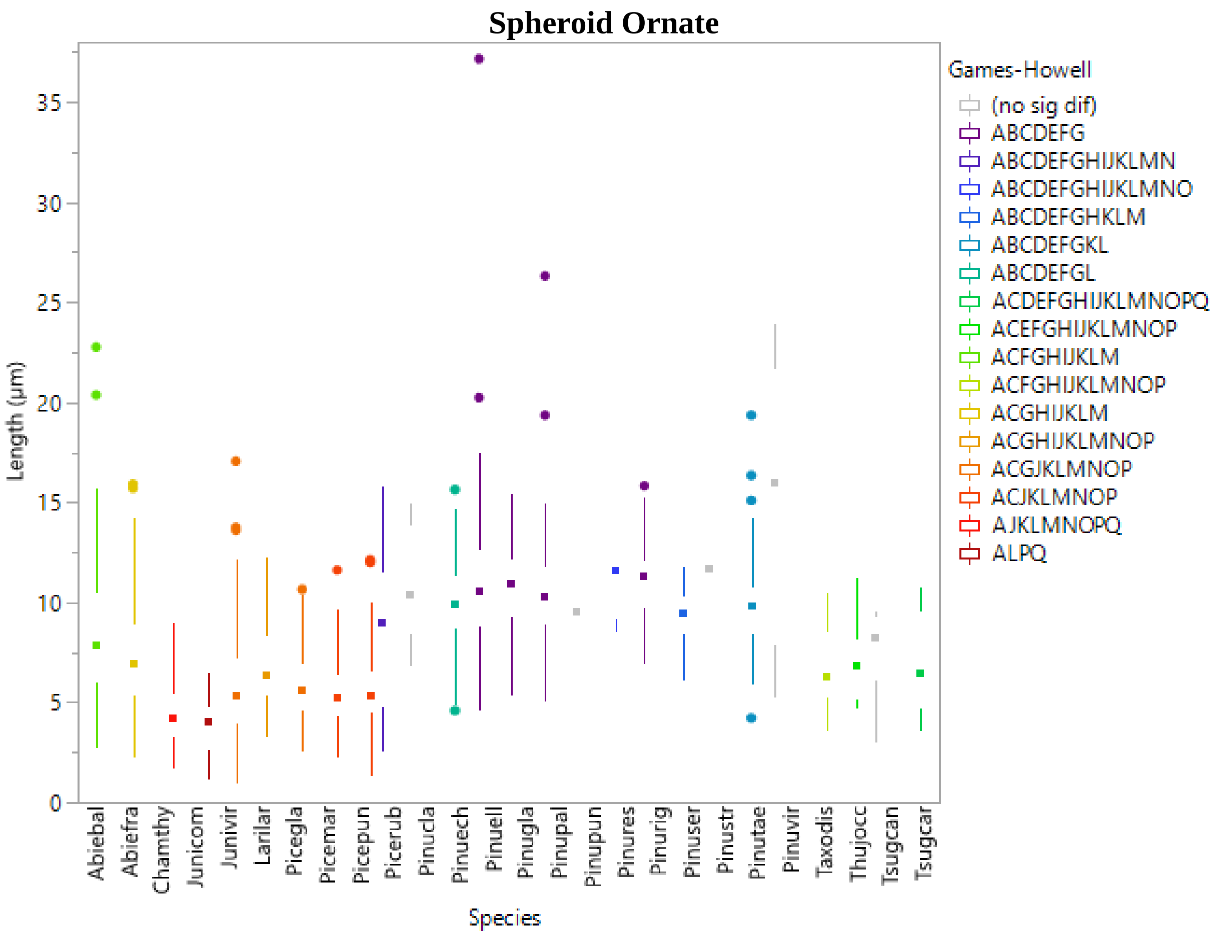


Figure 1.9: Length of spheroid ornate phytolith morphotype by species. Whiskers indicate +/- 1.5*(interquartile range). Squares indicate means. Dots indicate outliers (beyond 1.5*interquartile range). Colors indicate significant difference as determined by Welch's ANOVA followed by Games-Howell HSD.

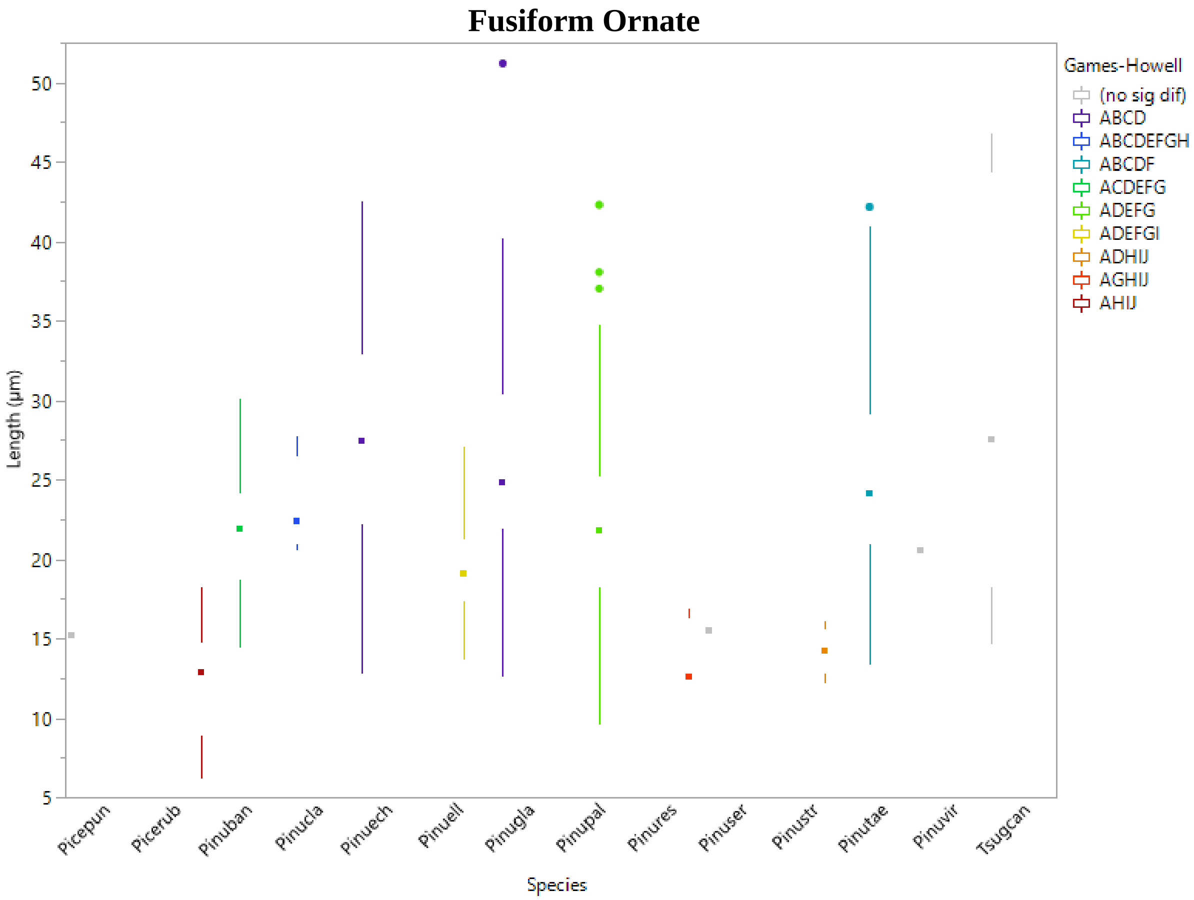


Figure 1.10: Length of Fusiform Ornate phytolith morphotype by species. Whiskers indicate +/- 1.5*(interquartile range). Squares indicate means. Dots indicate outliers (beyond 1.5*interquartile range). Colors indicate significant difference as determined by Welch's ANOVA followed by Games-Howell HSD.

Prismatic Psilate

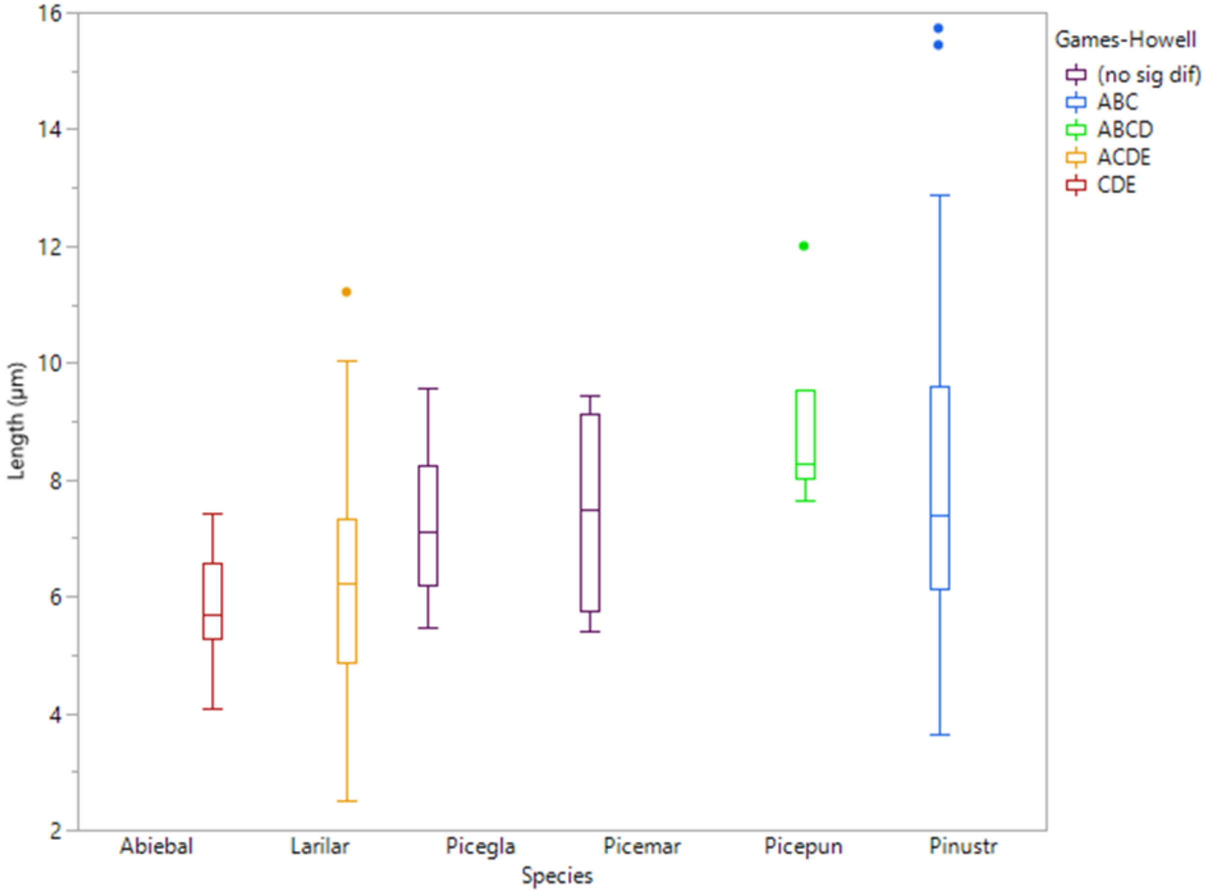


Figure 1.11: Length of prismatic psilate phytolith morphotype by species. Whiskers indicate +/- 1.5*(interquartile range). Dots indicate outliers (beyond 1.5*interquartile range). Colors indicate significant difference as determined by Welch's ANOVA followed by Games-Howell HSD.

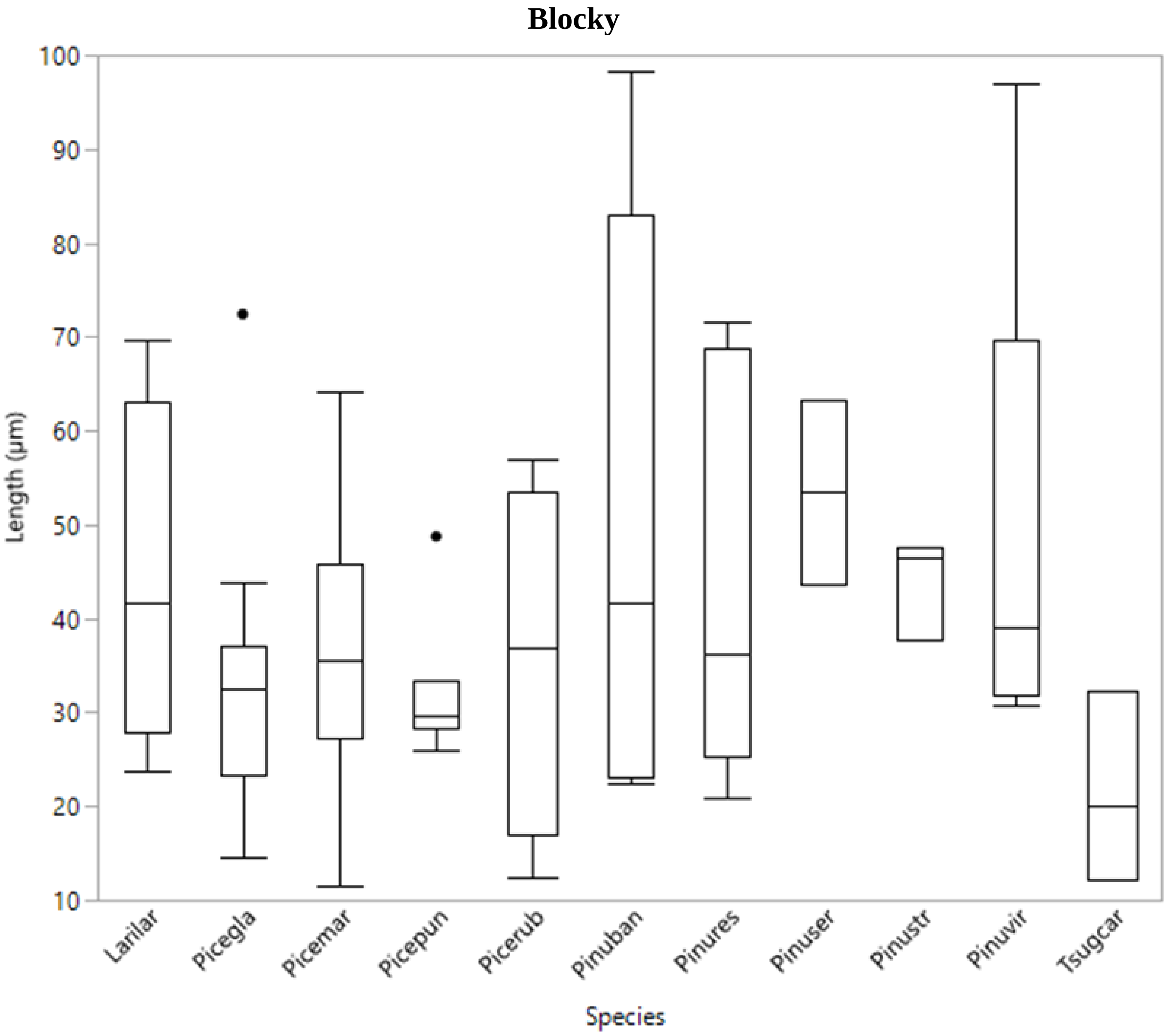
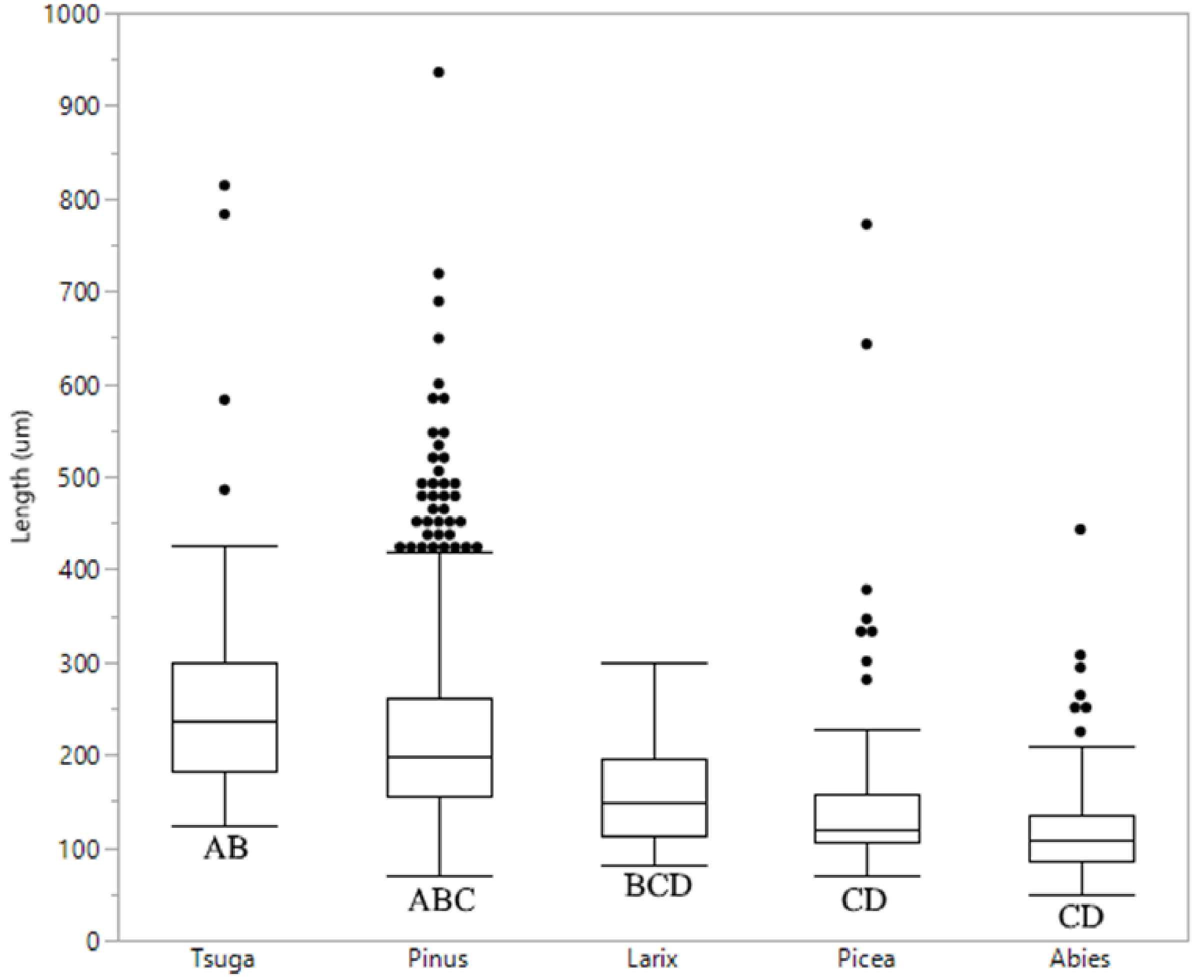


Figure 1.12: Length of blocky phytolith morphotype by species. Whiskers indicate +/- 1.5*(interquartile range). Dots indicate outliers (beyond 1.5*interquartile range). No significant difference was found between species (Welch's ANOVA).



Elongate Entire Assessed by Genus

Figure 1.12: Length of elongate entire phytolith morphotype by genus. Whiskers indicate +/- 1.5*(interquartile range). Dots indicate outliers (beyond 1.5*interquartile range). Significant difference was assessed by a Welch's ANOVA followed by Games-Howell HSD. Letters indicate connecting letter report from Games-Howell HSD.

CHAPTER 2: Shade-tolerance Classification of the Upland Herbaceous Flora of the Carolina and Virginia Piedmont

ABSTRACT

In the absence of disturbance, uplands of the southeastern United States Piedmont become dominated by closed-canopy forest. However, historical accounts describe savanna-like conditions over portions of the region dating at least as far back as the 1500s. These open habitats are thought to have declined because of human development, fire suppression, and loss of native grazing animals, but their legacy is evident in the rich diversity of persisting heliophytes in areas of primarily human-maintained open habitats, such as power-line rights-of-way and roadsides. Conservation practices required to restore and sustain Piedmont savanna are hampered by our current rudimentary understanding of community assembly and maintenance dynamics. Such understanding would be facilitated by a robust classification of species into specialist and generalist guilds related to canopy openness, a classification that is currently unavailable on a broad scale. Our objective was to develop a shade-tolerance classification for the upland Piedmont herbaceous flora of the Carolinas and Virginia, based on quantitative plot data from the region. A dataset of plot records (representing natural and semi-natural vegetation) was obtained from the Carolina Vegetation Survey. Following quality control, the dataset contained 1300 plots and 1550 species (including 835 native herbaceous species after single occurrences were removed), with species abundances in plots reported in cover classes. We estimated the canopy cover of each plot from the cover codes of its tree species. We assigned each plot to open (<25% canopy cover; n = 63), semi-open (25–75% canopy cover; n = 140), or closed (>75% canopy cover; n = 1097) habitat shade classes.

We calculated point biserial correlation coefficients (r_{pb}), which provided a positive or negative value for each species, dependent on its abundance and habitat association. We considered single (open, semi-open, or closed) and combined (open+semi-open, closed+semi-open, or open+closed) habitat classes during our analysis. A permutation test was employed to test the significance of the association between each species and the habitat shade class (or combination of classes) for which it had the largest positive coefficient. Species with $p< 0.1$ were considered generalists (no significant habitat association), those with $p<0.05$ were considered strong specialists, and those with $0.05<p<0.1$ were considered weak specialists. Of the 835

native herbaceous species in the dataset, we found 141 (17%) to be heliophytes associated with very open habitats (canopy cover <25%), and only 81 (10%) to be shade-tolerant species associated with closed habitats (canopy cover >75%), despite 84% of plots in the dataset being classified as closed habitats. This work suggests that open and semi-open habitats may contain a disproportionate diversity of regional herbaceous flora and provides the first quantitative shade-tolerance assessment of over 800 herbaceous species.

INTRODUCTION

Eastern United States Piedmont upland prairies, savannas, and woodlands with a heliophytic flora of Midwest prairie affinity trace an arc beginning with the Blackland prairies of Mississippi and Alabama (Roslund 1957; Barone 2005), through Georgia (Echols and Zomlefer 2010), and into the Carolinas and Virginia (Radford et al. 1968; Barden 1997; Davis et al. 2002; Schafale 2012; Weakley 2015; Fleming et al. 2017). Evidence from historical accounts, paleoecology, dendrochronology, and floristics (Rostlund 1957; Delcourt and Delcourt 1997; Juras 1997; Frost 2001; Barone 2005; Noss 2012) supports the historical existence of these now-rare communities, although the formation, timing, previous extent, and historical ecological dynamics are yet unclear. Early accounts describe savanna-like conditions in the southeastern United States Piedmont at least as far back as the 1500s (Rostlund 1957; Barden 1997; Barone 2005). In North Carolina, these systems likely once stretched along the Piedmont Crescent, which traces a historical Native American trading route (Dobbs 2006) near where many prairie remnant communities are now found (Davis et al. 2002; Benson 2011; Schafale 2012; Stanley 2019), and potentially over a broader area from the fall line to the foothills of the mountains (see De L’Isle 1718). Given the variation in climate, geology, soils and topography across the Piedmont, these communities were likely heterogeneous in plant composition.

Various remnants of previously widespread open vegetation are classified under different natural community types (Schafale 2012), of which a number are considered imperiled, including: Diabase Glade, Ultramafic Outcrop Barren, and Xeric Hardpan Forest. Considering the likely vast reduction in acreage due to disruption of historical fire occurrence (Delcourt and Delcourt 1997; Frost 2001), extirpation of native grazers such as bison (Barden 1997), and heavy settlement of the region, it is not surprising that many state- and federally-listed threatened and endangered plant species in the Piedmont are associated with open habitats. For example, at least

76 of approximately 210 state-listed Piedmont rare plant species in North Carolina are associated with habitats such as glades, barrens, meadows, and/or woodlands (Robinson 2018). These rare species continue to occur in a series of small, fragmented habitats (such as roadsides and powerline rights-of-way), of which very few sites are of considerable acreage and quality. Most of these sites likely remained open and relatively unaltered due to stressful underlying soils (often alfisols with vertic properties) that make them generally unsuitable for agriculture and development (see Hardison and Long 1910), and that naturally reduce the growth of woody vegetation while promoting the persistence of grasses and forbs through drought stress (Juras 1997). Open habitats usually offer orders of magnitude more pollinator resources than the more pervasive closed-canopy forests (see Hanula et al. 2015), giving them great value as forage for pollinators and other wildlife and prompting great interest in their conservation and restoration.

Restoration of open and semi-open habitats in the region has received much attention (Juras 1997; Davis 2002; Alley 2004; Taecker 2007; Sigmon-Chatham 2015), but scientific attention has lagged regarding the dynamics of plant species assembly and demography in response to restoration interventions in these systems. Due to the rarity of remaining natural examples, the dynamics of these ecosystems remain largely unclear, and it is difficult to formulate appropriate management and restoration practices. Understanding demographic patterns, including colonization, at various scales, from species to guild, is critical to developing and evaluating the success of different management and restoration strategies. However, such understanding is predicated on a robust classification of species into habitat specialist and generalist guilds reflecting shade tolerance, which is not currently available on a broad scale. In order to help fill this gap, our objective was to develop a shade-tolerance classification of upland Piedmont herbaceous plant species of the Carolinas and Virginia based on quantitative vegetation plot data from throughout the region.

METHODS

Dataset Compilation

An initial dataset containing 2914 plots representing natural and semi-natural Piedmont vegetation was retrieved from the Carolina Vegetation Survey (CVS) database (Peet et al. 2012). As the CVS project seeks to “document the composition and status of the natural vegetation” of the region, plots are sampled non-randomly but are intended to capture the greatest quality and diversity of natural and semi-natural vegetation in the region. Plots were surveyed between 1977 and 2015 following CVS methodology (Peet et al. 1998) or comparable Virginia Natural Heritage methodology (DCR-DNH 2011). Plant species abundance in plots is reported in CVS cover class codes that reflect ranges of percent cover: 1 = 0–0.1% (trace), 2 = 0.1–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95% and 10 > 95%. Plots vary in total size from 10 to 1000 m^2 based on area occupied by the plant community and resources of the surveyors.

We performed multiple quality control steps to obtain our final dataset. Taxonomy was standardized so each taxon was as closely equivalent to species rank as possible (Appendix A) and followed taxonomic concepts in Weakley (2015). For example, the taxa *Coreopsis* sp., *Coreopsis major*, *Coreopsis major* var. *major*, and *Coreopsis major* var. *rigida* were all present in the dataset. We chose to recognize the two subspecific taxa as records of *Coreopsis major* and discard records of the poor resolution *Coreopsis* sp. We also discarded records of non-vascular plants (e.g., mosses) and non-plant taxa (e.g., lichens) because they were inconsistently recorded, and confidence in their identification varied greatly. Any plots that contained a discarded taxon with a cover code >6 (i.e., >25% cover) were removed from the dataset because of loss of substantial information. Because our focus here was on upland vegetation, we removed any plots with survey notes indicating they were located in bottomland positions (e.g., streamside, floodplain, etc.). Our final dataset contained 1300 plots with 1550 vascular plant species and represented Piedmont upland vegetation of the Carolinas and Virginia (Figure 2.1). Additional details of the dataset preparation steps can be found in Appendix A.

Species were categorized as tree, shrub, vine, or herb based on assignments in the CVS database and cross-referenced with the USDA Plants database (USDA 2019) for species with lacking CVS designations. These growth-form assignments were hard categories, with each species assigned to only one form. For species that are sometimes considered to have more than one growth form (e.g., shrub or small tree), we categorized them as the larger growth form (“tree” in this example). Native or exotic status of each species was also retrieved from the CVS database and cross-referenced with the USDA Plants database.

We calculated an estimate of total plot canopy cover from the cover codes of tree species present in each plot. Cover codes were converted to the geometric mean of the endpoints of their associated cover class (ranges of % cover as previously listed) and summed to produce a canopy cover estimate for each plot. Plots were assigned to habitat shade classes based on the estimated total canopy cover: open (<25%), semi-open (25–75%), or closed (>75%). While a variety of canopy cover ranges have been used to define categories of vegetation structure, our breakpoints were chosen as a compromise between biological relevance and limitations of the coarse resolution of the cover class system. While this summation of percentages yields a better estimate than directly summing the cover codes, the total cover estimated for a given plot can (and often does) exceed 100%, because we are not accounting for potential overlap. While methods to account for random overlap in cover estimates have been proposed (Daniëls et al. 2011), we chose not to make assumptions about the overlap of species in our plots. Our tree cover estimates may have a bias toward higher percentages.

Statistical Analyses

We focused our analysis on only the herbaceous species because we were interested in using plot data to assess shade-tolerance associations of species (by proxy of estimated canopy cover), and woody species are more likely to persist in sub-optimal light conditions. By this, we mean that the presence of woody species in plots potentially represents landscape history rather than present conditions (Schwartz 2007; Nowacki and Abrams 2008; Rackham 2008). Point-biserial correlation coefficients (r_{pb}) relating species abundance patterns to plot habitat shade classes were calculated following De Cáceres and Legendre (2009) using the R package *indicspecies* (package version 1.7.6 with R version 3.6.0). This coefficient provides a positive or negative value for each species quantifying the strength of its association to each habitat shade class. For our purposes, only the habitat shade class with the highest coefficient (i.e., the strongest positive association) for each species was considered. A permutation test with 9999 iterations was used to test if the magnitude of a species-habitat association was greater than 95% of those obtained by chance alone (i.e., when species occurrences are randomly shuffled between plots). Following Burst et al. (2017), we classified each species as habitat shade class specialists or generalists based on the significance of their highest r_{pb} coefficient. Species with a significant association with a habitat shade class were considered strong specialists (r_{pb} coefficient with $p<0.05$). We also considered those with less significant but still notable habitat associations to be weak specialists (r_{pb} coefficient with $0.05<p<0.1$). Species with no significant or notable habitat shade class association were considered generalists (r_{pb} coefficient with $p>0.1$). Species with only a single occurrence were considered infrequent species and removed from the analysis. Following De Cáceres et al. (2010), we considered both single and combined habitat shade classes. Our single classes were open, semi-open and closed, while our combined classes were open+semi-open, open+closed, and closed+semi-open. The combined classes allowed for better detection of species with broader distributions of interest (open+semi-open, closed+semi-open) or even the rarely anticipated bimodal distributions (open+closed) that would otherwise be classified as generalists if only our open, semi-open, and closed classes were considered. The R script used for these analyses can be found in Appendix A.

Other Assessments

We examined conservation and hydrophytic status for specialist and generalist herbaceous species in the dataset. We use the term “conserved” species loosely here to indicate any species that is federally listed or that appears on at least one state’s rare species list for North Carolina (Robinson 2018), South Carolina (SCDNR 2015), or Virginia (Townsend 2019), indicating it has been identified as a consideration or priority for conservation. The degree of protection of these species usually varies from state to state and by the assessed rarity. Hydrophyte status was assessed based on The National Wetland Plant List (Lichvar et al. 2016). Hydrophytes are obligate (OBL), facultative wetland (FACW) or facultative (FAC) species, while nonhydrophytes are facultative upland (FACU) or upland (UPL) species (Lichvar et al. 2016).

RESULTS

Plot habitat classification

Based on their estimated canopy cover, 1097/1300 (84%) plots were classified as closed habitat, while only 140/1300 (11%) and 63/1300 (5%) were classified as semi-open and open habitat, respectively (Table 2.2).

Species shade-tolerance classification

Herbaceous plants made up 892/1163 (77%) of the total species in the dataset after infrequent species (those with only a single occurrence) were removed (Table 2.1). Detailed overviews of the 892 herbaceous species and their habitat shade class associations, conservation status, and hydrophytic status, can be found in Tables 2.3 and 2.4.

Eight hundred and thirty-five (94%) of the herbaceous species in the dataset were native species (Table 2.1). Of those 835 native herbaceous species, 461 (55%) were determined to have no significant (p>0.1) association to any habitat shade class and were considered generalists, 141 (17%) were determined to be specialists of open habitats (estimated canopy <25%), 77 (9%) were determined to be specialists of semi-open habitats (estimated canopy 25–75%), and 81 (10%) were determined to be specialists of closed habitats (estimated canopy >75%; Table 2.3). When considering combined habitat shade classes, an additional 47 (6%) native herbaceous species were determined to be associated with open+semi-open habitat (estimated canopy <75%), and 27 (3%) were determined to be associated with semi-open+closed habitats (estimated canopy >25%; Table 2.3). One species, *Galium obtusum* Bigelow, was unexpectedly found to have a weak association with the bimodal combination open+closed (estimated canopy <25% and >75%; Table 2.4).

One hundred and five (13%) native herbaceous species in the dataset were found to be rare species of conservation concern appearing on at least one state rare species list and/or as a federally listed species. Most (73 spp., 70%) were determined to be habitat shade class generalists. The most common specialist association for these rare species was found to be open (14 spp., 13% of rare species). Six rare species (8%) were determined to be associated with closed habitats (Table 2.3).

Only 57 (6%) of herbaceous species in the dataset were found to be exotics. Of these exotic species, the majority (54%) were determined to be habitat shade class generalists. Open habitats were the most common association among exotic specialists, representing 16 (28%) of the exotic species. Only two (4%) exotic species were found to be associated with closed habitats (Table 2.3).

Of the 892 total herbaceous species (infrequent species excluded) in this upland dataset, 320 (36%) were found to be hydrophytes according to Lichvar et al. (2016). The majority (202 spp., 63%) of hydrophytes were found to be habitat shade class generalists, but 59 (18%) were determined to be associated with open habitats, and 19 (6%) were determined to be associated with closed habitats (Table 2.3).

DISCUSSION

Plots representing open and semi-open habitats were relatively rare in our dataset, together representing only 16% of the plots. However, we found 141 species (17%) of our native herbaceous flora in the dataset to be heliophytes associated with very open habitats (canopy cover <25%), and 265 species (31%) to be associated with habitats with canopy cover <75%. Only 81 native herbaceous species (10%) in the dataset were found to be associated with closed habitats (canopy cover >75%), despite those habitats representing a clear majority (84%) of plots in the dataset. Open and semi-open habitats also contained 24 (23%) of the rare species specialists (state and/or federally listed) identified in this dataset, as opposed to only six (6%) rare species specialists strictly associated with closed habitats. These data suggest open and semi-open habitats may hold a disproportionate diversity of our native specialist herbaceous flora and provide critical habitat for rare species.

We also identified a potentially surprising number of hydrophytes, representing as much as 36% of all herbaceous species in the dataset. The inclusion of wetland species in this dataset of upland plots is understandable in the context of the heterogeneity of the Piedmont upland. Soils with water-restrictive features (e.g. shrink-swell clays) can lead to the development of hydrophytic upland vegetation such as Mixed Moisture Hardpan Forest, Upland Depression Swamp Forest, and Upland Pool communities (see Schafale 2012).

Another surprising result was the bimodal habitat association of *Galium obtusum* Bigelow, that was found to be associated with both open and closed habitats but avoiding semi-open habitats (25-75% canopy cover). There is no clear biological explanation for this pattern and, given the association was found to be “weak” ($0.05<p<0.1$), it is likely an artefact of the dataset preparation or misidentification. One subspecies of *G. obtusum*, *G. obtusum* var. *filifolium* (Wiegand) Fernald, is recognized in the eastern Piedmont region (Weakley 2015). Both varieties are associated with marshes and swamps, but var. *filifolium* is also associated with creekbanks and alluvial forests (Weakley 2015). As we only treated taxa at the species level in our dataset, subspecific taxa with greatly differing habitat requirements would potentially weaken our analysis. This could also represent a case of Type I error, where *G. obtusum* was simply misclassified by chance.

There are a few considerations that could weaken conclusions drawn from our analysis. Some perennial heliophytes may be able to persist in sub-optimal habitat under fire-suppression but be unable to reproduce, and this would weaken the power of r_{pb} to correctly identify these as shade-intolerant species that rely on open habitat to complete their life cycle. With this consideration in mind, it is likely the true number of open and semi-open specialist species is greater than the numbers found here. Another concern is the low sample sizes of some rare species. For example, the rare prairie-affinity heliophyte *Echinacea laevigata* (Boynton & Beadle) Blake (smooth coneflower) may represent a species having both persistence in sub-optimal shaded habitat and low sample size. In our dataset, it occurred in only two plots and was found to be weakly ($0.05<p<0.01$) associated with open habitat, which is thought to be necessary for successful reproduction and recruitment of seedlings (Gaddy 1991).

The eastern Piedmont has long been considered part of the eastern forest vegetation region, characterized by succession moving toward a forest climax in the absence of disturbance (Oosting 1948; Braun 1950; Dyer 2006). Given the number of native species we found that depend on open and semi-open habitat in the Carolina and Virginia Piedmont, we should continue to re-evaluate our understanding of the history of the landscape and the role of natural (and semi-natural) disturbances in creating and maintaining forest – woodland/savanna/grassland mosaics in place of the traditional concept of unbroken forest.

This work represents the first purely quantitative assessment of the shade-tolerance, by proxy of habitat association, of the breadth of Piedmont native herbs, and it can serve as a valuable resource for ecological and conservation-focused studies in the field. This work draws further attention to the diversity of our native heliophyte communities and provides quantitative assessment of the habitat associations of over 800 of our native herbs.

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TABLES

Table 2.1: Overview of the vascular plant taxa present in the 1300-plot final dataset following quality control and taxonomic homogenization steps. The plots represent natural and semi-natural vegetation of the Piedmont uplands of the Carolinas and Virginia. Infrequent (single occurrence) species are excluded.

Growth Form	*Native Species*	*Exotic Species*	*Totals*
Herb	835	57	*892*
Shrub	6	14	*20*
Tree	157	12	*169*
Vine	67	15	*82*
Totals	*1065*	*98*	*1163*

Table 2.2: Number of vegetation plots assigned to each habitat shade class as determined from estimated total tree cover of each plot.

Habitat Shade Class	*Number of vegetation plots assigned*	*Estimated Canopy Coverage*
Open	63	<25%
Semi-open	140	25–75%
Closed	1097	>75%
Total	*1300*	

Table 2.3: Various assessments of the 892 herbaceous species in the dataset (infrequent species excluded). Specialist status is determined by point biserial correlation coefficients (r_{pb}) followed by a permutation test to assess strength of the association. "Gen." indicates generalist species. "Conserved" indicates species that appear on state and/or federal rare species lists. Hydrophytes and nonhydrophytes were assessed based on Lichvar et al. (2016).

	Open	*Open+ Semi-Open*	*Semi-open*	*Semi-open+ Closed*	*Closed*	*Open+ Closed*	*Gen.*	*Totals*
Strong Specialist	133	38	62	16	72	0	N/A	*321*
Weak Specialist	24	11	21	11	11	1	N/A	*79*
Native	141	47	77	27	81	1	461	*835*
Exotic	16	2	6	0	2	0	31	*57*
Conserved	14	4	6	2	6	0	73	*105*
Hydrophyte	59	16	19	4	19	1	202	*320*
Nonhydrophyte	47	11	18	12	37	0	118	*243*

Table 2.4: Herbaceous species and their habitat shade class associations as determined by point biserial correlation coefficients (r_{pb}). * indicates an exotic species. Only the highest r_{pb} coefficient for each species is listed. The p-values are obtained from a permutation and represent the proportion of r_{pb} coefficients that exceeded the highest r_{pb} coefficient observed when species occurrences were shuffled randomly among plots 9999 times. "Cons." indicates conservation status: NP = Not Protected, SL = State Listed (State abbreviations in parentheses), FL = Federally Listed. "Wetland" indicates the assignment of each taxon based on Lichvar et al. (2016).

Taxon	**Shade Class**	**r_{pb}**	**p-value**	**n**	**Cons.**	**Wetland**
Actaea racemosa	Strong Closed	0.226908568	0.0002	154	NP	N/A
Adiantum pedatum	Strong Closed	0.146009894	0.0118	84	NP	FAC
Agrimonia rostellata	Strong Closed	0.17172982	0.003	83	NP	FACU
*Alliaria petiolata**	Strong Closed	0.156020331	0.0044	67	NP	FACU
Amianthium muscitoxicum	Weak Closed	0.113498534	0.0547	24	NP	FAC
Anemone americana	Strong Closed	0.178967312	0.0023	124	NP	N/A
Arisaema [pusillum + quinatum + stewardsonii + triphyllum]	Strong Closed	0.199324283	0.0008	258	NP	N/A
Asarum [acuminatum + canadense + reflexum]	Strong Closed	0.131335196	0.0185	52	NP	N/A
Athyrium asplenioides	Strong Closed	0.160456303	0.007	105	NP	FAC
Botrypus virginianus	Strong Closed	0.237100827	0.0002	253	NP	FACU
Brachyelytrum erectum	Strong Closed	0.191179748	0.0008	154	NP	FACU
Cardamine concatenata	Strong Closed	0.226200618	0.0001	96	NP	FACU
Carex albicans	Strong Closed	0.15534832	0.0108	105	NP	UPL
Carex amphibola	Weak Closed	0.102910374	0.0981	38	SL (SC)	FAC
Carex blanda	Strong Closed	0.155178347	0.0119	133	NP	FAC
Carex cephalophora	Strong Closed	0.152172417	0.0112	77	NP	FACU
Carex digitalis	Strong Closed	0.297988261	0.0001	183	NP	UPL
Carex laxiculmis	Strong Closed	0.176554157	0.0021	66	NP	N/A
Carex laxiflora	Strong Closed	0.209217616	0.0005	89	NP	FACU
Carex physorhyncha	Strong Closed	0.237753629	0.0001	115	NP	N/A
Carex planispicata	Weak Closed	0.100552734	0.0764	28	NP	N/A
Carex platyphylla	Weak Closed	0.101845203	0.0991	19	NP	N/A
Carex rosea	Strong Closed	0.240433046	0.0002	114	NP	FACU
Carex virescens	Weak Closed	0.108478539	0.0742	34	NP	N/A
Carex willdenowii	Strong Closed	0.173219919	0.0021	51	NP	UPL
Caulophyllum thalictroides	Weak Closed	0.103468576	0.0743	28	SL (SC)	N/A
Circaea canadensis	Strong Closed	0.205926349	0.0005	116	NP	FACU
Claytonia virginica	Strong Closed	0.173479369	0.0026	69	NP	FAC
Collinsonia canadensis	Strong Closed	0.163290135	0.0036	73	NP	FAC
Conopholis americana	Strong Closed	0.149443098	0.0074	39	NP	N/A
Cynoglossum virginianum	Strong Closed	0.132952469	0.0276	69	NP	N/A
Dicentra canadensis	Weak Closed	0.100072983	0.084	21	NP	N/A
Epifagus virginiana	Strong Closed	0.215514799	0.0004	98	NP	N/A

Table 2.4: (Continued).

Erythronium americanum	Strong Closed	0.117357656	0.0388	34	NP	N/A
Euonymus americanus	Strong Closed	0.3058523	0.0001	233	NP	FAC
Eurybia divaricata	Strong Closed	0.25810283	0.0001	185	NP	N/A
Eutrochium purpureum	Strong Closed	0.123698629	0.0312	35	NP	FAC
Festuca subverticillata	Strong Closed	0.285422179	0.0001	176	NP	FACU
Galearis spectabilis	Strong Closed	0.134824659	0.0178	33	NP	N/A
Galium aparine	Strong Closed	0.185571704	0.0019	142	NP	FACU
Galium circaezans	Strong Closed	0.224785763	0.0002	539	NP	UPL
Galium concinnum	Weak Closed	0.11016005	0.0597	22	NP	UPL
Galium triflorum	Strong Closed	0.215731458	0.0003	166	NP	FACU
Geum virginianum	Strong Closed	0.143952981	0.0121	63	NP	FAC
Goodyera pubescens	Strong Closed	0.292198157	0.0001	262	NP	FACU
Hexastylis minor	Weak Closed	0.112047837	0.0525	37	NP	N/A
Hexastylis virginica	Strong Closed	0.115977122	0.0429	35	NP	FACU
Hydrophyllum virginianum	Weak Closed	0.10098507	0.0919	19	NP	FAC
Hylodesmum nudiflorum	Strong Closed	0.28394894	0.0001	447	NP	N/A
Hypopitys monotropa	Strong Closed	0.11936465	0.037	36	NP	N/A
Liparis liliifolia	Strong Closed	0.152442308	0.0083	42	SL (SC)	FACU
Maianthemum racemosum	Strong Closed	0.469607495	0.0001	555	NP	FACU
Medeola virginiana	Strong Closed	0.173429292	0.003	100	NP	FAC
Mitchella repens	Strong Closed	0.24673501	0.0001	284	NP	FACU
Muhlenbergia sobolifera	Weak Closed	0.108019371	0.0623	30	SL (NC)	N/A
Osmorhiza claytonii	Strong Closed	0.17335626	0.002	52	SL (SC)	FACU
Osmorhiza longistylis	Strong Closed	0.13337985	0.0187	53	NP	FACU
Panax quinquefolius	Strong Closed	0.129530937	0.0258	29	SL (SC)	N/A
Parathelypteris noveboracensis	Strong Closed	0.119044022	0.049	59	NP	FAC
Persicaria virginiana	Strong Closed	0.155013232	0.0127	93	NP	FAC
Phegopteris hexagonoptera	Strong Closed	0.176627344	0.001	86	NP	FAC
Phryma leptostachya	Strong Closed	0.256309982	0.0001	165	NP	FACU
Poa cuspidata	Strong Closed	0.16940637	0.0035	73	NP	N/A
Poa sylvestris	Strong Closed	0.13184096	0.025	30	NP	FACW
Podophyllum peltatum	Strong Closed	0.272392669	0.0001	177	NP	FACU
Polygonatum biflorum	Strong Closed	0.389980514	0.0001	658	NP	FACU
Polystichum acrostichoides	Strong Closed	0.384036394	0.0001	506	NP	FACU
Ranunculus abortivus	Strong Closed	0.20424315	0.0007	72	NP	FACW
Sanguinaria canadensis	Strong Closed	0.20204479	0.0002	144	NP	UPL
Sanicula canadensis	Strong Closed	0.233150485	0.0003	249	NP	UPL
Sceptridium dissectum	Strong Closed	0.142264953	0.0114	37	NP	FAC
Scutellaria elliptica	Strong Closed	0.206901611	0.0004	152	NP	N/A

Table 2.4: (Continued).

