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RESEARCH PAPER

Floristics of Virginia's Northern and Central Piedmont grasslands

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Abstract

Aims: The grasslands of the North American Piedmont host diverse communities of sun-loving plants, but more than 90% of these grasslands have been lost across the region. Grasslands of the northern and central Piedmont of Virginia have received little formal study, but they are likely to be as diverse and threatened as they are in other parts of the eastern United States. To conserve the remaining Piedmont grasslands, we need to characterize floristic communities, identify the edaphic factors and disturbance regimes that drive their persistence, and develop methods to restore degraded grasslands. **Study Area:** Northern and Central Virginia Piedmont, USA. **Methods:** We surveyed plant communities and collected soil samples in 132 grasslands in old fields, powerline clearings, and roadsides. We used cluster analysis, indicator species analysis, and non-metric multidimensional scaling overlaid with soil and environmental variables to identify community groups. **Results:** We identified 695 plant taxa (87% of which are native) including 13 species that are rare in Virginia, two of which are globally critically imperiled (*Pycnanthemum clinopodioides* and *P. torreyi*). Six of our study sites contained 100 or more species with a maximum of 114 species in a single plot, making them among the most species-rich 100 m^2 plots recorded in the United States. Cluster analysis and ordination indicated four community groups, which we refer to as the Northern Prairies, Central Prairies, Savanna/Woodlands, and Wet Grasslands. **Conclusions:** The descriptions of these community groups can be used as reference information to inform grassland restoration in Virginia. Virginia's Piedmont grasslands are threatened by fire suppression, development, invasive species, and inappropriate management by utility companies. Swift action to conserve high quality grasslands and restore degraded ones is required to save these diverse plant communities.

Taxonomic reference: Weakley et al. (2012).

Abbreviations: NMDS = non-metric multidimensional scaling; PERMANOVA = permutational multivariate analysis of variance.

Keywords

biodiversity, cluster analysis, floristics, grassland, ordination, Piedmont grasslands, savanna, Southeastern grasslands, Virginia, woodland

Introduction

Temperate grasslands are the most threatened biome globally, with high rates of habitat loss and low levels of protection (Hoekstra et al. 2005). Worldwide, an estimated 45.8% of temperate grasslands have been lost to development or converted to agricultural land, and 49% of all grasslands have experienced degradation due to human activities and climate change (Hoekstra et al. 2005; Gang et al. 2014; Bardgett et al. 2021). The remaining temperate grasslands receive little conservation effort, in part due to the perception that they represent degraded forests and the assumption that grasslands can recover quickly after degradation (Veldman et al. 2015a, 2015b; Dudley et al. 2020; Buisson et al. 2022). This bias has led some scientists and organizations to misclassify extant grasslands as areas for potential reforestation, which would create forests at the expense of historic grasslands (Veldman et al. 2015b). To address this, conservation ecologists have called for increased recognition, restoration, and protection of grassland ecosystems during and beyond the United Nations Decade on Ecosystem Restoration (2020–2030) (Veldman et al. 2015b; Dudley et al. 2020; Török et al. 2021).

Grasslands host an array of plant and animal species, and their conservation and restoration can help address the 53% decline in North American grassland bird populations since the 1970s (Rosenberg et al. 2019). In addition to their conservation value, grasslands provide resources for livestock production and a range of ecosystem services, including water supply regulation, erosion control, and pollination (Bengtsson et al. 2019). In the face of global climate change, grasslands account for up to 34% of the global terrestrial carbon storage, the majority of which is in underground root and soil stores that are less susceptible to release by fire than the carbon stored above-ground in forest vegetation (White et al. 2000).

Among the temperate grasslands in need of increased recognition and study are the grasslands of the southeastern United States. These often-overlooked yet old ecosystems range from open tallgrass prairies to extensive savannas to open woodlands, glades, and barrens, all of which were historically common across the South (Barden 1997; Juras 1997; Noss 2013; Noss et al. 2015; Hanberry et al. 2020; Hanberry and Noss 2022; Krings et al. 2023; Szakacs et al. 2024). The savannas, open woodlands, and grasslands across the Piedmont uplands were maintained in part by relatively frequent, low-intensity fires originating from both dormant-season lightning strikes and early spring cultural burns conducted by Native American peoples to prepare land for hunting and agriculture (Spooner et al. 2021). Though we have lost most of these grasslands to modern-day agricultural expansion, land development, fire suppression, and forest encroachment, those that remain include some of the most endemic-species-rich habitats in eastern North America with higher native plant diversity than the tallgrass prairies of the American Great Plains (Noss 2013; Noss et al. 2015, 2021). In the remaining grasslands and rocky outcrops in the Virginia Piedmont, this species richness includes 52 globally and/or state-