Solidago caesia	Strong Closed	0.290603126	0.0001	240	NP	FACU
Solidago flexicaulis	Strong Closed	0.117471371	0.0456	26	NP	FACU
Stellaria pubera	Strong Closed	0.247976101	0.0001	180	NP	N/A
Thalictrum thalictroides	Strong Closed	0.193118587	0.0008	154	NP	FACU
Tipularia discolor	Strong Closed	0.174575551	0.0027	84	NP	FACU
Trillium catesbaei	Strong Closed	0.131418445	0.0221	46	NP	N/A
Uvularia perfoliata	Strong Closed	0.265448598	0.0001	348	NP	FACU
*Veronica hederifolia**	Strong Closed	0.140275907	0.0095	40	NP	N/A
Viola palmata	Strong Closed	0.157259647	0.0112	110	NP	FACU
Viola pubescens	Strong Closed	0.118491618	0.0405	25	NP	FACU
Viola sororia	Strong Closed	0.172556074	0.0055	180	NP	FAC
Ageratina altissima	Weak Closed+Semi-open	0.117531055	0.0693	62	NP	FACU
Agrimonia pubescens	Strong Closed+Semi-open	0.144892801	0.0217	88	SL (SC)	N/A
Agrostis perennans	Strong Closed+Semi-open	0.132030488	0.0378	77	NP	FACU
Asplenium platyneuron	Strong Closed+Semi-open	0.199891003	0.002	314	NP	FACU
Boechera laevigata	Weak Closed+Semi-open	0.107649508	0.089	39	NP	N/A
Bromus pubescens	Strong Closed+Semi-open	0.133450151	0.0336	77	NP	FACU
Carex hirsutella	Strong Closed+Semi-open	0.142929367	0.0226	93	NP	N/A
Carex nigromarginata	Strong Closed+Semi-open	0.136993603	0.0288	65	NP	UPL
Carex radiata	Weak Closed+Semi-open	0.11481872	0.079	66	NP	FAC
Desmodium perplexum	Strong Closed+Semi-open	0.12233891	0.0475	59	NP	N/A
Desmodium rotundifolium	Strong Closed+Semi-open	0.155227396	0.0138	114	NP	N/A
Dichanthelium boscii	Strong Closed+Semi-open	0.226333703	0.0003	331	NP	N/A
Dichanthelium dichotomum	Weak Closed+Semi-open	0.118022194	0.0643	261	NP	FAC
Elymus hystrix	Weak Closed+Semi-open	0.123391876	0.0518	78	NP	UPL
Endodeca serpentaria	Strong Closed+Semi-open	0.325634779	0.0001	394	NP	UPL
Euphorbia pubentissima	Weak Closed+Semi-open	0.107412457	0.0649	34	NP	N/A
Galium uniflorum	Weak Closed+Semi-open	0.119723701	0.0509	54	NP	FACU
Geranium maculatum	Strong Closed+Semi-open	0.138060345	0.0277	85	NP	FACU
Geum canadense	Strong Closed+Semi-open	0.158232758	0.0106	107	NP	FACU

Table 2.4: (Continued).

Hieracium venosum	Weak Closed+Semi-open	0.106918416	0.0997	153	NP	N/A
Nabalus serpentarius	Weak Closed+Semi-open	0.111301858	0.0924	58	NP	N/A
Rosa carolina	Strong Closed+Semi-open	0.152858308	0.0146	247	NP	FACU
Sanicula smallii	Strong Closed+Semi-open	0.142279426	0.0231	103	NP	N/A
Solidago arguta	Strong Closed+Semi-open	0.141632543	0.0161	72	NP	UPL
Solidago ulmifolia	Weak Closed+Semi-open	0.109015221	0.0982	50	SL (NC)	N/A
Tiarella cordifolia	Strong Closed+Semi-open	0.127507505	0.0432	78	NP	FAC
Uvularia sessilifolia	Weak Closed+Semi-open	0.114971286	0.0715	100	NP	FAC
Acalypha gracilens	Generalist	0.058981185	0.6163	13	NP	FAC
Acalypha virginica	Generalist	0.091059168	0.1417	26	NP	FACU
Achillea [borealis + millefolium]	Generalist	0.077184731	0.2339	14	NP	N/A
Aconitum uncinatum	Generalist	0.041103913	0.9263	3	SL (SC)	FAC
Actaea pachypoda	Generalist	0.066987424	0.4428	8	NP	UPL
Agrimonia microcarpa	Generalist	0.040125776	0.9815	5	NP	N/A
Agrimonia parviflora	Generalist	0.052696604	0.6659	6	NP	FACW
Allium [burdickii + tricoccum]	Generalist	0.068556004	0.3584	10	NP	N/A
Allium canadense	Generalist	0.036787247	0.7783	16	NP	FACU
Amsonia tabernaemontana	Generalist	0.074431262	0.2987	11	NP	FAC
Anchistea virginica	Generalist	0.06435876	0.1846	2	NP	OBL
Andropogon [capillipes + dealbatus]	Generalist	0.036709729	1	3	NP	N/A
Andropogon glomeratus	Generalist	0.07807822	0.1811	4	NP	FACW
Andropogon tenuispatheus	Generalist	0.060919512	0.2849	2	NP	N/A
Anemone acutiloba	Generalist	0.044395346	0.7952	4	NP	N/A
Anemone lancifolia	Generalist	0.07619791	0.177	7	NP	N/A
Anemone quinquefolia	Generalist	0.05516533	0.7331	5	NP	FACU
Angelica venenosa	Generalist	0.080824081	0.2647	12	NP	N/A
Antennaria parlinii	Generalist	0.078275528	0.2827	11	NP	N/A
Aphyllon uniflorum	Generalist	0.034873703	1	2	NP	N/A
Aplectrum hyemale	Generalist	0.071254284	0.397	9	NP	FAC
Apocynum sibiricum	Generalist	0.077506561	0.1329	4	NP	N/A
Arabidopsis lyrata	Generalist	0.042717883	1	3	NP	FACU
Aralia nudicaulis	Generalist	0.044395346	0.793	4	NP	FACU
Aralia racemosa	Generalist	0.040272765	1	3	NP	FACU
*Arenaria serpyllifolia**	Generalist	0.038347445	1	4	NP	FAC

Table 2.4: (Continued).

Arisaema dracontium	Generalist	0.080750869	0.2281	18	NP	FACW
Arnoglossum reniforme	Generalist	0.033083093	1	2	SL (VA)	N/A
*Artemisia vulgaris**	Generalist	0.040272765	1	3	NP	UPL
Aruncus dioicus	Generalist	0.05206512	0.8008	5	NP	FACU
Arundinaria [gigantea + tecta]	Generalist	0.072679472	0.3732	25	NP	N/A
Arundinaria appalachiana	Generalist	0.05911423	0.5584	7	NP	N/A
Asclepias quadrifolia	Generalist	0.059830891	0.6408	14	NP	N/A
Asclepias syriaca	Generalist	0.060919512	0.2925	2	NP	FACU
Asclepias variegata	Generalist	0.065811166	0.4132	34	NP	FACU
Aureolaria flava	Generalist	0.05381235	0.3938	3	NP	N/A
Aureolaria laevigata	Generalist	0.067487552	0.4854	17	NP	N/A
Aureolaria pedicularia	Generalist	0.062725034	0.2279	3	NP	N/A
Aureolaria virginica	Generalist	0.043522552	0.6542	80	NP	N/A
Avenella flexuosa	Generalist	0.061028976	0.184	4	NP	FACU
Bidens comosa	Generalist	0.034873703	1	2	NP	N/A
Bidens discoidea	Generalist	0.041103913	0.9229	3	NP	FACW
Bidens frondosa	Generalist	0.080057579	0.2356	19	NP	FACW
Blephilia ciliata	Generalist	0.029836062	0.9659	11	NP	N/A
Boehmeria cylindrica	Generalist	0.053755315	0.5311	85	NP	FACW
*Bromus commutatus**	Generalist	0.084631842	0.1081	3	NP	N/A
Callitriche heterophylla	Generalist	0.065850048	0.1946	2	NP	OBL
Campanula americana	Generalist	0.033083093	1	2	NP	N/A
Campanula divaricata	Generalist	0.098709581	0.1164	18	NP	N/A
Cardamine angustata	Generalist	0.074612594	0.3068	11	NP	FACU
Cardamine bulbosa	Generalist	0.049043077	0.2829	2	NP	OBL
*Cardamine hirsuta**	Generalist	0.04923941	0.8409	11	NP	FACU
Cardamine parviflora	Generalist	0.080582133	0.1502	6	NP	FACU
Carex alata	Generalist	0.036743179	0.9927	4	NP	OBL
Carex allegheniensis	Generalist	0.05516533	0.7239	5	NP	N/A
Carex appalachica	Generalist	0.034873703	1	2	SL (SC)	N/A
Carex atlantica	Generalist	0.060577925	0.4723	10	NP	FACW
Carex bromoides	Generalist	0.037017962	0.9267	3	NP	FACW
Carex careyana	Generalist	0.034196079	1	2	NP	N/A
Carex caroliniana	Generalist	0.034557642	0.8167	39	NP	FACW
Carex communis	Generalist	0.091865846	0.1427	16	NP	N/A
Carex complanata	Generalist	0.033088274	0.7908	48	NP	FACU
Carex corrugata	Generalist	0.038702302	0.9883	5	NP	FACW
Carex crebriflora	Generalist	0.060439789	0.6279	6	NP	FACW
Carex crinita	Generalist	0.04785413	0.6421	35	NP	OBL

Table 2.4: (Continued).

Carex cumberlandensis	Generalist	0.069878269	0.472	23	NP	N/A
Carex debilis	Generalist	0.052458067	0.5661	46	NP	FAC
Carex festucacea	Generalist	0.03554216	0.8057	17	NP	FAC
Carex flaccosperma	Generalist	0.077132568	0.3981	26	NP	FAC
Carex glaucodea	Generalist	0.077033697	0.3939	27	NP	FAC
Carex gracilescens	Generalist	0.034028302	0.9805	5	SL (SC)	N/A
Carex gracillima	Generalist	0.05516533	0.6802	6	SL (SC)	FACU
Carex granularis	Generalist	0.043637518	0.8635	4	SL (SC)	FACW
Carex grayi	Generalist	0.059824923	0.498	11	NP	FACW
Carex grisea	Generalist	0.055568479	0.62	7	NP	FACU
Carex howei	Generalist	0.059998572	0.2594	5	NP	N/A
Carex intumescens	Generalist	0.081206572	0.292	34	NP	FACW
Carex jamesii	Generalist	0.076390798	0.2934	11	SL (NC)	N/A
Carex kraliana	Generalist	0.077471775	0.3553	23	NP	N/A
Carex laevivaginata	Generalist	0.050796924	0.6192	22	NP	OBL
Carex leavenworthii	Generalist	0.067721735	0.1534	2	NP	N/A
Carex leptalea	Generalist	0.054502421	0.705	13	NP	OBL
Carex louisianica	Generalist	0.059084618	0.5539	9	NP	OBL
Carex lurida	Generalist	0.038585146	0.747	22	NP	OBL
Carex mitchelliana	Generalist	0.037177033	0.845	3	NP	OBL
Carex muehlenbergii	Generalist	0.085404856	0.1815	22	NP	N/A
Carex normalis	Generalist	0.045138482	0.9328	5	NP	FACW
Carex oxylepis	Generalist	0.047786877	0.8486	10	NP	FACW
Carex pellita	Generalist	0.041049925	0.8036	4	NP	OBL
Carex pigra	Generalist	0.052526478	0.3751	5	NP	FACW
Carex plantaginea	Generalist	0.047887952	0.926	4	SL (SC)	N/A
Carex prasina	Generalist	0.047044767	0.9273	4	SL (SC)	OBL
Carex retroflexa	Generalist	0.048677487	0.8132	11	NP	FACU
Carex seorsa	Generalist	0.033070319	0.8557	15	NP	FACW
Carex sparganioides	Generalist	0.042717883	1	3	NP	FACU
Carex squarrosa	Generalist	0.055605457	0.5871	10	NP	FACW
Carex stipata	Generalist	0.083876253	0.1131	10	NP	OBL
Carex striatula	Generalist	0.092426521	0.1338	18	NP	N/A
Carex stricta	Generalist	0.032052478	1	2	SL (SC)	OBL
Carex styloflexa	Generalist	0.061470148	0.5095	13	NP	FACW
Carex superata	Generalist	0.057568826	0.6452	6	NP	FAC
Carex swanii	Generalist	0.087336972	0.2606	35	NP	FACU
Carex texensis	Generalist	0.034873703	1	2	NP	N/A
Carex tonsa	Generalist	0.068747333	0.5305	8	NP	N/A

Table 2.4: (Continued).

Carex tribuloides	Generalist	0.087809946	0.1573	26	NP	FACW
Carex typhina	Generalist	0.080173877	0.2545	27	NP	FACW
Carex umbellata	Generalist	0.040044228	0.9882	5	NP	N/A
Carex vulpinoidea	Generalist	0.034873703	1	2	NP	OBL
Carex woodii	Generalist	0.052045624	0.2781	2	SL (SC)	UPL
*Cerastium glomeratum**	Generalist	0.034873703	1	2	NP	UPL
Chaerophyllum procumbens	Generalist	0.050765945	0.7251	5	NP	FACW
Chaerophyllum tainturieri	Generalist	0.060919512	0.2836	2	NP	FAC
Chamaelirium luteum	Generalist	0.102550421	0.1372	47	NP	FAC
Chasmanthium latifolium	Generalist	0.047877376	0.6318	41	NP	FACU
Chasmanthium laxum	Generalist	0.060177147	0.4782	57	NP	FAC
Chelone glabra	Generalist	0.051201746	0.7682	11	NP	OBL
Chimaphila umbellata	Generalist	0.098082114	0.1015	19	NP	N/A
Chrysogonum virginianum	Generalist	0.010565869	0.97	67	NP	N/A
Cicuta maculata	Generalist	0.079056499	0.2095	15	NP	OBL
Cinna arundinacea	Generalist	0.037954635	0.7311	55	NP	FACW
Cirsium horridulum	Generalist	0.081820255	0.1155	4	NP	FACU
Coleataenia anceps	Generalist	0.030755826	0.8313	22	NP	FAC
Collinsonia tuberosa	Generalist	0.033083093	1	2	SL (NC)	N/A
Collinsonia verticillata	Generalist	0.034873703	1	2	SL (NC/SC/VA)	N/A
Comandra umbellata	Generalist	0.081132407	0.2926	11	NP	FACU
*Commelina communis**	Generalist	0.036743179	0.9925	4	NP	FAC
Commelina virginica	Generalist	0.051345076	0.6804	18	NP	FACW
Corallorhiza odontorhiza	Generalist	0.034873703	1	2	NP	N/A
Coreopsis delphiniifolia	Generalist	0.053943156	0.1918	2	SL (VA)	N/A
Coreopsis grandiflora	Generalist	0.066462116	0.1033	2	SL (NC)	N/A
Coreopsis verticillata	Generalist	0.095798897	0.1366	55	NP	N/A
Corydalis flavula	Generalist	0.067161293	0.4608	17	NP	FACU
Cryptotaenia canadensis	Generalist	0.03915383	0.7098	36	NP	FAC
Cubelium concolor	Generalist	0.055982181	0.5424	7	NP	N/A
Cuthbertia rosea	Generalist	0.089659384	0.1256	4	NP	N/A
Cyperus echinatus	Generalist	0.081758547	0.1331	7	NP	FACU
Cyperus lancastriensis	Generalist	0.071256569	0.1461	3	NP	FAC
Cyperus lupulinus	Generalist	0.066462116	0.1052	2	NP	UPL
Cyperus odoratus	Generalist	0.066462116	0.1116	2	NP	FACW
Cyperus pseudovegetus	Generalist	0.074570325	0.2278	5	NP	FACW

Table 2.4: (Continued).

Cypripedium acaule	Generalist	0.054033446	0.7511	14	NP	FACU
Cypripedium parviflorum	Generalist	0.052744705	0.6939	5	SL (NC)	FACW
Cystopteris protrusa	Generalist	0.088243635	0.1453	17	NP	FAC
*Dactylis glomerata**	Generalist	0.087095506	0.1326	4	NP	FACU
Danthonia compressa	Generalist	0.041103913	0.9235	3	NP	FACU
Dendrolycopodium obscurum	Generalist	0.076811878	0.316	10	NP	FACU
Dennstaedtia punctilobula	Generalist	0.0840309	0.1932	14	NP	FACU
Deparia acrostichoides	Generalist	0.092818334	0.144	16	NP	FAC
Desmodium canescens	Generalist	0.064549762	0.2529	6	NP	N/A
Desmodium obtusum	Generalist	0.068784844	0.4283	9	NP	N/A
*Dianthus armeria**	Generalist	0.062725034	0.2247	3	NP	UPL
Dicentra cucullaria	Generalist	0.071537438	0.3788	22	SL (SC)	N/A
Dichanthelium aciculare	Generalist	0.058490051	0.1884	3	SL (SC)	FACU
Dichanthelium angustifolium	Generalist	0.060919512	0.2919	2	NP	N/A
Dichanthelium annulum	Generalist	0.077378834	0.1497	4	SL (NC)	N/A
Dichanthelium bicknellii	Generalist	0.084215525	0.1663	5	SL (NC)	N/A
Dichanthelium clandestinum	Generalist	0.069822351	0.4567	24	NP	FAC
Dichanthelium commutatum	Generalist	0.063253173	0.4094	269	NP	FACU
Dichanthelium ensifolium	Generalist	0.065850048	0.1882	2	NP	N/A
Dichanthelium linearifolium	Generalist	0.027047458	0.8739	17	NP	N/A
Dichanthelium longiligulatum	Generalist	0.06435876	0.1874	2	NP	N/A
Dichanthelium lucidum	Generalist	0.047887952	0.7202	5	NP	N/A
Dichanthelium polyanthes	Generalist	0.037863673	0.9022	12	NP	N/A
Dichanthelium ravenelii	Generalist	0.046462941	0.9223	4	NP	FACU
Dichanthelium strigosum	Generalist	0.084631842	0.1098	3	NP	FAC
Dichanthelium tenue	Generalist	0.066462116	0.1058	2	NP	N/A
Dichanthelium yadkinense	Generalist	0.046799366	0.8546	4	NP	N/A
*Digitaria ischaemum**	Generalist	0.069771935	0.2711	6	NP	UPL
Diodia [harperi + virginiana]	Generalist	0.033467925	0.9872	5	NP	N/A
Diphasiastrum digitatum	Generalist	0.0904411	0.1267	26	NP	N/A
Doellingeria infirma	Generalist	0.078098028	0.3156	25	NP	N/A
Drosera brevifolia	Generalist	0.069251913	0.1492	3	NP	OBL
Dryopteris carthusiana	Generalist	0.037177033	0.8466	3	SL (SC)	FAC
Dryopteris cristata	Generalist	0.074559278	0.2046	6	NP	FACW
Dryopteris intermedia	Generalist	0.048666178	0.8615	5	SL (SC)	FACU
Dryopteris marginalis	Generalist	0.073100016	0.3361	55	NP	FACU
Eleocharis obtusa	Generalist	0.052039174	0.1944	2	NP	OBL

Table 2.4: (Continued).

Eleocharis tenuis	Generalist	0.087250896	0.1968	14	NP	FACW
Eleocharis tortilis	Generalist	0.060919512	0.2955	2	NP	FACW
Elephantopus carolinianus	Generalist	0.033112945	0.7758	54	NP	FACU
Elephantopus nudatus	Generalist	0.077210014	0.1965	7	NP	FAC
Elephantopus tomentosus	Generalist	0.066466233	0.3933	72	NP	N/A
Elymus villosus	Generalist	0.047692892	0.8395	10	NP	FACU
Enemion biternatum	Generalist	0.034873703	1	2	SL (NC/SC/VA)	FACU
Eragrostis hirsuta	Generalist	0.084631842	0.1084	3	NP	UPL
Eragrostis spectabilis	Generalist	0.070366658	0.2607	6	NP	UPL
Erianthus alopecuroides	Generalist	0.063550345	0.1916	2	NP	FAC
Erianthus contortus	Generalist	0.029901547	1	2	NP	N/A
Erigenia bulbosa	Generalist	0.055703622	0.5316	7	SL (NC)	N/A
Erigeron pulchellus	Generalist	0.058695493	0.6139	19	NP	FACU
Erythronium umbilicatum	Generalist	0.045670314	0.9274	4	NP	FAC
Eupatorium compositifolium	Generalist	0.062778276	0.1669	3	NP	FAC
Euphorbia commutata	Generalist	0.033083093	1	2	SL (NC)	FACU
*Euphorbia marginata**	Generalist	0.033083093	1	2	NP	UPL
Euphorbia mercurialina	Generalist	0.049333865	0.7338	4	SL (NC)	N/A
Eurybia mirabilis	Generalist	0.042717883	1	3	SL (NC)	N/A
Eurybia schreberi	Generalist	0.033083093	1	2	NP	N/A
Euthamia caroliniana	Generalist	0.065850048	0.1875	2	NP	FAC
Euthamia graminifolia	Generalist	0.033083093	1	2	NP	FAC
Eutrochium fistulosum	Generalist	0.071531296	0.4968	22	NP	FACW
Fimbristylis autumnalis	Generalist	0.065502914	0.1222	3	NP	FACW
Fleischmannia incarnata	Generalist	0.072360023	0.1516	3	SL (NC/VA)	FAC
Fragaria virginiana	Generalist	0.087362187	0.2209	65	NP	FACU
Frasera caroliniensis	Generalist	0.091831978	0.145	3	SL (NC/SC)	N/A
Galax urceolata	Generalist	0.074050195	0.3314	24	NP	FACU
Galium lanceolatum	Generalist	0.033083093	1	2	NP	N/A
Galium latifolium	Generalist	0.040307439	0.7014	22	NP	N/A
Galium tinctorium	Generalist	0.039581612	0.9196	11	NP	OBL
Gentiana saponaria	Generalist	0.04457785	0.8558	4	NP	FACW
Gentiana villosa	Generalist	0.104876515	0.1111	18	NP	N/A

Table 2.4: (Continued).

Gillenia trifoliata	Generalist	0.059383326	0.6309	18	NP	N/A
*Glechoma hederacea**	Generalist	0.065712471	0.4625	19	NP	FACU
Glyceria septentrionalis	Generalist	0.034660277	1	2	NP	OBL
Glyceria striata	Generalist	0.052368876	0.5539	42	NP	OBL
Gratiola neglecta	Generalist	0.034873703	1	2	NP	OBL
Gratiola virginiana	Generalist	0.0787408	0.1172	10	NP	OBL
Gymnopogon ambiguus	Generalist	0.062778276	0.1729	3	NP	N/A
Hackelia virginiana	Generalist	0.033083093	1	2	SL (NC/ SC)	FACU
Hedeoma pulegioides	Generalist	0.045944834	0.8371	8	NP	N/A
Helenium brevifolium	Generalist	0.038636574	1	3	SL (NC/ SC/ VA)	OBL
Helianthus decapetalus	Generalist	0.042107096	1	5	NP	FACU
Helianthus laevigatus	Generalist	0.034873703	1	2	SL (NC/ SC)	N/A
Helianthus microcephalus	Generalist	0.030157101	1	3	NP	UPL
Helianthus schweinitzii	Generalist	0.062778276	0.1695	3	FL	N/A
Heliopsis helianthoides	Generalist	0.057396373	0.607	8	NP	FACU
Heuchera caroliniana	Generalist	0.034873703	1	2	SL (VA)	N/A
Hexastylis arifolia	Generalist	0.075396917	0.2999	154	NP	FAC
Hexastylis heterophylla	Generalist	0.044246576	1	6	NP	N/A
Hexastylis lewisii	Generalist	0.047887952	0.9237	4	NP	N/A
Hexastylis naniflora	Generalist	0.05381235	0.4066	3	FL	N/A
Hibiscus laevis	Generalist	0.066462116	0.107	2	NP	OBL
Hieracium gronovii	Generalist	0.068609771	0.4674	23	NP	UPL
Hieracium marianum	Generalist	0.047887952	0.93	4	NP	N/A
Hieracium paniculatum	Generalist	0.059226301	0.6056	6	NP	N/A
Homalosorus pycnocarpos	Generalist	0.041370928	1	3	NP	N/A
Houstonia caerulea	Generalist	0.01419818	0.9661	83	NP	FACU
Houstonia purpurea	Generalist	0.010056973	0.9741	135	NP	N/A
Huperzia lucidula	Generalist	0.069811111	0.3504	8	NP	FACW
Hydrastis canadensis	Generalist	0.034730397	1	2	SL (NC)	N/A
Hydrophyllum canadense	Generalist	0.093467243	0.121	19	SL (SC)	FACU
Hylodesmum glutinosum	Generalist	0.052674445	0.7477	12	NP	N/A
Hylodesmum pauciflorum	Generalist	0.066487637	0.5056	8	NP	N/A
*Hypericum perforatum**	Generalist	0.065850048	0.1947	2	NP	FAC
Hypericum virgatum	Generalist	0.033083093	1	2	NP	FACU

Table 2.4: (Continued).

Hypericum walteri	Generalist	0.054229966	0.6412	11	NP	OBL
Hypoxis hirsuta	Generalist	0.040057738	0.6966	57	NP	FAC
Impatiens capensis	Generalist	0.045197734	0.6487	50	NP	FACW
Impatiens pallida	Generalist	0.09638902	0.105	19	SL (SC)	FACW
Iris cristata	Generalist	0.077539398	0.2867	48	NP	N/A
*Iris pseudacorus**	Generalist	0.059705909	0.2704	4	NP	OBL
Iris verna	Generalist	0.054602895	0.5134	49	NP	N/A
Isoetes engelmannii	Generalist	0.08309559	0.1432	3	NP	OBL
Isoetes melanopoda	Generalist	0.080465787	0.112	3	FL	OBL
Isotria verticillata	Generalist	0.068747333	0.5296	8	NP	FACU
Jeffersonia diphylla	Generalist	0.062166963	0.4931	8	SL (NC)	N/A
Juncus [effusus + pylaei]	Generalist	0.058668928	0.4469	38	NP	N/A
Juncus acuminatus	Generalist	0.071302645	0.3544	9	NP	OBL
Juncus biflorus	Generalist	0.061175988	0.2635	5	NP	N/A
Juncus coriaceus	Generalist	0.028152856	0.8467	22	NP	FACW
Juncus tenuis	Generalist	0.040616813	0.7186	19	NP	FAC
Krigia dandelion	Generalist	0.096911451	0.142	16	NP	FAC
*Kummerowia stipulacea**	Generalist	0.060919512	0.2949	2	NP	FACU
Lactuca biennis	Generalist	0.065850048	0.187	2	NP	FACU
Lactuca canadensis	Generalist	0.087144126	0.172	26	NP	FACU
Lactuca floridana	Generalist	0.065128553	0.3931	12	NP	FACU
Laportea canadensis	Generalist	0.088738358	0.13	18	NP	FAC
Lechea minor	Generalist	0.066462116	0.1079	2	NP	N/A
Lechea pulchella	Generalist	0.060919512	0.2816	2	NP	N/A
Lechea racemulosa	Generalist	0.060848393	0.2389	5	NP	N/A
Leersia oryzoides	Generalist	0.049005564	0.7239	6	NP	OBL
Leersia virginica	Generalist	0.091798378	0.1758	77	NP	FACW
Lespedeza angustifolia	Generalist	0.066462116	0.108	2	NP	FAC
Lespedeza violacea	Generalist	0.083907753	0.2285	59	NP	N/A
Liatris aspera	Generalist	0.034873703	1	2	SL (NC)	N/A
Liatris pilosa	Generalist	0.058367164	0.5223	10	NP	N/A
Liatris squarrosa	Generalist	0.060302881	0.224	4	NP	N/A
Liatris virgata	Generalist	0.049043077	0.2943	2	NP	N/A
Ligusticum canadense	Generalist	0.101543243	0.1463	45	NP	FAC
Lilium michauxii	Generalist	0.084605785	0.1969	23	NP	FAC
Lilium superbum	Generalist	0.033083093	1	2	NP	FACW
Lindernia monticola	Generalist	0.086867588	0.1022	2	NP	OBL
Linum striatum	Generalist	0.084631842	0.1064	3	NP	FACW

Table 2.4: (Continued).

Lithospermum virginianum	Generalist	0.05381235	0.3961	3	SL (VA)	N/A
Lobelia cardinalis	Generalist	0.057252896	0.5853	10	NP	FACW
Lobelia georgiana	Generalist	0.042481579	1	5	NP	N/A
Lobelia inflata	Generalist	0.049736203	0.7828	13	NP	FACU
Lobelia spicata	Generalist	0.05454625	0.61	10	NP	FAC
*Lolium arundinaceum**	Generalist	0.089488483	0.1444	17	NP	N/A
Lorinseria areolata	Generalist	0.025504708	0.897	20	NP	FACW
Luzula acuminata	Generalist	0.061899787	0.5747	20	NP	FAC
Luzula bulbosa	Generalist	0.03804977	0.9892	5	NP	FACU
Luzula echinata	Generalist	0.105176332	0.1307	52	NP	FACU
Luzula multiflora	Generalist	0.047526301	1	4	NP	FACU
Lycopodioides apodum	Generalist	0.084631842	0.1101	3	NP	N/A
Lycopus americanus	Generalist	0.055875378	0.3074	5	NP	OBL
Lycopus rubellus	Generalist	0.034873703	1	2	NP	OBL
Lycopus virginicus	Generalist	0.061055571	0.4531	58	NP	OBL
Lysimachia ciliata	Generalist	0.087315024	0.1865	29	NP	FACW
Lysimachia lanceolata	Generalist	0.081820255	0.1165	4	NP	FAC
*Lysimachia nummularia**	Generalist	0.03748773	0.9265	10	NP	FACW
Lysimachia quadrifolia	Generalist	0.047621268	0.5903	29	NP	FACU
Malaxis unifolia	Generalist	0.065292372	0.6049	7	NP	FAC
Mecardonia acuminata	Generalist	0.060437259	0.2311	4	NP	OBL
Melica mutica	Generalist	0.106329449	0.1018	113	NP	N/A
Mentha canadensis	Generalist	0.045805216	0.3235	3	NP	N/A
Mertensia virginica	Generalist	0.06002478	0.4814	7	NP	FACW
Micranthes virginiensis	Generalist	0.040816497	0.6833	37	NP	FAC
*Microstegium vimineum**	Generalist	0.04117504	0.6718	177	NP	FAC
Mimulus alatus	Generalist	0.060919512	0.2861	2	NP	OBL
Monarda clinopodia	Generalist	0.05815428	0.6052	6	NP	FACU
Monarda fistulosa	Generalist	0.082193928	0.1621	6	NP	UPL
Monotropa uniflora	Generalist	0.104999259	0.1165	51	NP	FACU
Monotropsis odorata	Generalist	0.033083093	1	2	SL (NC/SC)	N/A
Muhlenbergia frondosa	Generalist	0.066462116	0.1046	2	NP	FAC
Muhlenbergia schreberi	Generalist	0.041103913	0.9237	3	NP	FAC
Muhlenbergia sylvatica	Generalist	0.065850048	0.1922	2	NP	FAC
Muhlenbergia tenuiflora	Generalist	0.041103913	0.9247	3	NP	FACU
*Murdannia keisak**	Generalist	0.053959227	0.5931	9	NP	OBL
Myosotis macrosperma	Generalist	0.053733623	0.7472	13	NP	FAC
Nabalus altissimus	Generalist	0.051117323	0.5523	135	NP	FACU

Table 2.4: (Continued).

Nemophila aphylla	Generalist	0.058221691	0.5467	7	NP	FACW
Obolaria virginica	Generalist	0.046613082	0.8107	4	NP	N/A
Onoclea sensibilis	Generalist	0.068321027	0.4285	18	NP	FACW
Ophioglossum pycnostichum	Generalist	0.046613082	0.8044	4	NP	N/A
Osmunda claytoniana	Generalist	0.065292372	0.6079	7	NP	FAC
Osmunda spectabilis	Generalist	0.075738224	0.3185	25	NP	OBL
Osmundastrum cinnamomeum	Generalist	0.04414326	0.6563	46	NP	FACW
Oxalis dillenii	Generalist	0.100204853	0.1349	138	NP	FACU
Oxalis florida	Generalist	0.042717883	1	3	NP	N/A
Oxalis stricta	Generalist	0.07636819	0.2938	46	NP	FACU
Oxalis violacea	Generalist	0.03532834	0.7544	75	NP	N/A
Oxypolis rigidior	Generalist	0.055190763	0.6342	7	NP	OBL
Packera obovata	Generalist	0.072333336	0.3443	10	NP	FACU
Paronychia canadensis	Generalist	0.038347445	1	4	NP	N/A
Paronychia montana	Generalist	0.060919512	0.2779	2	NP	N/A
Parthenium auriculatum	Generalist	0.066535633	0.2314	8	SL (NC)	N/A
Paspalum laeve	Generalist	0.064917778	0.1604	3	NP	FAC
Paspalum setaceum	Generalist	0.075487554	0.1288	5	NP	FACU
Pedicularis canadensis	Generalist	0.034873703	1	2	NP	FACU
Pellaea atropurpurea	Generalist	0.065850048	0.1869	2	SL (SC)	N/A
Peltandra virginica	Generalist	0.056749481	0.6505	15	NP	OBL
*Perilla frutescens**	Generalist	0.065969671	0.188	4	NP	FACU
*Persicaria longiseta**	Generalist	0.00314931	0.9955	35	NP	FAC
Persicaria pensylvanica	Generalist	0.07737496	0.1692	4	NP	FACW
Persicaria setacea	Generalist	0.08237805	0.1284	6	NP	OBL
Phacelia covillei	Generalist	0.037177033	0.8506	3	SL (NC/VA)	FACW
Phlox divaricata	Generalist	0.054274187	0.6752	5	NP	FACU
Physalis longifolia	Generalist	0.040272765	1	3	NP	N/A
Physalis pubescens	Generalist	0.055427291	0.6053	8	NP	FACU
Physalis virginiana	Generalist	0.029065094	0.8232	31	NP	N/A
Physostegia virginiana	Generalist	0.060250141	0.2426	4	NP	FAC
Phytolacca americana	Generalist	0.085335742	0.2311	54	NP	FACU
Pilea fontana	Generalist	0.041534864	0.9222	4	SL (SC)	FACW
Pilea pumila	Generalist	0.060811789	0.5099	28	NP	FACW
*Pilosella caespitosa**	Generalist	0.034873703	1	2	NP	N/A
*Pilosella officinarum**	Generalist	0.033083093	1	2	NP	N/A
*Plantago aristata**	Generalist	0.058602353	0.1955	2	NP	N/A
Platanthera clavellata	Generalist	0.005832966	1	10	NP	FACW

Table 2.4: (Continued).

Platanthera lacera	Generalist	0.033083093	1	2	SL (SC)	FACW
Pleopeltis michauxiana	Generalist	0.080199127	0.2552	48	NP	N/A
Pluchea camphorata	Generalist	0.043655707	0.4048	3	NP	FACW
*Poa annua**	Generalist	0.065850048	0.1962	2	NP	FACU
Poa autumnalis	Generalist	0.092896376	0.1954	37	NP	FAC
*Poa compressa**	Generalist	0.081708311	0.3046	30	NP	FACU
*Poa pratensis**	Generalist	0.066979385	0.3872	15	NP	FACU
Polygala curtissii	Generalist	0.071826612	0.1071	3	NP	N/A
Polygala senega	Generalist	0.047887952	0.9263	4	NP	FACU
Polymnia canadensis	Generalist	0.036709729	1	3	NP	N/A
Polypodium appalachianum	Generalist	0.07526033	0.2116	6	NP	N/A
Polypodium virginianum	Generalist	0.082159166	0.2265	23	NP	N/A
*Potentilla indica**	Generalist	0.036635274	0.7619	25	NP	FACU
Potentilla simplex	Generalist	0.078122367	0.2814	61	NP	FACU
Prosartes lanuginosa	Generalist	0.054274187	0.6782	5	NP	N/A
Pycnanthemum montanum	Generalist	0.065850048	0.1923	2	SL (SC)	N/A
Pycnanthemum pycnanthemoides	Generalist	0.07641209	0.1625	6	NP	N/A
Ranunculus hispidus	Generalist	0.054051032	0.7444	13	NP	FAC
Ranunculus micranthus	Generalist	0.05815428	0.6084	6	SL (NC)	FACU
Ranunculus recurvatus	Generalist	0.10320157	0.1436	43	NP	FAC
Rhexia mariana	Generalist	0.066462116	0.1104	2	NP	OBL
Rhexia nashii	Generalist	0.066462116	0.1061	2	NP	OBL
Rhynchosia tomentosa	Generalist	0.068125119	0.1966	5	NP	N/A
Rhynchospora caduca	Generalist	0.050420422	0.1926	2	NP	OBL
Rhynchospora capitellata	Generalist	0.077378834	0.1563	4	NP	OBL
Rhynchospora corniculata	Generalist	0.066462116	0.1047	2	NP	OBL
Rhynchospora recognita	Generalist	0.066462116	0.1119	2	NP	FACW
Rudbeckia laciniata	Generalist	0.092195373	0.1208	18	NP	FACW
Ruellia caroliniensis	Generalist	0.08489693	0.2303	97	NP	FACU
Ruellia humilis	Generalist	0.036337222	1	4	SL (NC)	FACU
Ruellia purshiana	Generalist	0.062142427	0.5914	19	SL (NC)	N/A
Sagittaria australis	Generalist	0.060919512	0.2934	2	NP	OBL
Sagittaria fasciculata	Generalist	0.032052478	1	2	FL	OBL
Sanguisorba canadensis	Generalist	0.048374703	0.8608	4	SL (SC)	FACW
Sanicula marilandica	Generalist	0.041103913	0.9216	3	NP	FACU
Sanicula odorata	Generalist	0.07670057	0.3672	29	NP	FACU
Sanicula trifoliata	Generalist	0.081898212	0.3006	11	SL (SC)	N/A
*Saponaria officinalis**	Generalist	0.078011895	0.1373	4	NP	FACU

Table 2.4: (Continued).

Saururus cernuus	Generalist	0.086059132	0.2153	34	NP	OBL
Sceptridium biternatum	Generalist	0.075142624	0.2607	19	NP	FAC
Scirpus atrovirens	Generalist	0.037669813	0.9247	3	NP	OBL
Scirpus polyphyllus	Generalist	0.04650927	0.7886	4	NP	OBL
Scleria oligantha	Generalist	0.079725179	0.2603	171	NP	FACU
Scrophularia marilandica	Generalist	0.047526301	1	4	NP	FACU
Scutellaria leonardii	Generalist	0.04119273	0.9346	4	SL (NC)	N/A
Scutellaria nervosa	Generalist	0.059226301	0.616	6	SL (NC/ SC)	FAC
Scutellaria ovata	Generalist	0.043840004	0.9439	8	NP	FACU
Scutellaria serrata	Generalist	0.060612796	0.5221	14	NP	N/A
Sedum glaucophyllum	Generalist	0.071217228	0.1988	8	SL (NC)	N/A
Sedum ternatum	Generalist	0.057244282	0.6846	15	NP	FACU
*Setaria faberi**	Generalist	0.066462116	0.1031	2	NP	UPL
Silene caroliniana	Generalist	0.049510101	0.7289	7	NP	N/A
Silene stellata	Generalist	0.094519301	0.1321	28	NP	N/A
Silene virginica	Generalist	0.095319361	0.1624	34	NP	N/A
Silphium asteriscus	Generalist	0.052509814	0.6095	23	NP	N/A
Silphium reniforme	Generalist	0.034873703	1	2	NP	N/A
Sisyrinchium albidum	Generalist	0.060919512	0.291	2	NP	FAC
Sisyrinchium dichotomum	Generalist	0.033083093	1	2	FL	N/A
Sisyrinchium mucronatum	Generalist	0.049045655	0.8112	12	NP	FAC
Sisyrinchium nashii	Generalist	0.063509177	0.1898	4	NP	FAC
Smallanthus uvedalia	Generalist	0.048576484	0.808	11	NP	N/A
Solidago curtisii	Generalist	0.058544637	0.5337	11	NP	FACU
Solidago flaccidifolia	Generalist	0.033083093	1	2	NP	N/A
Solidago gigantea	Generalist	0.058554773	0.632	6	NP	FACW
Solidago juncea	Generalist	0.099166129	0.1012	24	NP	N/A
Solidago pinetorum	Generalist	0.059545742	0.4449	12	NP	N/A
Solidago ptarmicoides	Generalist	0.05507472	0.288	2	SL (NC/ SC)	N/A
Solidago puberula	Generalist	0.033083093	1	2	NP	FACU
Solidago radula	Generalist	0.05381235	0.4137	3	SL (NC)	N/A
Solidago virgata	Generalist	0.066462116	0.1039	2	NP	N/A
Sphenopholis intermedia	Generalist	0.033083093	1	2	NP	FAC
Sphenopholis nitida	Generalist	0.064663863	0.4028	38	NP	FAC
Sphenopholis pensylvanica	Generalist	0.092102788	0.1112	3	NP	OBL

Table 2.4: (Continued).

Spigelia marilandica	Generalist	0.062472796	0.4572	13	SL (NC)	N/A
Spiranthes lacera	Generalist	0.060919512	0.2857	2	NP	FACU
Stachys latidens	Generalist	0.034873703	1	2	NP	FAC
Stachys tenuifolia	Generalist	0.034873703	1	2	SL (NC/SC)	FACW
Steinchisma hians	Generalist	0.08309559	0.1381	3	SL (VA)	FACW
*Stellaria media**	Generalist	0.09349234	0.1676	39	NP	UPL
Symphyotrichum concolor	Generalist	0.068111064	0.1939	4	NP	N/A
Symphyotrichum cordifolium	Generalist	0.081372603	0.244	24	NP	N/A
Symphyotrichum laeve	Generalist	0.034873703	1	2	SL (NC/SC)	FACU
Symphyotrichum lanceolatum	Generalist	0.052222512	0.6761	5	NP	FACW
Symphyotrichum lateriflorum	Generalist	0.098534364	0.144	129	NP	FACW
Symphyotrichum puniceum	Generalist	0.077919134	0.1687	6	NP	OBL
Symphyotrichum undulatum	Generalist	0.089828023	0.1947	57	NP	N/A
Symplocarpus foetidus	Generalist	0.043239721	0.7177	25	NP	OBL
Tephrosia spicata	Generalist	0.064294183	0.2092	4	NP	N/A
Teucrium canadense	Generalist	0.051789444	0.7685	5	NP	FACW
Thalictrum [hepaticum + pubescens]	Generalist	0.046144436	0.8769	9	NP	N/A
Thalictrum clavatum	Generalist	0.033083093	1	2	NP	FACW
Thalictrum dioicum	Generalist	0.071200351	0.3638	9	NP	FAC
Thalictrum pubescens	Generalist	0.042717883	1	3	NP	FACW
Thaspium barbinode	Generalist	0.070545958	0.502	22	NP	FACU
Thaspium trifoliatum	Generalist	0.059107197	0.6009	19	NP	N/A
Thelypteris palustris	Generalist	0.042481579	1	5	NP	FACW
Tradescantia hirsuticaulis	Generalist	0.05381235	0.3912	3	NP	N/A
Tradescantia subaspera	Generalist	0.055062731	0.7237	14	NP	N/A
Tradescantia virginiana	Generalist	0.051789444	0.7701	5	SL (NC/SC)	FACU
Trautvetteria caroliniensis	Generalist	0.05803487	0.3111	3	SL (SC)	FACW
Trichophorum planifolium	Generalist	0.043349636	0.9019	7	NP	N/A
Trichostema brachiatum	Generalist	0.034873703	1	2	SL (NC)	N/A
Trichostema dichotomum	Generalist	0.07737496	0.1718	4	NP	UPL
Trillium cuneatum	Generalist	0.040272765	1	3	NP	N/A
Trillium discolor	Generalist	0.042107096	1	5	SL (NC/SC)	N/A
Trillium erectum	Generalist	0.034873703	1	2	NP	FACU

Table 2.4: (Continued).

Trillium rugelii	Generalist	0.042717883	1	3	SL (SC)	N/A
Trillium sessile	Generalist	0.095297054	0.1087	18	SL (NC)	UPL
Triosteum angustifolium	Generalist	0.050932881	0.7508	5	NP	FAC
Tripsacum dactyloides	Generalist	0.0727532	0.1562	4	NP	FACW
*Urtica dioica**	Generalist	0.05381235	0.4075	3	NP	FACU
Uvularia puberula	Generalist	0.05080588	0.5799	36	NP	FACU
Veratrum parviflorum	Generalist	0.033083093	1	2	NP	N/A
Veratrum virginicum	Generalist	0.051203614	0.4223	4	NP	FACW
Verbesina alternifolia	Generalist	0.074700467	0.3849	26	NP	FAC
Vernonia acaulis	Generalist	0.049200783	0.6253	9	NP	N/A
Vernonia glauca	Generalist	0.102946767	0.1268	47	NP	N/A
Veronica anagallis-aquatica	Generalist	0.067483759	0.189	2	NP	OBL
Viola affinis	Generalist	0.041217243	0.9212	3	NP	FACW
Viola canadensis	Generalist	0.043411822	0.878	6	NP	FAC
Viola cucullata	Generalist	0.064092122	0.565	18	NP	FACW
Viola eriocarpa	Generalist	0.084768793	0.2026	14	NP	N/A
Viola hastata	Generalist	0.02722783	0.9503	10	NP	UPL
Viola hirsutula	Generalist	0.091483852	0.1738	15	NP	FACU
Viola pedata	Generalist	0.04440598	0.7787	7	NP	FACU
Viola rotundifolia	Generalist	0.039281117	1	4	NP	FAC
Viola sagittata	Generalist	0.070497869	0.1639	7	NP	FAC
Viola subsinuata	Generalist	0.047810317	0.888	10	NP	FACU
Viola tripartita	Generalist	0.033083093	1	2	SL (SC)	N/A
Xanthium strumarium	Generalist	0.058602353	0.1934	2	NP	FAC
Xerophyllum asphodeloides	Generalist	0.048016521	0.7309	5	SL (SC)	N/A
Zephyranthes atamasco	Generalist	0.043411822	0.8744	6	NP	FACW
Zizia aptera	Generalist	0.042531678	0.9136	10	NP	FAC
Zizia trifoliata	Generalist	0.041271615	0.7211	20	NP	FACU
Agalinis tenuifolia	Strong Open	0.120165403	0.0158	8	NP	FAC
Aletris farinosa	Strong Open	0.090724705	0.0465	2	NP	FAC
*Allium vineale**	Strong Open	0.136666173	0.0107	13	NP	FACU
Andropogon gyrans	Strong Open	0.157624475	0.0017	13	NP	FACU
Andropogon ternarius	Strong Open	0.095483226	0.0265	5	NP	FACU
Andropogon virginicus	Strong Open	0.315312205	0.0001	58	NP	FACU
*Anthoxanthum odoratum**	Strong Open	0.195560372	0.0001	10	NP	FACU
Apocynum cannabinum	Strong Open	0.191782033	0.0004	52	NP	FACU
Aristida dichotoma	Strong Open	0.26226237	0.0001	13	NP	UPL
Aristida purpurascens	Strong Open	0.231113313	0.0001	7	NP	FAC
*Artemisia annua**	Strong Open	0.13392187	0.005	5	NP	FACU

Table 2.4: (Continued).

Asclepias tuberosa	Strong Open	0.102748165	0.0441	13	NP	N/A
Asplenium resiliens	Weak Open	0.097436923	0.0996	2	NP	N/A
Baptisia australis	Strong Open	0.15447653	0.0022	7	NP	FACU
Baptisia tinctoria	Strong Open	0.237676601	0.0001	15	NP	N/A
Bidens aristosa	Strong Open	0.140151759	0.0072	10	NP	FACW
Bidens cernua	Strong Open	0.138675049	0.0034	2	NP	OBL
Bidens laevis	Strong Open	0.138675049	0.0021	2	NP	OBL
Bryodesma rupestre	Strong Open	0.204738226	0.0001	8	NP	N/A
Bulbostylis capillaris	Strong Open	0.251873747	0.0001	8	NP	FACU
Carex abscondita	Weak Open	0.093319639	0.0759	4	NP	FAC
Chamaecrista nictitans	Strong Open	0.239019503	0.0001	32	NP	FACU
Cleistesiopsis [divaricata + oricamporum]	Strong Open	0.100950871	0.0437	2	NP	N/A
Commelina erecta	Strong Open	0.171389073	0.001	20	NP	FAC
Conoclinium coelestinum	Weak Open	0.095362469	0.0895	3	NP	FAC
Coreopsis auriculata	Strong Open	0.135259647	0.0088	6	NP	N/A
Croton willdenowii	Strong Open	0.317978174	0.0001	15	NP	N/A
Danthonia sericea	Strong Open	0.312391293	0.0001	101	NP	FACU
Danthonia spicata	Strong Open	0.238380916	0.0002	430	NP	N/A
*Datura stramonium**	Weak Open	0.087671758	0.0968	2	NP	N/A
*Daucus carota**	Strong Open	0.228429807	0.0001	8	NP	UPL
Desmodium lineatum	Strong Open	0.136923368	0.0052	4	NP	N/A
Desmodium strictum	Strong Open	0.358082321	0.0001	14	SL (VA)	N/A
Desmodium tenuifolium	Weak Open	0.087671758	0.0945	2	SL (VA)	FAC
Diamorpha smallii	Strong Open	0.175992759	0.0001	3	SL (VA)	FACW
Dichanthelium acuminatum	Strong Open	0.262391295	0.0001	41	NP	FAC
Dichanthelium consanguineum	Strong Open	0.186328245	0.0001	5	SL (VA)	FACU
Dichanthelium laxiflorum	Strong Open	0.267335818	0.0001	182	NP	FACU
Dichanthelium leucothrix	Strong Open	0.148962944	0.0006	4	NP	FACW
Dichanthelium meridionale	Strong Open	0.090644796	0.0411	6	NP	N/A
Dichanthelium oligosanthes	Strong Open	0.146254485	0.0028	2	NP	FACU
Dichanthelium ovale	Weak Open	0.084926527	0.0751	3	NP	FACU
Dichanthelium scoparium	Strong Open	0.185293262	0.0003	16	NP	FACW
Dichanthelium sphaerocarpon	Strong Open	0.155882135	0.0037	21	NP	FACU
Dichanthelium villosissimum	Weak Open	0.099342494	0.0619	15	NP	N/A
Diodella teres	Strong Open	0.208259435	0.0001	9	NP	N/A
Echinacea laevigata	Weak Open	0.093171508	0.05	2	FL	N/A
Echinochloa muricata	Strong Open	0.117417461	0.0101	3	NP	FACW

Table 2.4: (Continued).

Eclipta prostrata	Strong Open	0.097300088	0.0189	4	NP	FAC
Eleocharis compressa	Strong Open	0.11420499	0.0197	4	NP	OBL
Elymus virginicus	Strong Open	0.144412376	0.0064	41	NP	FACW
Erianthus giganteus	Strong Open	0.129070479	0.0026	3	NP	FACW
Erigeron annuus	Weak Open	0.099342494	0.0616	15	NP	FACU
Eupatorium altissimum	Strong Open	0.091719635	0.0309	5	NP	N/A
Eupatorium capillifolium	Strong Open	0.249585652	0.0001	37	NP	FACU
Eupatorium hyssopifolium	Strong Open	0.260900352	0.0001	56	NP	N/A
Eupatorium perfoliatum	Strong Open	0.098641477	0.0422	3	NP	FACW
Eupatorium rotundifolium	Strong Open	0.340599914	0.0001	23	NP	FAC
Eupatorium torreyanum	Strong Open	0.230427383	0.0001	12	NP	N/A
Euphorbia corollata	Strong Open	0.181721817	0.0021	156	NP	N/A
Euphorbia humistrata	Strong Open	0.117417461	0.0101	3	NP	FAC
Festuca octoflora	Strong Open	0.171563827	0.0001	5	NP	UPL
Geranium carolinianum	Strong Open	0.143654329	0.0002	4	NP	N/A
Gillenia stipulata	Strong Open	0.099914363	0.0429	2	SL (NC/VA)	N/A
Gymnopogon brevifolius	Strong Open	0.163824771	0.0016	6	NP	FACU
Helianthus occidentalis	Strong Open	0.093482158	0.0489	4	NP	UPL
*Holcus lanatus**	Strong Open	0.10222528	0.0425	2	NP	FAC
Houstonia pusilla	Strong Open	0.138185907	0.008	4	NP	FAC
Houstonia tenuifolia	Strong Open	0.161441363	0.0029	18	NP	N/A
Hypericum drummondii	Strong Open	0.112367938	0.0083	3	NP	UPL
Hypericum gentianoides	Strong Open	0.347970113	0.0001	29	NP	UPL
Hypericum mutilum	Strong Open	0.130637091	0.0066	4	NP	FACW
Hypericum setosum	Weak Open	0.086867588	0.0985	2	SL (VA)	OBL
*Hypochaeris radicata**	Weak Open	0.084926527	0.0704	3	NP	UPL
Juncus brachycarpus	Strong Open	0.146254485	0.0022	2	NP	FACW
Juncus debilis	Strong Open	0.135259647	0.0101	6	NP	OBL
Juncus marginatus	Strong Open	0.195587471	0.0001	5	NP	FACW
Justicia americana	Strong Open	0.136583302	0.0061	3	NP	OBL
Krigia virginica	Strong Open	0.15344824	0.0029	7	NP	UPL
*Kummerowia striata**	Strong Open	0.094357084	0.0163	4	NP	FACU
*Lespedeza bicolor**	Strong Open	0.129092757	0.0021	5	NP	N/A
*Lespedeza cuneata**	Strong Open	0.253460342	0.0001	39	NP	FACU
Lespedeza repens	Strong Open	0.13546747	0.0297	99	NP	N/A
Lespedeza stuevei	Strong Open	0.274507312	0.0001	16	NP	N/A
*Leucanthemum vulgare**	Strong Open	0.265543885	0.0001	9	NP	UPL
Liatris squarrulosa	Strong Open	0.100950871	0.0446	2	SL (NC)	N/A

Table 2.4: (Continued).

Lobelia puberula	Strong Open	0.134425614	0.0018	3	NP	FACW
Manfreda virginica	Strong Open	0.116748696	0.0211	11	NP	N/A
Marshallia legrandii	Strong Open	0.101839204	0.045	2	SL (NC/VA)	N/A
Mononeuria glabra	Strong Open	0.276784355	0.0001	9	NP	N/A
Muhlenbergia capillaris	Strong Open	0.248122666	0.0001	9	NP	FACU
Myosotis verna	Weak Open	0.095362469	0.0886	3	NP	FAC
Myriopteris lanosa	Strong Open	0.197548834	0.0001	21	NP	N/A
Nabalus trifoliolatus	Strong Open	0.157766982	0.003	13	NP	N/A
Nothoscordum bivalve	Weak Open	0.087671758	0.096	2	NP	FACU
Nuttallanthus canadensis	Strong Open	0.212236173	0.0003	17	NP	N/A
Oenothera fruticosa complex	Strong Open	0.27963434	0.0001	29	NP	N/A
Orontium aquaticum	Weak Open	0.095362469	0.0882	3	NP	OBL
Packera aurea	Strong Open	0.244721367	0.0001	19	NP	FACW
Packera paupercula	Strong Open	0.118706765	0.0195	17	SL (NC)	FAC
Panicum dichotomiflorum	Strong Open	0.287658114	0.0001	28	NP	FACW
Panicum philadelphicum	Strong Open	0.168665842	0.0007	6	NP	FAC
Parthenium integrifolium	Strong Open	0.265860933	0.0001	45	NP	N/A
Paspalum floridanum	Weak Open	0.097436923	0.0957	2	NP	FACW
Persicaria lapathifolia	Strong Open	0.134425614	0.0034	3	NP	FACW
Persicaria punctata	Strong Open	0.121088383	0.0146	15	NP	OBL
Phemeranthus piedmontanus	Strong Open	0.203642472	0.0001	5	SL (NC/VA)	N/A
Phemeranthus teretifolius	Strong Open	0.281732808	0.0001	15	NP	N/A
Plantago virginica	Strong Open	0.193004445	0.0001	5	NP	UPL
Polygala lutea	Strong Open	0.117417461	0.0072	3	NP	FACW
Polygala verticillata	Strong Open	0.155109343	0.0005	5	NP	UPL
Polypremum procumbens	Strong Open	0.18324106	0.0001	5	NP	UPL
Potentilla canadensis	Strong Open	0.318842466	0.0001	181	NP	N/A
Prunella vulgaris	Strong Open	0.147053516	0.0028	14	NP	FACU
Pseudognaphalium obtusifolium	Strong Open	0.368522348	0.0001	45	NP	N/A
Ptilimnium capillaceum	Strong Open	0.138675049	0.0018	2	NP	OBL
Pycnanthemum tenuifolium	Strong Open	0.244610736	0.0001	47	NP	FACW
Rhynchospora globularis	Strong Open	0.109442988	0.0333	8	NP	FACW
Rudbeckia hirta	Weak Open	0.08584594	0.0994	3	NP	FACU
*Rumex acetosella**	Strong Open	0.142150344	0.0043	3	NP	UPL
*Rumex crispus**	Strong Open	0.097377293	0.0469	4	NP	FAC
Sagittaria latifolia	Strong Open	0.108637156	0.0257	5	NP	OBL

Table 2.4: (Continued).

Salvia lyrata	Weak Open	0.118296851	0.0694	69	NP	FACU
Schizachyrium scoparium	Strong Open	0.413384594	0.0001	111	NP	FACU
Scleria ciliata	Strong Open	0.176274065	0.0001	6	NP	FAC
Scleria pauciflora	Strong Open	0.23107721	0.0001	23	NP	FACU
Scutellaria integrifolia	Strong Open	0.250620571	0.0002	115	NP	FACW
*Setaria viridis**	Strong Open	0.101194062	0.0096	3	NP	N/A
Silphium compositum	Strong Open	0.254685206	0.0001	14	NP	N/A
Silphium terebinthinaceum	Weak Open	0.083532011	0.0952	7	SL (NC/SC/VA)	FACU
Sisyrinchium angustifolium	Strong Open	0.16584037	0.002	23	NP	FACW
Solanum carolinense	Strong Open	0.108001366	0.0471	21	NP	FACU
Solidago [patula + salicina]	Strong Open	0.192710533	0.0001	6	NP	N/A
Solidago altissima	Strong Open	0.117039593	0.0152	7	NP	FACU
Solidago bicolor	Weak Open	0.109835196	0.0559	30	SL (SC)	N/A
Solidago petiolaris	Weak Open	0.096104398	0.0624	10	NP	N/A
Solidago speciosa	Strong Open	0.150480263	0.0035	11	NP	N/A
Sorghastrum nutans	Strong Open	0.277745206	0.0001	45	NP	FACU
Sphenopholis obtusata	Strong Open	0.10803648	0.0271	6	NP	FAC
Spiranthes cernua	Weak Open	0.095362469	0.0855	3	NP	FACW
Sporobolus vaginiflorus	Strong Open	0.112384835	0.0167	5	NP	N/A
Stylosanthes biflora	Strong Open	0.171278885	0.0019	34	NP	N/A
Symphyotrichum phlogifolium	Weak Open	0.097436923	0.0937	2	NP	N/A
Symphyotrichum pilosum	Strong Open	0.267898307	0.0001	24	NP	FAC
Symphyotrichum racemosum	Strong Open	0.112500149	0.0235	11	NP	FACW
Taenidia integerrima	Weak Open	0.092431354	0.062	8	NP	N/A
Tephrosia virginiana	Strong Open	0.193192667	0.0007	54	NP	N/A
Tradescantia ohiensis	Strong Open	0.142150344	0.0054	3	NP	FAC
Tridens flavus	Strong Open	0.271279725	0.0001	16	NP	FACU
*Trifolium campestre**	Strong Open	0.130674304	0.0031	2	NP	N/A
*Trifolium repens**	Strong Open	0.134425614	0.0019	3	NP	FACU
Triodanis perfoliata	Strong Open	0.143383808	0.0043	13	NP	FAC
Veratrum viride	Weak Open	0.076512416	0.0985	2	NP	FACW
Verbena simplex	Strong Open	0.201668971	0.0001	5	SL (SC)	N/A
Vernonia noveboracensis	Strong Open	0.095800749	0.0282	5	NP	FACW
Viola primulifolia	Strong Open	0.139482984	0.0116	22	NP	FAC
Zizia aurea	Strong Open	0.149558242	0.0035	17	NP	FAC
Galium obtusum	Weak Open+Closed	0.117085943	0.0745	59	NP	FACW
Acalypha rhomboidea	Weak Open+Semi-open	0.098385978	0.0639	9	NP	FACU

Table 2.4: (Continued).

Allium cernuum	Strong Open+Semi-open	0.149951155	0.0058	25	SL (SC)	FACU
Ambrosia artemisiifolia	Strong Open+Semi-open	0.14849293	0.009	45	NP	FACU
Andropogon gerardi	Strong Open+Semi-open	0.147608851	0.0041	17	NP	FAC
Anemone virginiana	Strong Open+Semi-open	0.125894951	0.0165	17	NP	FACU
Aquilegia canadensis	Strong Open+Semi-open	0.121097552	0.0125	10	NP	FAC
*Arthraxon hispidus**	Strong Open+Semi-open	0.099797137	0.0335	6	NP	FAC
Asclepias verticillata	Strong Open+Semi-open	0.159604997	0.0034	24	NP	FACU
Chrysopsis mariana	Strong Open+Semi-open	0.178125175	0.0008	27	NP	UPL
Conyza canadensis	Weak Open+Semi-open	0.097797415	0.0623	18	NP	N/A
Coreopsis major	Strong Open+Semi-open	0.201471697	0.0004	92	NP	N/A
Coreopsis tripteris	Strong Open+Semi-open	0.104589451	0.0397	8	NP	FAC
Cyperus strigosus	Strong Open+Semi-open	0.090967138	0.0467	6	NP	FACW
Desmodium ciliare	Strong Open+Semi-open	0.136019668	0.0107	23	NP	N/A
Dichanthelium depauperatum	Strong Open+Semi-open	0.213961686	0.0001	63	NP	N/A
Erigeron strigosus	Strong Open+Semi-open	0.195773479	0.0004	30	NP	FACU
Eupatorium pilosum	Weak Open+Semi-open	0.089175025	0.0577	7	NP	FACW
Eupatorium serotinum	Strong Open+Semi-open	0.132252156	0.019	21	NP	FAC
Gamochaeta purpurea	Strong Open+Semi-open	0.132553583	0.0137	20	NP	UPL
Helianthus divaricatus	Strong Open+Semi-open	0.126833286	0.0258	53	NP	N/A
Hypericum punctatum	Weak Open+Semi-open	0.108510468	0.0578	26	NP	FAC
Hypericum stragulum	Strong Open+Semi-open	0.138357991	0.0253	77	NP	N/A
Ionactis linariifolia	Strong Open+Semi-open	0.108677412	0.0437	13	NP	N/A
Juncus dichotomus	Strong Open+Semi-open	0.12834289	0.0193	17	NP	FACW
Lespedeza procumbens	Strong Open+Semi-open	0.134233519	0.0144	47	NP	N/A
Lespedeza virginica	Strong Open+Semi-open	0.151093423	0.0085	52	NP	N/A
Lobelia nuttallii	Weak Open+Semi-open	0.083491802	0.0971	9	NP	FACW
Ludwigia alternifolia	Weak Open+Semi-open	0.087703	0.0778	9	NP	FACW
Ludwigia palustris	Weak Open+Semi-open	0.103692197	0.0549	16	NP	OBL

Table 2.4: (Continued).

Marshallia obovata	Weak Open+Semi-open	0.092880307	0.0514	8	NP	N/A
*Melilotus albus**	Strong Open+Semi-open	0.093410863	0.0302	5	NP	N/A
Myriopteris tomentosa	Strong Open+Semi-open	0.105475504	0.0468	15	NP	N/A
Packera anonyma	Strong Open+Semi-open	0.188856921	0.0008	49	NP	UPL
Panicum virgatum	Strong Open+Semi-open	0.132128364	0.0116	14	NP	FAC
Penstemon laevigatus	Strong Open+Semi-open	0.124263978	0.0205	25	NP	FACU
Phlox subulata	Weak Open+Semi-open	0.099246515	0.0509	9	SL (NC)	N/A
Pityopsis [graminifolia + tracyi]	Strong Open+Semi-open	0.132925632	0.0128	27	NP	N/A
Sericocarpus asteroides	Strong Open+Semi-open	0.114338129	0.0388	30	NP	N/A
Sericocarpus linifolius	Strong Open+Semi-open	0.12891419	0.0181	29	NP	N/A
Setaria parviflora	Weak Open+Semi-open	0.087134548	0.0739	7	NP	FAC
Solidago nemoralis	Strong Open+Semi-open	0.121130853	0.0352	29	NP	N/A
Solidago odora	Strong Open+Semi-open	0.126965517	0.0285	52	NP	N/A
Solidago racemosa	Strong Open+Semi-open	0.122011925	0.0152	12	SL (VA)	N/A
Solidago rugosa	Strong Open+Semi-open	0.125815931	0.0256	43	NP	FAC
Sporobolus clandestinus	Weak Open+Semi-open	0.097972929	0.0521	8	NP	N/A
Symphyotrichum dumosum	Strong Open+Semi-open	0.115614995	0.0317	19	NP	FAC
Symphyotrichum grandiflorum	Strong Open+Semi-open	0.096379718	0.0408	6	NP	N/A
Symphyotrichum patens	Strong Open+Semi-open	0.120408761	0.0369	43	NP	N/A
Veronicastrum virginicum	Strong Open+Semi-open	0.119287589	0.0178	9	SL (SC)	FACU
Ageratina aromatica	Strong Semi-open	0.103210059	0.038	12	NP	N/A
Allium cuthbertii	Strong Semi-open	0.095514903	0.0163	3	SL (SC)	N/A
Antennaria plantaginifolia	Strong Semi-open	0.212385786	0.0007	114	NP	N/A
Arnoglossum atriplicifolium	Weak Semi-open	0.089136196	0.0994	11	NP	N/A
Asclepias amplexicaulis	Strong Semi-open	0.107268027	0.0232	5	NP	N/A
Asclepias viridiflora	Weak Semi-open	0.088932387	0.0601	7	NP	N/A
Asplenium trichomanes	Strong Semi-open	0.109404889	0.016	4	NP	FAC
*Barbarea vulgaris**	Strong Semi-open	0.105076197	0.0156	4	NP	FACU
Bidens bipinnata	Weak Semi-open	0.097108404	0.0632	11	NP	FACU
Boechera canadensis	Strong Semi-open	0.124349926	0.0132	18	NP	N/A
Boechera missouriensis	Strong Semi-open	0.110093764	0.0146	4	SL (NC)	N/A

Table 2.4: (Continued).

Brickellia eupatorioides	Weak Semi-open	0.088480669	0.0652	5	NP	N/A
*Bromus japonicus**	Strong Semi-open	0.097823198	0.0151	2	NP	N/A
Cardamine pensylvanica	Strong Semi-open	0.124305885	0.0109	8	NP	OBL
Carex joorii	Strong Semi-open	0.13271933	0.0114	13	NP	OBL
Carex lupulina	Weak Semi-open	0.090997509	0.0807	13	NP	OBL
Carex pensylvanica	Strong Semi-open	0.209099503	0.0002	83	NP	N/A
Carex straminea	Strong Semi-open	0.097823198	0.0132	2	NP	OBL
Cerastium velutinum	Strong Semi-open	0.145908799	0.003	7	NP	N/A
Chamaecrista fasciculata	Strong Semi-open	0.139336952	0.0092	15	NP	FACU
Chasmanthium sessiliflorum	Strong Semi-open	0.110513342	0.0335	18	NP	FAC
Cirsium discolor	Strong Semi-open	0.110913864	0.021	5	NP	UPL
Clematis ochroleuca	Strong Semi-open	0.13591518	0.0153	54	NP	N/A
Coreopsis pubescens	Strong Semi-open	0.142935949	0.0007	5	NP	FACU
Desmodium glabellum	Strong Semi-open	0.117796187	0.0294	22	NP	N/A
Desmodium laevigatum	Strong Semi-open	0.135477511	0.0139	35	NP	N/A
Desmodium marilandicum	Strong Semi-open	0.121002492	0.0227	9	NP	N/A
Desmodium nuttallii	Strong Semi-open	0.180767908	0.0007	16	NP	N/A
Desmodium paniculatum	Strong Semi-open	0.146386616	0.0161	86	NP	FACU
Desmodium viridiflorum	Weak Semi-open	0.092758462	0.0859	11	NP	N/A
Elymus riparius	Strong Semi-open	0.114998053	0.0143	4	SL (SC)	FACW
Erechtites hieraciifolius	Strong Semi-open	0.170519468	0.0054	114	NP	N/A
Eupatorium [album + subvenosum + sullivaniae + vaseyi]	Strong Semi-open	0.135565381	0.0088	22	NP	N/A
Eupatorium godfreyanum	Strong Semi-open	0.123454961	0.0229	21	NP	N/A
Eupatorium pubescens	Strong Semi-open	0.162088317	0.0024	18	NP	N/A
Eupatorium saltuense	Strong Semi-open	0.119952029	0.0078	3	SL (NC)	N/A
Eupatorium sessilifolium	Strong Semi-open	0.174328757	0.0012	29	NP	N/A
Euphorbia maculata	Weak Semi-open	0.096616383	0.0582	7	NP	FACU
Galium pilosum	Weak Semi-open	0.108508051	0.0994	115	NP	N/A
Geum [donianum + fragarioides]	Strong Semi-open	0.104052789	0.0403	10	NP	N/A
Helianthus atrorubens	Strong Semi-open	0.119306395	0.0177	6	NP	N/A
Helianthus porteri	Weak Semi-open	0.089681955	0.066	3	SL (SC)	N/A
Helianthus strumosus	Weak Semi-open	0.082462583	0.0774	5	NP	FACU
Heuchera americana	Strong Semi-open	0.160587559	0.0054	71	NP	FACU
Houstonia longifolia	Strong Semi-open	0.155852614	0.0033	21	NP	N/A
Hydatica petiolaris	Strong Semi-open	0.155230105	0.0007	5	NP	N/A
Hypericum radfordiorum	Strong Semi-open	0.097823198	0.0141	2	SL (NC)	N/A
Juncus scirpoides	Strong Semi-open	0.097823198	0.013	2	NP	FACW

Table 2.4: (Continued).

Lepidium virginicum	Strong Semi-open	0.115393151	0.0068	3	NP	FACU
Lespedeza capitata	Strong Semi-open	0.130046126	0.0071	4	NP	FACU
Lespedeza frutescens	Strong Semi-open	0.112836182	0.0212	10	NP	N/A
Lespedeza hirta	Strong Semi-open	0.119813088	0.0362	44	NP	N/A
Liatris spicata	Weak Semi-open	0.090080424	0.0661	4	NP	FAC
Oxalis grandis	Strong Semi-open	0.126197621	0.0224	7	NP	N/A
Penstemon canescens	Strong Semi-open	0.156391846	0.0023	10	NP	N/A
Persicaria hydropiperoides	Strong Semi-open	0.11228555	0.0204	5	NP	OBL
Phacelia dubia	Weak Semi-open	0.086672396	0.068	4	NP	N/A
Phlox nivalis	Weak Semi-open	0.100453962	0.0666	14	NP	N/A
Physalis heterophylla	Strong Semi-open	0.117065375	0.0279	9	NP	N/A
Piptochaetium avenaceum	Strong Semi-open	0.193692667	0.0013	162	NP	UPL
Platanthera ciliaris	Strong Semi-open	0.097823198	0.0117	2	NP	FACW
*Poa trivialis**	Strong Semi-open	0.103001891	0.0451	12	NP	FACW
Pteridium latiusculum	Strong Semi-open	0.115667747	0.0462	56	NP	N/A
Pycnanthemum incanum	Strong Semi-open	0.113478642	0.0319	10	NP	N/A
Ranunculus pusillus	Weak Semi-open	0.096624049	0.0501	6	NP	OBL
Rudbeckia fulgida	Strong Semi-open	0.095514903	0.0166	3	NP	FAC
Salvia urticifolia	Weak Semi-open	0.088032059	0.0848	11	NP	N/A
Scirpus cyperinus	Weak Semi-open	0.089681955	0.0596	3	NP	FACW
Scirpus georgianus	Weak Semi-open	0.091574974	0.0646	9	NP	OBL
Scleria triglomerata	Strong Semi-open	0.168244847	0.0011	28	NP	FAC
Scutellaria lateriflora	Weak Semi-open	0.098540215	0.0741	16	NP	FACW
Solanum ptychanthum	Strong Semi-open	0.148351788	0.0008	5	NP	FACU
Solidago erecta	Strong Semi-open	0.11288984	0.0462	28	NP	N/A
Solidago sphacelata	Strong Semi-open	0.098179849	0.0319	7	NP	N/A
Sophronanthe pilosa	Strong Semi-open	0.097823198	0.0134	2	NP	FACU
*Stellaria graminea**	Strong Semi-open	0.097823198	0.0153	2	NP	FACU
*Taraxacum officinale**	Weak Semi-open	0.102870118	0.0585	15	NP	FACU
Thalictrum revolutum	Strong Semi-open	0.134705524	0.0086	11	NP	FAC
Triosteum aurantiacum	Weak Semi-open	0.089681955	0.0594	3	NP	N/A
Triosteum perfoliatum	Strong Semi-open	0.102360281	0.0258	5	NP	N/A
*Verbascum thapsus**	Strong Semi-open	0.127070278	0.0137	12	NP	FACU
Verbesina occidentalis	Strong Semi-open	0.1354896	0.0141	45	NP	FACU
Woodsia obtusa	Weak Semi-open	0.096041012	0.0508	10	NP	N/A

FIGURES

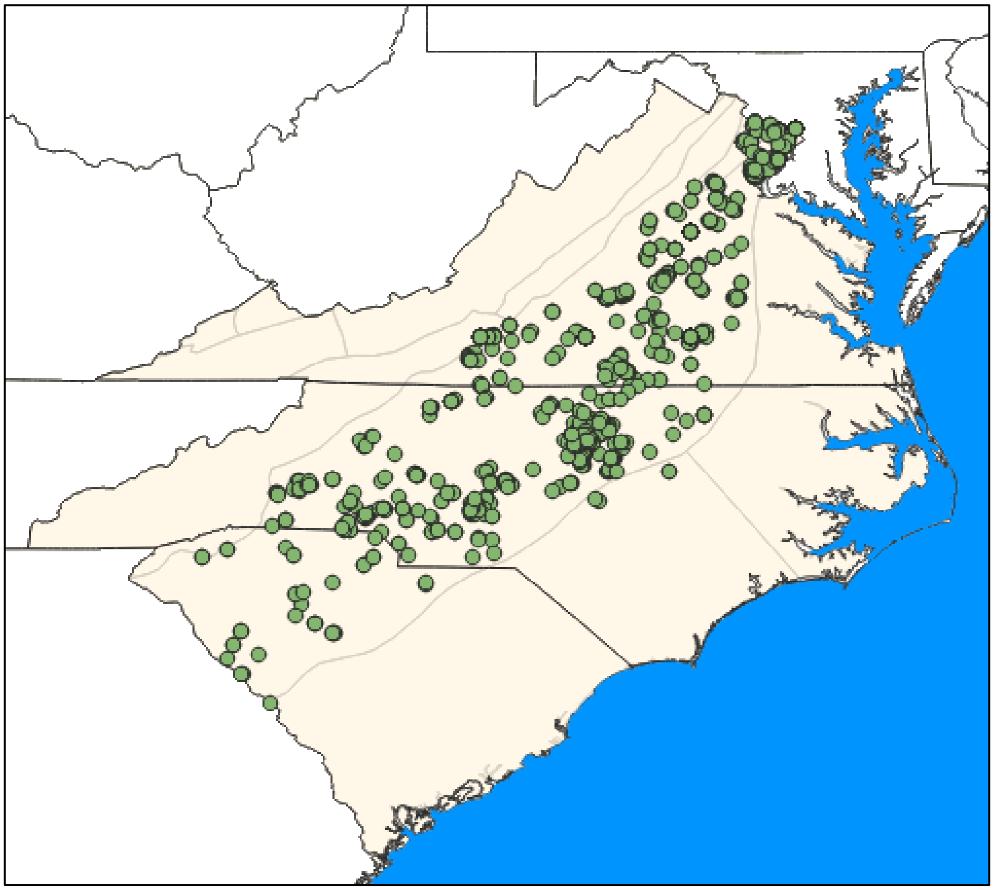

Figure 2.1: Location of the 1300 plots in the Virginia, North Carolina, and South Carolina Piedmont. Some plots have masked locations and their coordinates are only rough approximations of the true location. Figure generated with QGIS.

CHAPTER 3: Long-term Monitoring of Vegetation Plots and *Echinacea laevigata* at Picture Creek Diabase Barrens (Granville Co., NC).

ABSTRACT

Picture Creek Diabase Barrens (PCDB) hosts communities of regionally and globally rare heliophytes, including the federally-listed endangered *Echinacea laevigata* (smooth purple coneflower). Vegetation monitoring plots were established in 1993 to capture vegetation composition and response of *E. laevigata* to prescribed fire. We present the results of a 2018 resurvey that sought to address the following questions: 1) How have *E. laevigata* populations changed over time? 2) How has the associated vegetation changed over time? 3) What biotic and abiotic factors might explain any observed changes? 4) Is current management appropriate or are adjustments needed to promote more suitable habitat for the rare heliophytes? Four 0.1 hectare plots at PCDB were resurveyed using previous survey methodology. We identified all vascular plants, recorded DBH and dominance classes for woody stems, recorded counts of *E. laevigata* individuals and reproductive stems, and recorded visual cover estimates for herbaceous species in sets of 1 m^2 intensive modules (10 per plot). We also estimated coverage of additional environmental information such as canopy openings and bare soil. Due to recent (2017) prescribed fire, the previously fire-suppressed vegetation at PCDB is moving toward a more savanna-like structure with lower density of woody stems and greater coverage of herbaceous species. Fires have eliminated *Juniperus virginiana* and greatly reduced *Liquidambar styraciflua*, both previously prevalent understory and midstory "weedy" tree species. We observed steep declines (79–94%) in *E. laevigata* individuals in all plots from 2001 to 2018. However, anecdotal evidence suggests the declines are due to loss of seedlings (not counted separately from adult plants), leaving open the possibility that the total number of adult plants has remained stable. We observed increased (160–3800%) numbers of reproductive stems, and remaining individuals in the 2018 survey were mature and well-positioned to produce seed as conditions continue to move toward what is thought to be more optimal habitat. Changes in seedling recruitment and/or survival rates are not captured in lump counts of individuals or flowering stems. Future surveys should collect finer demographic information to better understand seedling recruitment dynamics and long-term population trajectory.

INTRODUCTION

In the absence of disturbance, uplands of the southeastern United States Piedmont become dominated by closed-canopy hardwood forest (Oosting 1942; Keever 1950; Christensen and Peet 1984; Nowacki and Abrams 2008). Historical accounts from early explorers suggest there was once a mosaic of both open and forested vegetation in the region, including perhaps some large extents of savanna-like vegetation. These open areas likely varied in structure (from open grasslands to woodlands and savannas) and were given many names, but they have come to be loosely called the “Piedmont prairies” (Barden 1997; Davis et al. 2002) or “Piedmont savannas” (Adams 2012) in recent literature. The earliest accounts of the Piedmont prairies in the Carolinas come from members of the 1540s De Soto expedition who, in part, passed through the Piedmont of what is now North and South Carolina. Expedition member Rodrigo de Ranjel used the terms *savana* and *llano* (grassy plain) to describe the landscape of several locations in the region, while others remarked on the ease of movement through the relatively open terrain and the abundance of grazing land for their animals (Rostlund 1947). The Piedmont prairies largely disappeared during European settlement and subsequent fire suppression of the region (Davis et al. 2002), but prairie or savanna-like vegetation could have once been maintained through fire (both natural and human set), stressful soil conditions, and grazing by now extinct or extirpated large herbivores (Juras 1997; Barden 1997; Frost 2000). Today, native heliophytes, many with midwestern Prairie Peninsula affinities, persist in areas where primarily human-mediated disturbances, such as mowing and herbicide application, reduce woody plant dominance and maintain open vegetation in an otherwise forested landscape. There are at least 277 native plant species recognized as of prairie-affinity in the Carolinas (Davis et al. 2002). Many of these prairie-affinity species are of conservational concern and include federally-listed, eastern Piedmont endemic species such as *Echinacea laevigata* (C.L. Boynton & Beadle) S.F. Blake (smooth purple coneflower), *Marshallia legrandii* Weakley (tall Barbara’s buttons), and *Helianthus schweinitzii* Torr. & A. Gray (Schweinitz’s sunflower). These heliophyte communities harbor vanishing regional biodiversity, serve as habitat for wildlife, and provide abundant pollinator resources not found in closed-canopy forests. The imperiled native prairie-affinity flora have sparked great interest in the conservation and restoration of Piedmont prairies, savannas, and woodlands thought to historically have been their natural habitats (Schmidt and Barnwell 2002; Taecker 2007; Tompkins et al. 2010a; Tompkins et al. 2010b; Benson 2011;

Tompkins 2013; Stanley et al. 2019). However, the restoration and maintenance of suitable heliophyte habitat requires intensive and knowledgeable management, and unknowns remain about the historical distribution, composition, and general ecology of the Piedmont prairies. Thorough documentation and long-term studies of present Piedmont prairie remnant flora are critical to successful management of these imperiled plant communities. Here we report on a resurvey of 25-year-old vegetation monitoring plots at a robust Piedmont prairie remnant site in order to address the following questions:

1. How have *Echinacea laevigata* populations in plots changed over time?
2. How has other vegetation in the plots changed over time?
3. What biotic and abiotic factors might explain any observed changes?
4. Is current management appropriate or are adjustments needed to promote more suitable habitat for the rare heliophytes?

METHODS

Study Site

Picture Creek Diabase Barrens (PCDB) is a natural area located in Granville County, North Carolina, currently owned and managed by the North Carolina Department of Agriculture and Consumer Services (NCDA and CS) Research Stations Division with the primary goal of increasing the amount of suitable habitat for the rare species. The site contains an example of the globally imperiled Xeric Hardpan Forest (Northern Prairie Barren Subtype) natural community (Schafale 2012) and what is thought to be remnant Piedmont prairie flora (Stanley et al. 2019). PCDB is considered a Nationally Significant Natural Heritage Area by the North Carolina Natural Heritage Program. At least 48 rare species, including the largest known population of *E. laevigata*, are found at PCDB (Stanley et al. 2019). Long-term vegetation monitoring plots were first established at the site in 1993 (Barnett-Lawrence 1995) to study shifts in vegetation composition and *E. laevigata* populations in response to site management over time. The plots were resurveyed in 2001 (Lunsford 2002) and most recently by the present authors in 2018.

PCDB encompasses 407.4 acres of mostly flat to gently rolling land adjacent to the stream Picture Creek, near the town of Butner. Elevation ranges from 94–116 m (310–380 ft) above sea level and the site experiences a mild climate with average daily minimum temperature of the coldest month being -0.5°C (see Stanley et al. 2019). Average annual precipitation is 110.1

cm (43.34 in) and, on average, the area experiences one tropical cyclone every 3–4 years (see Stanley et al. 2019).

The site occurs in the Durham subbasin of the Deep River Triassic basin, one of the geological rifts that formed during the Late Triassic as the Pangea supercontinent broke apart (Oakley et al. 1995; Olsen et al. 1991). These rifts allowed intrusions of magma to form patches of mafic rocks, such as the diabase sill that underlies PCDB. Mafic rocks are rare in the region and estimated to only represent around 10% of the North Carolina Piedmont (Oakley 1995). Due to the weathering of the diabase parent material, most of PCDB is mapped as occurring on Iredell soil series (an Alfisol), which is characterized by higher concentrations of iron, magnesium, and calcium than surrounding, more typical Piedmont Ultisols which usually originate from felsic parent materials such as granite. This soil is also characterized by a shrink-swell clay horizon that can cause a perched water table during wetter months. Some areas of the site are mapped as the soil series Picture, a Mollisol which is similar to Iredell but occurs along ephemeral drainages and has a mollic epipedon. Mollisols are soils that are usually found beneath grasslands but it is still unclear if the presence of the Picture Mollisol is an indication that the area historically harbored significant grassland vegetation in the past.

Artifacts such as numerous arrowheads (see Stanley et al. 2019) suggest the site was once traversed by Native Americans, although their type and intensity of usage of the area has not been critically studied. The site is located near the estimated route of a Native American trading path, which follows a settlement corridor called the Piedmont Crescent, and which once traversed the state in an arc roughly from Northeast to Southwest, roughly parallel to, if not coinciding in part with, present-day I-85 (Dobbs 2006). European settlement of the vicinity took place in the early 1700s and tobacco cultivation became increasingly popular in the region from 1850 onward. It is unknown if PCDB was ever ploughed, but the Iredell soils in the area were considered undesirable for most agricultural pursuits and generally described as "wild-grass pasture" (Hardison and Long 1910). By the early 1900s, lands over "Iredell clay loam" were characterized by dominance of "blackjack oak" (*Quercus marilandica*) accompanied by "shortleaf pine" (probably referring to *Pinus echinata*, but the term was sometimes also used for *Pinus taeda*) and an understory of "broom sedge" (probably *Andropogon virginicus,* but may refer to a variety of grasses currently or once classified within *Andropogon* and *Schizachyrium)* (Hardison and Long 1910). The parcels of land that now make up PCDB were privately owned until purchased by the government in 1942 to establish Camp Butner and eventually transferred to the state of North Carolina following Camp Butner's closure in 1947. Land surveys in the early 1980s revealed that numerous rare plant species were present, and the PCDB SNHA was established in 1986 to conserve them. The site is currently bounded by Picture Creek to the west, a railroad to the east, and roads to the north and south. A powerline was constructed in the early 1980s and runs through the center of the site. Rare heliophytes are currently found primarily within the powerline corridor and "glade" areas within the surrounding woods. Aerial photographs from 1940 onward and dendrochronology show some areas of the site that are now densely forested once had a more open canopy and were dominated by shade intolerant trees such as *Pinus echinata* and *Quercus stellata* (Sigmon-Chatham 2015). Current management seeks to create more savanna-like habitat for the rare heliophytes.

Plot descriptions and histories

Five 0.1-hectare permanent plots were established at PCDB in 1993 to monitor vegetation response to site management (Barnett-Lawrence 1995). At least one plot was located in each of the four Burn Units (with two plots located in Burn Unit 2) (Figure 3.1). Plot locations were chosen to capture populations of *E. laevigata*, with the exception of Burn Unit 4, which contained no *E. laevigata* at the time (Barnett-Lawrence 1995). Plots were named PCG ("Picture Creek Glade") 01–05. All of the plots are located in currently forested areas outside the powerline corridor. PCG05 was burned in 1994 and all plots were burned in 2017. No other fires are known to have affected the plots in this timeframe. There was a burn planned for 2002 that did not occur. A burn did occur in the powerline corridor in 2012 but it was generally unsuccessful in penetrating into the forest and did not carry to any of the monitoring plots (Stanley et al. 2019; Schnake 2019 pers. comm.). There have been ongoing forestry activities to selectively thin some stands and restore them to a more open structure based on the results of Sigmon-Chatham (2015). These forestry activities are currently restricted to a northern portion of the site and have not affected any of the PCG monitoring plots.

PCG01 is located within Burn Unit 4 just off the central access road (Figure 3.1). It is the only plot that has never been known to contain *E. laevigata* but did contain other prairie heliophytes (especially *Baptisia australis* var. *aberrans*) at the time of establishment. This plot was resurveyed in 2001, but we chose not to resurvey it in 2018 due to lack of *E. laevigata*. It is currently under closed-canopy forest, and no prairie species were apparent during a cursory walkthrough in March 2019.

PCG02 is located within Burn Unit 3 just inside the tree line to the south of tower 3 and is parallel to the powerline corridor (Figure 3.1). Aerial photos from 1972 (and earlier) and map drawings from 1973 show the western access road once continued south, passing a saw mill, and eventually connecting to 33rd street. This road may have once passed through the current location of PCG02 based on georeferenced hand-drawn maps and the relationship of PCG02 to the western access road. *Echinacea laevigata* and other prairie species are found on the edge of the plot closest to the powerline corridor (and are prevalent within this section of the corridor). PCG02 was resurveyed by Barnett-Lawrence in 1995 before a planned burn that unfortunately was not performed. This plot was last burned in the 2017 early spring fire and char was estimated to reach 6 to 9 m high on the northeast-facing side of most trees in the plot. It falls within Dry-Mesic Basic Oak-Hickory Forest as delineated in Stanley et al. (2019) and is in the vicinity of Stand 1 in Sigmon-Chatham (2015).

PCG03 is located within Burn Unit 2 to the west of the western access road (Figure 3.1). An old logging loop road passes through the plot and prairie-affinity species, including *Echinacea laevigata*, are found along the ruts. This plot was burned in the 2017 early spring fire and char was estimated to have reached about 5–8 m high on the east-facing side of most trees in the plot. PCG03 falls within an area of Xeric Hardpan Forest as delineated in Stanley et al. (2019), and would be near Stand 2 in Sigmon-Chatham (2015). In terms of landscape position, this plot is on a mid-slope above a Picture Creek tributary stream but below the top of the ridge.

PCG04 is also located within Burn Unit 2 to the west of the western access road but north of PCG03 (Figure 3.1). PCG04 is located in a glade area that is on higher ground and canopy trees are visibly shorter than PCG03, which is downslope. Prairie-affinity species, including smooth purple coneflower, are found mostly on the side of the plot facing the western access road, where they are abundant within the road. This plot was burned in the 2017 early-spring fire, and char was estimated to reach about 7–9 m high on many trees in the plot. PCG04 falls within one an area of Xeric Hardpan Forest as delineated in Stanley et al. (2019) and would be in the vicinity of Stand 2 in Sigmon-Chatham (2015). Lunsford (2002) described PCG04 as a control plot to the more frequently burned PCG05.

PCG05 is located within Burn Unit 1 and is to the east of the western access road (Figure 3.1). This plot was burned in 1994 (Barnett-Lawrence 1995), and Barnett-Lawrence performed pre- and post-burn surveys. Despite additional attempts to continue regular prescribed burns in the following decades (Frost pers. com. 2019), the next successful burn to affect this plot was not until spring 2017. This plot was burned in the 2017 early spring fire and we estimate char to be only 3 m high, indicating this plot was the least affected by this burn. The plot is generally considered part of the "glade" region of the site and falls within an of Xeric Hardpan Forest as delineated in Stanley et al. (2019). Lunsford (2002) noted "In plot PCG05, there is in fact a strong edge effect. Much of the center of the plot is almost savanna-like in its openness and grassiness, while the edges have a much more dappled light, limiting the grass cover. The rosettes [of *E. laevigata*] nearer the grassy midline of the plot are mostly not well developed. A robust population of a *Marshallia* species flourishes there instead. It is in the dappled shade that the majority of *Echinacea* flowering occurred in (and around) PCG05 in 2001."

Survey methodology

Each plot is a 20 x 50 m (0.1 ha) rectangle divided into ten, 100-m^2 subplots, with each 100-m^2 subplot having a 1-m^2 and 10-m^2 nested intensive module in one corner (Figure 3.2). We relocated plots from their six permanent metal stakes (or plastic in the case of PCG03) that are placed every 10 m along the centerline from 0 to 50 m. We resurveyed plots PCG02–05 during October (fall season) of 2018. Previous surveys also had been undertaken in the fall, with Barnett-Lawrence (1995) from October to November of 1993, and Lunsford (2002) from September to November of 2001. There was a prescribed burn in early 2017 that affected all plots and our 2018 survey took place two growing seasons post-burn.

We followed Barnett-Lawrence (1995) and Lunsford (2002) with a few modifications to increase our survey speed: we did not perform full nested species presence inventories or map *Echinacea laevigata* (Lunsford 2002). All vascular plants we encountered were identified to species, if possible. We surveyed the 1-m^2 modules for herbaceous species cover and tree seedling (≤25 cm in height) cover and stem counts. We surveyed the 10-m^2 modules for "shrub" (any woody stem between 25 cm and 1 m in height) cover and tree sapling (any woody stem reaching 1 m but < breast height, or reaching breast height but with a diameter < 1 cm DBH) stem counts.

All living trees reaching breast height (1.3 m) and at least 1 cm DBH were measured using diameter tape. The positions of all trees (living or standing dead) ≥ 9.5 cm DBH were recorded (GPS coordinates and hand drawn maps) and these large trees were also assigned a dominance class. Dominance classes are: 1) Dominant, above average canopy height; 2) Codominant, at average canopy height; 3) Subdominant, below average canopy height; 4) Heavily damaged or suppressed; and 5) Standing dead. We did not record fallen or small (< 9.5 cm DBH) dead trees. If a tree had more than one stem, where both stems originated from the ground, we recorded each stem as a separate tree. If a tree had a split or forked stem, with the split/fork occurring above the ground, we only recorded the largest stem.

We compiled a full species list for each plot by recording the presence of any species not captured in the intensive modules or tree surveys (but we did not record any cover or stem counts for these "residual" species). All visual estimates of cover were recorded in cover classes using Barnett-Lawrence (1995): 0%, 0–5%, 5–25%, 25–50%, 50–75%, 75–95%, and 95–100%. Taxonomy follows Stanley et al. (2019), which is based on Weakley (2015) but provides updated taxonomy for species with recent taxonomic revisions.

Echinacea counts

We walked the entirety of each 100 m^2 subplot and recorded the number of individuals of *E. laevigata* and any reproductive stems encountered (i.e., heads in fruit at this time of year). *Echinacea laevigata* is a basal-rosette-forming perennial herb that sends up a flowering stalk that supports a single head inflorescence (however, one plant may produce multiple flowering stalks). The plant has a tap root system that often branches to form side shoots, resulting in clumps of rosettes from the same individual. We defined an individual as a solitary rosette, a seedling, or a clump of closely overlapping rosettes that were likely derived from the same root.

Other data collected

Following Lunsford (2002), we recorded additional environmental data for each 100 m^2 subplot, as follows. We recorded visual cover estimates (using the previously defined cover classes) for total herbaceous cover, bare area, bryophytes and lichens, rocks, and canopy openings. Because bare soil is thought to be important for *Echiancea laevigata* seedling establishment (Gadd 1991), we chose to record both unvegetated ground and bare soil.

Unvegetated ground can be covered by a layer of duff and/or leaf litter, and we felt it was important to distinguish it from bare soil. The difference between strictly bare soil and duff or litter covered ground is unclear for previous surveys.

Analyses

A species list was compiled, tree data were tabulated, and stem density and basal area (BA) were calculated for trees reaching at least 9.5 cm DBH. We examined trends in overall species richness, and we compiled more detailed summaries of trends in rare and exotic species presence. We also examined trends in the number of prairie indicator species (*sensu* Davis et al. 2002) and shade-tolerance guilds (see Chapter 2) in plots.

Nonmetric multidimensional scaling (NMDS) ordination was used to visualize trends in vegetation composition of the 1-m^2 nested modules and overall species presence. We performed three ordinations, one for a dataset of the 1-m^2 nested modules (cover codes), one for a subset of the 1-m^2 nested modules with only survey data from 2001 and 2018 (to search for compositional trends related to environmental data that were not surveyed in 1993 or 1994), and one for whole-plot species presence (presence/absence). A Bray-Curtis distance matrix was computed for each dataset and used for NMDS ordinations in PC-ORD (version 6.22) using the “slow and thorough” autopilot settings.

RESULTS

Echinacea laevigata population trends

The number of individuals of *E. laevigata* declined in all plots in 2018 when compared to 2001 (Table 3.1). Declines were 79.4 to 94.2%, with the greatest number of individuals lost in PCG05, from 8352 in 2001 to 1724 in 2018. However, the number of reproductive stems, as well as the ratio of reproductive stems to total individuals, increased in all plots in 2018 when compared to 2001 (Table 3.1). PCG05 had the highest numbers of individuals and reproductive stems in both 2001 and 2018. PCG02 had the lowest number of individuals and reproductive stems in 2001 and the lowest number of individuals in 2018, but PCG03 had the lowest number of reproductive stems in 2018. In the 1993 survey, individuals were only counted for PCG02, and no reproductive stems were counted for any plot, making PCG02 the only plot to have three time points for *E. laevigata* counts. The number of individuals counted in PCG02 increased from

232 in 1993 up to 281 in 2001 then decreased to only 31 in 2018 (Table 3.1). It must be noted that our 2018 counts included very few seedlings. We did not encounter any recognizable *E. laevigata* seedlings in PCG02 or PCG03, but we did encounter some smaller *E. laevigata* in PCG04 and PCG05 that were included in the tally of individuals counted. Following the methods of Lunsford (2002), we did not keep a separate tally for seedlings, so the exact number of seedlings included in our counts is uncertain.

Species richness trends

A total of 254 taxa, excluding poor resolution taxa (e.g., *Acer* sp.), were reported across all plots and years. Total species richness showed a few different trends across plots. PCG02 and PCG04 followed the same pattern, wherein species richness continually increased from 1993 to 2018 (Figure 3.3). PCG03 showed an increase from 1993 to 2001, followed by a decrease in species richness from 2001 to 2018. PCG05 was the only plot to be surveyed in all four years and showed a decrease from 1993 to the 1994 post-burn survey, an increase from 1994 to 2001, and a decrease from 2001 to 2018. When species richness values by growth habits are considered separately, most follow the pattern of the plot total species richness with some notable exceptions (Figure 3.3). Tree richness declined in PCG02 and PCG04 in 2018 while richness of most other habits increased. Shrub richness also declined in PCG04 in 2018, which was contrary to the overall trend of increasing richness. The trend in graminoid richness in PCG03 generally ran counter to all other growth habits in all surveys, declining from 1993 to 2001 (when richness of most habits increased) and increasing from 2001 to 2018 (when richness of most habits decreased). Overall, PCG02 saw increasing richness in all habits but trees (which declined), PCG03 saw increases followed by decreases in richness of all habits except for graminoids (which declined, then increased), and PCG04 saw increases in richness all habits followed by a decline in woody species. PCG05, which experienced greater fire frequency than the other plots, showed a decline in richness across all habits (and overall richness) in years immediately following burns (i.e., 1994 and 2018), and showed increasing richness for all habits in 2001, the year with the longest time since last fire.

For the NMDS ordination of species presence/absence in plots, the autopilot chose a 3-dimensional solution with the axes capturing a total of 86.7% of the compositional variation in the dataset (Figure 3.4). The first axis captured 62.4% of the compositional variation while the second axis captured 13.0% and the third captured 11.4%. The first and most informative axis showed a trend of compositional variation through time; most pronounced was the separation of the 2018 survey from the previous surveys. Species with changes in presence that were most correlated with the first axis were *Carex flaccosperma* ($r^2 = 0.887$), which showed increasing presence in the direction of the 2018 survey, and *Chimaphila maculata* ($r^2 = 0.887$), which showed an opposing trend of decreasing presence (Figure 3.4).

Rare species trends

Eleven state-listed (one also federally listed) rare species were observed across all plots and survey years. *Echinacea laevigata* (federally listed as endangered) and *Silphium terebinthinaceum* were both present in all plots in all survey years. One rare species, *Panicum flexile*, is new to the plots (but not the site) and was found in PCG04 and PCG05 during our 2018 survey. *Liatris squarrulosa* had a new appearance in PCG02 in 2018 but previously occurred in PCG03 in 2001 and PCG04 in 2001 and 2018. *Baptisia australis* var. *aberrans* and *Symphyotrichum depauperatum* are two rare taxa that were lost from the plots. Both were found in at least one plot in 1993 and 2001 but were not found in any plots in 2018. *Baptisia australis* var. *aberrans* was previously found in PCG03, PCG04, and PCG05 in 1993 and 2001. *Symphyotrichum depauperatum* was previously found in all plots in 1993, still found in the post-burn 1994 survey of PCG05, but was only ever found again in PCG04 in 2001. *Marshallia legrandii* was first found in PCG03, PCG04, and PCG05 in 2001, and was again found in these plots in 2018, but has never been found in PCG02. *Lithospermum canescens* has been continuously found in PCG03 and PCG05 in all survey years but has never been found in PCG02 or PCG04. *Matelea decipiens* was found in PCG02 in 1993 but never found again, although it is still found elsewhere at PCDB. *Parthenium auriculatum* was previously found in PCG03 in 1993, not seen in 2001, and was a new appearance in PCG05 in 2018. *Solidago ptarmicoides* was found in PCG03 in 1993 and 2001, but it was not seen in this plot in 2018. It was found in PCG04 in 2001 and 2018 and in PCG05 in the post-burn 1994, 2001, and 2018 surveys. A tabulated summary of this information can be found in Table 3.2.

Exotic species trends

Eleven exotic species were observed across all plots and survey years, representing around 4% (11/254) of the total species richness. *Lespedeza cuneata* was found in all plots in 2018 and had a continuous presence in PCG03 in all surveys. *Lonicera japonica* had a continuous presence in PCG02, PCG04, and PCG05 in all surveys (including the post-burn 1994 survey for PCG05), but was only found in PCG03 in 1991 and 2001. For 2018, *Hypochaeris radicata*, *Ligustrum sinense,* and *Taraxacum officinale* were new appearances in PCG02, while *Albizia julibrissin* and *Sonchus oleraceus* were new appearances for PCG03. *Potentilla indica* was a new appearance in PCG02 and PCG04. *Microstegium vimineum* was first found in PCG03 in 2001 and was still present in 2018. *Cirsium vulgare* and *Kummerowia striata* were previously present in at least one plot each but were not found during the 2018 survey. *Cirsium vulgare* was previously found in PCG03 and PCG04 in 1993 and PCG05 in 2001, while *Kummerowia striata* was previously found in PCG05 in 1993 and PCG03 in 2001. A tabulated summary of this information can be found in Table 3.3.

Prairie-affinity and heliophilic species trends

It is difficult to define remnant Piedmont prairie species, but a few tentative assignments exist. Davis et al. (2002) provided a list of Piedmont prairie indicator species based on extensive field work at six sites considered to be putative Piedmont prairie remnants. In that work, species were determined to be indicators (further categorized as "strong" or "weak") based on their known habitat affinities and presence at the six sites. PCDB was not included in the Davis et al. (2002) study, but we can use their indicator determinations to look for trends in heliophytes in the plots.

The monitoring plots at PCDB contained a total of 111 prairie indicator species *sensu* Davis et al. (2002), 51 being strong indicators and 60 being weak indicators, representing about 44% (111/254) of the total species richness. The trend in overall prairie indicator richness of each plot mirrors the trend in overall species richness, increasing from 1993 to 2001, but usually declining in surveys that occurred one growing season after burns (i.e., 1994 and 2018; Figure 3.5). PCG04 is the only plot that experienced continuous increase in indicator richness from 1993 to 2018. Some of the declines in overall number of indicators in 2018 can be attributed to the loss of previously frequent *Chimaphila maculata* (strong), *Fragaria virginiana* (weak), *Oenothera fruticosa* (strong), *Potentillia canadensis* (strong), and *Rhus aromatica* (strong), all species previously occurring in at least three of the four plots in 1993 and 2001, but not observed in 2018. Frequent and stable (i.e., present in all surveys or at least the 2001 and 2018 surveys) indicators are the woody species *Carya tomentosa* (weak), *Fraxinus americana* (weak), *Juniperus virginiana* (strong), *Parthenocissus quinquefolia* (weak), *Pinus taeda* (weak), *Prunus serotina* (strong), *Quercus alba* (weak), *Quercus falcata* (weak), *Quercus stellata* (strong), *Rhus copallinum* (weak), and *Toxicodendron radicans* (weak), and the herbaceous species *Chrysogonum virginianum* (strong), *Danthonia spicata* (weak), *Echinacea laevigata* (weak), *Eupatorium hyssopifolium* (strong), *Lespedeza procumbens* (strong), *Lespedeza repens* (strong), *Melica mutica* (strong), *Rudbeckia fulgida* (weak), *Ruellia caroliniensis* (strong), *Scutellaria integrifolia* (strong), *Silphium terebinthinaceum* (strong), *Tragia urticifolia* (strong), and *Tridens flavus* (strong).

Of the 175 herbaceous species occurring in the four PCDB monitoring plots, 150 (86%) received a shade-tolerance association (see Chapter 3). Examining trends in these species over time shows generalists and open specialists consistently have the greatest richness in all plots, although there is some crossover as to which one is highest in each plot at any given time. PCG02, PCG03, and PCG04 are all experiencing increasing open specialists while PCG05 experienced a decline from 2001 to 2018. Closed specialists declined from 2001 to 2018 while semi-open specialists are increasing in the same timeframe. Other habitat specialists are variable in their trends (Figure 3.6).

Understory vegetation trends

For the NMDS ordination of the 1 m^2 nested modules, the autopilot chose a 3-dimensional solution with these axes capturing a total of 62.7% of the compositional variation in the dataset (Figure 3.7). The first axis captures 27.1%, the second axis captures 22.0%, and the third captured 13.5%. The first axis seems to have captured compositional variation between plots, especially showing PCG05 separating from the other plots. Prairie-affinity species such as *Echinacea laevigata* ($r^2 = 0.287$) and *Schizachyrium scoparium* ($r^2 = 0.204$) were correlated with this first axis and show greater abundance in the direction of PCG05 (Figure 3.7). This axis was also correlated with total herbaceous cover ($r^2 = 0.287$) which increases in the direction of PCG05. The second axis seems to have captured compositional variation between survey years and suggests there is change occurring through time. *Dichanthelium laxiflorum* ($r^2 = 0.281$) and *Cercis canadensis* ($r^2 = 0.268$) are correlated with this second axis and show greater abundance in the direction of 2018 (Figure 3.7). The third axis seems to primarily have captured compositional variation within surveys but the 1994 survey of PCG05 also separated from the rest on this axis.

The NMDS ordination of only the 2001 and 2018 nested modules also chose a 3-dimensional solution. The axes of this ordination captured a total of 63.4% of the compositional variation in the dataset (Figure 3.8). The first axis captured 25.2%, the second axis captured 21.5%, and the third axis captured 16.6%. The first axis seems related to variation between plots (PCG05 separating from the rest) and is correlated with unvegetated ground ($r^2 = 0.471$), which decreases in the direction of PCG05, and canopy opening ($r^2 = 0.427$), which increases in the direction of PCG05 (Figure 3.8). Total herbaceous cover is also correlated with the first axis ($r^2 = 0.361$) and is decreasing in the direction of PCG05 (Figure 3.8). The second axis seems primarily related to variation between the 2001 and 2018 surveys, but PCG05 and PCG02 also separated from the other plots on this axis. Several species are correlated with this axis, such as Strophostyles umbellata ($r^2 = 0.300$) and *Potentillia canadensis* ($r^2 = 0.227$), both increasing in the direction of the 2001 survey of PCG05 (Figure 3.8). The third axis seems related to unexplained variation within surveys.

Midstory and canopy vegetation trends

Tree total basal area (BA) showed different trends between PG05 and all other plots (Figure 3.9). In PCG05, BA declined in the 1994 post-burn survey, but it increased in all other years (including the 2018 post-burn survey). PCG05 saw the greatest BA in 1993, decreased by 2001, then increased by 2018. In all other plots, BA increased from 1993 to 2001 but declined in the post-burn 2018 survey. In general, *Pinus echinata* and *Pinus taeda* showed the greatest overall increases in BA from 2001 to 2018 (Figure 3.9). Standing dead stems were a greater portion of the total BA in most plots from 2001 to 2018, a result of the 2017 prescribed fire.

PCG02, PCG03, and PCG04 all show a similar trend for tree stem density (Figure 3.9). These plots had their lowest stem density in 1993, which rose by 2001, and then plummeted by 2018. PCG05 again shows a different trend for stem density. Stem density in PCG05 started highest in 1993 and decreased in 1994, 2001, and 2018. Overall, stem density increased in intervals without fire and decreased in surveys in years immediately following fires (i.e., 1994 and 2018). Stems of *Juniperus virginiana* and *Liquidambar styraciflua* were prevalent in 2001, but they were mostly eliminated by 2018 (Figure 3.9). Tree basal area and stem density are also summarized in Table 3.4.

Other biotic and abiotic metrics

Cover estimates of additional metrics collected in all survey years are presented in Table 3.5. Total herbaceous cover is the only metric consistently reported for all plots in all survey years. PCG02, PCG03, and PCG04 follow a similar pattern (Figure 3.10) where, in general, herbaceous cover increased with time across survey years. PCG05 shows a slightly different pattern, wherein herbaceous cover decreased in surveys following prescribed burns (i.e. 1994 and 2018). Canopy openings generally increased greatly from 2001 to 2018, with the exception of PCG05, which experienced a decline in openings. In 2001, bryophyte and lichen cover was reported to be greater than 25% in some subplots of PCG02, PCG03, and PCG04, with greater than 95% in two PCG04 subplots. In 2018, no greater than 5% bryophyte and lichen cover was encountered in any plot, suggesting a dramatic decline. The amount of downed wood increased from 2001 to 2018.

There is some uncertainty related to the reporting of "bare area" in Lunsford (2002). Her report describes this measure as "…how much is bare soil…," but it seems this may have been an estimate of unvegetated ground (Lunsford Jones pers. comm. 2019). In this case, bare area would include both bare soil and areas where the soil is covered by duff and/or leaf litter. We chose to report estimates of both unvegetated ground and strictly bare soil separately in our 2018 survey. If we compare our estimates of unvegetated ground to Lunsford's (2002) "bare area," then the amount of unvegetated ground has generally declined in all plots except for PCG05, which saw an increase. We also found that very little (always smallest cover class) of the unvegetated area was bare soil, with most of this area being covered by duff and/or litter. It is difficult to be certain how Lunsford's (2002) bare area estimates relate to bare soil, so direct comparisons should be viewed with caution.

DISCUSSION

1. How have *Echinacea laevigata* populations in plots changed over time?

We observed an apparent decline in *E. laevigata* populations in all plots from 2001 to 2018. However, the plants we encountered in 2018 were generally mature and many had multiple reproductive stems, sometimes five or more flowering stems originating from a single large rosette or clump counted as one individual. Lunsford (2002) stated that she counted "…even rosette seedlings the size of a fingernail…" and noted that "…much of the count for PCG05 was comprised of such seedlings." Personal communications with her suggest the total number of mature plants has remained closer to stable from 2001 to 2018, because she estimated that around 80% of her counts were seedlings (Erin Lunsford Jones, pers. comm. 2019). It seems the apparent declines in individuals can be attributed to fluctuations in seedlings and a lack of seedling establishment and/or survival in the years between 2001 and 2018. This leads to new questions such as: What is the lifespan of this species? Are some of the plants encountered in Lunsford (2001) the same individuals we encountered in 2018, or did these 2018 plants establish in the intervening years? What events triggered the establishment of so many seedlings in 2001? What factors most contributed to their mortality in the following years? Herbchronology, aging perennial herbaceous plants that produce annual growth signatures (Dietz and Ullmann 1997; von Arx and Dietz 2006), could address some of these questions, provided *E. laevigata* produces a discernable annual growth signature. Other monitoring efforts at PCDB have shown cycles of increases and decreases in flowering stem counts for the "glade" area (encompasses PCG05, and surrounding area) from 2008 to 2018 (Wilson et al. 2018). Total flowering stems of the glade area generally fluctuated between a few hundred to around 2,000 before showing a dramatic increase up to 10,000 flowering stems in 2018 (Wilson et al. 2018). The 2018 increase in flowering stems was likely a response to the 2017 prescribed burn.

2. How has other vegetation in the plots changed over time?

Despite the uncertainties of whether populations of *Echinacea laevigata* were stable or declining, other rare heliophytes have experienced some clear declines in certain plots. For example, PCG03 lost rare heliophytes, such as *Baptisia australis* var. *aberrans*, *Liatris squarrulosa*, *Parthenium auriculatum*, *Solidago ptarmicoides*, and *Symphyotrichum depauperatum*, which were reported to occur in the plot in prior surveys. As these prairie heliophytes all grow abundantly in the powerline corridor that experiences frequent disturbances, including mowing every three years and multiple burns in the last ten years, their loss from plots like PCG03 is likely due to competition and/or fire suppression prior to 2017. Two rare species had new appearances in one or more plots in 2018, suggesting they are colonizing new areas. *Liatris squarrulosa* was a new appearance in PCG02, and given its abundance in the nearby powerline, this likely represents colonization of an adjacent area. However, the appearance of *Panicum flexile* in PCG04 and PCG05 may represent a new colonization event or it may have been overlooked or misidentified in the past. Lunsford (2002) reported *Panicum flexile* on her species list, but it is not listed in the plot reports, so it cannot be directly attributed to a plot. Despite the fluctuations in rare heliophyte occurrences in some plots, total herbaceous cover is generally increasing over time (Figure 3.10). Open and semi-open specialists are increasing in diversity in most plots, while closed-canopy specialists are generally decreasing in diversity (Figure 3.6).

There were also new appearances of exotic species in several plots. PCG02 and PCG03, together, gained six new occurrences of exotic species. Fortunately, these exotic species were generally low in abundance (lowest cover class for those that appeared in the 1 m^2 modules). However, the new appearances of *Albizia julibrissin* and *Ligustrum sinense* are concerning because they can both be aggressive and invasive species. While *Ligustrum sinense* was already known from PCDB, *Albizia julibrissin* is a new occurrence at the site. PCG05 has the lowest number of exotic species, so it is possible that higher fire frequency has a positive effect on excluding exotic species. This could be a result of the exotic species being fire-intolerant (Just et al. 2017).

Other changes have been observed in the woody vegetation. The prescribed fires have clearly reduced stem density and altered woody species composition in plots. All plots continue to have a canopy dominated by *Pinus echinata* and *P. taeda*, and this was unchanged by the 2017 fire. However, the less fire-resistant species, such as *Juniperus virginiana* and *Liquidambar styraciflua*, saw dramatic declines in all plots following the 2017 fire. Both *Juniperus virginiana* and *Liquidambar styraciflua* are woody species that tend to establish in open areas following disturbances. *Liquidamabar styraciflua* was observed to be slightly more fire resistant, with frequent resprouts observed in PCG05, but *Juniperus virginiana* experienced near-total mortality for trees of all sizes following the 2017 fire. A similar pattern was observed following the 1994 burn of PCG05 (Barnett-Lawrence 1995; Figure 2.10). As Barnett-Lawrence (1995) pointed out, the extreme sensitivity of *Juniperus virginiana* to fire suggests it is not a stable part of these communities, which would have historically persisted in regions of the landscape that experienced periodic fires (Barden 1997, Frost 2000). It is perhaps better to view *Juniperus virginiana* as an invader that enters these systems in times of fire suppression. This brings into question its inclusion as a "strong" prairie indicator species in Davis et al. (2002), but such is more understandable in the context of it being a potential indicator of previously open patches in the landscape.

3. What biotic and abiotic factors might explain any observed changes?

Perhaps the greatest concern with regard to long-term habitat quality of PCDB is the inferred reduction in seedling establishment for *Echinacea laevigata*. One explanation is that young plants and seedlings were killed in the 2017 prescribed burn, but this does not fully explain why there were so few seedlings apparent the next year or why populations of mature plants apparently are not expanding. *Echinacea laevigata* produces flowering heads from May to July and fruit (cypselas) from late June to September (Gaddy 1991). The dispersal mechanism is still uncertain, but birds and rodents presumably scatter the cypselas, which lack any obvious appendages for dispersal. The cypselas overwinter and seedlings usually emerge during the following growing season, but can emerge without stratification. Other monitoring efforts at PCDB show *E. laevigata* flowering stems decreased in the glade area (encompassing PCG05 and the surrounding area) in 2017, the year the burn took place (Wilson et al. 2018), so this might explain the lack of seedlings we observed in 2018. Another issue is the inherent difficulty in identifying seedlings. *Echinacea laevigata* seedlings could potentially be confused with other members of the Asteraceae, of which there are many present in and around the plots. It is possible we were too conservative in our evaluation of seedlings and excluded some that were likely *E. laevigata*. Additional studies of seedling development and identification of *E. laevigata* versus other Asteraceae seedlings are warranted.

This work also underscores the need for further study on the life cycle and demographics of *Echinacea laevigata*. The accumulation of litter and duff at PCDB may be a factor reducing the establishment of *E. laevigata* seedlings in periods of fire suppression. While recent prescribed fires have done much to reduce the duff layer, there is still abundant duff and litter present, and it is unclear if this is impeding seedling establishment. Walker (2009) conducted germination experiments to search for viable seeds in soil and leaf litter samples. He found *E. laevigata* seedlings germinated from sifted leaf litter but not soil, suggesting *E. laevigata* seeds are not reaching the soil seedbank or are not persisting. This pattern was also observed in other prairie heliophytes, such as *Solidago ptarmicoides*. Walker (2009) also observed reduced germination rates from spring litter compared to fall litter, although very low numbers of seeds were recovered in both seasons. Seeds of *E. laevigata* are potentially being caught in the leaf litter and it is unclear if seedlings can successfully establish in conditions where significant litter and duff layers are present.

Gaddy (1991) suggested *E. laevigata* seedlings require bare soil, preferably rich in magnesium and/or calcium, to successfully establish themselves. He even recommended plowing or raking around areas near mature plants to provide bare soil for seedling establishment. In 1994, fire breaks around PCG05 were cleared and raked down to mineral soil in preparation for the prescribed burn and Barnett-Lawrence (1995) reported "…the removal of litter and minor soil disturbance has resulted in many *E. laevigata* plants sprouting rosettes." He also reported that other prairie-affinity heliophytes such as *Silphium terebinthinaceum* and *Eryngium yuccifolium* responded positively to the fire lane clearing. It is possible this disturbance of the firebreaks also facilitated the movement of *Marshallia legrandii* into the nearby plots. This species name was not published until 2012 (Weakley and Poindexter 2012), but by the time of the 2001 survey it was already known there was a *Marshallia* sp. nov. present at PCDB. This species was not reported in any plots in 1993 but was found in PCG04 and PCG05 in 2001. *Marshallia legrandii* is currently abundant in the powerline right-of-way, the western access trail used as a fire break adjacent to PCG03-PCG05, and inside the bounds of PCG04 and PCG05. It is possible the robust populations of *M. legrandii* and *E. laevigata* observed in these plots in 2001 was a long-term response to the 1994 disturbances that would have uncovered significant bare soil.

However, it is unclear if the high number of seedlings apparently present in the 2001 survey was due to the general disturbance, uncovered soil, or both. Lunsford (2002) commented that she was counting a great number of seedlings, and she also reported 50–100% bare area in most of her 10 m^2 subplots. However, she reported the least amount of bare area in PCG05 (0–5% in 9 of the 10 subplots) where she would have encountered the most seedlings, but this might be attributed to the seedlings covering ground that would otherwise be counted as bare. Without more detail on leaf litter, duff depth, seedlings counts, and optimal seedling recruitment conditions, it is difficult to say for certain. The uncertainty in the past survey estimates of "bare area" precludes direct comparisons, but we found bare soil was only present in very small patches, primarily around tree-falls, during our 2018 survey, and most unvegetated ground was covered in leaf litter and a duff layer. We frequently reported unvegetated ground covered in leaf litter or duff to have 50% or greater coverage of 100 m^2 subplots, while bare soil was never greater than 5% (Table 2.5). Future surveys should consistently report the presence of bare soil and unvegetated ground as these could be influencing *E. laevigata* seedling recruitment. Future studies should also examine demographics more carefully to determine which life stages are most critical to population growth and how long mature plants can persist in various conditions. We wonder how many, if any, of the large plants we counted in 2018 were young plants counted by Lunsford in 2001. It is still unclear what factors led to what may have been an unusually large crop of seedlings in 2001 and what their survival rate was in the following years. It must also be noted that 2001 was a drought year for Granville County and it is possible the young seedlings encounterd in the 2001 survey were not able to survive. Droughts also occurred in 2007, 2010–2012, and 2017 which could have reduced seedling recruitment between 2001 and 2018.

Overall, fire is likely the single most influencial factor affecting both *E. laevigata* and associated vegetation at PCDB. All monitoring plots saw dramatic reductions in stem density in response to the 2017 fire that eliminated nearly all saplings from plots (leading to ~95% reduction in most plots), and basal area was also reduced for most plots due to the loss of many fire-intolerant trees of varying sizes. The exception to these trends was PCG05, where stem density was not as dramically reduced (only ~69% reduction) and basal area actually increased. This makes sense, given that the 2017 fire seemed to not carry through PCG05 with the same intensity as in the other plots. Fire reduces woody dominance (Table 3.4), increases canopy openings (Figure 3.8), and seems to increase *E. laevigata* reproductive stems in later growing seasons (Table 3.1; Wilson et al. 2018). It probably also plays a key role in creating bare soil suitable for recruitment of *E. laevigata* seedlings (Gaddy 1991).

4. Is current management appropriate or are adjustments needed to promote more suitable habitat for the rare heliophytes?

Targeted restoration requires clear reference conditions, something that continues to be an issue with Piedmont prairie remnant flora due to the lack of "pristine" examples upon which to base idealized descriptions. Based on estimates of historical fire return intervals (~3-5 years) in the region (Frost 2000) and the variable but generally stressful soils at PCDB, the historical vegetation structure is thought to have been a mosaic of open barrens and *Pinus echinata* savanna and/or woodland (Frost pers. comm. 2019). Dendrochronology and historical aerial photography support the idea that at least portions of the site were more open within the last ~100 years and *Pinus echinata* was an important component of the landscape (Sigmon-Chatham 2015). Current management seeks to conduct prescribed burns every 3 years, and thinning is being conducted in portions of the site (currently avoiding directly impacting rare species) to reduce basal area. Target basal area post-thinning is 35 to 60 ft^2/acre (~8–14 m^2/hectare) consisting of primarily large trees, with an intent to create "natural savannah stand structure, with some localized variability in stand density (Schnake et al. 2011)." The PCG plots are currently not targeted for thinning operations but they experience prescribed fire. Our results show most plots are experiencing a reduction in basal area (as much as 23.4%; Table 2.5) just from the prescribed fire. It is important to note that regularly prescribed fires are a relatively recent occurrence at PCDB, the 1994 fire being the first and various challenges preventing regular burns for at least the next decade (Frost, pers. comm. 2019).

Current vegetation structure in plots is still quite dense, with the lowest basal area being 19.1 m^2/ha in PCG04 (Table 2.5) – still outside the target range of ~8–14 m^2/hectare. Overall, our results suggest all plots are moving toward an open woodland or savanna-like vegetation structure, with fewer woody stems and greater cover of understory herbaceous vegetation. This corresponds well with what is currently estimated to be ideal habitat for *E. laevigata* and other rare prairie-affinity heliophytes. While the apparent declines in total *E. laevigata* population, loss of some heliophytes from plots, and appearance of new exotic species are concerning, these are most likely symptoms of the long years of fire suppression most plots have faced in the last decades. As PCG05 shows, abundant *E. laevigata* persist in conditions where burns have been more frequent, and plants are mature and well-positioned to recruit new seedlings as conditions presumedly become more optimal. Based on the vegetation trends in the monitoring plots, the changes observed in vegetation structure are consistent with manangement goals to reduce basal area and improve conditions for rare heliophytes. We recommend that management continue with the current plans to transition parts of PCDB to a savanna structure that should provide suitable habitat for the rare heliophyte species. Regular future observations of the monitoring plots will be key to understanding how the heliophytes and other vegetation are responding to the increased fire frequency that should be reducing competition and increasing light availability by reducing plot stem density and increasing canopy openings. We also recommend further study of *Echinacea laevigata* demographics and seedling establishment in the future.

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TABLES

Table 3.1: Counts for *Echinacea laevigata* individuals and reproductive stems. Reproductive stems were not counted in 1993, and individuals were only counted in PCG02. All reproductive stems and individuals were counted in each plot in 2001 and 2018.

Year	Plot	Individuals	gain/loss	% gain/loss
1993	PCG02	232	n/a	n/a
2001	PCG02	281	49	21.1%
2018	PCG02	31	-250	-89.0%
2001	PCG03	1006	n/a	n/a
2018	PCG03	58	-948	-94.2%
2001	PCG04	1950	n/a	n/a
2018	PCG04	355	-1595	-81.8%
2001	PCG05	8352	n/a	n/a
2018	PCG05	1724	-6628	-79.4%

Year	Plot	Reproductive Stems	gain/loss	% gain/loss
1993	PCG02	n/a	n/a	n/a
2001	PCG02	1	n/a	n/a
2018	PCG02	39	38	3800.0%
2001	PCG03	10	n/a	n/a
2018	PCG03	26	16	160.0%
2001	PCG04	85	n/a	n/a
2018	PCG04	286	201	236.5%
2001	PCG05	386	n/a	n/a
2018	PCG05	1389	1003	259.8%

Table 3.2: Summary of rare species found in the monitoring plots at PCDB.

Taxon	Conservation Status	Trend
Baptisia australis (L.) R. Br. var. *aberrans* (Larisey) M.G. Mendenh.	G5 T2 S2 NC State-Listed	Lost from plots. Was found in PCG03, PCG04, and PCG05 in 1993 and 2001 but no occurrences in any plot in 2018. Has never been found in PCG02.
Echinacea laevigata (C.L. Boynton & Beadle) S.F.	G2G3 S1S2 NC State-Listed Federally-Listed Endangered	Continuously present in all plots (PCG02, PCG03, PCG04, and PCG05) in all survey years.
Liatris squarrulosa Michx.	G4G5 S2 NC State-Listed	New appearance in PCG02 in 2018 but transient or variable in other plots. Only found in PCG03 in 2001. Found in PCG04 for 2001 and 2018. Never found in PCG05.
Lithospermum canescens (Michx.) Lehm.	G5 S2 NC State-Listed	Continuously present in PCG03 and PCG05 in all survey years. Never found in PCG02 or PCG04.
Marshallia legrandii Weakley	G1 S1 NC State-Listed Endangered	Found in PCG03, PCG04, and PCG05 in 2001 and 2018. Never found in PCG02.
Matelea decipiens (Alexander) Woodson	G5 S3 NC State-Listed	Found in PCG02 only in 1993. Never found in any other plots.
Panicum flexile (Gatt.) Scribn.	G5 S1 NC State-Listed	New appearance in PCG04 and PCG05 in 2018.
Parthenium auriculatum Britton	G3G4 S3 NC State-Listed	Found in PCG03 in 1993 but not seen again. New appearance in PCG05 in 2018.
Silphium terebinthinaceum Jacq.	G4G5 S2 NC State-Listed	Continuously present in all plots (PCG02, PCG03, PCG04, and PCG05) in all survey years.
Solidago ptarmicoides (Torr. & A. Gray) B. Boivin	G5 S1 NC State-Listed	Found in PCG03 in 1993 and 2001 but not seen in 2018. Found in PCG04 in 2001 and 2018. Found in PCG05 in the post-burn 1994 survey and again in 2001 and 2018.
Symphyotrichum depauperatum (Fernald) G.L. Nesom	G2 S1 NC State-Listed	Lost from all plots. Was found in all plots in 1993 and still found in the post-burn 1994 survey of PCG05, but only found again in PCG04 in 2001. Not found in any plot in 2018.

Table 3.3: Summary of exotic species found in the monitoring plots at PCDB.

Taxon	**Trend**
Albizia julibrissin Durazz.	New appearance in PCG03 in 2018.
Cirsium vulgare (Savi) Ten.	Lost from plots. Found in PCG03 and PCG04 in 1993 and in PCG05 in 2001. Not found in any plots in 2018.
Hypochaeris radicata L.	New appearance in PCG02 in 2018.
Kummerowia striata (Thunb.) Schindl.	Lost from plots. Found in PCG05 in 1993 and in PCG03 in 2001. Not found in any plots in 2018.
Lespedeza cuneata (Dum. Cours.) G. Don	Found in all plots in 2018. Continuously found in PCG03 in all surveys but variable appearance in other plots. Found in PCG02 and PCG04 in 1993 and 2018. Found in PCG05 in 2001 and 2018.
Ligustrum sinense Lour.	New appearance in PCG02 in 2018.
Lonicera japonica Thunb.	Found continuously in PCG02, PCG04, and PCG05 in all surveys (including the post-burn 1994 survey for PCG05). Found in PCG03 in 1991 and 2001 but not in 2018.
Microstegium vimineum (Trin.) A. Camus	Found in PCG03 in 2001 and 2018.
Potentilla indica (Andrews) Th. Wolf	New appearances in PCG02 and PCG04 in 2018.
Sonchus oleraceus L.	New appearance in PCG03 in 2018.
Taraxacum officinale F.H. Wigg.	New appearance in PCG02 in 2018.

Table 3.4: Overstory summary statistics based on measurements of all living trees reaching at least 9.5cm DBH in each plot. Basal area and stem density are extrapolated from 0.1 ha measurements to 1 ha estimates. All plots experienced prescribed fire in 2017, and PCG05 also experienced fire in 1994. The 1994 post-fire survey was only conducted for PCG05.

PCG02	**Tree Species**	**Difference**	**Stem Density (/ha)**	**%Difference**	**Basal Area (m^2/ha)**	**%Difference**
1993	26		5740		25.3	
2001	26	0	6520	+6.4%	31.8	+11.4%
2018	8	-18	330	-90.4%	26.7	-8.7%

PCG03	**Tree Species**	**Difference**	**Stem Density (/ha)**	**%Difference**	**Basal Area (m^2/ha)**	**%Difference**
1993	27		6700		24.0	
2001	33	+6	6870	+1.3%	29.6	+10.3%
2018	8	-25	410	-88.7%	22.7	-13.2%

PCG04	**Tree Species**	**Difference**	**Stem Density (/ha)**	**%Difference**	**Basal Area (m^2/ha)**	**%Difference**
1993	25		6980		25.0	
2001	29	+4	8570	+10.2%	30.7	+10.2%
2018	5	-24	400	-91.08%	19.1	-23.4%

PCG05	**Tree Species**	**Difference**	**Stem Density (/ha)**	**%Difference**	**Basal Area (m^2/ha)**	**%Difference**
1993	18		6700		24.2	
1994	6	-12	600	-83.6%	16.3	-19.4%
2001	14	+8	2710	+63.7%	18.4	+6.1%
2018	9	-5	830	-53.1%	24.0	+13.0%

Table 3.5: Visual estimates of cover were recorded in cover classes: 0%, 1-5%, 5-25%, 25-50%, 50-75%, 75-95%, and 95-100% where the classes are named based on the midpoints. Red = decrease from previous survey; Green = increase from previous survey. It was unclear in the 1994 and 2001 surveys if "bare area" indicated bare soil or unvegetated ground (potentially covered in litter or duff).

Survey	Plot	Metric	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10
1993	PCG02	Total Herb Cover	0	3	3	3	3	3	3	3	0	3
1993	PCG03	Total Herb Cover	37	3	37	15	3	15	15	0	0	3
1993	PCG04	Total Herb Cover	3	3	3	3	3	3	3	15	3	3
1993	PCG05	Total Herb Cover	15	15	15	62	0	85	62	62	62	37
1994	PCG05	Bare Area	15	0	15	3	15	0	15	15	3	3
1994	PCG05	Bryophyte/Lichen	0	0	0	0	0	0	0	0	3	0
1994	PCG05	Total Herb Cover	37	15	15	37	3	62	37	15	37	62
2001	PCG02	Bare Area	85	62	97	85	97	97	97	85	97	85
2001	PCG02	Bryophyte/Lichen	0	37	0	0	0	0	0	3	0	0
2001	PCG02	Canopy Opening	0	62	3	37	0	0	3	3	0	3
2001	PCG02	Logs/Trees	15	0	0	15	0	0	3	3	0	3
2001	PCG02	Rock	0	0	0	0	0	0	0	0	0	0
2001	PCG02	Total Herb Cover	3	3	3	3	3	3	3	3	3	3
2001	PCG03	Bare Area	0	85	62	85	62	85	62	85	37	97
2001	PCG03	Bryophyte/Lichen	62	15	0	0	3	3	3	0	3	3
2001	PCG03	Canopy Opening	62	0	3	3	3	3	3	0	15	0
2001	PCG03	Logs/Trees	0	0	3	0	0	3	3	3	37	0
2001	PCG03	Rock	0	0	0	0	0	0	0	0	0	0
2001	PCG03	Total Herb Cover	62	3	37	3	37	3	15	3	37	3
2001	PCG04	Bare Area	37	97	85	0	97	0	85	85	85	85
2001	PCG04	Bryophyte/Lichen	37	0	0	97	3	97	3	3	3	3
2001	PCG04	Canopy Opening	15	0	0	3	0	0	0	0	0	0
2001	PCG04	Logs/Trees	0	0	3	0	0	3	3	0	0	0
2001	PCG04	Rock	0	0	0	0	0	0	0	0	0	0
2001	PCG04	Total Herb Cover	3	3	15	15	3	3	3	3	3	3
2001	PCG05	Bare Area	0	0	0	3	85	3	0	0	0	15
2001	PCG05	Bryophyte/Lichen	0	0	3	0	0	0	3	0	0	0
2001	PCG05	Canopy Opening	85	62	97	97	0	85	97	85	97	85
2001	PCG05	Logs/Trees	3	37	0	0	3	0	0	0	0	37
2001	PCG05	Rock	0	0	0	0	0	0	0	0	0	0
2001	PCG05	Total Herb Cover	97	97	97	97	3	97	97	97	97	97
2018	PCG02	Bare Soil	3	3	3	3	3	3	3	3	3	3
2018	PCG02	Bryophyte/Lichen	0	0	0	0	0	0	0	3	3	3
2018	PCG02	Canopy Opening	15	15	37	15	15	15	15	37	37	62
2018	PCG02	Logs/Trees	15	15	15	15	15	3	3	3	15	15
2018	PCG02	Rock	0	0	0	3	0	3	3	0	0	0
2018	PCG02	Total Herb Cover	37	37	62	37	37	62	15	62	62	37
2018	PCG02	Unvegetated Ground	37	37	15	37	62	37	62	37	37	37
2018	PCG03	Bare Soil	3	3	3	3	3	3	3	3	3	3
2018	PCG03	Bryophyte/Lichen	3	3	3	3	3	3	3	3	3	3
2018	PCG03	Canopy Opening	62	62	37	15	37	15	15	15	37	62
2018	PCG03	Logs/Trees	15	15	15	3	3	15	3	3	3	3
2018	PCG03	Rock	3	3	3	3	3	3	3	3	3	3
2018	PCG03	Total Herb Cover	85	62	37	15	37	37	37	37	37	62
2018	PCG03	Unvegetated Ground	15	37	62	85	62	62	62	62	62	37
2018	PCG04	Bare Soil	3	3	3	3	3	3	3	3	3	3

Table 3.5: (Continued).

2018	PCG04	Bryophyte/Lichen	3	0	0	3	3	3	3	3	3	3
2018	PCG04	Canopy Opening	62	37	62	62	37	62	62	85	85	85
2018	PCG04	Logs/Trees	3	15	3	3	3	3	3	3	15	15
2018	PCG04	Rock	0	3	0	0	0	0	0	0	0	0
2018	PCG04	Total Herb Cover	37	3	85	15	37	62	62	37	37	15
2018	PCG04	Unvegetated Ground	62	62	37	37	37	15	15	37	37	62
2018	PCG05	Bare Soil	3	3	3	3	3	3	3	3	3	3
2018	PCG05	Bryophyte/Lichen	3	0	0	0	0	3	3	0	3	0
2018	PCG05	Canopy Opening	37	37	62	62	37	62	62	37	62	37
2018	PCG05	Logs/Trees	3	15	15	3	3	3	15	3	3	3
2018	PCG05	Rock	0	0	0	0	0	0	0	0	0	3
2018	PCG05	Total Herb Cover	85	37	37	37	37	62	62	62	37	62
2018	PCG05	Unvegetated Ground	15	62	62	62	62	37	37	37	62	62

FIGURES

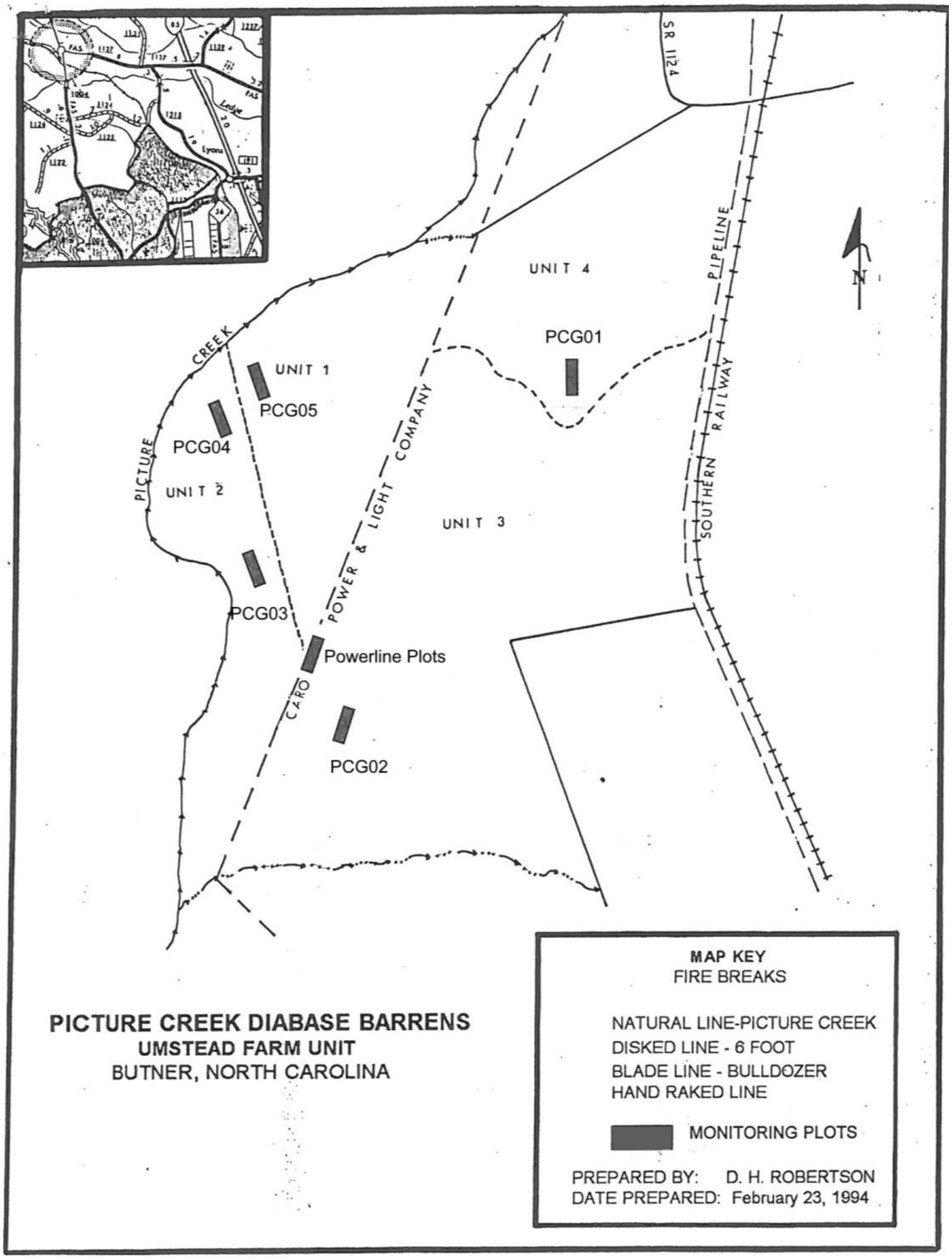

Figure 3.1: Locations of the five Picture Creek Glade (PCG) plots at Picture Creek Diabase Barrens. Figure adapted from Barnette-Lawrence 1995.

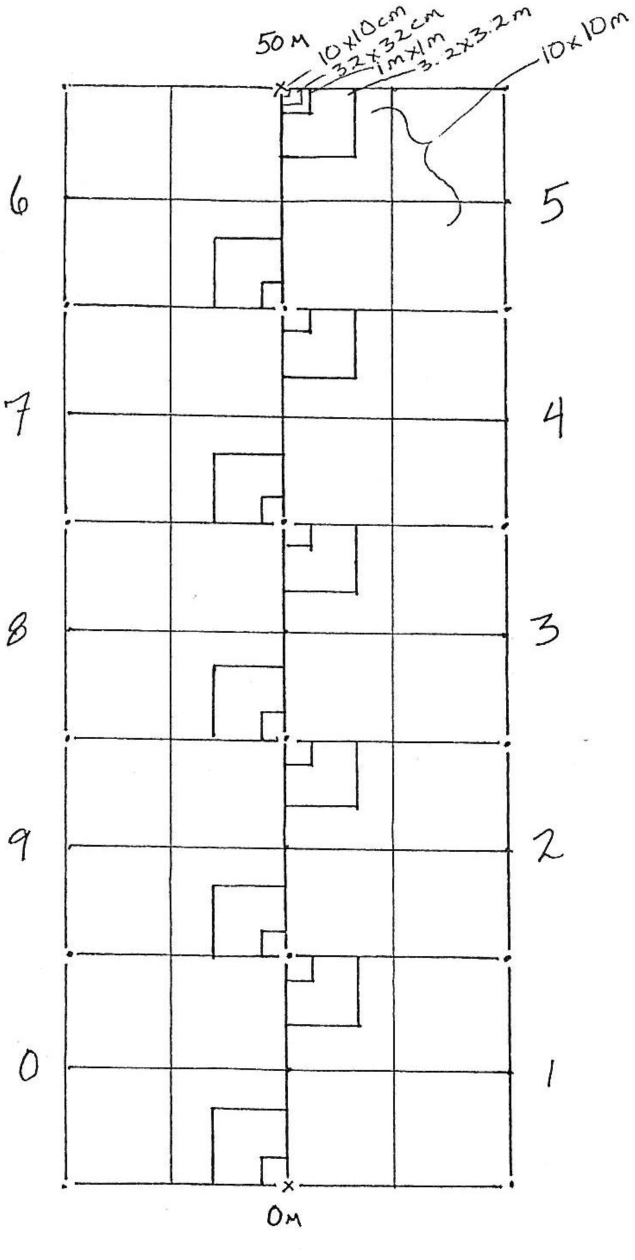

Figure 3.2: Figure from Lunsford (2002) showing layout of 0.1 ha plots with nested modules.

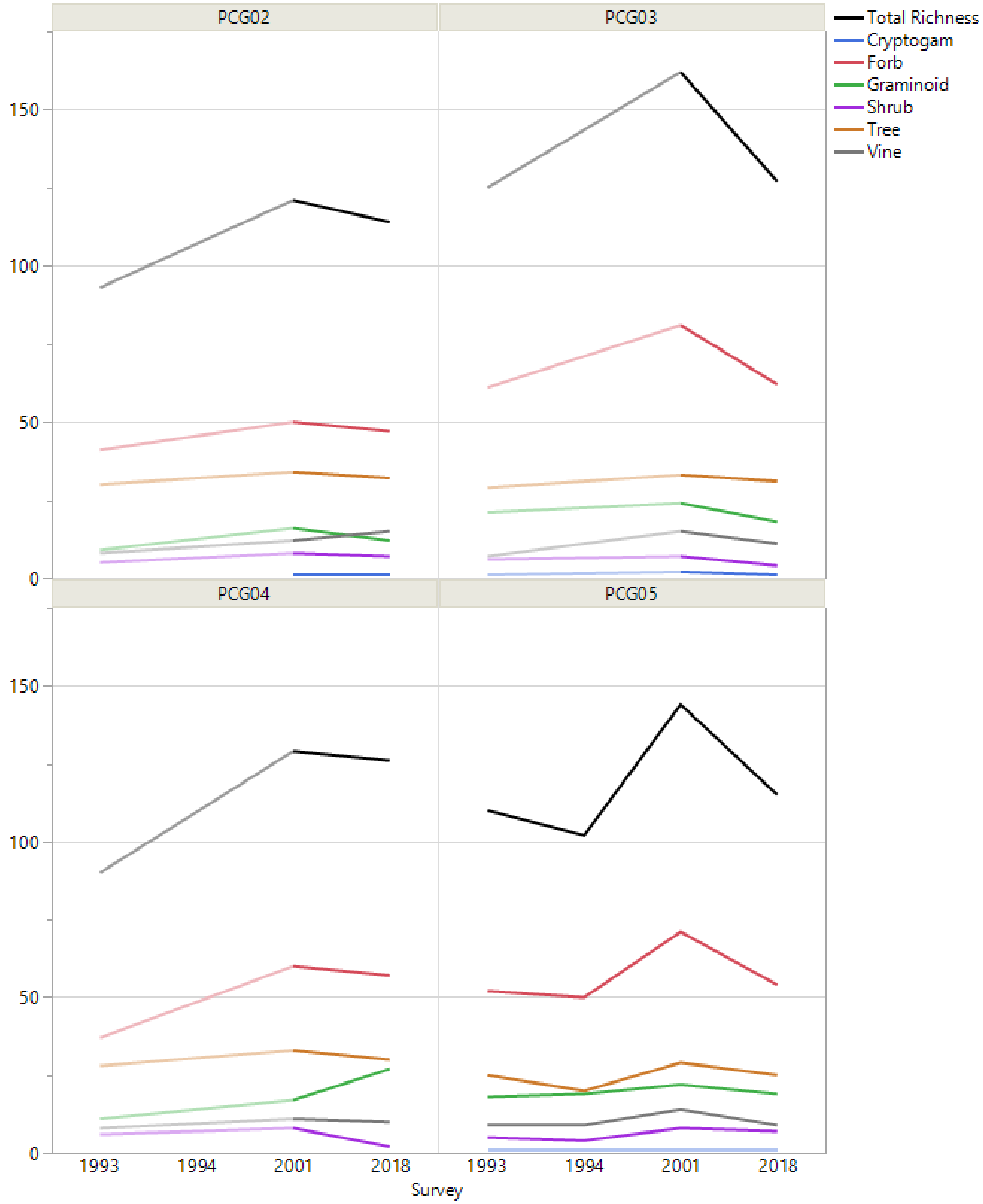

Figure 3.3: Plot species richness by growth habit over time. Only PCG05 had a 1994 survey, indicated by the faded section of the other plots.

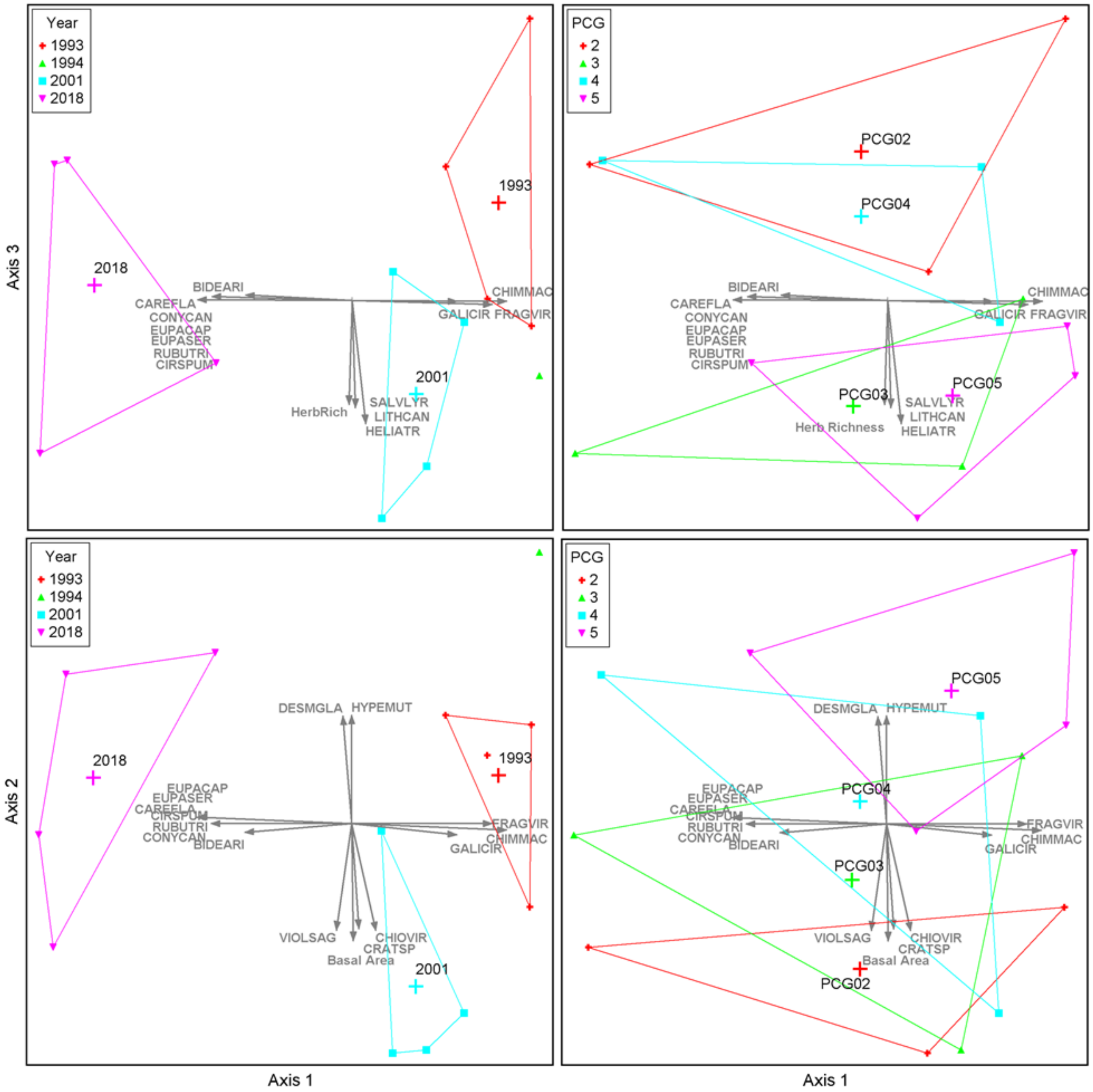

Figure 3.4: NMDS ordination of plot-level species presence over three survey years. Points represent individual plots (n = 13) and are colored by survey year. Left-side panels are colored by survey year, while right-side panels are colored by plot. Hulls encompass points of the same year/plot. Vectors indicate trends in species occurrence (presence/absence).

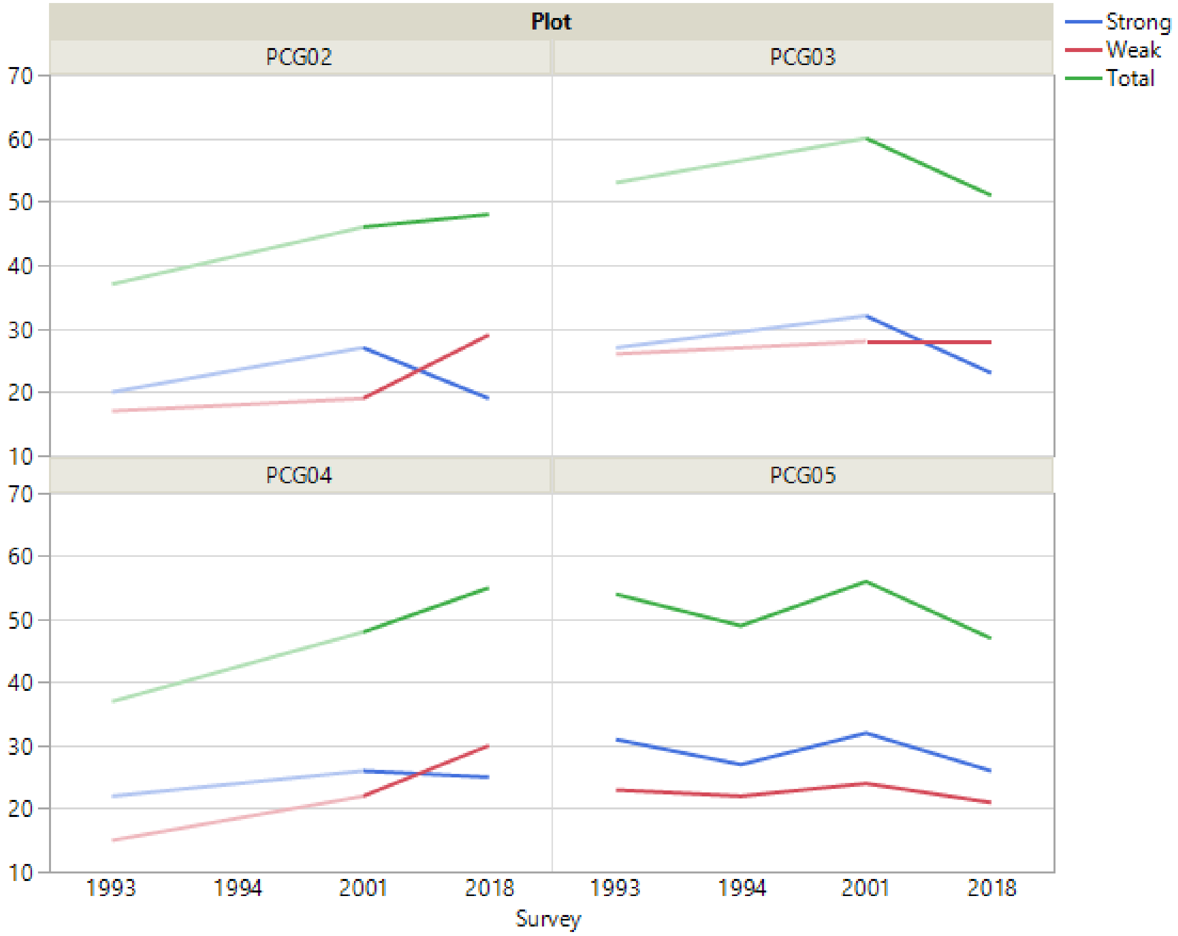

Figure 3.5: Trends in Piedmont prairie indicator species richness. Indicator species are defined based on Davis et al. (2002) and divided into "strong" and "weak" indicators. PCG05 is the only plot with a 1994 survey.

Figure 3.6: Trends in habitat shade class associations of the herbaceous species found in PCDB monitoring plots. 150 total species across all plots and years. Includes both native and exotic (only 3 exotic species). All plots experienced prescribed fire in 2017. PCG05 also experienced fire in early 1994 (survey is one growing season post-burn).

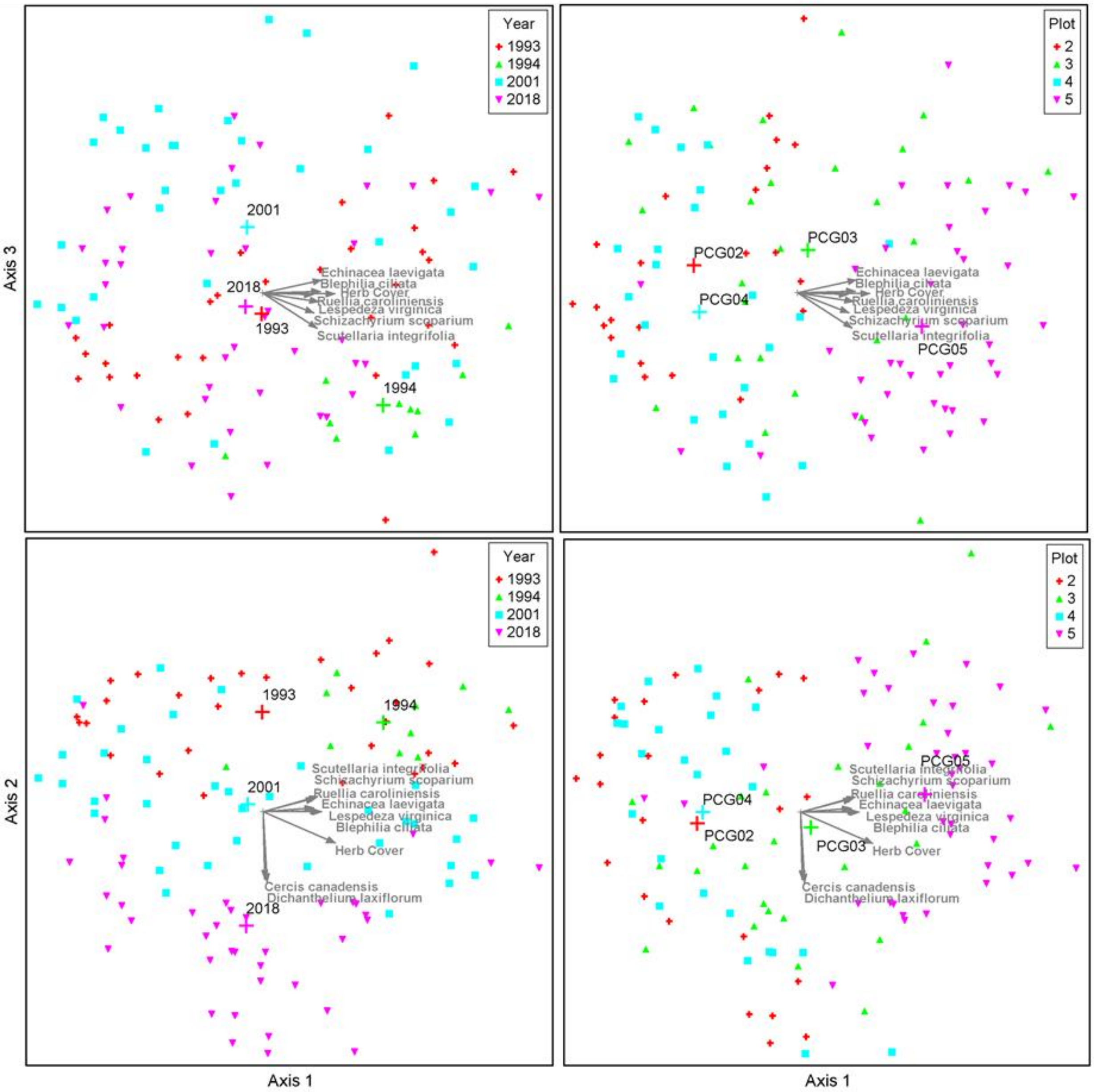

Figure 3.7: NMDS ordination of 1 m^2 nested modules. Points represent individual modules (n = 117). Left-side panels are colored by survey year, while right-side panels are colored by plot. Vectors represent trends in species abundance and environmental metrics.

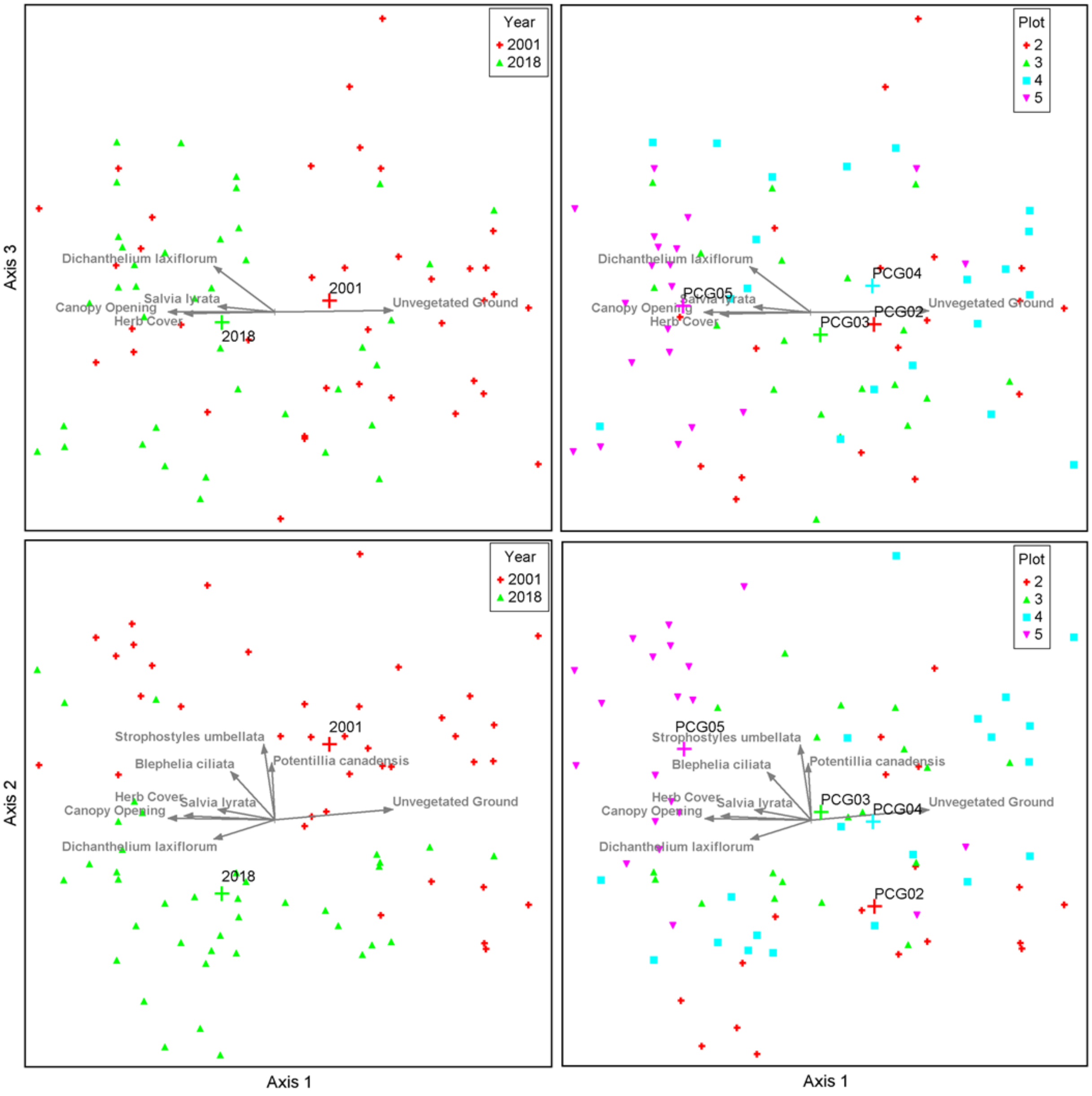

Figure 3.8: NMDS ordination of 1 m^2 nested modules for 2001 and 2018 suveys. Points represent individual modules (n = 77). Left-side panels are colored by survey year, while right-side panels are colored by plot. Vectors represent trends in species abundance and environmental metrics.

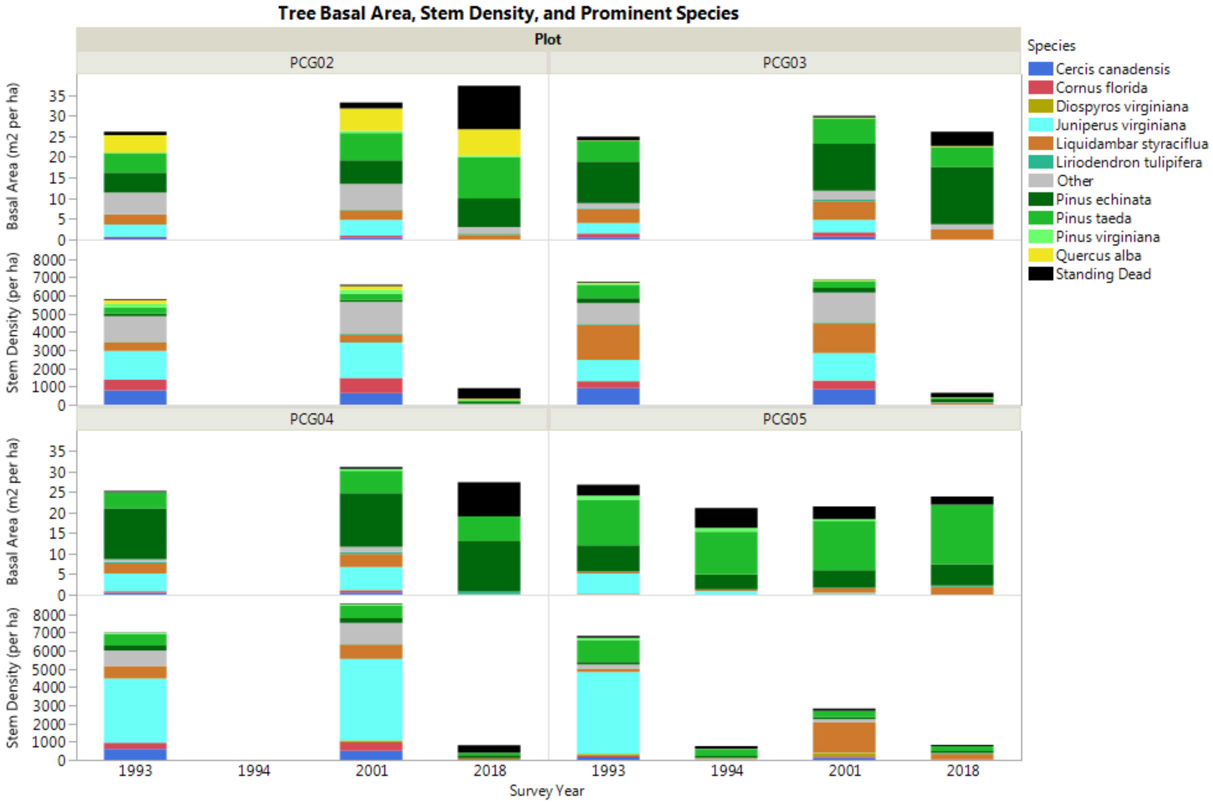

Figure 3.9: Overstory summary statistics based on measurements of all living trees reaching at least 9.5cm DBH in each plot. Basal area and stem density are extrapolated from 0.1 ha measurements to 1 ha estimates. All plots experienced prescribed fire in 2017, and PCG05 also experienced fire in 1994. The 1994 post-fire survey was only conducted for PCG05.

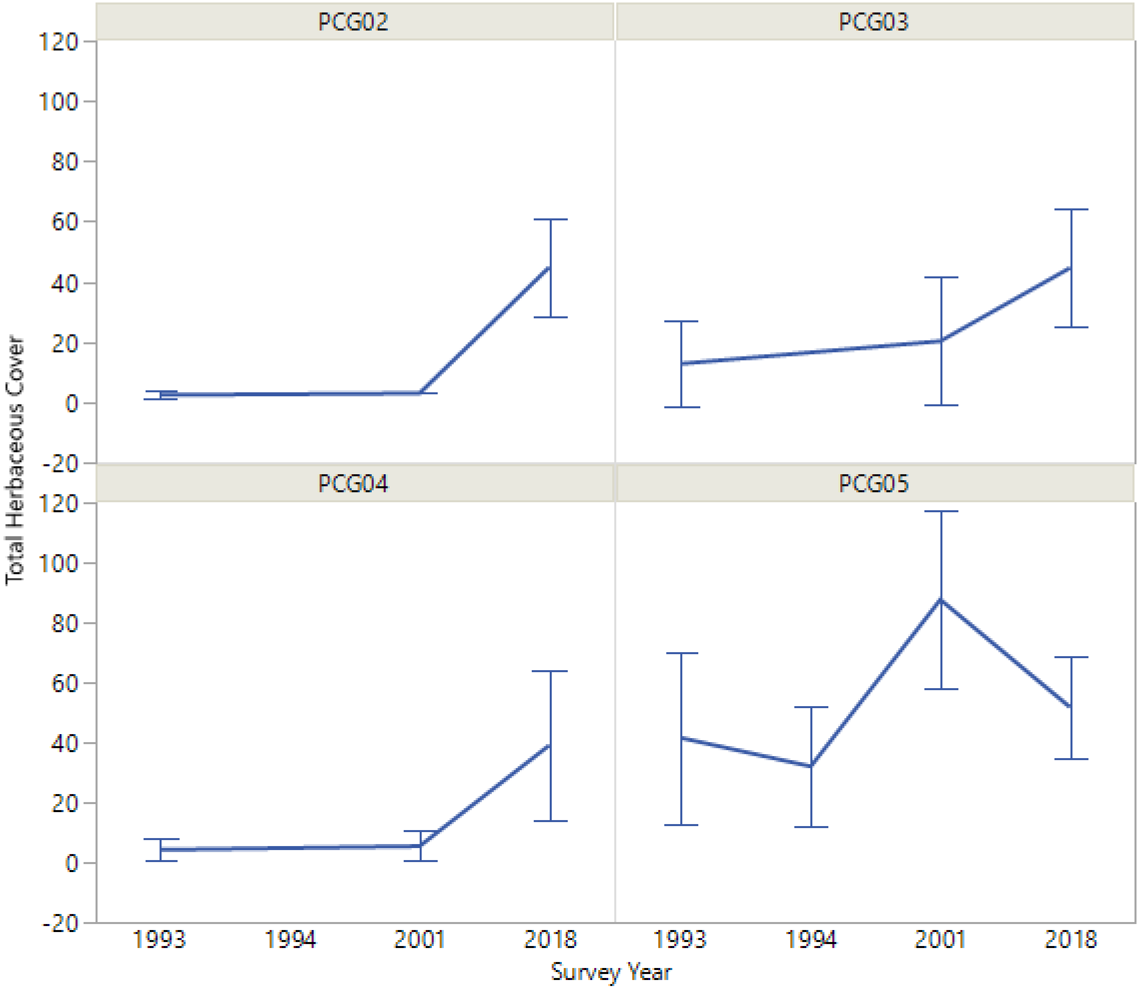

Figure 3.10: Average total herbaceous cover of subplots. Points represent averages of cover estimates of total herbaceous cover from the 10 subplots of each plot. Error bars represent +/- one standard deviation. Total herbaceous coverage was initially estimated in cover codes representing ranges in percent cover. Only PCG05 was surveyed in 1994.

CHAPTER 4: In Search of the “Piedmont prairies”: Multivariate Analyses of Heliophilic Plant Communities of the Eastern Piedmont of North America.

ABSTRACT

Although vegetation succession in the eastern Piedmont of North America favors closed-canopy forest in the absence of disturbance, historical evidence suggests upland vegetation of the region was once characterized by areas of heliophilic vegetation such as prairies, savannas, and/or woodlands. At present, native heliophilic flora persists in areas where primarily anthropogenic disturbances (such as mowing) maintain open conditions, and the semi-natural state of these remnant patches creates a challenge for community classification, conservation, and restoration efforts that rely on an understanding of natural reference dynamics and community structure. While much work has been done to characterize individual or small groups of these heliophilic vegetation communities, there has been no comprehensive and quantitative study to characterize the full breadth of the heterogeneous heliophilic vegetation in the eastern Piedmont. We seek to partially address this issue using plot data from the Carolina Vegetation Survey (CVS) to quantitatively characterize the non-forest, upland communities of the Piedmont region of the Carolinas and Virginia (a well-surveyed portion of the eastern Piedmont) and address the following objectives: 1) identify and characterize the major types of extant Piedmont, upland, heliophilic vegetation; 2) offer a definition and characterization of extant vegetation colloquially known as “Piedmont prairie” and discuss how it relates to other types of heliophilic vegetation. Our final dataset consisted of 195 plots obtained from the CVS database and representing non-forest, upland vegetation of the Carolina and Virginia Piedmont. Through hierarchical clustering (flexible-β) and stride analysis (plotting the PARTANA ratio and silhouette width) we determined the optimal number of partitions for our dataset to be 12 clusters. The r-package *optpart* was used to move plots between clusters to further ensure plots are members of their best-fit cluster. Nonmetric multidimensional scaling (NMDS) ordination was used to visualize compositional trends in the dataset. Through primarily quantitative means, we identified 12 major types of heliophilic vegetation that can be roughly lumped into five larger groupings: Piedmont Oak-Hickory and Red Cedar Woodlands, Piedmont Glades, Piedmont Pine Woodlands, Piedmont Savannas and Grasslands, and Piedmont River Terrace Glades.

INTRODUCTION

Naturally open plant communities are currently rare in the eastern Piedmont of North America, a region where succession favors closed-canopy forest in the absence of disturbance. However, historical evidence suggests the uplands of the region were once home to more open-canopied plant communities with significant components of heliophilic forbs and grasses. Rostlund (1957) and Barden (1997) brought attention to and summarized the historical accounts from early explorers, traders, and settlers who described "prairies, savannas, plains, or old fields (Barden 1997)" in the Piedmont uplands. The persistence of heliophilic vegetation in the eastern Piedmont requires some form of disturbance (such as fire and/or grazing) to maintain an open vegetation structure. The heliophilic plant communities described in the historical accounts largely disappeared during European settlement and subsequent fire suppression of the region (Barden 1997; Frost 2002; Davis et al. 2002). While no pristine examples of the historical plant communities are known to exist today, heliophilic flora persist in areas where primarily anthropogenic disturbances (such as mowing or herbicide application) maintain open conditions (Davis et al. 2002). Because of the present anthropogenic influences on and rarity of natural heliophilic assemblages, many uncertainties remain about the natural species composition, community structure, ecological dynamics, and historical distribution of these heliophyte communities.

Classification and appropriate management of heliophilic vegetation in the region remains a challenging issue. As Barden (1997) summarized, many names have been applied to the open vegetation encountered during the time of early exploration and European settlement, yet the name "Piedmont prairie" stands out in current general usage. Today it is not uncommon to hear vegetation described as a "Piedmont prairie remnant" (Barden 1997; Fleming et al. 2001; Davis et al. 2002; Thompkins et al. 2010; Benson 2011; Stanley et al. 2019), yet there exists no single definition of "Piedmont prairie" as a plant community in the present landscape. The species list compiled by Davis et al. (2002) provided a good starting point for recognizing heliophilic vegetation in the region, but it did not offer community classification or ecological analyses of assemblages they referred to as "Piedmont prairie remnants." Benson (2011) provided a characterization of some "Piedmont prairie" sites but did not give a formal definition of these communities or how they relate to the broader context of other Piedmont heliophilic vegetation. Adams (2012) documented and characterized vegetation he named relict "Piedmont savanna" flora, but it remains unclear how this flora relates to other Piedmont heliophilic assemblages such as "Piedmont prairies." While these efforts have done much to document and characterize specific assemblages, none have led to more comprehensive definition and characterization of the breadth of extant Piedmont heliophilic vegetation.

Efforts to document, characterize, and classify vegetation of the region are vital to understanding these now rare communities. A robust vegetation classification system supports communication, conservation, restoration, and ecological work. Traditional regional classifications were based primarily on expert judgement and field observations. As more and more quantitative plot data become available through the efforts of regionally-based groups, such as natural heritage programs and the Carolina Vegetation Survey (CVS), we can now use multivariate computational tools to help refine existing traditional classification systems and to search for compositional patterns that may have been previously overlooked. The advent of the USNVC has also stimulated the movement toward standardized classification systems backed by quantitative analyses (Peet et al. 2012). Quantitative analyses can address conflicts between regional classification systems, the USNVC, and colloquial perceptions of vegetation. These analyses can also address questions of whether vegetation colloquially identified as "Piedmont prairie" differs in floristic composition from "Piedmont savanna."

Here we use multivariate techniques and plot data from the CVS database to: 1) identify and characterize the major types of extant Piedmont, upland, heliophilic vegetation; 2) offer a definition and characterization of extant vegetation colloquially known as "Piedmont prairie" and discuss how it relates to other types of heliophilic vegetation.

METHODS

Study Area

The eastern Piedmont plateau is a gently rolling geographic region located on the eastern coast of North America. It is bordered on the east by the Atlantic Coastal Plain and on the west by the Appalachian Mountains. Within the Piedmont region, the eastern edge is often referred to as the "outer" or "lower" Piedmont as it gently slopes downward toward the lower elevation of the Coastal Plain. The Fall Line serves as the dividing line between the most eastern edge of the Piedmont and the western edge of the Coastal Plain. The western edge of the Piedmont is also known as the "inner" or "upper" Piedmont as it slopes up into the Appalachian Mountains, the dividing line here being the Blue Ridge Escarpment. The Piedmont stretches north-south from New York to Alabama, but we focus on the portion that lies within Virginia and the Carolinas.

Data Preparation

The final dataset is a subset of the larger dataset used in Chapter 2, but preparation steps are summarized here: An initial dataset containing 2914 “Piedmont” plots was retrieved from the CVS database. Part of the CVS mission is to document natural and semi-natural vegetation of the Carolinas and surrounding region. Plots were surveyed between 1977 and 2015 following CVS methodology (Peet et al. 1998) or comparable Virginia Natural Heritage methodology (DCR-DNH 2011). Species abundance in plots is reported in CVS cover class codes that reflect ranges of percent cover: 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% and 10 > 95%. Plots vary in total size from 10 to 1000 m^2 based on area occupied by the plant community and resources of the surveyors. The CVS has assigned all plots to USNVC Associations based on expert judgement. For our analysis, plots with missing cover data were removed from the initial dataset. We used Weakley (2015) as our taxonomic reference and we standardized each entity to be as closely equivalent to species rank as possible for our analyses (Appendix S4.1). For example, the taxa *Acer* sp., *Acer rubrum*, *Acer rubrum* var. *rubrum*, and *Acer rubrum* var. *trilobum* were all present in the dataset. We chose to treat the two subspecific taxa as records of *Acer rubrum* and discard records of the poor resolution *Acer* sp. Any plot records that contained a discarded taxon with a cover code >6 were removed from the dataset due to missing information. From the remaining plots, we extracted all those classified as a non-forest association (i.e., woodlands, shrublands, herbaceous vegetation, or sparse vegetation) that were representative of upland, terrestrial, open or semi-open vegetation. This final dataset contained 195 plots and 957 taxa (hereafter referred to as “species”) from Virginia, North Carolina, and South Carolina.

Data Analysis

A Bray-Curtis dissimilarity matrix was calculated based on the species compositions of the 195 plots and used in an agglomerative hierarchical clustering with flexible-beta group linkage (β = -0.25). Hierarchical clustering was performed in R (package *hclust*), and stride analysis (package *optpart*; Roberts 2010) was used to identify the most “optimal” partition solutions. Stride simultaneously plots silhouette width (Rousseeuw 1987) and the PARTANA ratio (Aho et al. 2008), two different geometric measures of within versus between cluster similarity, over a range of partition solutions (i.e., cluster membership at each level of the hierarchical clustering dendrogram). A mathematically optimal partition solution achieves high values of the two ratios. In some cases, several possible solutions will achieve different combinations of the two ratios that appear favorable. We considered partition solutions here that were both mathematically optimal and comparable in scope to existing classification units (e.g. USNVC Groups). We then used the optpart function (package *optpart*; Roberts 2010) to further optimize our chosen partition by moving plots between clusters to maximize the PARTANA ratio and silhouette width. This movement of plots between clusters breaks the hierarchical relationship that was generated by the initial clustering, so we performed a second round of hierarchical clustering (flexible-beta group linkage; $\beta = -0.25$) using a Bray-Curtis dissimilarity matrix calculated from the average cover of each species in each optimized cluster. To calculate the average cover of each species, we converted the cover codes to the geometric mean of their ranges (of percent cover) and averaged them before transforming them back into cover codes.

Once our partition solution was chosen and each cluster was geometrically optimized, species indicator values (IndVals) for each cluster were calculated in PC-ORD (version 6.22) based on Dufrêne and Legendre (1997). Species IndVals can range from 0 (no indicator value) to 100 (perfect indicator) for a given species in a given cluster. The Dufrêne and Legendre IndVal is a combination of relative frequency, the percentage of plots in a given cluster in which a species occurs, and relative abundance, the proportion of species abundance (based on cover class codes in our dataset) that is concentrated in the given cluster versus other clusters. A randomized Monte Carlo test with 10,000 runs was used to assess significance of the observed IndVals versus IndVals obtained by randomly shuffling plots between clusters.

Nonmetric Multidimensional Scaling (NMDS) ordination was used to visualize species compositional trends in the 195-plot dataset. NMDS ordination was performed in PC-ORD using the “slow and thorough” autopilot procedure. The 195 plots from the CVS database came with associated metadata for a range of measurements such as elevation and soil chemistry. These environmental variables were overlain on the NMDS ordination.

Other considerations

We also examined the occurrence of habitat shade class specialists (as identified in Chapter 2), estimated canopy cover (as calculated from cover of tree taxa in Chapter 2), occurrence of Davis et al. (2002) prairie indicator species, and calculated 1 m^2 average species richness for our clusters identified through hierarchical clustering.

RESULTS

NMDS Ordination

The NMDS ordination autopilot chose a three-dimensional solution (Figure 4.1) that captured a total of 74.7% of the compositional variation in the dataset. The first axis captured 33.6% of the compositional variation and is correlated with pH ($r^2 = 0.278$) and the abundances of *Acer rubrum* ($r^2 = 0.394$), *Nyssa sylvatica* ($r^2 = 0.387$), and *Oxydendrum arboreum* ($r^2 = 0.288$). Clusters 3, 5, 6, 11, and 12 separated toward the end of the axis characterized by higher pH and lower abundance of *A. rubrum, N. sylvatica, and O. arboreum*. Clusters 7 and 8 separated toward the opposite end of this axis. The second axis captured 23.8% of the compositional variation in the dataset and is correlated with the abundance of *Dichanthelium boscii* ($r^2 = 0.288$) and total estimated tree cover ($r^2 = 0.244$). Cluster 9 separated in the direction of greater abundance of *D. boscii* and higher estimated tree cover while clusters 6, 5, and 12 separated in the opposite direction. The third axis captured 19.1% of the compositional variation in the dataset and is correlated with the abundance of *Liquidambar styraciflua* (r2 = 0.322), *Quercus montana* ($r^2 = 0.248$), *Eupatorium hyssopifolium* ($r^2 = 0.240$), and *Rhus copallinum* ($r^2 = 0.240$). Clusters 2, 3, 4, and 6 separated toward the direction of *Q. montana* while clusters 7, 9, 10, and 11 separated toward the direction of greater abundance of *L. styraciflua*, *E. hyssopifolium*, and *R. copallinum*.

Hierarchical Clustering

The stride analysis output (Figure 4.2) suggested a range of optimal partition solutions to consider, and we chose to focus here on 12 clusters (Figure 4.3; Table 4.1). This number of clusters corresponded to a peak in both silhouette width and PARTANA ratio, suggesting a geometrically favorable solution, and roughly matched the number of USNVC Groups assigned in the dataset (13 Groups, if those represented by only a single plot in a priori assignments to associtions are not considered). Groups represent a lower-middle level of the USNVC hierarchy and are meant to convey regional groupings of communities (as opposed to local or continental groupings). Given the rather heterogeneous nature of the 195-plot dataset, clusters that might capture regional variation seem appropriate. The geographic locations of the plots in each cluster are found in Figure 4.4.

Indicator Values and Cluster Characterization

Of the 957 species in the dataset, 304 (32%) had a significantly high IndVal for at least one cluster ($p<0.05$). These significantly high IndVals ranged from 14.2 (*Scutellaria elliptica* for cluster 1) to 84.5 (*Desmodium paniculatum* for cluster 9). The detailed results of the indicator species analysis are presented in Table 4.2.

A characterization of the 12 clusters and some of their properties follows. Clusters have been organized into five larger groupings based on the second round of hierarchical clustering (Figure 4.3). We provide cluster names derived from the general location, frequent species, indicator species, perceived vegetation structure, and colloquial vegetation names for the majority of plots in each cluster. Most clusters contain a diversity of communities, so these names do not necessarily fit every plot in a given cluster. We further provide names in the format of the USNVC naming system (FGDC 2008; Jennings et al. 2009), consisting of a series of species names (e.g., those with high frequency, indicator values, and/or cover values) connected by "-" to indicate they are within the same vertical stratum or separated by "/" to indicate they are in different vertical strata.

We summarize the major compositional characters of each cluster, their distribution, how they relate to existing regional classification systems, and various environmental information, as available for plots. Soil pH measurements are summarized here using USDA soil reaction classes (Soil Science Division Staff 2017) defined as Ultra Acid (<3.5), Extremely acid (3.5–4.4), Very Strongly Acid (4.5–5.0), Strongly Acid (5.1–5.5), Moderately Acid (5.6–6.0), Slightly Acid (6.1–6.5), and Neutral (6.6–7.3). Summaries of environmental data and other plot information are found in Table 4.3 and Figures 4.5–4.8.

Grouping 1: Piedmont Oak-Hickory and Red Cedar Woodlands

Cluster 1 (72 plots) – Piedmont Red Cedar-Post Oak Woodlands

Juniperus virginiana – Quercus stellata – Carya glabra / *Viburnum prunifolium* / *Danthonia spicata*

This is the largest cluster (72 plots) and represents a variety of oak woodlands found throughout the Virginia and Carolina Piedmont. Many plots of this cluster are colloquially referred to as "montmorillonite woodlands (Schafale and Weakley 1990)" or "hardpan forest (Schafale 2012)," both names indicating the underlying soil might have a shrink-swell clay layer that can restrict the movement of water or the growth of plant roots. Mean estimated tree canopy cover is 90% (range = 38–100%; Table 4.3), the highest mean of any cluster.

Important tree species are *Juniperus virginiana* (96% frequency), *Carya glabra* (90% frequency) and a variety of *Quercus* spp., with the most frequent being *Quercus stellata* (94% frequency; IndVal = 27.3). *Carya carolinae-septentrionalis* (state-listed in Virginia; Townsend 2019) is a rare species with a significant IndVal (= 26.6) in this cluster. *Viburnum prunifolium* (IndVal = 27.8) is the highest indicator species. Common herbs are *Danthonia spicata* (83% frequency) and *Piptochaetium avenaceum* (63% frequency; IndVal = 19.2). *Endodeca serpentaria* (57% frequency; IndVal = 23.3) is the highest indicator herb, but *Galium circaezans* (58% frequency; IndVal = 18.9) and *Polygonatum biflorum* (56% frequency) are sometimes also present. In addition to the notable indicator species, this cluster is distinguished from the other clusters in this grouping by the higher frequency of *Quercus stellata*, *Quercus alba*, and *Diospyros virginiana*. Just under half (32/72; 44%) of the plots have soil series information and 20 plots (28%) occur on Altisols, some (Iredell) have a shrink-swell clay layer. Soil pH ranges from Extremely to Moderately Acid (Figure 4.7). This type of vegetation is expressed in portions of the following notable sites: Rock Hill Blackjacks Heritage Preserve, Umstead State Park, Yadkin River, Hurdle Mills Flats, Duke Forest, Donnelley Hardpan Bog, and Rockyface Mountain.

Cluster 2 (14 plots) – Inner Piedmont Chestnut Oak Woodlands

Quercus montana – Quercus rubra – Carya glabra – Pinus virginiana / *Danthonia spicata – Carex pensylvanica*

This cluster captures a diversity of oak-pine woodlands in Virginia and North Carolina. Some of the plots in this cluster fit descriptions of Shale Slope Woodlands (Schafale 2012) or Shale Barrens (Fleming et al. 2017), but others would be better characterized as flatrock or outcrop communities. Mean estimated canopy cover is 69% (range = 34–100%; Table 4.3), the 3rd highest mean of any cluster. Important tree species are *Quercus montana* (IndVal = 35.2), *Quercus rubra* (IndVal = 24.5), and/or *Pinus virginiana* (IndVal = 23.5). *Carya glabra* (79% frequency), *Fraxinus* (88% frequency), and *Prunus serotina* (frequency 71%) also tend to be present. Understory vegetation includes *Danthonia spicata* (93% frequency) and *Carex pensylvanica* (IndVal = 49.4). *Solidago ulmifolia* (IndVal = 17.5; state-listed in North Carolina; Robinson 2018), *Solidago bicolor* (IndVal = 15.2; state-listed in South Carolina; SCDNR 2015), *Pellaea atropurpurea* (IndVal = 14.3; state-listed in South Carolina; SCDNR 2015), *Solidago racemosa* (IndVal = 14.3; state-listed in Virginia; Townsend 2019) are notable rare species found in some of these plots. In addition to the notable indicator species, this cluster is distinguished from the other clusters in this grouping by the lower frequency of *Juniperus virginiana* and *Ulmus alata*, and the higher frequency of *Quercus montana* and *Pinus virginiana*. This cluster also lacks *Dichanthelium laxiflorum*, which occurs in the other two clusters in this grouping. Only one plot has soil series information and it occurs on Ayersville (Dystrudept), a poorly developed soil. Soil pH ranges from Extremely Acid to Moderately Acid (Figure 4.7) and survey notes often describe exposed bedrock being present. This type of vegetation is expressed in portions of the following notable sites: Box Creek, Rocky Face Mountain, Cedar Mountain, and South Mountains.

Cluster 3 (9 plots) – Piedmont Red Cedar-Ash Woodlands

Juniperus virginiana – Fraxinus sp. / *opuntia / *Danthonia spicata* Woodland

This cluster captures a variety of woodlands in North and South Carolina characterized by *Juniperus virginiana* (100% frequency), *Fraxinus* sp. (89% frequency), *Ulmus alata* (78% frequency), and *Carya glabra* (78% frequency). Understory vegetation includes a variety of forbs such as *Coreopsis pubescens* (Indval = 55.6), *Houstonia longifolia* (IndVal = 33.3), *Galium pilosum* (67% frequency), and *Packera anonyma* (56% frequency). The grasses *Danthonia spicata* (89% frequency) and *Dichanthelium laxiflorum* (78% frequency) are frequent. *Chionanthus virginicus* (IndVal = 23.2), *Pinus pungens* (IndVal = 25.5), and *Quercus imbricaria* (Indval = 29.6) are notable woody indicator species. *Opuntia mesacantha* (IndVal = 37.9) is a significant indicator species occurring in 67% of plots. *Hypericum densiflorum* (IndVal = 43.8; state-listed in Virginia; Townsend 2019), *Coreopsis grandiflora* (IndVal = 22.2; state-listed in North Carolina; Robinson 2018), and *Dichanthelium bicknellii* (IndVal = 20.9; state-listed in North Carolina; Robinson 2018) are notable rare species found in some of these plots. In addition to the notable indicator species, this cluster is distinguished from the other clusters in this grouping by the lower frequency of *Quercus* spp. (*Quercus imbricaria* is the most frequent at only 33%), and lower estimated tree cover (Table 4.3). This cluster also lacks *Pinus virginiana* and *Vaccinium* spp. which are generally present in the other clusters. Only four (44%) plots have soil series information and they mostly (3) occur on Ultisols. Soil pH ranges from Extremely Acid to Moderately Acid (Figure 4.7). Several (4; 44%) plots are located in the Brushy Mountains. Two plots are "oak-hickory gaps" surveyed by Nick Adams (Adams 2012). This type of vegetation is expressed in portions of the following notable sites: Brushy Mountains, Joe Mountain, and Glassy Mountain Heritage Preserve.

Grouping 2: Piedmont Glades

Cluster 4 (10 plots) – Outer Piedmont Red Cedar Cliff Glades

Juniperus virginiana – Vaccinium arboreum / Hieracium venosum

This cluster captures a variety of woodlands found on cliffs or slopes in the Outer Piedmont of North and South Carolina. This is one of the most depauperate clusters, with an average species richness of only 6 spp./m^2 (Table 4.3). This cluster is characterized by *Juniperus virginiana* (100% frequency) and *Quercus* spp. (especially *Quercus stellata* [70% frequency]). *Acer leucoderme* (IndVal = 51), *Pleopeltis michauxiana* (IndVal = 45.4), and *Vaccinium arboreum* (IndVal = 39.3, 90% frequency) are notable indicator species. Many of these plots have been invaded by species such as *Ailanthus altissima* (50% frequency) and *Lonicera japonica* (70% frequency). Understory vegetation includes species, such as *Phytolacca* *americana* (IndVal = 35.3) and *Hieracium venosum* (IndVal = 35.5), which are commonly found in disturbed margins. *Boechera missouriensis* (state-listed species in North Carolina; Robinson 2018) and *Tillandsia usneoides* (state-listed species in Virginia; Townsend 2019) occur in a few plots (each with 20% frequency). In addition to the notable indicator species, this cluster is distinguished from the other clusters in this grouping by the higher frequency of *Vaccinium* spp. (especially *V. arboreum*) and the lower frequency of *Schizachyrium scoparium*. The soil series reported at most (90%) sites are Dystrudepts, well-drained soils with weak development that are weathered from felsic material found in the Carolina Slate Belt. Soil pH ranges from Extremely to Strongly Acid (Figure 4.7). This type of vegetation is expressed in portions of the following notable sites: Richardson Creek Slopes, Uwharrie River Cliffs, Morgan's Bluff, and the Savannah River Bluffs Heritage Preserve.

Cluster 5 (9 plots) -- Piedmont Flatrock and Outcrop Glades

Schizachyrium scoparium – Phemeranthus teretifolius – Aristida dichotoma herbaceous vegetation

This cluster captures a variety of herbaceous-dominated vegetation found on shallow soils associated with flatrocks or rock outcrops on both the Inner and Outer Piedmont of Virginia and North Carolina. These plots generally fit descriptions of the perennial herbaceous zone of granitic flatrock communities found in Schafale (2012) and Fleming et al. (2017). Plots of this cluster have a very high occurrence of open habitat specialists, representing 45% of all occurrences (Figure 4.5). The most prevalent species are *Schizachyrium scoparium* (89% frequency), *Phemeranthus teretifolius* (IndVal = 31.7, 78% frequency), and *Aristida dichotoma* (IndVal = 50.9, 78% frequency). *Juniperus virginiana* (56% frequency) is sometimes present. No plots have soil series information, but soil pH ranges from Extremely Acid to Neutral (Figure 4.7). Survey notes describe shallow soils, often with exposed bedrock, and sometimes with ponding depressions. This type of vegetation is expressed in portions of the following notable sites: Uwharrie National Forest and Rocky Face Mountain.

Cluster 6 (7 plots) – Inner Piedmont Red Cedar Glades

Juniperus virginiana / *Myriopteris lanosa*

This small cluster captures a variety of glade vegetation restricted to outcrops in the Inner Piedmont of Virginia and North Carolina. Beyond some general compositional similarities to outcrop glades or barrens, the indicator and prevalent species for this cluster do not clearly correspond to any specific communities described in Schafale (2012) or (Fleming et al. 2017). *Juniperus virginiana* (86% frequency) and *Fraxinus* sp. (57% frequency) are common woody species. The herbaceous understory is characterized by species such as *Myriopteris lanosa* (IndVal = 49.4), *Schizachyrium scoparium* (71% frequency), and *Allium cernuum* (IndVal = 49.8; state-listed in South Carolina; SCDNR 2015). The invasive species *Ligustrum sinense* (57% frequency) and *Ailanthus altissima* (57% frequency) are present at several sites. In addition to the notable indicator species, this cluster is distinguished from the other clusters in this grouping by the lack of *Vaccinium arboreum*, which is common in cluster 4 and occasionally occurs in cluster 5. Unfortunately, no plots have soil series information, but pH ranges from Extremely to Strongly Acid (Figure 4.7) and survey notes indicate many sites have exposed rock. This type of vegetation is expressed in portions of the following notable sites: Rocky Face Mountain, and Gwaltwaneys Outcrops.

Grouping 3: Piedmont Pine Woodlands

Cluster 7 (9 plots) Piedmont Longleaf Pine Woodlands

Acer rubrum – Liquidambar styraciflua – Nyssa sylvatica – Pinus palustris / *Vaccinium fuscatum – Gaylussacia frondosa*

This is a small cluster (9 plots) scattered across the Virginia and Carolina Piedmont and capturing Piedmont *Pinus palustris* (Longleaf Pine) sites. Many (>50%) of these sites have facultative wetland flora (Lichvar et al. 2016) such as *Osmundastrum cinnamomeum* (IndVal = 66.7) and *Aronia arbutifolia* (IndVal = 60.8), and they fit well with descriptions of Wet Piedmont Longleaf Pine Forest (Schafale 2012). *Acer rubrum* (100% frequency) is also present. In addition to the notable indicator species, this cluster is distinguished from the other cluster in this grouping by the higher frequency of *Vaccinium tenellum* and *V. fuscatum* rather than *V. pallidum* and/or *V. stamineum.* Only two sites have soil series information, and they are located on Georgeville (Kanhapludult), an Ultisol with low-activity kaolinitic clay horizon. Soil pH ranges from Extremely to Very Strongly Acid (Figure 4.7). This type of vegetation is expressed in portions of the following notable sites: Pleasant Grove Longleaf, Black Ankle Bog, and Franconia Bog.

Cluster 8 (26 plots) – Piedmont Virginia Pine-Oak Woodlands

Acer rubrum – Nyssa sylvatica – Pinus virginiana – Quercus spp. / *Vaccinium pallidum* / *Smilax glauca*

This cluster captures a variety of acidic woodlands found in both the Inner and Outer Piedmont of Virginia and the Carolinas. These plots generally fit the description of "Acidic Shale Slope Woodland (Schafale 2012)." Mean estimated canopy cover is 76% (range = 26–100%), the 2nd highest. There are no herbaceous species with a frequency of at least 50% and this is one of the most depauperate clusters, with an average species richness of only 6 spp./m2 (Table 4.3). This cluster is characterized by *Pinus virginiana* (73% frequency), *Pinus echinata* (58% frequency). *Acer rubrum* (92% frequency) is also present. Herbaceous vegetation is generally absent, and common understory species include the shrubs *Vaccinium pallidum* (88% frequency) and *V. stamineum* (69% frequency). The highest indicator species are *Oxydendrum arboreum* (IndVal = 36.9), *Quercus coccinea* (IndVal = 36.8), and *Vaccinium pallidum* (IndVal = 35.5). In addition to the notable indicator species, this cluster is distinguished from the other clusters in this grouping by the general lack of herbaceous vegetation and the higher frequency of *Vaccinium stamineum.* Soil pH ranges from Ultra to Strongly Acid (Figure 4.7). The few (7; 27%) plots that have soil series information are located on Uwharrie, a deep, cobbly/bouldery Ultisol formed from colluvium. Individual plot survey notes often reference disturbances such as pine beetle outbreaks or evidence of past logging. This type of vegetation is expressed in portions of the following notable sites: Little Mountain, Gold Hill Flats, Crowders Mountain State Park, Lake Wheeler, Uwharrie National Forest, Pilot Mountain State Park, and Parsons Mountain.

Grouping 4: Piedmont Savannas and Grasslands

Cluster 9 (8 plots) – Outer Piedmont Oak-Hickory Savannas

Quercus alba – Cornus florida – Carya tomentosa / *Rhus michauxii – Rubus flagellaris* / *Schizachyrium scoparium – Desmodium* spp.

This cluster captures savanna and grassland vegetation in the Outer Piedmont of Virginia and North Carolina. Plots of this cluster generally fit well with descriptions of Oak-Hickory Woodlands and Savannas (Fleming et al. 2017). One plot of this cluster has the highest species richness in the dataset at 37 spp/m^2 (Table 4.3). Unfortunately, the other plots lack the necessary information to calculate species richness at 1 m^2, so it is not possible to compute an average richness for this cluster. Common tree species are *Quercus* spp. (especially *Q. alba* [100% frequency]) and *Carya* spp. (especially *C. tomentosa* [100% frequency]). Understory vegetation include the federally-listed endangered *Rhus michauxii* (IndVal = 75), a low-growing shrub endemic to the Southeast. The understory also includes an incredible diversity of herbs with over twenty herbaceous species that are significant indicators (based on IndVal; Table 4.1). Some highlights include *Desmodium* spp. (especially *D. paniculatum* [IndVal = 84.5]), *Apocynum cannabinum* (IndVal = 35.9), *Schizachyrium scoparium* (88% frequency), and *Solidago nemoralis* (IndVal = 41.9). In addition to the notable indicator species, this cluster is distinguished from other clusters of this grouping by the lack of *Juniperus virginiana* and the higher frequency of *Quercus velutina*. Unfortunately, most plots lack specific soil series information but the majority (7/8; 88%) have pH in the Moderately Acid to Neutral range (Figure 4.7), making this the most basic cluster. Nearly all (7/8; 86%) plots are located at Fort Pickett in Virginia, a military installation that supports fire-dependent vegetation, including the largest known population of *Rhus michauxii*, on land regularly burned by training activities (Emrick and Hill 1997). The solitary North Carolina plot is located near Durham and is part of the Eno River Diabase Sill Preserve (Reed 2018).

Cluster 10 (18 plots) – Piedmont Ruderal Native Grasslands

Liquidambar styraciflua – Acer rubrum / *Schizachyrium scoparium – Danthonia spicata*

This cluster captures a variety of herbaceous vegetation found in primarily ruderal sites (e.g., roadsides and powerline corridors) of North Carolina. All plots were surveyed by Adams

(2012) to document native savanna remnant vegetation in right-of-ways. Mean estimated canopy cover is 13% (range= 6–29%), the 2nd lowest (Table 4.3). These plots are dominated by grasses such as *Schizachyrium scoparium* (94% frequency), *Danthonia spicata* (89% frequency), and *Andropogon virginicus* (IndVal = 22.8). Forbs are variable and include *Eupatorium rotundifolium* (IndVal = 77.8), *Pseudognaphalium obtusifolium* (IndVal = 44.4), *Chrysopsis mariana* (IndVal = 38.2), *Baptisia tinctoria* (IndVal = 38.1), *Potentilla canadensis* (IndVal = 38), *Silphium compositum* (IndVal = 36.1). Saplings of *Liquidambar styraciflua* (94% frequency) and *Acer rubrum* (83% frequency) are common. *Lonicera japonica* (72% frequency) is a frequent invasive species reported in plots. In addition to the notable indicator species, this cluster is distinguished from other clusters of this grouping by the higher frequency of *Nyssa sylvatica*, *Lonicera japonica*, and *Prunus serotina*. Most plots have soil information and many (15/18; 83%) are found on Ultisols. Of these, most (12/18, 67%) are found on Kanhapludults, Ultisols with a low-activity kaolinitic clay horizon. The pH of plots was reported to be Extremely to Strongly Acid (Figure 4.7).

Cluster 11 (8 Plots) – Piedmont Prairie Barrens

Quercus phellos – Juniperus virginiana – Ulmus alata – Fraxinus americana / Oenothera fruticosa – Silphium terebinthinaceum

This cluster captures "prairie-like" vegetation in the Piedmont of North and South Carolina. Most plots fit the description of Xeric Hardpan Forest (Northern and Southern Prairie Barren Subtypes) in Schafale (2012). This cluster has a mean richness of 19 spp./m2 (range = 11–26 spp./m2), the 2nd highest (Table 4.3). Tree species that characterize this cluster are *Quercus* spp. (especially *Q. phellos* [88% frequency], or *Q. stellata* [50% frequency]), and *Pinus* spp. (*P. echinata* [50% frequency] or *P. taeda* [50% frequency]). *Juniperus virginiana* (88% frequency) and *Acer rubrum* (50% frequency) also occur in some plots. The understory is diverse, and notable indicators are *Silphium terebinthinaceum* (IndVal = 39.7; state-listed in North Carolina, South Carolina, and Virginia; Townsend 2019; Robinson 2018; SCDNR 2015), *Oenothera fruticosa* (IndVal = 33.9), *Scleria pauciflora* (IndVal = 18.5), *Houstonia tenuifolia* (IndVal = 21.1). Some of these plots also contain the invasive vine, *Lonicera japonica* (63% frequency). In addition to the notable indicator species, this cluster is distinguished from other clusters of this grouping by the lower frequency of *Schizachyrium scoparium* (only 25%) and the presence of *Quercus phellos* instead of *Q. alba*. All plots have soil series information and half (4/8 50%) are located on Iredell (Oxyaquic Vertic Hapludalf), an Alfisol with a shrink-swell clay layer. One plot is located on Picture (Vertic Argiaquoll), a soil series similar to Iredell but with a mollic epipedon. Soil pH ranges from Extremely to Slightly Acid (Figure 4.7). Plots in this cluster capture portions of vegetation at several notable "prairie" sites: Picture Creek Diabase Barrens (see Chapter 3; Stanley 2019), Rock Hill Blackjacks Heritage Preserve (Schmidt and Barnwell 2002), Mineral Springs Barrens (Davis et al. 2002), and Suther Prairie (Tompkins et al. 2010; Davis et al. 2002).

Grouping 5: Piedmont River Terrace Glades

Cluster 12 (5 plots) – Piedmont River Terrace Glades

Croton willdenowii – Hypericum gentianoides – Bulbostylis capillaris

This is a small cluster that captures a variety of nearly treeless glade vegetation found on old river terraces in Virginia and North Carolina. Mean estimated canopy cover is 3% (range = 1–8%), the lowest of any cluster (Table 4.3). This cluster has the highest occurrence of open habitat specialists (54% of all occurrences across plots of the cluster; Figure 4.5). Only three species have a frequency of at least 50%, but all are specialists of open habitat: *Croton willdenowii* (IndVal = 56.2), *Hypericum gentianoides* (IndVal = n.s.), and *Bulbosylis capillaris* (IndVal = 31.8). While these species are each characteristic of different outcrop, dome, or glade communities (Schafale 2012; Fleming et al. 2017), there is no clear synonymy to existing types for this cluster. Two plots, surveyed by Adams (2012) in the vicinity of Butner, NC, have soil series information and are located on Picture (Vertic Argiaquoll). Plot survey notes often describe areas of shallow soil and exposed rock. Many are in the vicinity of a river and are on river terraces. Soil pH is highly variable and ranges from Extremely to Moderately Acid (Figure 4.7). This type of vegetation is expressed in portions of the following notable sites: Sandy Mush Flat Rock and Overton Flat Rock.

DISCUSSION

1) Identify and characterize the major types of extant Piedmont, upland, heliophilic vegetation.

Through primarily quantitative means, we identified 12 major types of Piedmont vegetation that contain significant components of heliophilic vegetation (Table 4.1). These vegetation types range in structure from woodlands (clusters 1, 2, 3, 7, and 8), to savannas/barrens (clusters 9 and 11), to grasslands/glades (clusters 4, 5, 6, 10, and 12). We use the term “woodlands” here to broadly describe plots with high tree cover (generally estimated to be >60%) but normally not so closed as to completely exclude understory vegetation. Regionally, the terms “savanna” and/or “barren” are used to indicate a variety of vegetation with sparse to moderate tree cover and an herbaceous understory (Juras 1997; Fleming 2017; Schafale 2012; Tyndall and Hull 1999), although “barren” sometimes implies trees are stunted due to shallow or otherwise stressful soil (Adams 2012; Fralish et al. 1999). Savannas are transitional between open grasslands and more closed woodlands, with tree cover generally varying from 10–60% and an understory with shade-intolerant plant species (Adams 2012). We use the terms savanna and barren here to indicate vegetation with intermediate tree cover but apply the terms to separate vegetation clusters in accordance with colloquial names traditionally applied to the sites represented by plots of those clusters. We use the terms “grassland” and “glade” here to indicate different types of treeless (or nearly treeless) vegetation dominated by herbaceous species. A glade refers to all or part of a vegetational complex that forms on shallow soil in areas where rock, usually granite in the Piedmont, is close to the surface (Ware 2002). If the rock feature is flat it may be called a “flatrock,” otherwise it is often called a dome (if rounded) or outcrop. We use “grassland” here to indicate herbaceous-dominated vegetation not associated with exposed rock features.

Maintaining and restoring open vegetation is desirable due to the diversity of species associated with these community types (Table 4.2). Grazing, fire, and stressful edaphic conditions are thought to be the primary factors that currently maintain or once maintained open vegetation in the Piedmont (Davis et al. 2002; Juras 1997; Taecker 2007; Schafale 2012; Benson 2011; Delcourt and Delcourt 1997; Frost 2001). Because many large grazers, such as bison and elk, have been extirpated from the Piedmont (Barden 1997, Juras 1997), human disturbances that reduce woody dominance (e.g., mowing), fire (natural and anthropogenic), and edaphic conditions are now the primary factors maintaining open vegetation in the present landscape. We identified three clusters that likely occur over very shallow soil (based on survey notes describing the presence of exposed rock) and would be maintained by primarily edaphic factors: Piedmont Flatrock and Outcrop Glades (cluster 5), Inner Piedmont Red Cedar Glades (cluster 6), and Piedmont River Terrace Glades (cluster 12). For deeper soil sites, periodic disturbances are necessary to prevent mesophtyification and eventual conversion to closed-canopy forest (Nowacki and Abrams 2008).

The high occurrence of fire-intolerant woody species such as *Juniperus virginiana* (found in 68% of all plots) and *Acer rubrum* (found in 65% of all plots) suggests most plots are currently experiencing fire suppression or lack natural ignition sources. *Juniperus virginiana* is particularly interesting as it can develop a fibrous root system that allows it to grow in very shallow soils (Lawson 1990) and establish in areas where edaphic factors otherwise prevent woody growth. However, thin bark makes *Juniperus virginiana* very susceptible to fire (Lawson 1990). Sites such as the piedmont savanna plots (Cluster 9) that experience periodic fire (Emrick and Hill 1997; Reed 2018) are notably lacking fire-intolerant species like *Juniperus virginiana*. The Adams (2012) grassland plots (cluster 10) are generally not maintained by fire or edaphic factors. Instead, these plots are kept nearly treeless by periodic mowing and/or the application of herbicides targeting woody species. Tree species are often present in these plots, but their extremely low cover (mean estimated canopy cover of only 13%; Table 4.3) suggests they are not reaching maturity and these occurrences mostly represent saplings. The most common type of vegetation identified in our dataset was Red Cedar-Oak-Hickory Woodlands (47% of plots in the dataset were placed into this cluster). These plots are generally forest-like in their structure, with high estimated canopy cover (mean of 90%; Table 4.3). However, the high frequency (94%; Table 4.1) of *Quercus stellata* suggests these plots were once more open-canopied in the past. Post oak is very shade-intolerant (Stransky 1990), although it can sometimes persist in closed forest once well-established. It is fire-tolerant and tends to resprout profusely (Stransky 1990). The high frequency of fire-intolerant *Juniperus virginiana* (96%) and *Acer rubrum* (75%) suggests these woodland sites are currently under fire suppression and experiencing mesophytification.

While we lack quantification of plot disturbance histories, it is still clear from the occurrence patterns of shade-tolerant, shade-intolerant, fire-tolerant, and fire-intolerant species that disturbance history is an important factor influencing community structure of plots in our dataset. Further analyses of disturbance histories and vegetation responses are needed in order to better understand how each different vegetation type is shaped by varying disturbances. Substrate, which affects soil depth and pH, is also an important factor influencing the vegetation types identified in our dataset.

2) Offer a definition and characterization of extant vegetation colloquially known as “Piedmont prairie” and discuss how it relates to other types of heliophilic vegetation.

Use of the term “Piedmont prairie” to describe heliophilic flora in the Carolinas was, in part, popularized by Barden (1997) and his review of the historical accounts of the presettlement Piedmont landscape as summarized in Rostlund (1947). Davis et al. (2002) documented “Piedmont prairie remnant” sites and created lists of prairie indicator species to assist in the recognition of this vegetation in the current landscape. Schafale and Weakley (1990) describe potentially “prairie-like” vegetation in relation to Xeric Hardpan Forest where present and/or past disturbances allowed the retention of a diverse herbaceous layer of “prairie-affinity” flora. While not all sites traditionally recognized as Piedmont prairies were represented in our dataset, we did have plots representing portions of Mineral Springs Barrens (Davis et al. 2002), Rock Hill Blackjacks Heritage Preserve (Schmidt and Barnwell 2002), Suther Prairie (Tompkins et al. 2010), Harrelson Parcel (Reed 2018), and Picture Creek Diabase Barrens (Stanley et al. 2019). These sites all occur in North or South Carolina and are associated with mafic soils derived from the Triassic basins. In our analyses, the plots representing these sites all grouped into one cluster (cluster 11 – Piedmont Prairie Barrens) with the exception of the plot representing the Harrelson Parcel. This plot was initially grouped with the other Piedmont prairie barren sites in the first round of hierarchical clustering but was moved into the Piedmont savanna cluster (cluster 9) during partition optimization using *optpart*.

The Piedmont savanna plots represent portions of vegetation occurring at the Fort Pickett military installation in Virginia. Portions of the site are regularly burned and are home to the largest known population of the federally-listed endangered *Rhus michauxii* (Emrick and Hill 1997). The inclusion of the Harrelson Parcel, a relatively small North Carolina site that is part of the Eno River Diabase Sill Preserve (Reed 2018), in this savanna cluster seems unusual. However, the Harrelson Parcel is also regularly maintained by prescribed fire and is one of several locations where *Rhus michauxii* occurs in the North Carolina Piedmont (Reed 2018). Interestingly, *Rhus michauxii* is not present in the Harrelson Parcel plot in our dataset but the plot still shares many other features with the Virginia Piedmont savanna plots such as the absence of *Juniperus virginiana* and the presence of *Desmodium paniculatum*. Whether the compositional similarities between the Harrelson Parcel and the Fort Pickett plots are primarily due to similar disturbance history or indicate a shared floristic history (i.e., were once part of a larger savanna system) is unclear. Historical documents indicate savanna-like vegetation may have once stretched across relatively broad regions of the Piedmont (see De L'Isle 1718; Juras 1997), however present "remnant" flora is generally only found in scattered patches of relatively small size. It is also possible Native American trading paths (see Dobbs 2006) could have once been important dispersal corridors for regional vegetation; however, this is currently speculation based on the relative positions of remnant sites.

As already discussed, the terms savanna and barren are often used regionally to indicate vegetation of intermediate tree cover between a (nearly) treeless grassland and a more heavily forested woodland, although barren is also sometimes used to specifically indicate stunted vegetation on stressful soils. We chose to maintain the name of cluster 9 as "Piedmont savanna" because its plots conform to this vegetation structure and "savanna" is the colloquial name for most of those plots (see Fleming et al. 2017). The naming of cluster 11 ("Piedmont prairie barrens") is more difficult because of the rather heterogeneous nature of the cluster. Because multiple sites are referred to as barrens (i.e., Mineral Springs Barrens and Picture Creek Diabase Barrens), and because the vegetation type in most (75%) plots of the cluster is currently recognized in Schafale (2012) as Xeric Hardpan Forest (Prairie Barren Subtypes), we chose to name the cluster accordingly. The Piedmont savanna and Piedmont prairie barren clusters separated in our analyses based on compositional factors such as the frequency of *Juniperus virginiana* (absent in the savanna plots), *Oenothera fruticosa* (frequent in the prairie barren plots), and the most frequent oak species (*Quercus phellos* is common in the prairie barren plots but is generally replaced by *Q. alba* in the savanna plots).

Adams (2012) defines Piedmont prairie as having <10% tree cover while Piedmont savanna has 10–60% tree cover. Often, prairie has been regionally used to indicate the presence of prairie-affinity flora rather than to indicate specific amounts of tree cover. What constitutes prairie-affinity flora may vary based on authority, but generally the term indicates species that are also characteristic of Midwest prairies. Examples of some midwestern prairie-affinity species that occur in Piedmont communities include: *Silphium terebinthinaceum*, *Solidago ptarmicoides*, *Lithospermum canescens*, and *Liatris squarrosa* (see review in Noss 2013; Weakley 2015; Schafale 2012). Prairie-affinity is also used to indicate eastern Piedmont endemic species that are congeners of characteristic Midwest prairie species such as: *Echinacea laevigata*, *Helianthus schweinitzii*, *Marshallia legrandii*, and *Baptisia australis* var. *aberrans* (see Weakley 2015). At "Piedmont prairie" sites such as Picture Creek Diabase Barrens, midwestern disjunct species and Piedmont endemic species occur together in the same communities (see Chapter 3; Stanley et al. 2019).

Regional prairie flora is sometimes also associated with glade communities such as Piedmont Basic Glade (Falls Dam Slope Subtype) (Schafale 2012) and alluvial communities such as Riverside Prairies (Fleming et al. 2017). Plots colloquially called "glades" in our dataset primarily sorted into Cluster 5 (Piedmont Flatrock and Outcrop Glades) and cluster 8 (Piedmont Pine-Oak Woodlands) and were compositionally distinct from the savanna (cluster 9), grassland (cluster 10), and prairie barren (cluster 11) clusters (Table 4.1). A plot located at Suther Prairie (Tompkins 2010) represented the only Riverside Prairie plot in our dataset, and it was placed into cluster 11 (Piedmont Prairie Barrens) during our analyses.

Based on field studies of six Piedmont prairie sites, two of which (Mineral Springs Barrens and Suther Prairie) were represented in our dataset, Davis et al. (2002) provided a list of prairie indicator species. These prairie indicator species were generally widespread in our dataset and at least some occurred in every cluster (Figure 4.6). Some of these prairie indicators were also significant indicator species (as determined by IndVal) for the savanna, grassland, and prairie barren clusters in our analyses (Table 4.1). Our analyses identified additional species that were significant indicators for these vegetation types (e.g., *Penstemon laevigatus*; Table 4.2).

A limitation of this work is that plots do not necessarily capture the full range of compositional variation of vegetation across a site. For example, the plot representing Picture Creek Diabase Barrens captures open vegetation occurring in a powerline right-of-way that bisects the site. This is generally where the greatest density of rare native heliophytes presently occurs at the site, but heliophytes also occur in areas of the site with a more woodland vegetation structure (see Chapter 3; Stanley 2019). However, some sites likely are quite well represented in our dataset. For example, Rock Hill Blackjacks Heritage Preserve is represented by eight plots that capture a range of vegetation across the site, including at least four plots that capture prairie-like vegetation.

Because our goals here were related to the characterization and colloquial naming conventions of Piedmont heliophilic flora, future work should extend these analyses to critically assess the classification of these vegetation types within the USNVC. While we did consider the rough number of USNVC Groups represented in the dataset when selecting a partition solution, the vegetation types identified here do not directly correspond to any units of the USNVC hierarchy. Additional analyses using more targeted plot selection and approaches such as supervised clustering could be used to further clarify this issue. Further analyses should also quantitatively explore the relationship of the vegetation types identified here to other vegetation types within North America. While this dataset captures a botanically well-surveyed portion of the Mid-Atlantic and Southeastern Piedmont, it lacks plots from other regions of the Piedmont also known to contain prairies (e.g., the Black Belt prairies of the Alabama Piedmont). Barone (2005) performed a broader analysis of prairie vegetation in North America using species presence-absence data, but the growth of resources such as VegBank (Peet et al. 2012) has made more detailed plot data available that would allow for a deeper study of this topic. Additional studies of the broader biogeography of prairie-affinity species also seem warranted to better understand historical community assembly dynamics and clarify what “prairie-affinity” truly means in the context of the Piedmont landscape.

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TABLES

Table 4.1: Frequency and average cover of species by cluster. Only species with frequency ≥ 50% are shown. Highlights indicate significant ($p<0.05$) indicator species as determined by IndVal (see Table 4.2). Shade Class was determined based on analyses in Chapter 2. Wetland indicator status is based on Lichvar et al. (2016). Prairie indicator status is based on Davis et al. (2002). * indicates an exotic species.

Grouping 1: Piedmont Oak-Hickory and Red Cedar Woodlands

Cluster 1 (72 plots) – Piedmont Red Cedar-Post Oak Woodlands

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Danthonia spicata	Herb	83	4	Strong Open	n/a	Weak
Asplenium platyneuron	Herb	67	2	Strong Closed+Semi-open	FACU	Weak
Dichanthelium boscii	Herb	64	2	Strong Closed+Semi-open	n/a	n/a
Piptochaetium avenaceum	Herb	63	6	Strong Semi-open	UPL	Strong
Galium circaezans	Herb	58	2	Strong Closed	UPL	n/a
Endodeca serpentaria	Herb	57	2	Strong Closed+Semi-open	UPL	n/a
Polygonatum biflorum	Herb	56	2	Strong Closed	FACU	n/a
Rosa carolina	Herb	56	2	Strong Closed+Semi-open	FACU	Strong
Dichanthelium laxiflorum	Herb	51	2	Strong Open	FACU	n/a
Vaccinium stamineum	Shrub	67	3	n/a	FACU	Strong
Juniperus virginiana	Tree	96	6	n/a	FACU	Strong
Quercus stellata	Tree	94	6	n/a	UPL	Strong
Carya glabra	Tree	90	6	n/a	FACU	Weak
Fraxinus [americana + biltmoreana + pennsylvanica + smallii]	Tree	88	5	n/a	n/a	Weak
Prunus serotina	Tree	86	2	n/a	FACU	Strong
Ulmus alata	Tree	86	6	n/a	FACU	n/a
Acer rubrum	Tree	75	4	n/a	FAC	n/a
Diospyros virginiana	Tree	71	2	n/a	FAC	Strong
Quercus alba	Tree	71	6	n/a	FACU	Weak
Quercus rubra	Tree	69	4	n/a	FACU	n/a
Carya tomentosa	Tree	67	5	n/a	n/a	Weak
Quercus phellos	Tree	63	3	n/a	FAC	n/a
Quercus velutina	Tree	63	4	n/a	n/a	Strong
Cornus florida	Tree	58	4	n/a	FACU	n/a
Cercis canadensis	Tree	57	5	n/a	FACU	n/a
Viburnum prunifolium	Tree	56	2	n/a	FACU	n/a
Liquidambar styraciflua	Tree	50	4	n/a	FAC	n/a
Parthenocissus quinquefolia	Vine	88	2	n/a	FACU	Weak
Muscadinia rotundifolia	Vine	75	4	n/a	n/a	n/a
Smilax bona-nox	Vine	74	2	n/a	FACU	n/a

Table 4.1 (Continued):

Toxicodendron radicans	Vine	67	2	n/a	FAC	Weak
Smilax glauca	Vine	61	2	n/a	FACU	n/a
**Lonicera japonica*	Vine	58	3	n/a	FACU	n/a
Smilax rotundifolia	Vine	57	2	n/a	FAC	n/a

Cluster 2 (14 plots) – Inner Piedmont Chestnut Oak Woodlands

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Carex pensylvanica	Herb	93	5	Strong Semi-open	n/a	n/a
Danthonia spicata	Herb	93	3	Strong Open	n/a	Weak
Polygonatum biflorum	Herb	79	2	Strong Closed	FACU	n/a
Asplenium platyneuron	Herb	71	2	Strong Closed+Semi-open	FACU	Weak
Schizachyrium scoparium	Herb	57	3	Strong Open	FACU	Strong
Euphorbia corollata	Herb	57	2	Strong Open	n/a	Strong
Rosa carolina	Herb	50	2	Strong Closed+Semi-open	FACU	Strong
Dichanthelium dichotomum	Herb	50	2	Weak Closed+Semi-open	FAC	Weak
Dichanthelium boscii	Herb	50	2	Strong Closed+Semi-open	n/a	n/a
Antennaria plantaginifolia	Herb	50	2	Strong Semi-open	n/a	Strong
Vaccinium stamineum	Shrub	64	5	n/a	FACU	Strong
Rubus [flagellaris]	Shrub	57	2	n/a	n/a	n/a
Vaccinium pallidum	Shrub	50	4	n/a	n/a	n/a
Quercus montana	Tree	93	6	n/a	UPL	n/a
Quercus rubra	Tree	86	4	n/a	FACU	n/a
Carya glabra	Tree	79	6	n/a	FACU	Weak
Pinus virginiana	Tree	79	7	n/a	n/a	n/a
Fraxinus [americana + biltmoreana + pennsylvanica + smallii]	Tree	71	6	n/a	n/a	Weak
Prunus serotina	Tree	71	2	n/a	FACU	Strong
Juniperus virginiana	Tree	57	5	n/a	FACU	Strong
Chionanthus virginicus	Tree	50	4	n/a	FAC	Weak
Acer rubrum	Tree	50	2	n/a	FAC	n/a
Parthenocissus quinquefolia	Vine	86	2	n/a	FACU	Weak
Toxicodendron radicans	Vine	50	2	n/a	FAC	Weak
Smilax glauca	Vine	50	2	n/a	FACU	n/a

Cluster 3 (9 plots) – Piedmont Red Cedar-Ash Woodlands

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Danthonia spicata	Herb	89	5	Strong Open	n/a	Weak
Dichanthelium laxiflorum	Herb	78	3	Strong Open	FACU	n/a
Galium pilosum	Herb	67	2	Weak Semi-open	n/a	Strong
Asplenium platyneuron	Herb	56	2	Strong Closed+Semi-open	FACU	Weak

Table 4.1 (Continued):

Packera anonyma	Herb	56	2	Strong Open+Semi-open	UPL	Strong
Verbesina occidentalis	Herb	56	2	Strong Semi-open	FACU	n/a
Houstonia longifolia	Herb	56	2	Strong Semi-open	n/a	Weak
Myriopteris tomentosa	Herb	56	2	Strong Open+Semi-open	n/a	n/a
Coreopsis pubescens	Herb	56	5	Strong Semi-open	FACU	n/a
Potentilla canadensis	Herb	56	2	Strong Open	n/a	Strong
Opuntia mesacantha	Shrub	67	2	n/a	n/a	n/a
Symphoricarpos orbiculatus	Shrub	56	4	n/a	FACU	Weak
Juniperus virginiana	Tree	100	6	n/a	FACU	Strong
Fraxinus [americana + biltmoreana + pennsylvanica + smallii]	Tree	89	5	n/a	n/a	Weak
Ulmus alata	Tree	78	6	n/a	FACU	n/a
Carya glabra	Tree	78	6	n/a	FACU	Weak
Chionanthus virginicus	Tree	67	3	n/a	FAC	Weak
Acer rubrum	Tree	56	2	n/a	FAC	n/a
Parthenocissus quinquefolia	Vine	89	2	n/a	FACU	Weak
Smilax glauca	Vine	56	2	n/a	FACU	n/a
**Lonicera japonica*	Vine	56	2	n/a	FACU	n/a

Grouping 2: Piedmont Glades

Cluster 4 (10 plots) – Outer Piedmont Red Cedar Cliff Glades

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Hieracium venosum	Herb	70	3	Weak Closed+Semi-open	n/a	Weak
Piptochaetium avenaceum	Herb	60	5	Strong Semi-open	UPL	Strong
Dichanthelium commutatum	Herb	60	3	Generalist	FACU	n/a
Asplenium platyneuron	Herb	60	2	Strong Closed+Semi-open	FACU	Weak
Phytolacca americana	Herb	60	3	Generalist	FACU	Weak
Pleopeltis michauxiana	Herb	60	2	Generalist	n/a	n/a
Callicarpa americana	Shrub	50	3	n/a	FACU	n/a
Juniperus virginiana	Tree	100	6	n/a	FACU	Strong
Vaccinium arboreum	Tree	90	4	n/a	FACU	Strong
Ulmus alata	Tree	80	2	n/a	FACU	n/a
Quercus stellata	Tree	70	6	n/a	UPL	Strong
Carya glabra	Tree	60	6	n/a	FACU	Weak
Pinus virginiana	Tree	60	5	n/a	n/a	n/a
Acer leucoderme	Tree	60	6	n/a	n/a	n/a
Quercus rubra	Tree	50	2	n/a	FACU	n/a
Quercus nigra	Tree	50	2	n/a	FAC	n/a
Celtis [laevigata + smallii]	Tree	50	2	n/a	n/a	n/a
**Ailanthus altissima*	Tree	50	6	n/a	FACU	n/a
Toxicodendron radicans	Vine	80	2	n/a	FAC	Weak
**Lonicera japonica*	Vine	70	2	n/a	FACU	n/a

Table 4.1 (Continued):

Bignonia capreolata	Vine	60	3	n/a	FAC	n/a
Parthenocissus quinquefolia	Vine	60	2	n/a	FACU	Weak
Smilax bona-nox	Vine	50	2	n/a	FACU	n/a
Campsis radicans	Vine	50	2	n/a	FAC	Weak

Cluster 5 (9 plots) -- Piedmont Flatrock and Outcrop Glades

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Schizachyrium scoparium	Herb	89	6	Strong Open	FACU	Strong
Phemeranthus teretifolius	Herb	78	2	Strong Open	n/a	Strong
Aristida dichotoma	Herb	78	3	Strong Open	UPL	n/a
Hypericum gentianoides	Herb	67	2	Strong Open	UPL	Strong
Croton willdenowii	Herb	67	3	Strong Open	n/a	n/a
Eupatorium capillifolium	Herb	56	2	Strong Open	FACU	Weak
Dichanthelium depauperatum	Herb	56	4	Strong Open+Semi-open	n/a	n/a
Packera anonyma	Herb	56	4	Strong Open+Semi-open	UPL	Strong
Juniperus virginiana	Tree	56	5	n/a	FACU	Strong

Cluster 6 (7 plots) – Inner Piedmont Red Cedar Glades

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Myriopteris lanosa	Herb	86	4	Strong Open	n/a	n/a
Schizachyrium scoparium	Herb	71	4	Strong Open	FACU	Strong
Oxalis dillenii	Herb	71	2	Generalist	FACU	n/a
Allium cernuum	Herb	71	2	Strong Open+Semi-open	FACU	Strong
Danthonia spicata	Herb	71	3	Strong Open	n/a	Weak
Hypericum gentianoides	Herb	57	4	Strong Open	UPL	Strong
Packera anonyma	Herb	57	4	Strong Open+Semi-open	UPL	Strong
Commelina erecta	Herb	57	3	Strong Open	FAC	n/a
Juniperus virginiana	Tree	86	6	n/a	FACU	Strong
Fraxinus [americana + biltmoreana + pennsylvanica + smallii]	Tree	57	4	n/a	n/a	Weak
**Ligustrum sinense*	Tree	57	3	n/a	FACU	n/a
**Ailanthus altissima*	Tree	57	2	n/a	FACU	n/a

Grouping 3: Piedmont Pine Woodlands

Cluster 7 (9 plots) Piedmont Longleaf Pine Woodlands

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Pteridium latiusculum	Herb	67	6	Strong Semi-open	n/a	n/a
Osmundastrum cinnamomeum	Herb	67	6	Generalist	FACW	n/a
Eupatorium pilosum	Herb	67	2	Weak Open+Semi-open	FACW	n/a
Danthonia sericea	Herb	67	4	Strong Open	FACU	Strong
Chasmanthium laxum	Herb	56	5	Generalist	FAC	n/a
Solidago odora	Herb	56	2	Strong Open+Semi-open	n/a	Strong
Gaylussacia frondosa	Shrub	78	3	n/a	FAC	n/a
Vaccinium fuscatum	Shrub	78	3	n/a	FAC	n/a

Table 4.1 (Continued):

Aronia arbutifolia	Shrub	67	2	n/a	FACW	n/a
Vaccinium tenellum	Shrub	56	4	n/a	UPL	Strong
Rubus pensilvanicus	Shrub	56	2	n/a	FAC	n/a
Liquidambar styraciflua	Tree	100	3	n/a	FAC	n/a
Acer rubrum	Tree	100	6	n/a	FAC	n/a
Nyssa sylvatica	Tree	100	5	n/a	FAC	n/a
Pinus palustris	Tree	78	6	n/a	FAC	n/a
Prunus serotina	Tree	67	2	n/a	FACU	Strong
Diospyros virginiana	Tree	67	2	n/a	FAC	Strong
Quercus alba	Tree	67	2	n/a	FACU	Weak
Pinus taeda	Tree	67	4	n/a	FAC	Weak
Quercus stellata	Tree	56	4	n/a	UPL	Strong
Carya glabra	Tree	56	2	n/a	FACU	Weak
Rhus copallinum	Tree	56	3	n/a	FACU	Weak
Liriodendron tulipifera	Tree	56	3	n/a	FACU	n/a
Oxydendrum arboreum	Tree	56	3	n/a	UPL	n/a
Ilex opaca	Tree	56	2	n/a	FACU	n/a
Smilax glauca	Vine	78	2	n/a	FACU	n/a
Muscadinia rotundifolia	Vine	67	5	n/a	n/a	n/a

Cluster 8 (26 plots) – Piedmont Virginia Pine-Oak Woodlands

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Vaccinium pallidum	Shrub	88	5	n/a	n/a	n/a
Vaccinium stamineum	Shrub	69	3	n/a	FACU	Strong
Acer rubrum	Tree	92	4	n/a	FAC	n/a
Nyssa sylvatica	Tree	85	5	n/a	FAC	n/a
Diospyros virginiana	Tree	77	3	n/a	FAC	Strong
Sassafras albidum	Tree	73	4	n/a	FACU	Weak
Pinus virginiana	Tree	73	6	n/a	n/a	n/a
Quercus marilandica	Tree	69	5	n/a	n/a	Strong
Oxydendrum arboreum	Tree	69	5	n/a	UPL	n/a
Quercus velutina	Tree	65	4	n/a	n/a	Strong
Quercus montana	Tree	65	6	n/a	UPL	n/a
Quercus alba	Tree	62	5	n/a	FACU	Weak
Quercus coccinea	Tree	62	4	n/a	n/a	Weak
Pinus echinata	Tree	58	5	n/a	n/a	Strong
Prunus serotina	Tree	54	2	n/a	FACU	Strong
Smilax glauca	Vine	88	2	n/a	FACU	n/a
Muscadinia rotundifolia	Vine	50	4	n/a	n/a	n/a
Smilax rotundifolia	Vine	50	4	n/a	FAC	n/a

Grouping 4: Piedmont Savannas and Grasslands

Cluster 9 (8 plots) – Outer Piedmont Oak-Hickory Savannas

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Desmodium paniculatum	Herb	100	2	Strong Semi-open	FACU	n/a
Schizachyrium scoparium	Herb	88	7	Strong Open	FACU	Strong
Apocynum cannabinum	Herb	88	2	Strong Open	FACU	Weak
Eupatorium hyssopifolium	Herb	88	2	Strong Open	n/a	Strong

Table 4.1 (Continued):

Dichanthelium boscii	Herb	88	3	Strong Closed+Semi-open	n/a	n/a
Chamaecrista nictitans	Herb	75	2	Strong Open	FACU	Weak
Lespedeza procumbens	Herb	75	2	Strong Open+Semi-open	n/a	Strong
Ambrosia artemisiifolia	Herb	75	2	Strong Open+Semi-open	FACU	Weak
Dichanthelium commutatum	Herb	75	2	Generalist	FACU	n/a
Eupatorium godfreyanum	Herb	75	2	Strong Semi-open	n/a	n/a
Desmodium nuttallii	Herb	75	2	Strong Semi-open	n/a	n/a
Desmodium laevigatum	Herb	75	2	Strong Semi-open	n/a	n/a
Desmodium ciliare	Herb	63	2	Strong Open+Semi-open	n/a	Weak
Solidago nemoralis	Herb	63	2	Strong Open+Semi-open	n/a	Weak
Desmodium marilandicum	Herb	63	2	Strong Semi-open	n/a	n/a
Solidago rugosa	Herb	63	2	Strong Open+Semi-open	FAC	Weak
Hypericum stragulum	Herb	63	2	Strong Open+Semi-open	n/a	n/a
Desmodium perplexum	Herb	63	3	Strong Closed+Semi-open	n/a	n/a
Eupatorium pubescens	Herb	63	2	Strong Semi-open	n/a	n/a
Vernonia glauca	Herb	63	2	Generalist	n/a	n/a
Galium pilosum	Herb	63	2	Weak Semi-open	n/a	Strong
Potentilla canadensis	Herb	63	2	Strong Open	n/a	Strong
**Lespedeza cuneata*	Herb	50	2	Strong Open	FACU	n/a
Dichanthelium dichotomum	Herb	50	2	Weak Closed+Semi-open	FAC	Weak
Symphyotrichum undulatum	Herb	50	3	Generalist	n/a	n/a
Hylodesmum nudiflorum	Herb	50	5	Strong Closed	n/a	n/a
Chrysogonum virginianum	Herb	50	2	Generalist	n/a	Strong
Oxalis dillenii	Herb	50	2	Generalist	FACU	n/a
Rubus [flagellaris]	Shrub	75	2	n/a	n/a	n/a
Rhus michauxii	Shrub	75	5	n/a	n/a	n/a
Carya tomentosa	Tree	100	5	n/a	n/a	Weak
Cornus florida	Tree	100	4	n/a	FACU	n/a
Quercus alba	Tree	100	5	n/a	FACU	Weak
Rhus copallinum	Tree	88	3	n/a	FACU	Weak
Diospyros virginiana	Tree	88	2	n/a	FAC	Strong
Liquidambar styraciflua	Tree	88	5	n/a	FAC	n/a
Quercus velutina	Tree	88	4	n/a	n/a	Strong
Sassafras albidum	Tree	88	2	n/a	FACU	Weak
Carya glabra	Tree	75	5	n/a	FACU	Weak
Ulmus alata	Tree	63	2	n/a	FACU	n/a
Quercus falcata	Tree	63	6	n/a	FACU	Weak

Table 4.1 (Continued):

Rhus glabra	Tree	63	4	n/a	n/a	Strong
Fraxinus [americana + biltmoreana + pennsylvanica + smallii]	Tree	50	3	n/a	n/a	Weak
Liriodendron tulipifera	Tree	50	4	n/a	FACU	n/a
Parthenocissus quinquefolia	Vine	75	2	n/a	FACU	Weak
Clitoria mariana	Vine	63	5	n/a	FACU	Strong
Vitis aestivalis	Vine	63	2	n/a	FACU	Weak
Galactia volubilis	Vine	50	2	n/a	FACU	Weak
Ipomoea pandurata	Vine	50	2	n/a	FACU	Strong
Vitis vulpina	Vine	50	2	n/a	FAC	n/a
Campsis radicans	Vine	50	2	n/a	FAC	Weak

Cluster 10 (18 plots) – Piedmont Ruderal Native Grasslands

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Schizachyrium scoparium	Herb	94	5	Strong Open	FACU	Strong
Danthonia spicata	Herb	89	5	Strong Open	n/a	Weak
Pseudognaphalium obtusifolium	Herb	83	3	Strong Open	n/a	Strong
Potentilla canadensis	Herb	83	5	Strong Open	n/a	Strong
Eupatorium rotundifolium	Herb	78	2	Strong Open	FAC	n/a
Eupatorium hyssopifolium	Herb	67	2	Strong Open	n/a	Strong
Andropogon virginicus	Herb	67	4	Strong Open	FACU	Strong
Danthonia sericea	Herb	61	6	Strong Open	FACU	Strong
Dichanthelium laxiflorum	Herb	56	4	Strong Open	FACU	n/a
Chrysopsis mariana	Herb	56	3	Strong Open+Semi-open	UPL	Strong
Sorghastrum nutans	Herb	50	3	Strong Open	FACU	Strong
Coreopsis major	Herb	50	3	Strong Open+Semi-open	n/a	Weak
Silphium compositum	Herb	50	4	Strong Open	n/a	Strong
Rubus pensilvanicus	Shrub	50	3	n/a	FAC	n/a
Liquidambar styraciflua	Tree	94	4	n/a	FAC	n/a
Acer rubrum	Tree	83	2	n/a	FAC	n/a
Nyssa sylvatica	Tree	72	2	n/a	FAC	n/a
Quercus alba	Tree	67	4	n/a	FACU	Weak
Prunus serotina	Tree	61	2	n/a	FACU	Strong
Rhus copallinum	Tree	56	2	n/a	FACU	Weak
Carya tomentosa	Tree	56	3	n/a	n/a	Weak
Quercus phellos	Tree	50	2	n/a	FAC	n/a
Juniperus virginiana	Tree	50	2	n/a	FACU	Strong
Muscadinia rotundifolia	Vine	78	4	n/a	n/a	n/a
**Lonicera japonica*	Vine	72	4	n/a	FACU	n/a
Smilax rotundifolia	Vine	72	3	n/a	FAC	n/a
Campsis radicans	Vine	67	2	n/a	FAC	Weak
Toxicodendron radicans	Vine	56	3	n/a	FAC	Weak
Parthenocissus quinquefolia	Vine	56	2	n/a	FACU	Weak

Cluster 11 (8 Plots) – Piedmont Prairie Barrens

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Oenothera fruticosa complex	Herb	88	2	Strong Open	n/a	n/a

Table 4.1 (Continued):

Scleria pauciflora	Herb	63	2	Strong Open	FACU	Weak
Dichanthelium laxiflorum	Herb	63	2	Strong Open	FACU	n/a
Danthonia spicata	Herb	63	2	Strong Open	n/a	Weak
Houstonia tenuifolia	Herb	50	2	Strong Open	n/a	n/a
Symphyotrichum pilosum	Herb	50	2	Strong Open	FAC	Strong
Dichanthelium acuminatum	Herb	50	2	Strong Open	FAC	Weak
Penstemon laevigatus	Herb	50	1	Strong Open+Semi-open	FACU	n/a
Rosa carolina	Herb	50	4	Strong Closed+Semi-open	FACU	Strong
Setaria parviflora	Herb	50	2	Weak Open+Semi-open	FAC	Weak
Solanum carolinense	Herb	50	2	Strong Open	FACU	Weak
Silphium terebinthinaceum	Herb	50	6	Weak Open	FACU	Strong
Paspalum setaceum	Herb	50	3	Generalist	FACU	Weak
Apocynum cannabinum	Herb	50	3	Strong Open	FACU	Weak
Sorghastrum nutans	Herb	50	3	Strong Open	FACU	Strong
Ulmus alata	Tree	88	5	n/a	FACU	n/a
Fraxinus [americana + biltmoreana + pennsylvanica + smallii]	Tree	88	3	n/a	n/a	Weak
Quercus phellos	Tree	88	3	n/a	FAC	n/a
Juniperus virginiana	Tree	88	5	n/a	FACU	Strong
Rhus copallinum	Tree	63	3	n/a	FACU	Weak
Diospyros virginiana	Tree	63	4	n/a	FAC	Strong
Liquidambar styraciflua	Tree	63	4	n/a	FAC	n/a
Quercus stellata	Tree	50	6	n/a	UPL	Strong
Pinus echinata	Tree	50	5	n/a	n/a	Strong
Pinus taeda	Tree	50	5	n/a	FAC	Weak
Acer rubrum	Tree	50	2	n/a	FAC	n/a
**Lonicera japonica*	Vine	63	4	n/a	FACU	n/a
Smilax bona-nox	Vine	50	2	n/a	FACU	n/a

Grouping 5: Piedmont River Terrace Glades

Cluster 12 (5 plots) – Piedmont River Terrace Glades

Taxon	Habit	Freq.	Cov.	Shade Class	Wetland	Prairie
Croton willdenowii	Herb	100	3	Strong Open	n/a	n/a
Hypericum gentianoides	Herb	60	2	Strong Open	UPL	Strong
Bulbostylis capillaris	Herb	60	2	Strong Open	FACU	n/a

Table 4.2: Species indicator values (IndVals). “Clus.” indicates the cluster for which each species scored the highest IndVal. Mean, Standard Deviation, and p-values are based on a Monte-Carlo randomization test (100000 interations). Only species with significant IndVal (p<0.05) are included here. Taxonomy follows Weakley (2015). * indicates an exotic species.

Species	Clus.	IndVal	Mean	StDev	p-value
Viburnum prunifolium	C1	27.8	8.5	3.34	0.0008
Quercus stellata	C1	27.3	10.5	2.2	0.0001
Carya carolinae-septentrionalis	C1	26.6	7.5	3.71	0.0019
Endodeca serpentaria	C1	23.3	8.6	3.24	0.0033
Ulmus alata	C1	21	10.6	2.63	0.0022
Cercis canadensis	C1	20.4	9.2	3.41	0.0103
Carya glabra	C1	19.9	10.7	2.13	0.0005
Fraxinus [americana + biltmoreana + pennsylvanica + smallii]	C1	19.9	10.5	2.39	0.0015
Piptochaetium avenaceum	C1	19.2	9.4	3.16	0.012
Galium circaezans	C1	18.9	8.9	3.1	0.0104
Prunus serotina	C1	16.9	10.4	2.1	0.0064
Carya ovata	C1	16.2	7.8	3.82	0.0379
Smilax bona-nox	C1	15.7	9.5	2.77	0.0314
Scutellaria elliptica	C1	14.2	7.2	3.81	0.0497
Carex pensylvanica	C2	49.4	8.1	3.79	0.0001
Quercus montana	C2	35.2	8.9	3.31	0.0001
Polygonatum biflorum	C2	24.7	9	3.09	0.001
Quercus rubra	C2	24.5	10	2.83	0.0004
Pinus virginiana	C2	23.5	9.6	3.15	0.0027
Silene stellata	C2	21.4	7.3	4.08	0.0114
Amelanchier spicata	C2	20.6	7.2	4.09	0.0119
Hypericum prolificum	C2	20.6	6.9	4.22	0.0175
Phacelia dubia	C2	20.4	7.2	4.1	0.0156
Vaccinium stamineum	C2	17.6	10	2.75	0.0168
Crataegus [buckleyi + craytonii + intricata]	C2	17.5	6.9	4.29	0.0271
Solidago ulmifolia	C2	17.5	6.8	4.07	0.0251
Robinia pseudoacacia	C2	16.6	6.9	4.21	0.0377
Heuchera americana	C2	15.5	7.1	3.87	0.0371
Coreopsis pubescens	C3	55.6	7.1	4.16	0.0001
Hydatica petiolaris	C3	44.4	7.1	3.95	0.0001
Oxalis grandis	C3	44.4	7.1	4.04	0.0001
Geum canadense	C3	43.8	7	4.12	0.0001
Hypericum densiflorum	C3	43.8	6.9	4.03	0.0001
Solanum ptychanthum	C3	40.7	7	4.14	0.0001
Opuntia mesacantha	C3	37.9	6.7	3.96	0.0003
Verbesina occidentalis	C3	35.5	7.1	4.21	0.0006
Houstonia longifolia	C3	33.3	7.1	4.04	0.0006

Table 4.2 (Continued):

Symphoricarpos orbiculatus	C3	32.7	7.4	4	0.0009
Boechera laevigata	C3	30.9	6.6	4.1	0.0012
Quercus imbricaria	C3	29.6	7	4.02	0.0036
Bidens bipinnata	C3	27.4	6.6	4.12	0.0024
Sanicula canadensis	C3	27	6.9	4	0.0033
Pinus pungens	C3	25.5	6.9	4.32	0.0067
Chionanthus virginicus	C3	23.2	8.5	3.46	0.0046
**Bromus japonicus*	C3	22.2	7.3	4.23	0.0123
Coreopsis grandiflora	C3	22.2	7.3	4.04	0.0078
Cyperus lupulinus	C3	22.2	7.3	4.12	0.0091
Ipomoea coccinea	C3	22.2	7.2	4.11	0.0099
Lepidium virginicum	C3	22.2	7.3	4.11	0.0095
Polypodium appalachianum	C3	22.2	7.3	4.18	0.0101
Myriopteris tomentosa	C3	21.2	6.9	4.06	0.0098
Dichanthelium bicknellii	C3	20.9	7.3	4.04	0.0166
Thalictrum revolutum	C3	19	7.1	4.02	0.0187
Penstemon canescens	C3	18.8	6.8	4.2	0.022
Polygala curtissii	C3	18.7	7.4	4.19	0.0267
Galium pilosum	C3	18.4	8.4	3.19	0.0152
Dryopteris marginalis	C3	18.3	7	4.28	0.0257
Agalinis tenuifolia	C3	18.2	6.7	4.13	0.0241
Dichanthelium laxiflorum	C3	17.6	9.4	2.97	0.0168
Commelina virginica	C3	17.5	7.1	4.05	0.0308
Juniperus virginiana	C3	17.5	10.8	1.82	0.0009
Ulmus americana	C3	16.2	6.8	4.26	0.034
Anemone virginiana	C3	15.2	6.7	4.17	0.0418
Acer leucoderme	C4	51	7.3	4.02	0.0001
Pleopeltis michauxiana	C4	45.4	7.2	4	0.0001
Vaccinium arboreum	C4	39.3	8.6	3.47	0.0001
Hieracium venosum	C4	35.5	8.5	3.31	0.0001
Phytolacca americana	C4	35.3	7.1	3.91	0.0005
Bignonia capreolata	C4	32.8	7.8	4.01	0.0007
**Ailanthus altissima*	C4	29.9	8	4.13	0.0024
Callicarpa americana	C4	26.9	6.9	4.1	0.003
Celtis [laevigata + smallii]	C4	26.8	6.8	3.96	0.003
Thyrsanthella difformis	C4	20.4	6.9	4.13	0.0153
Galium tinctorium	C4	20	7.3	4.17	0.0131
Oxalis stricta	C4	20	6.8	4	0.0113
Symphyotrichum phlogifolium	C4	20	7.3	4.1	0.0117
Tillandsia usneoides	C4	20	7.3	4.32	0.0146

Table 4.2 (Continued):

Boechera missouriensis	C4	19.1	7.4	4.07	0.0215
Quercus nigra	C4	18.7	7.3	3.79	0.017
Galium aparine	C4	15.6	7	4.13	0.0437
Aristida dichotoma	C5	50.9	6.9	4.18	0.0001
Phemeranthus teretifolius	C5	31.7	6.9	3.96	0.0013
Aristida purpurascens	C5	23.5	6.8	4.04	0.0084
Lindernia monticola	C5	22.2	7.3	4.19	0.0089
Eupatorium capillifolium	C5	21.4	7.3	4.07	0.0109
Houstonia pusilla	C5	20.9	7.3	4.05	0.0161
Schizachyrium scoparium	C5	19.5	9.5	3.08	0.0113
Hypericum gentianoides	C5	17.7	7.5	3.71	0.0219
Dichanthelium depauperatum	C5	16.3	8.5	3.58	0.0399
Allium cernuum	C6	49.8	7	4.11	0.0002
Myriopteris lanosa	C6	49.4	7.4	4.05	0.0002
Festuca octoflora	C6	38.2	7	3.98	0.0002
Phemeranthus piedmontanus	C6	35.9	7	4.08	0.0009
Bryodesma rupestre	C6	28.9	6.9	4.19	0.0031
Dichanthelium ovale	C6	28.6	7.2	4.18	0.0011
Sporobolus vaginiflorus	C6	24.7	7.3	4.08	0.0036
**Ligustrum sinense*	C6	23.5	7.7	3.87	0.0052
Commelina erecta	C6	20.9	7.1	4.03	0.0113
Sporobolus clandestinus	C6	20.9	7.1	3.97	0.01
Clematis viorna	C6	20.6	7.2	3.96	0.0119
Celtis occidentalis	C6	18	7.4	4	0.0234
Sedum glaucophyllum	C6	16.6	6.7	4.17	0.0302
Plantago virginica	C6	16.1	7.2	4.08	0.044
Aquilegia canadensis	C6	15.1	6.9	4.1	0.0488
Oxalis dillenii	C6	14.7	8.3	3.33	0.0445
Vaccinium fuscatum	C7	70.7	6.7	4.13	0.0001
Eupatorium pilosum	C7	66.7	6.8	4.15	0.0001
Osmundastrum cinnamomeum	C7	66.7	7.1	4.22	0.0001
Pinus palustris	C7	61.9	6.8	4.13	0.0001
Aronia arbutifolia	C7	60.8	6.8	4.29	0.0001
Chasmanthium laxum	C7	46.6	7.1	4.49	0.0003
Pteridium latiusculum	C7	45.5	7.5	4.12	0.0002
Viburnum nudum	C7	44.4	7.1	4.02	0.0001
Amelanchier canadensis	C7	43.1	6.8	4.03	0.0003
Gaylussacia frondosa	C7	43	7.4	4.29	0.0002
Alnus serrulata	C7	33.3	7.4	4.13	0.0016
Drosera brevifolia	C7	33.3	7.4	4.09	0.0014

Table 4.2 (Continued):

Polygala lutea	C7	33.3	7.3	4.03	0.0024
Smilax laurifolia	C7	33.3	7.3	3.99	0.0019
Eubotrys racemosus	C7	33	7.4	4.14	0.0021
Rhododendron viscosum	C7	32.7	7.3	4.1	0.0019
Nyssa sylvatica	C7	30.6	9.9	2.76	0.0001
Ilex verticillata	C7	29.6	6.9	4.08	0.0029
Acer rubrum	C7	28.9	11.1	2.24	0.0001
Vaccinium tenellum	C7	27.4	7.7	3.88	0.0024
Solidago odora	C7	26.9	7.3	3.85	0.0028
Anchistea virginica	C7	22.2	7.3	4.16	0.0101
Carex leptalea	C7	22.2	7.3	4.21	0.0115
Carex lurida	C7	22.2	7.3	4.21	0.0115
Carex seorsa	C7	22.2	7.3	4.13	0.0102
Hypericum setosum	C7	22.2	7.3	4.33	0.0134
Lespedeza capitata	C7	22.2	7.3	4.19	0.0091
Magnolia virginiana	C7	22.2	7.1	4.4	0.0102
Platanthera ciliaris	C7	22.2	7.3	4.16	0.0107
Rhexia nashii	C7	22.2	7.3	4.19	0.0105
Sophronanthe pilosa	C7	22.2	7.3	4.11	0.0088
Ilex opaca	C7	22.1	7.8	3.79	0.008
Juncus coriaceus	C7	19.8	7.2	4	0.0183
Panicum virgatum	C7	19.7	7	4.11	0.0168
Lyonia mariana	C7	19	6.8	4.15	0.021
Iris verna	C7	18.6	6.8	4.07	0.0215
Vaccinium corymbosum	C7	18.1	6.9	4.19	0.0255
Pinus taeda	C7	15.7	8.6	3.57	0.0457
Oxydendrum arboreum	C8	36.9	8.2	3.7	0.0002
Quercus coccinea	C8	36.8	7.7	3.86	0.0004
Vaccinium pallidum	C8	35.5	9.4	3.06	0.0001
Quercus marilandica	C8	26.9	9	3.32	0.0011
Kalmia latifolia	C8	26.1	7.1	4.31	0.0043
Gaylussacia baccata	C8	22.4	7	4.12	0.0103
Gaylussacia dumosa	C8	20.1	7	4.38	0.0192
Smilax glauca	C8	19.9	9.8	2.52	0.0021
Pinus echinata	C8	18.9	8.8	3.33	0.0148
Symplocos tinctoria	C8	15.2	6.9	4.16	0.0458
Chimaphila maculata	C8	15.1	7.5	3.84	0.0439
Desmodium paniculatum	C9	84.5	7	3.99	0.0001
Rhus michauxii	C9	75	6.8	4.06	0.0001
Desmodium laevigatum	C9	66.2	6.7	4.09	0.0001

Table 4.2 (Continued):

Eupatorium godfreyanum	C9	59	6.7	3.91	0.0001
Vernonia glauca	C9	58.9	6.5	4	0.0001
Desmodium nuttallii	C9	54.9	6.6	4.12	0.0001
Desmodium marilandicum	C9	54.2	6.8	4.05	0.0001
Desmodium perplexum	C9	51.6	7.1	4.04	0.0001
Chrysogonum virginianum	C9	48.2	6.8	4.11	0.0001
Rhus glabra	C9	46.2	7.2	4.33	0.0001
Lespedeza procumbens	C9	44	7	3.88	0.0002
Solidago nemoralis	C9	41.9	6.7	4.02	0.0002
Eupatorium pubescens	C9	41	6.7	4.08	0.0003
Cirsium discolor	C9	37.5	7.3	4.01	0.0011
Eupatorium saltuense	C9	37.5	7.3	3.99	0.0008
Carya tomentosa	C9	37.2	10	2.87	0.0001
Cornus florida	C9	37.1	9.6	3.05	0.0001
Desmodium viridiflorum	C9	36.2	7.1	3.97	0.0009
Ipomoea pandurata	C9	36	6.6	4.05	0.0006
Apocynum cannabinum	C9	35.9	7.3	3.73	0.0005
Hylodesmum nudiflorum	C9	35.8	7.3	4.24	0.0005
Sanicula smallii	C9	35.8	7	4.03	0.0003
Physalis heterophylla	C9	35.5	6.9	4.02	0.001
Quercus velutina	C9	34.8	9.9	2.96	0.0001
Vitis aestivalis	C9	34.7	7.2	3.97	0.0005
Eupatorium hyssopifolium	C9	34.1	7.7	3.84	0.0013
Solidago pinetorum	C9	33.7	7.2	3.99	0.0013
Vitis vulpina	C9	31.7	7.2	3.91	0.0008
Rubus occidentalis	C9	31.6	6.7	3.97	0.0008
Sassafras albidum	C9	31.5	8.4	3.63	0.0007
Quercus alba	C9	31.4	10.4	2.61	0.0001
Ambrosia artemisiifolia	C9	30.8	7.5	3.62	0.0006
Lactuca canadensis	C9	30.5	6.7	4.27	0.002
Desmodium ciliare	C9	29.5	6.9	3.96	0.0023
Ageratina aromatica	C9	29.2	7.1	4.33	0.0021
Clitoria mariana	C9	29.2	8.6	3.41	0.0003
Quercus falcata	C9	28.6	8.7	3.51	0.0009
Symphyotrichum undulatum	C9	28.4	7	3.94	0.0023
Symphyotrichum lateriflorum	C9	28.1	6.9	3.99	0.003
Hypericum stragulum	C9	27.3	7.9	3.54	0.0014
Solidago rugosa	C9	26.5	7.2	3.9	0.003
Brickellia eupatorioides	C9	25	7.3	4.07	0.0038
Erianthus alopecuroides	C9	25	7.3	4.2	0.0038

Table 4.2 (Continued):

Dichanthelium boscii	C9	24.5	9.4	2.87	0.001
Rhus copallinum	C9	24	8.5	3.37	0.0036
Salvia urticifolia	C9	23.8	7.3	4.23	0.007
Amphicarpaea bracteata	C9	23.7	7	4.35	0.0091
Asclepias variegata	C9	23.7	7.2	4	0.0055
Carex striatula	C9	23.7	7.3	3.93	0.0074
Phryma leptostachya	C9	23.7	7.3	3.95	0.0068
Juglans nigra	C9	23.2	7	4.27	0.0095
Liquidambar styraciflua	C9	22.8	10	2.8	0.002
Dioscorea villosa	C9	22.5	7.2	4.07	0.0098
Solidago erecta	C9	22	6.7	3.99	0.0077
Chamaecrista nictitans	C9	21.9	7.5	3.84	0.0084
Cyperus echinatus	C9	21.1	6.9	4.09	0.0132
Rubus [flagellaris]	C9	21	8.5	3.35	0.0074
Uvularia perfoliata	C9	20.8	7.3	4.07	0.0131
Lespedeza violacea	C9	20.7	7	3.94	0.0096
Liriodendron tulipifera	C9	20.7	8	3.98	0.0143
Tephrosia spicata	C9	20	7.3	3.93	0.0154
Silphium asteriscus	C9	19.7	6.9	4.11	0.0171
Eupatorium sessilifolium	C9	17.1	6.8	4.09	0.0336
Botrypus virginianus	C9	16.9	6.9	4.18	0.0329
Desmodium glabellum	C9	16.7	6.7	4.24	0.0313
Gymnopogon ambiguus	C9	16.7	7.3	3.92	0.0401
Helianthus atrorubens	C9	16.7	7	4.17	0.0327
Sphenopholis nitida	C9	16.7	6.6	4.12	0.0301
Sisyrinchium mucronatum	C9	16.4	7.2	3.99	0.0426
Diospyros virginiana	C9	16.3	10.2	2.38	0.0213
Dichanthelium commutatum	C9	15.8	9.3	3.24	0.0432
Viola sororia	C9	15.5	6.8	4.1	0.0438
Desmodium rotundifolium	C9	15	6.6	4.12	0.0457
Carya ovalis	C9	14.9	7	4.2	0.049
Agrimonia pubescens	C9	14.5	6.7	4.13	0.049
Eupatorium rotundifolium	C10	77.8	6.9	4.05	0.0001
Pseudognaphalium obtusifolium	C10	44.4	7.7	3.89	0.0002
Chrysopsis mariana	C10	38.2	7.1	3.85	0.0002
Baptisia tinctoria	C10	38.1	6.8	4.17	0.0006
Potentilla canadensis	C10	38	9	3.55	0.0001
Silphium compositum	C10	36.1	7	4.22	0.0006
**Anthoxanthum odoratum*	C10	33.3	6.8	4.12	0.0006
Desmodium strictum	C10	33.3	6.7	4.11	0.0008

Table 4.2 (Continued):

Muhlenbergia capillaris	C10	33.3	6.9	4.13	0.0009
Lespedeza stuevei	C10	33.1	6.8	4.17	0.0008
Symphyotrichum racemosum	C10	27.8	7	4.14	0.0046
Rubus cuneifolius	C10	24.3	7	4.14	0.0068
Parthenium integrifolium	C10	23.2	7.3	4.09	0.0072
Andropogon virginicus	C10	22.8	8.1	3.83	0.0077
Pycnanthemum tenuifolium	C10	21.5	7.6	4.14	0.0115
**Albizia julibrissin*	C10	21.3	6.8	4.25	0.0145
Eupatorium torreyanum	C10	18.7	6.8	4.21	0.0223
Coreopsis major	C10	17.4	8.4	3.54	0.0238
Danthonia spicata	C10	17.2	10.6	2.09	0.0073
**Daucus carota*	C10	17	7	4.24	0.0336
Bidens aristosa	C10	16.7	7.3	4.13	0.0404
Dichanthelium leucothrix	C10	16.7	7.4	4.02	0.0386
Gymnopogon brevifolius	C10	16.7	7.4	4	0.0386
Nabalus trifoliolatus	C10	16.7	7.3	3.96	0.0408
Tridens flavus	C10	16.7	6.7	3.98	0.0339
Tephrosia virginiana	C10	16.5	7.7	3.77	0.0338
Campsis radicans	C10	16.3	9	3.15	0.0337
Packera aurea	C10	15.9	6.8	4.16	0.0379
Sorghastrum nutans	C10	15.8	7.7	3.67	0.0399
Dichanthelium consanguineum	C10	15.4	6.9	4.07	0.0447
Nabalus altissimus	C10	15.3	6.9	4.2	0.0439
Paspalum setaceum	C11	42.5	7.1	4.05	0.0002
Silphium terebinthinaceum	C11	39.7	6.9	4.19	0.0004
Mecardonia acuminata	C11	37.5	7.4	4.09	0.0005
Oenothera fruticosa complex	C11	33.9	7.4	4.01	0.0005
Prunella vulgaris	C11	30.7	7.2	4.27	0.0036
Euphorbia curtisii	C11	29.6	7.1	3.91	0.0024
Setaria parviflora	C11	26	6.9	4.23	0.0061
Penstemon laevigatus	C11	25.9	6.9	4.21	0.005
Cornus amomum	C11	25	7.3	4.21	0.0047
Juncus brachycarpus	C11	25	7.3	4.13	0.0042
Quercus phellos	C11	25	9.9	2.96	0.0007
Rhynchospora caduca	C11	25	7.2	4.47	0.0057
Solidago ptarmicoides	C11	25	7.3	4.17	0.0047
Rudbeckia hirta	C11	24.5	7.4	4.27	0.0067
Paspalum laeve	C11	24.3	7.4	4.01	0.0045
Helianthus schweinitzii	C11	23.7	7.3	3.92	0.0074
Juncus biflorus	C11	23.7	7.3	4.01	0.0079

Table 4.2 (Continued):

Solanum carolinense	C11	22.6	6.7	4.09	0.0085
Houstonia tenuifolia	C11	21.1	6.7	4.13	0.0111
Andropogon gyrans	C11	18.7	7.2	4.4	0.0276
Scleria pauciflora	C11	18.5	7.1	4.13	0.0214
Dichanthelium acuminatum	C11	16.7	7.1	3.91	0.0247
Ruellia humilis	C11	16.1	7.2	4.07	0.0467
Rhynchospora globularis	C11	15.9	7.1	4.11	0.0459
Eragrostis hirsuta	C11	15.7	7.4	4	0.047
Symphyotrichum pilosum	C11	15.3	7	3.98	0.044
Croton willdenowii	C12	56.2	6.9	4.04	0.0001
**Rumex acetosella*	C12	40	7.3	4.09	0.0003
Diamorpha smallii	C12	32.7	7.3	3.9	0.0012
Bulbostylis capillaris	C12	31.8	6.6	3.98	0.0011
Carex muehlenbergii	C12	30.7	6.7	4.13	0.0013
Polypremum procumbens	C12	28.7	7.1	4.17	0.0037
Verbena simplex	C12	27.7	7.1	3.96	0.0035
Dichanthelium villosissimum	C12	25.5	6.8	4.18	0.0059
**Lolium arundinaceum*	C12	24.5	7.1	4.23	0.0079
Tragia urticifolia	C12	21.4	7.5	4.09	0.0122
Panicum dichotomiflorum	C12	20.1	6.8	4.21	0.0183
Digitaria ciliaris	C12	20	6.1	4.89	0.0259
Fimbristylis autumnalis	C12	20	6.2	4.91	0.0257
Lechea minor	C12	20	6.2	4.87	0.023
Packera tomentosa	C12	20	6.2	4.85	0.0215
Eupatorium compositifolium	C12	18.7	7.3	4.13	0.0302
Dichanthelium sphaerocarpon	C12	18.5	6.9	4.06	0.0197
Mononeuria glabra	C12	16.7	6.7	4.1	0.0322

Table 4.3: Mean (and range) species richness and estimated tree cover for the 12 clusters representing Piedmont heliophilic vegetation. * indicates less than 50% of plots had the information necessary to calculate this metric, so the mean and range do not represent the entire cluster.

Cluster	Species Richness (spp./m^2)	Estimated Tree Cover (%)
C1: Piedmont Red Cedar-Post Oak Woodlands	11 (4-25)	90 (38-100)
C2: Inner Piedmont Chestnut Oak Woodlands	*8 (6-10)	69 (34-100)
C3: Piedmont Red Cedar-Ash Woodlands	17 (6-27)	43 (4-100)
C4: Outer Piedmont Red Cedar Cliff Glades	6 (2-11)	55 (18-100)
C5: Piedmont Flatrock and Outcrop Glades	9 (6-12)	14 (0-55)
C6: Inner Piedmont Red Cedar Glades	*8 (6-10)	17 (0-36)
C7: Piedmont Longleaf Pine Woodlands	14 (10-27)	48 (10-100)
C8: Piedmont Virginia Pine-Oak Woodlands	6 (2-9)	76 (26-100)
C9: Outer Piedmont Oak-Hickory Savanna	*37	58 (26-99)
C10: Piedmont Ruderal Native Grasslands	10 (6-15)	13 (6-29)
C11: Piedmont Prairie Barrens	19 (11-26)	40 (3-100)
C12: Piedmont River Terrace Glades	11 (5-15)	3 (1-8)

FIGURES

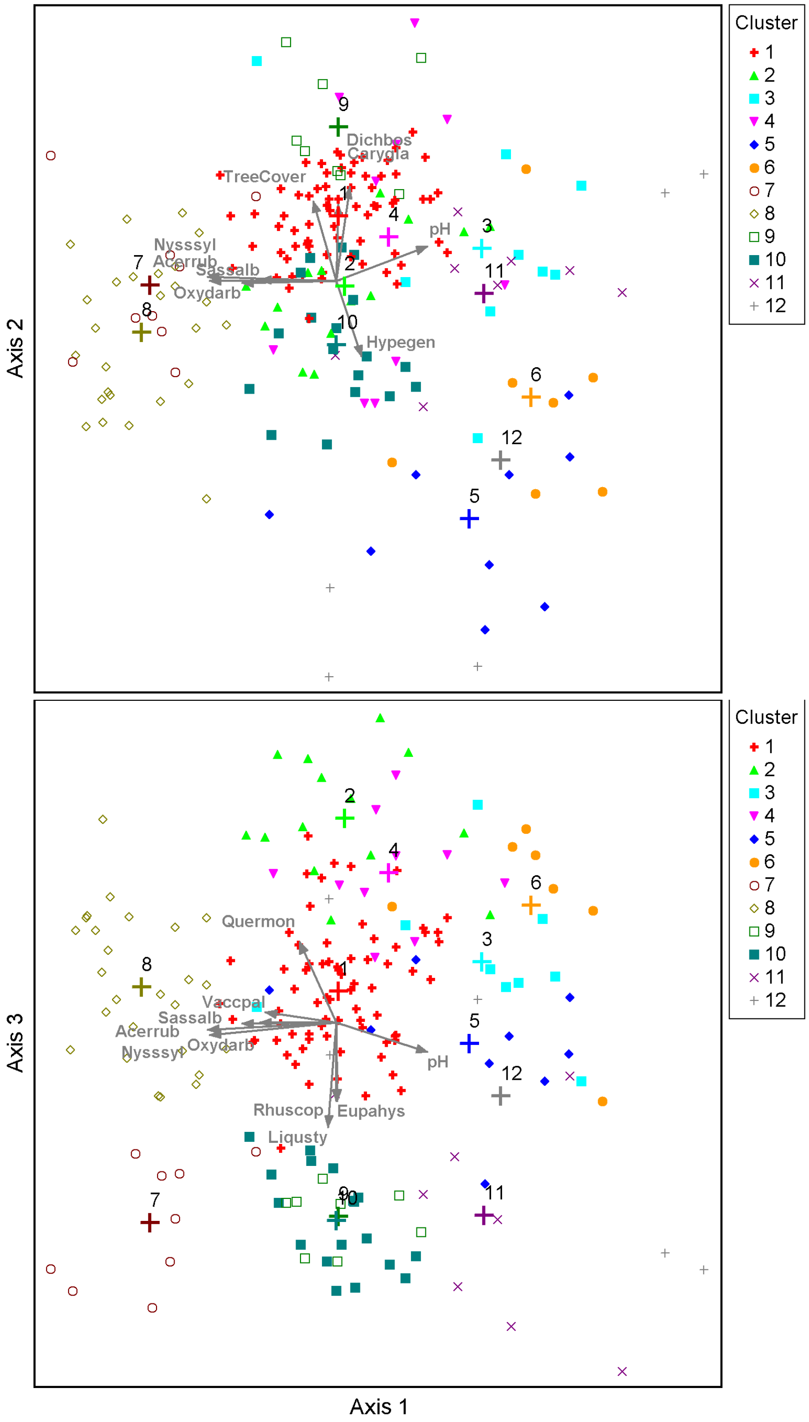

Figure: 4.1: NMDS Ordination. Points represent the position of individual plots in compositional space and are colored based on cluster membership. Labeled pluses indicate cluster centroids. Vectors indicate trends in species abundances and environmental data. n = 195 plots.

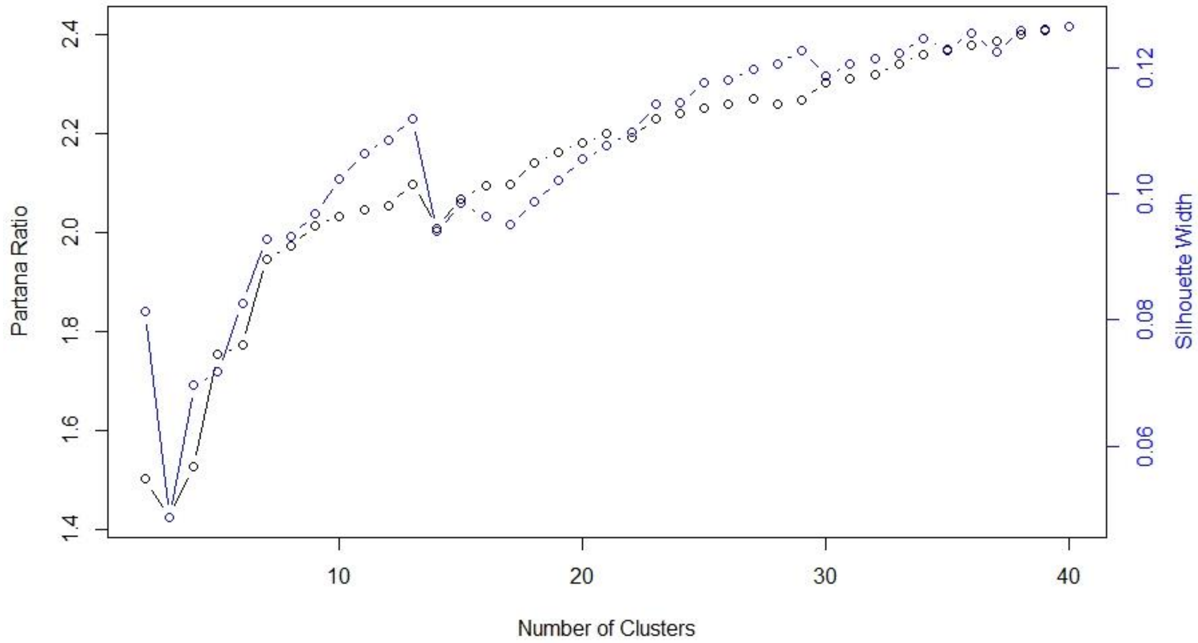

Figure 4.2: Stride for Flexible-beta showing a peak in both measurements corresponding to 12 clusters.

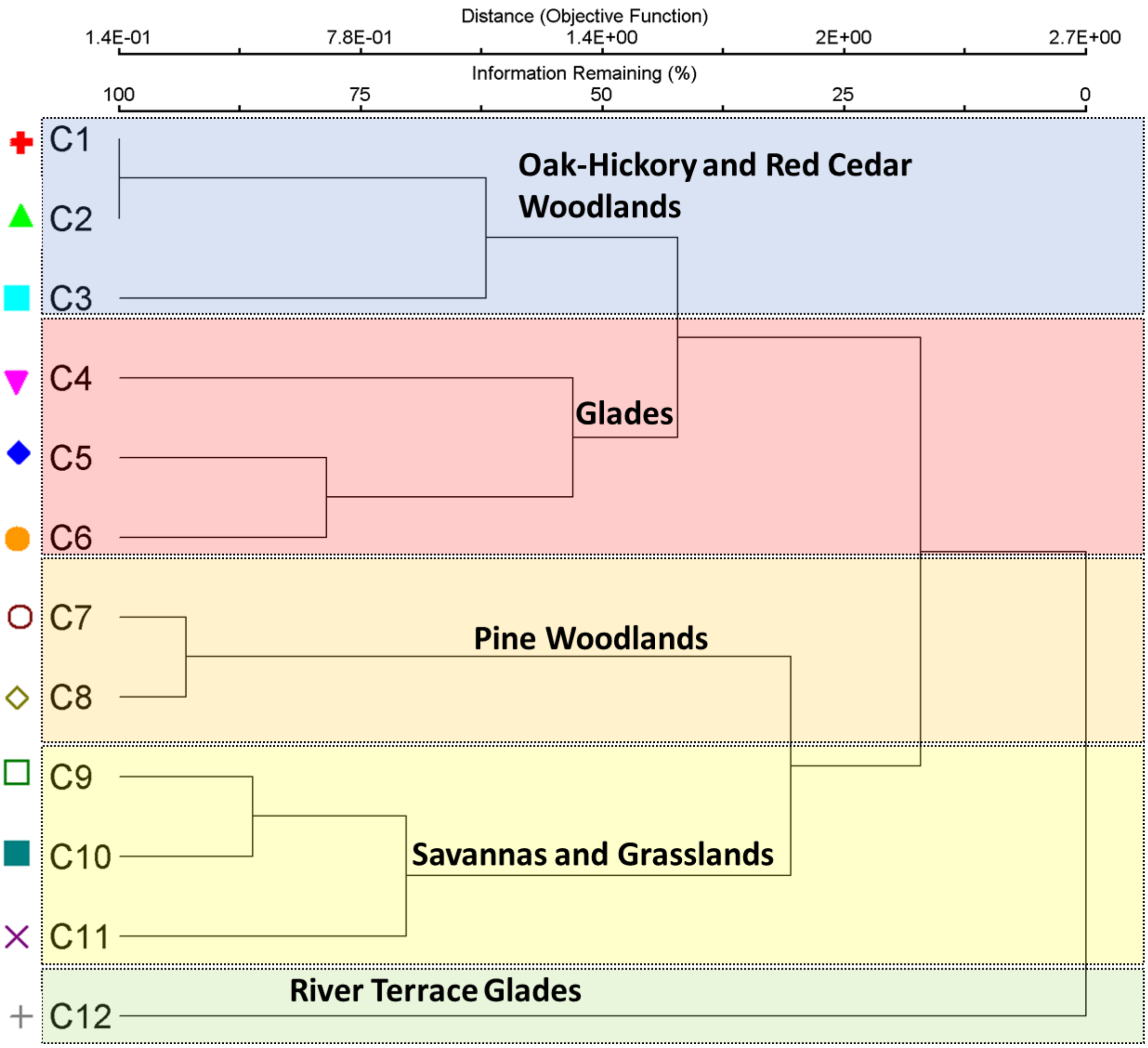

Figure 4.3: Hierarchical cluster (Flexible-beta, beta = -0.25) of the 12 clusters. Icons correspond to the icons in the NMDS ordination summary (Figure 4.4).

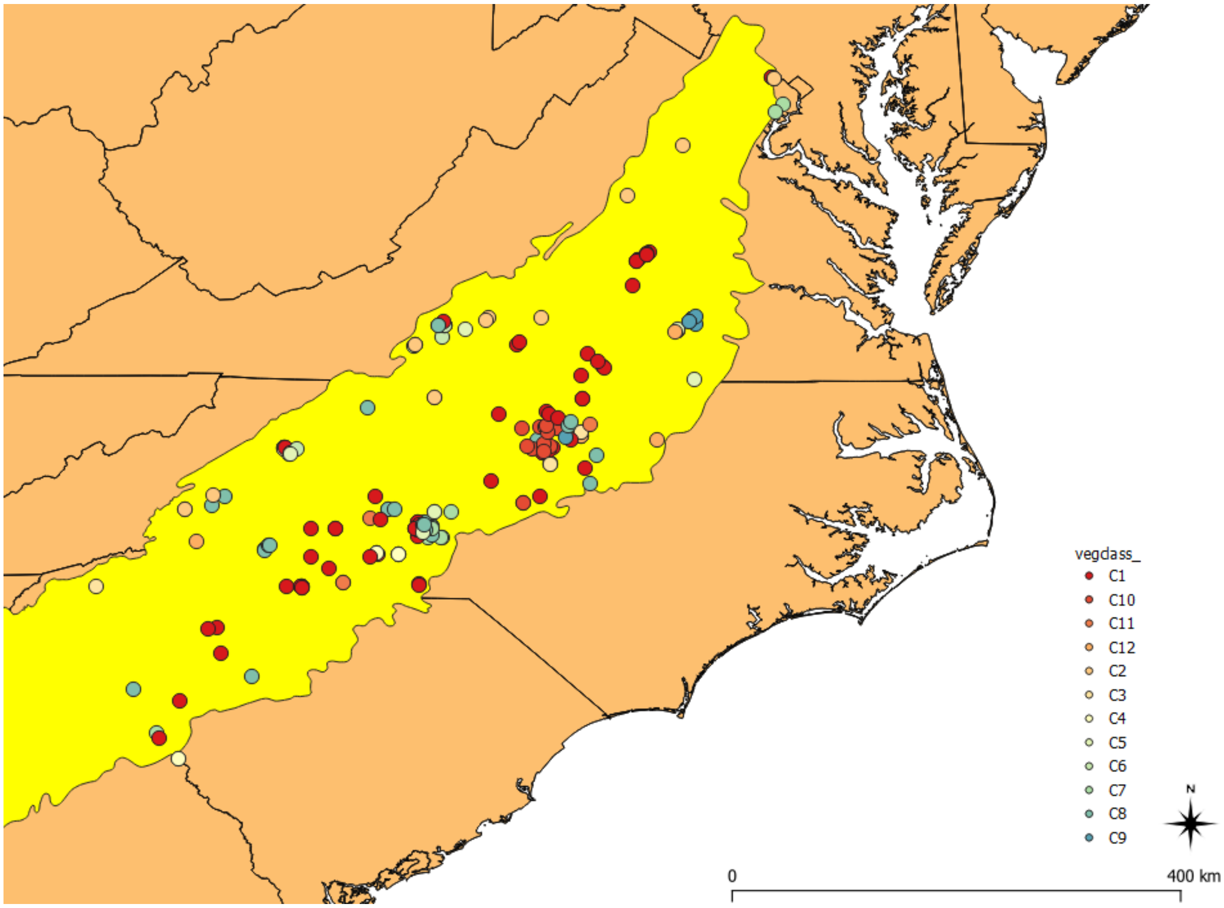

Figure 4.4: Geographic locations of the plots and their cluster membership.

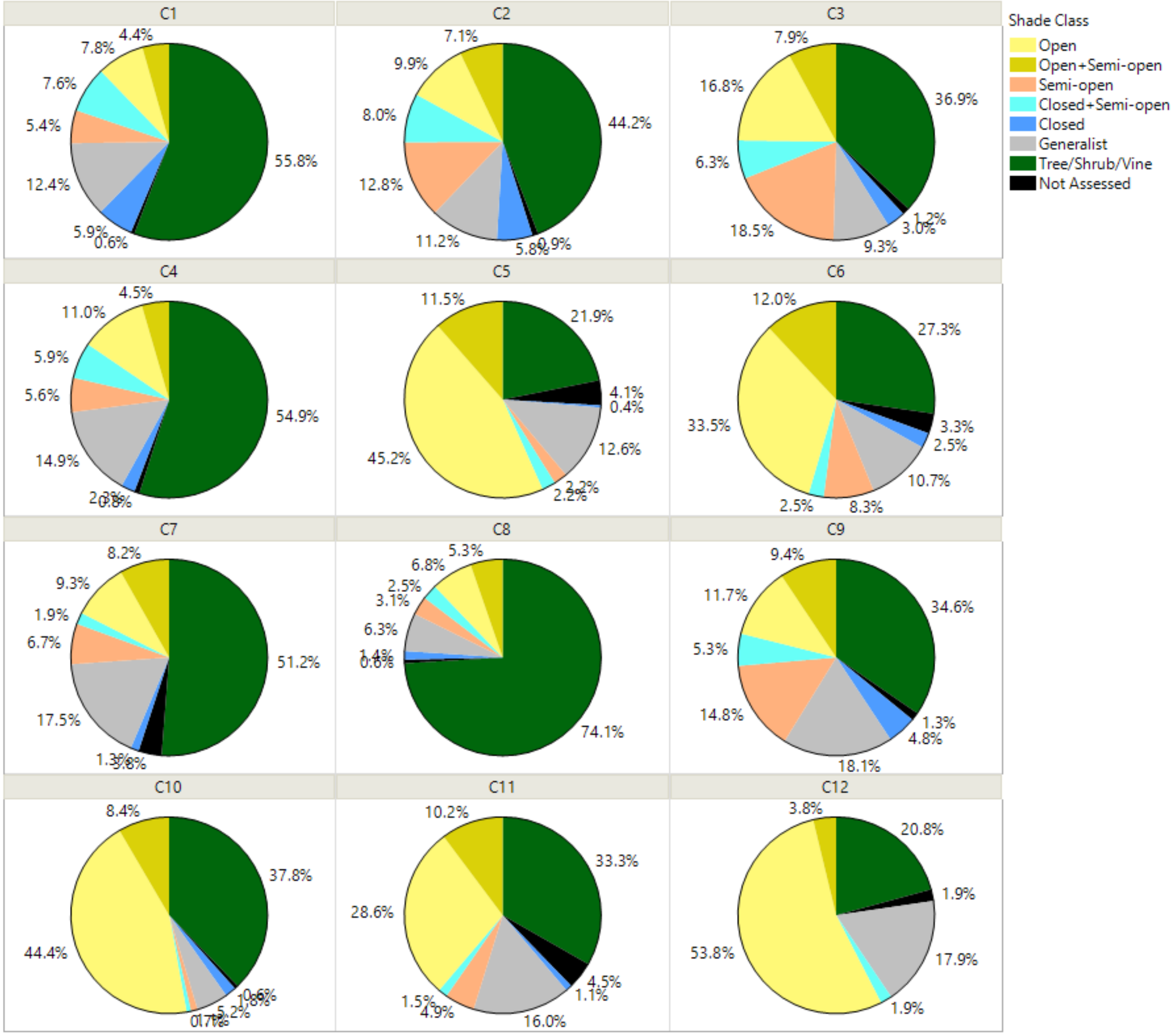

Figure 4.5: Shade class occurrences by cluster. An occurrence is a record of a species in a plot. Species shade classes were determined based on analyses in Chapter 2.

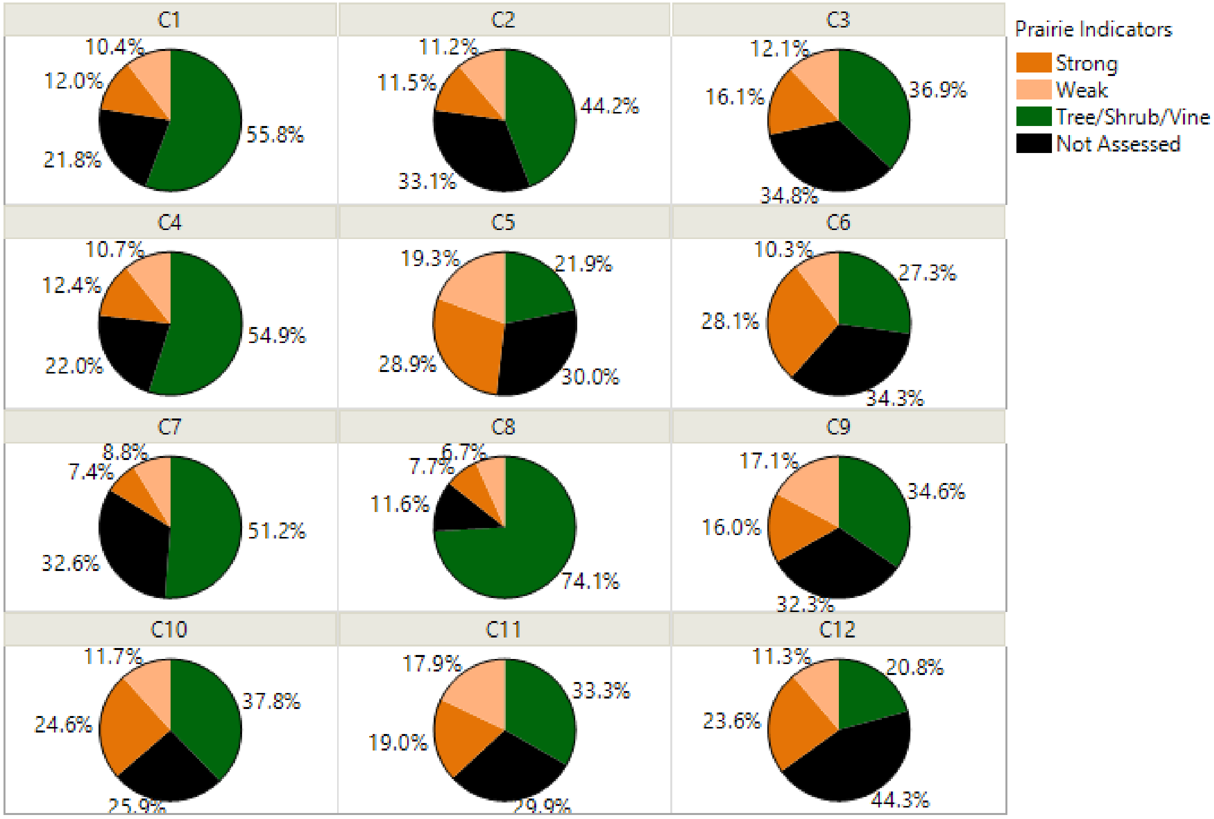

Figure 4.6: Prairie indicator occurrences by cluster. An occurrence is a record of a species in a plot Prairie indicator species were determined based on Davis et al. (2002).

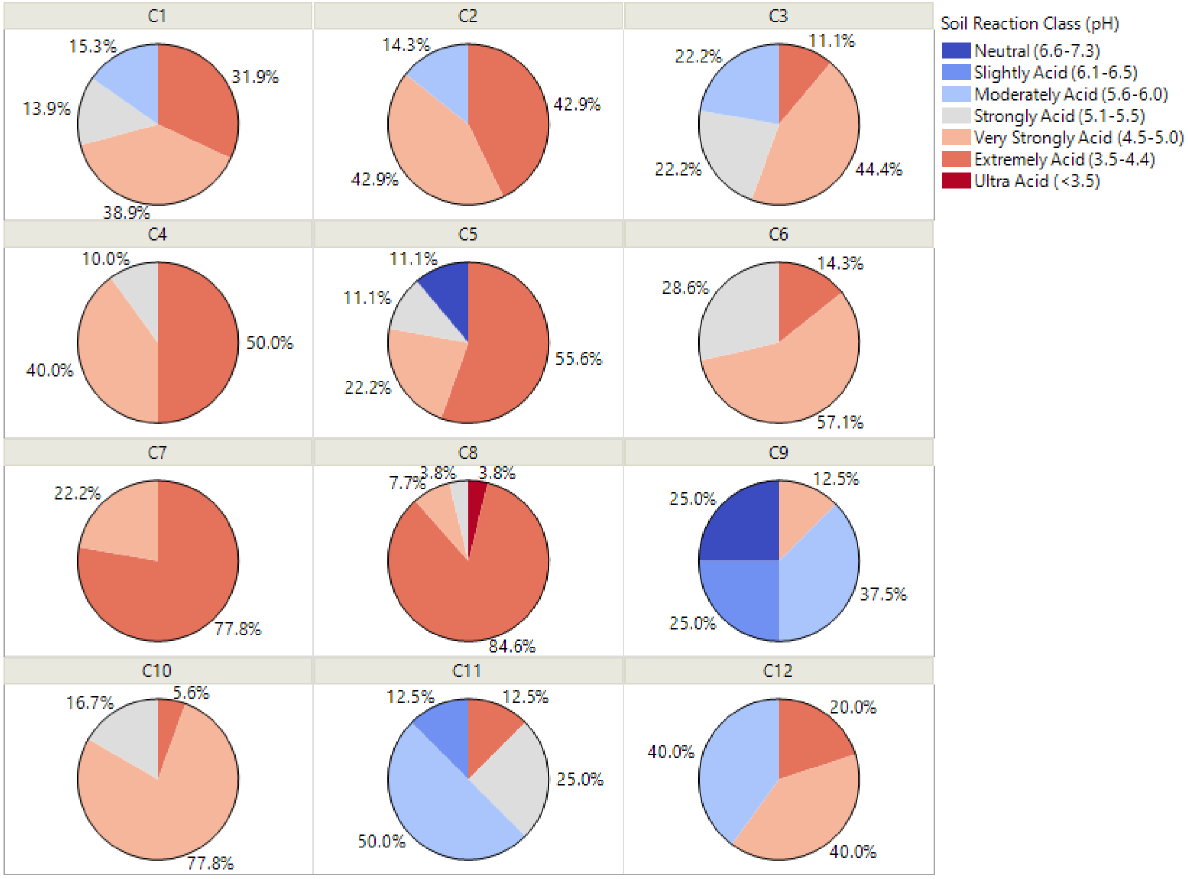

Figure 4.7: Soil reaction classes of plots in each cluster.

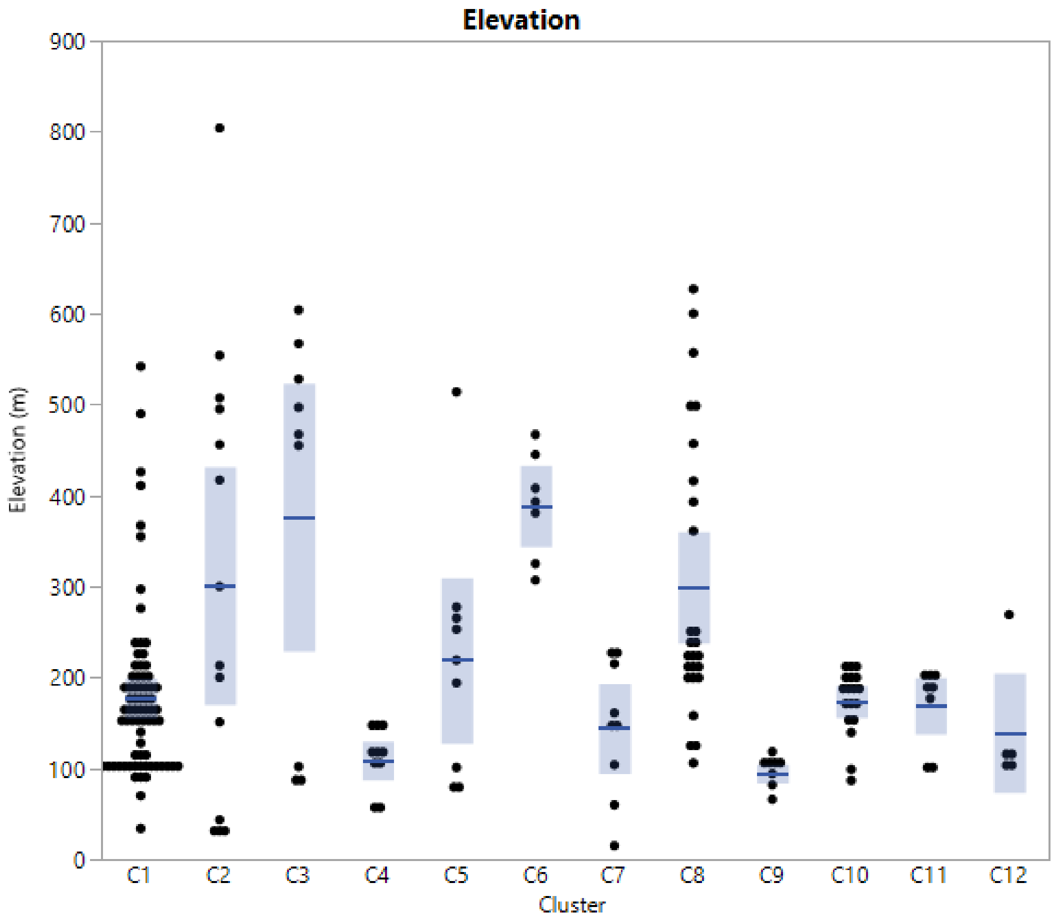

Figure 4.8: Elevation of plots in each cluster. Horizontal lines indicate means and shaded areas are confidence intervals. n=195 plots.

APPENDICES

APPENDIX A

Taxonomic homogenization rules for preparation of the 1300-plot dataset obtained from the Carolina Vegetation Survey.

Goal: Taxonomy should be as closely representative of the species level as possible.

1. Drop anything that is not a vascular plant (e.g. “Cladonia”)
2. Drop any “unknowns” and unranked taxa (e.g. “forb”).
3. Drop any taxon at a rank of genus or higher (e.g. “Acer”) unless a particular group is only represented by a genus-level taxon.
4. Merge subspecific taxa into parent species.
5. If a subgenus exists alongside its subordinate taxa and has more records than the subordinates, merge all together. If the subordinate taxa have more records, drop the subgenus. If a subgenus exists without a subordinate taxon, leave as is. Merge on ties.
6. Drop hybrids.

Weakley (2015) was used as a taxonomic reference.

Detailed preparation of the 1300-plot dataset obtained from the Carolina Vegetation Survey.

- ➔ Received initial file with 2914 plots and 2720 taxonomic entities.
- ➔ Dropped 274 plots with no cover information and went down to 2640 plots.
- ➔ These 2640 plots contained 2673 taxonomic entities. I cleaned up the taxonomy (see appendix) and ended with 1965 taxonomic entities (as representative of species level as possible).
- ➔ Plots with observations to be dropped (based on taxonomic cleaning) that have cover value >5 (i.e. >10% cover) were flagged to be dropped (107 plots).
- ➔ First PC-Ord import is 2532 plots x 1936 taxa.
- ➔ "Outliers" identified and flagged for dropping following multiple rounds of NMDS quick ordinations. Outliers were defined as those plots whose inclusion in the dataset resulted in the autopilot selecting a one-dimensional solution. Outliers were removed at each round of ordination and this continued until a multi-dimensional solution was recommended. (12 plots dropped over four rounds of ordination; see appendix).
- ➔ Discovered some plots have multiple copies from resurveys. Went back and flagged the previous surveys to drop (284 plots).
- ➔ Dropping 195 plots with no soil data. I can't logically impute soil data and it is likely an important environmental factor. All AL and GA plots were dropped (no soil data!).
- ➔ Drop 144 more plots without soil data (soil data is all 0, previous drops were based on blanks).

-Concise Drop Record-
274 dropped for no cover data
163 dropped for being a previous survey with the most current survey in the dataset
327 dropped for no soil data
107 dropped for poor taxonomic resolution (mostly granite communities with lichen dominants)
12 dropped in NMS outlier passes
\----------
883 total drops

- ➔ 2031 plots remaining in dataset (with 1965 species)

288 additional plots later removed for being located outside the Piedmont

- ➔ 1743 plots remain in dataset (with 1718 species).

443 plots removed for representing bottomland (alluvial) vegetation

- ➔ 1300 plots in final dataset (with 1550 species)

Dataset preparation – identification of outlier plots using NMDS ordinations.

“Outliers” identified and flagged for dropping following multiple rounds of NMDS “quick and dirty” autopilot ordinations using PC-Ord. Outliers were defined as those plots whose inclusion in the dataset resulted in the autopilot selecting a one-dimensional solution. Outliers were removed and the new dataset was subjected to another round of NMDS ordination. This continued until a multi-dimensional solution was recommended.

First cut: 2527 plots remain
Plots removed:
111d1345
85MADS22
081d1015
4b0154
082c1104

Second cut: 2524 plots remain
Plots removed:
85GFNP19
85FRAN3
67CHA80

Third Cut: 2521 plots remain
Plots removed:
85KzRR4
85NO3
85FRAN1

Fourth Cut: 2520 remain
Plot removed:
85URK31

Fifth ordination has a multi-dimensional solution.

R script for the point biserial correlation coefficients analysis.

```
##Employing the point biserial correlation coefficient to classify habitat specialization of the
vascular flora of the Piedmont of the Carolinas and Virginia

##Methods: Starting dataset from Szakacs included 1300 plots from CVS that had been culled
from the 20K plot CVS database and subsequently quality controlled by Szakacs and AK. Plots
were assigned to "Habitat Classes" based on total estimated cover of tree species (<25% = open,
25-75% = semi-open, and >75% = closed). The dataset was formatted into a Plot by Species
matrix (1300 x 1550) and the point biserial correlation coefficient was then calculated. Data
manipulation and calculation scripts are provided below.

## Load libraries
library(indicspecies)
library(permute)

## Do you need to clean up your working environment?
## First, see what's currently there.

ls()

## If desired, remove (almost) everything in the working environment.
## You will get no warning, so don't do this unless you are really sure.

rm(list = ls())
ls()


## Increase output file size so that R shows complete results
options(max.print=10000000)


## Load data file
## My file is a plot x species matrix with species abundance reported in cover classes; the file
has row name and column name headers.
mydata <- read.csv("guilds_main_1300.csv", row.names=1, header=T)


##Add habitat type as a vector
##First, read in file: (my file is a two column table, first column is plot names and second is the
habitat class)
habitat_type = read.csv("guilds_1300_class.csv")


##...then, convert to vector (my file had two columns so I use $HabitatC to choose the
appropriate column)
```

```
habitat_type_vector<-habitat_type$HabitatC

## Begin sink to output file. Will write to file when sink ends.
sink("guilds_1300_Habitat_output_9999.txt", append=TRUE)

## Compute point biserial correlation coefficient (group equalized) for abundance data.
## NOTE: increase number of permutations to 9999 for final run.
phi <- multipatt(mydata, habitat_type_vector, func = "r.g", control = how(nperm=9999))

phi

## Stop writing to file
## Note: the file output here is very very large if using the Level 1 dataset (>300MB).
sink()

## Write the matrix with association strength for all combinations studied to file.
## Note: the column labels for this spreadsheet may end up off by 1 in excel. Just shift them
over. Values and rows are correct.
write.table(phi$str, "guilds_1300_habitat_output_9999_str.csv", sep=",", col.names=TRUE,
row.names=TRUE)

## Write the data table with the best matching group and permutation test results to file.
## Note: the column labels for this spreadsheet may end up off by 1 in excel. Just shift them
over. Values and rows are correct.
write.table(phi$sign, "guilds_1300_habitat_output_9999_sign.csv", sep=",", col.names=TRUE,
row.names=TRUE)
```

APPENDIX B

Table 3.6: Full taxonomy and species codes used for the study of Picture Creek Diabase Barrens *Echinacea laevigata* monitoring plots. Taxonomy follows Stanley et al. (2019).

CODE	Full Taxon Name	Comment
ACALGRA	*Acalypha gracilens* A. Gray	
ACALVIR	*Acalypha virginica* L.	
ACERFLO	*Acer floridanum* (Chapm.) Pax	
ACERRUB	*Acer rubrum* L.	
ACERSP	*Acer* sp.	
AGRIPAR	*Agrimonia parviflora* Aiton	
AGRIPUB	Agrimonia pubescens Wallr.	
AGRIROS	Agrimonia rostellata Wallr.	
AGRISP	Agrimonia sp.	
AGROPER	Agrostis perennans (Walter) Tuck.	
AGROSP	Agrostis sp.	
ALBIJUL	Albizia julibrissin Durazz.	Exotic
AMBRART	Ambrosia artemisiifolia L.	
AMELARB	Amelanchier arborea (F. Michx.) Fernald	
AMPHBRA	Amphicarpaea bracteata (L.) Fernald	
ANDRGYR	Andropogon gyrans Ashe	
ANDRSP	Andropogon sp.	
ANDRVIR	Andropogon virginicus L.	
ANEMVIR	Anemone virginiana L.	
ANGEVEN	Angelica venenosa (Greenway) Fernald	
ANGRPER	Agrostis perennans (Walter) Tuck.	
ANTEPAR	Antennaria parlinii Fernald	
ANTEPLA	Antennaria plantaginifolia (L.) Richardson	
ANTESP	Antennaria sp.	
APOCCAN	Apocynum cannabinum L.	
ARISDIC	Aristida dichotoma Michx.	
ARISPUR	Aristida purpurascens Poir.	
ARISSP	Aristida sp.	
ARONARB	Aronia arbutifolia (L.) Pers.	
ASCLSP	Asclepias sp.	
ASCLVER	Asclepias verticillata L.	
ASPLPLA	Asplenium platyneuron (L.) Britton, Sterns & Poggenb.	
BAPTAUSA	Baptisia australis (L.) R. Br. var. aberrans (Larisey) M.G. Mendenh.	
BIDEARI	Bidens aristosa (Michx.) Britton	
BLEPCIL	Blephilia ciliata (L.) Benth.	

Table 3.6: (Continued).

BOTRDIS	Sceptridium dissectum (Spreng.) Lyon	
BOTRVIR	Botrypus virginianus (L.) Michx.	
CAMPRAD	Campsis radicans (L.) Bureau	
CAREAMP	Carex amphibola Steud.	
CARECAR	Carex caroliniana Schwein.	
CAREFLA	Carex flaccosperma Dewey	
CARELAX	Carex laxiflora Lam.	
CARESP	Carex sp.	
CARPCAR	Carpinus caroliniana Walter	
CARYGLA	Carya glabra (Mill.) Sweet	
CARYOVA	Carya ovata (Mill.) K. Koch	
CARYSP	Carya sp.	
CARYTOM	Carya tomentosa (Poir.) Nutt.	
CEANAME	Ceanothus americanus L.	
CELTLAE	Celtis laevigata Willd.	
CELTTEN	Celtis tenuifolia Nutt.	
CENTSP	Centrosema sp.	
CENTVIR	Centrosema virginianum (L.) Benth.	
CEONAME	Ceanothus americanus L.	
CERCCAN	Cercis canadensis L.	
CHAMFAS	Chamaecrista fasciculata (Michx.) Greene	
CHAMNIC	Chamaecrista nictitans (L.) Moench	
CHIMMAC	Chimaphila maculata (L.) Pursh	
CHIOVIR	Chionanthus virginicus L.	
CHRYVIR	Chrysogonum virginianum L.	
CIRCSP	Cirsium sp.	
CIRSPUM	Cirsium pumilum (Nutt.) Spreng.	
CIRSSP	Cirsium sp.	
CIRSVUL	Cirsium vulgare (Savi) Ten.	Exotic
CLEMOCH	Clematis ochroleuca Aiton	
COLEANC	Coleataenia anceps (Michx.) Soreng	
CONYCAN	Conyza canadensis (L.) Cronquist	
CORAODO	Corallorhiza odontorhiza (Willd.) Poir.	
COREAUR	Coreopsis auriculata L.	
CORNFLO	Cornus florida L.	
CORYAME	Corylus americana Walter	
CRATSP	Crataegus sp.	
CRATUNI	Crataegus uniflora Münchh.	
CROTPUR	Crotalaria purshii DC.	
CROTSAG	Crotalaria sagittalis L.	

Table 3.6: (Continued).

DANTSPI	Danthonia spicata (L.) P. Beauv. ex Roem. & Schult.
DESMCIL	Desmodium ciliare (Muhl. ex Willd.) DC.
DESMGLA	Desmodium glabellum (Michx.) DC.
DESMLIN	Desmodium lineatum DC.
DESMMAR	Desmodium marilandicum (L.) DC.
DESMPAN	Desmodium paniculatum (L.) DC.
DESMROT	Desmodium rotundifolium (Michx.) DC.
DESPMSP	Desmodium sp.
DICHBOS	Dichanthelium boscii (Poir.) Gould & C.A. Clark
DICHCOM	Dichanthelium commutatum (Schult.) Gould
DICHDEP	Dichanthelium depauperatum (Muhl.) Gould
DICHDIC	Dichanthelium dichotomum (L.) Gould
DICHLAX	Dichanthelium laxiflorum (Lam.) Gould
DICHPOL	Dichanthelium polyanthes (Schult.) Mohlenbr.
DICHSCO	Dichanthelium scoparium (Lam.) Gould
DICHSP	Dichanthelium sp.
DIOSVIL	Dioscorea villosa L.
DIOSVIR	Diospyros virginiana L.
ECHILAE	Echinacea laevigata (C.L. Boynton & Beadle) S.F.
ELEPCAR	Elephantopus carolinianus Raeusch.
ELEPTOM	Elephantopus tomentosus L.
ELYMVIR	Elymus virginicus L.
ENDOSER	Endodeca serpentaria (L.) Raf.
ERAGSP	Eragrostis sp.
ERAGSPE	Eragrostis spectabilis (Pursh) Steud.
ERECHIE	Erechtites hieraciifolius (L.) Raf. ex DC.
ERYNYUC	Eryngium yuccifolium Michx.
EUONAME	Euonymus americanus L.
EUPACAP	Eupatorium capillifolium (Lam.) Small ex Porter & Britton
EUPAGOD	Eupatorium godfreyanum Cronquist
EUPAHYS	Eupatorium hyssopifolium L.
EUPAROT	Eupatorium rotundifolium L.
EUPASER	Eupatorium serotinum Michx.
EUPASP	Eupatorium sp.
EUPHCOR	Euphorbia corollata L.
EUPHPUB	Euphorbia pubentissima Michx.
FAGUGRA	Fagus grandifolia Ehrh.
FRAGVIR	Fragaria virginiana Mill.
FRAXAME	Fraxinus americana L.
GALAREG	Galactia regularis (L.) Britton, Sterns & Poggenb.

Table 3.6: (Continued).

GALICIR	Galium circaezans Michx.	
GALIPIL	Galium pilosum Aiton	
GALISP	Galium sp.	
GALIUNI	Galium uniflorum Michx.	
GELSSEM	Gelsemium sempervirens (L.) J. St.-Hil.	
GENTSP	Gentiana sp.	
GENTVIL	Gentiana villosa L.	
GEUMSP	Geum sp.	
GOODPUB	Goodyera pubescens (Willd.) R. Br.	
GYMNAMB	Gymnopogon ambiguus (Michx.) Britton, Sterns & Poggenb.	
HELIATR	Helianthus atrorubens L.	
HELIDEC	Helianthus decapetalus L.	
HELISP	Helianthus sp.	
HELISTR	Helianthus strumosus L.	
HIERGRO	Hieracium gronovii L.	
HIERSP	Hieracium sp.	
HOUSTEN	Houstonia tenuifolia Nutt.	
HYLONUD	Hylodesmum nudiflorum (L.) H. Ohashi & R.R. Mill	
HYPEHYP	Hypericum hypericoides (L.) Crantz	
HYPEMUT	Hypericum mutilum L.	
HYPEPUN	Hypericum punctatum Lam.	
HYPESP	Hypericum sp.	
HYPESTR	Hypericum stragulum W.P. Adams & N. Robson	
HYPEVIR	Hypericum virgatum Lam.	
HYPORAD	Hypochaeris radicata L.	Exotic
ILEXDEC	Ilex decidua Walter	
ILEXOPA	Ilex opaca Aiton	
ILEXVOM	Ilex vomitoria Aiton	
IPOESP	Ipoema sp.	
IPOMPAN	Ipomoea pandurata (L.) G. Mey.	
IRSISP	Iris sp.	
JUNIVIR	Juniperus virginiana L.	
KUMMSTR	Kummerowia striata (Thunb.) Schindl.	Exotic
LACTCAN	Lactuca canadensis L.	
LESPCUN	Lespedeza cuneata (Dum. Cours.) G. Don	Exotic
LESPPRO	Lespedeza procumbens Michx.	
LESPREP	Lespedeza repens (L.) W.P.C. Barton	
LESPVIR	Lespedeza virginica (L.) Britton	
LIATSQL	Liatris squarrulosa Michx.	
LIATSQU	Liatris squarrosa (L.) Willd.	

Table 3.6: (Continued).

LIGUSIN	Ligustrum sinense Lour.	Exotic
LINUMEDT	Linum medium (Planch.) Britton var. texanum (Planch.) Fernald	
LINUSTR	Linum striatum Walter	
LIPALIL	Liparis liliifolia (L.) Rich. ex Ker-Gawl.	
LIQUSTY	Liquidambar styraciflua L.	
LIRITUL	Liriodendron tulipifera L.	
LITHCAN	Lithospermum canescens (Michx.) Lehm.	
LOBEINF	Lobelia inflata L.	
LOBENUT	Lobelia nuttallii Schult.	
LOBESP	Lobelia sp.	
LOBESPI	Lobelia spicata Lam.	
LONIJAP	Lonicera japonica Thunb.	Exotic
LONISEM	Lonicera sempervirens L.	
LYSILAN	Lysimachia lanceolata Walter	
MARSLEG	Marshallia legrandii Weakley	
MATEDEC	Matelea decipiens (Alexander) Woodson	
MATESP	Matelea sp.	
MELIMUT	Melica mutica Walter	
MELISP	Melica sp.	
MENICAN	Menispermum canadense L.	
MICRVIM	Microstegium vimineum (Trin.) A. Camus	Exotic
MITCREP	Mitchella repens L.	
MORURUB	Morus rubra L.	
MORUSP	Morus sp.	
MUHLCAP	Muhlenbergia capillaris (Lam.) Trin.	
MUHLTEN	Muhlenbergia tenuiflora (Willd.) Britton, Sterns & Poggenb.	
MUSCROT	Muscadinia rotundifolia (Michx.) Small	
NYSSSYL	Nyssa sylvatica Marshall	
OBOLVIR	Obolaria virginica L.	
OENOFRU	Oenothera fruticosa L.	
OXALDIL	Oxalis dillenii Jacq.	
OXALSP	Oxalis sp.	
OXALSTR	Oxalis stricta L.	
PACKANO	Packera anonyma (Alph. Wood) W.A. Weber & Á. Löve	
PACKSP	Packera sp.	
PANIFLE	Panicum flexile (Gatt.) Scribn.	
PANISP	Panicum sp.	
PARTARI	Parthenium auriculatum Britton	
PARTQUI	Parthenocissus quinquefolia (L.) Planch.	
PASPFLO	Paspalum floridanum Michx.	

Table 3.6: (Continued).

PASPSP	Paspalum sp.	
PASSINC	Passiflora incarnata L.	
PASSLUT	Passiflora lutea L.	
PENSAUS	Penstemon australis Small	
PENSPAL	Penstemon pallidus Small	
PENSSP	Penstemon sp.	
PERSHYD	Persicaria hydropiperoides (Michx.) Small	
PHLOSP	Phlox sp.	
PHYSHET	Physalis heterophylla Nees	
PHYSVIR	Physostegia virginiana (L.) Benth.	
PHYTAME	Phytolacca americana L.	
PINUECH	Pinus echinata Mill.	
PINUSP	Pinus sp.	
PINUTAE	Pinus taeda L.	
PINUVIR	Pinus virginiana Mill.	
PLATOCC	Platanus occidentalis L.	
POLYBIF	Polygonatum biflorum (Walter) Elliott	
POLYSP	Polygala sp.	
POTECAN	Potentilla canadensis L.	
POTEIND	Potentilla indica (Andrews) Th. Wolf	Exotic
POTESIM	Potentilla simplex Michx.	
POTESP	Potentilla sp.	
PRUNSER	Prunus serotina Ehrh.	
PRUNSP	Prunus sp.	
PRUNVEL	Prunella vulgaris L.	
PSEUOBT	Pseudognaphalium obtusifolium (L.) Hilliard & B.L. Burtt	
PYCNSP	Pycnanthemum sp.	
PYCNTEN	Pycnanthemum tenuifolium Schrad.	
PYRRCAR	Pyrrhopappus carolinianus (Walter) DC.	
QUERALB	Quercus alba L.	
QUERBIC	Quercus bicolor Willd.	
QUERCOC	Quercus coccinea Münchh.	
QUERFAL	Quercus falcata Michx.	
QUERMAR	Quercus marilandica Münchh.	
QUERPHE	Quercus phellos L.	
QUERRUB	Quercus rubra L.	
QUERSP	Quercus sp.	
QUERSTE	Quercus stellata Wangenh.	
RHUSARO	Rhus aromatica Aiton	
RHUSCOP	Rhus copallinum L.	

Table 3.6: (Continued).

ROBIPSE	Robinia pseudoacacia L.	
ROSACAR	Rosa carolina L.	
ROSASP	Rosa sp.	
RUBUALL	Rubus allegheniensis Porter	
RUBUPEN	Rubus pensilvanicus Poir.	
RUBUSP	Rubus sp.	
RUBUTRI	Rubus trivialis Michx.	
RUDBFUL	Rudbeckia fulgida Aiton	
RUELCAR	Ruellia caroliniensis (J.F. Gmel.)	
RUMESP	Rumex sp.	
SABAANG	Sabatia angularis (L.) Pursh	
SACCALO	Saccharum alopecuroides (L.) Nutt.	
SACCBREC	Saccharum brevibarbe (Michx.) Pers. var. contortum (Elliott) R.D. Webster	
SALISP	Salix sp.	
SALVLYR	Salvia lyrata L.	
SANICAN	Sanicula canadensis L.	
SANISP	Sanicula sp.	
SCEPBIT	Sceptridium biternatum (Savigny) Lyon	
SCHISCO	Schizachyrium scoparium (Michx.) Nash	
SCLEOLI	Scleria oligantha Michx.	
SCLEPAU	Scleria pauciflora Muhl. ex Willd.	
SCLESP	Scleria sp.	
SCUTELL	Scutellaria elliptica Spreng.	
SCUTINT	Scutellaria integrifolia L.	
SCUTSP	Scutellaria sp.	
SILPAST	Silphium asteriscus L.	
SILPTER	Silphium terebinthinaceum Jacq.	
SISYMUC	Sisyrinchium mucronatum Michx.	
SMILBON	Smilax bona – nox L.	
SMILGLA	Smilax glauca Walter	
SMILROT	Smilax rotundifolia L.	
SOLACAR	Solanum carolinense L.	
SOLICAE	Solidago caesia L.	
SOLINEM	Solidago nemoralis Aiton	
SOLIPIN	Solidago pinetorum Small	
SOLIPTA	Solidago ptarmicoides (Torr. & A. Gray) B. Boivin	
SOLISP	Solidago sp.	
SONCOLE	Sonchus oleraceus L.	Exotic
SORGNUT	Sorghastrum nutans (L.) Nash	
STROUMB	Strophostyles umbellata (Muhl. ex Willd.) Britton	

Table 3.6: (Continued).

STYLBIF	Stylosanthes biflora (L.) Britton, Sterns & Poggenb.	
SYMPDEP	Symphyotrichum depauperatum (Fernald) G.L. Nesom	
SYMPDUM	Symphyotrichum dumosum (L.) G.L. Nesom	
SYMPLAT	Symphyotrichum lateriflorum (L.) Á. Löve & D. Löve	
SYMPPIL	Symphyotrichum pilosum (Willd.) G.L. Nesom	
SYMPSP	Symphyotrichum sp.	
TARAOFF	Taraxacum officinale F.H. Wigg.	Exotic
THASTRI	Thaspium trifoliatum (L.) A. Gray	
TIARCOR	Tiarella cordifolia L.	
TIPUDIS	Tipularia discolor (Pursh) Nutt.	
TOXIRAD	Toxicodendron radicans (L.) Kuntze	
TRAGURT	Tragia urticifolia Michx.	
TRICDIC	Trichostema dichotomum L.	
TRIDFLA	Tridens flavus (L.) Hitchc.	
ULMUALA	Ulmus alata Michx.	
ULMUAME	Ulmus americana L.	
UVULPER	Uvularia perfoliata L.	
UVULSES	Uvularia sessilifolia L.	
UVULSP	Uvularia sp.	
VACCPAL	Vaccinium pallidum Aiton	
VACCSTA	Vaccinium stamineum L.	
VERNGLA	Vernonia glauca (L.) Willd.	
VERNNOV	Vernonia noveboracensis (L.) Michx.	
VERNSP	Vernonia sp.	
VEROSP	Veronica sp.	
VIBUDEN	Viburnum dentatum L.	
VIBUPRU	Viburnum prunifolium L.	
VIBURAF	Viburnum rafinesquianum Schult.	
VIOLCUC	Viola cucullata Aiton	
VIOLSAG	Viola sagittata Aiton	
VIOLSOR	Viola sororia Willd.	
VIOLSP	Viola sp.	
VITICIN	Vitis cinerea (Engelm.) Engelm. ex Millardet	
VITISP	Vitis sp.	
ZIZIAUR	Zizia aurea (L.) Koch	

Figure 3.11: Photograph of PCG05 taken during the 2018 survey.

APPENDIX C

Table 4.4: Confusion matrix of USNVC Groups and clusters. Each cell indicates how many plots are assigned under each system.

		C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	*Tot*
G165	Piedmont-Central Atlantic Coastal Plain Oak Forest	53	1	1	5	0	0	0	5	1	12	7	0	*85*
G601	Chinquapin Oak - Shumard Oak - Blue Ash Alkaline Forest & Woodland	12	2	6	3	2	3	0	0	9	1	0	0	*38*
G670	Central & Southern Appalachian Rocky Outcrop	2	2	1	0	2	0	0	9	0	2	0	0	*18*
G162	Virginia Pine - Table Mountain Pine Woodland & Barrens	1	5	0	0	0	0	0	5	0	0	0	0	*11*
G180	Appalachian Mafic Glade	0	2	0	0	1	4	0	1	0	0	0	1	*9*
G012	Shortleaf Pine - Oak Forest & Woodland	0	0	0	0	0	0	2	6	0	0	0	0	*8*
G650	Northeastern Oak - Hickory Forest & Woodland	3	2	0	0	0	0	0	0	0	0	0	0	*5*
G671	Piedmont Dome & Flatrock Vegetation	0	0	0	0	3	0	0	0	0	0	0	2	*5*
G583	Southeastern Ruderal Grassland & Shrubland	0	0	1	0	0	0	0	0	0	3	0	0	*4*
G179	Central Interior Alkaline Open Glade & Barrens	0	0	0	0	1	0	0	0	0	0	0	2	*3*
G190	Wet-Mesic Longleaf Pine Open Woodland	0	0	0	0	0	0	3	0	0	0	0	0	*3*
G044	Central Interior-Appalachian Seepage Swamp	0	0	0	0	0	0	2	0	0	0	0	0	*2*
G045	Laurentian-Acadian-Appalachian Acidic Swamp	0	0	0	0	0	0	2	0	0	0	0	0	*2*
G842	Southeast Coastal Plain Cliff & Rock Vegetation	1	0	0	0	0	0	0	0	0	0	0	0	*1*
G753	Central Interior-Appalachian Riverscour Barrens & Prairie	0	0	0	0	0	0	0	0	0	0	1	0	*1*
	Totals	*72*	*14*	*9*	*8*	*9*	*7*	*9*	*26*	*10*	*18*	*8*	*5*	*195*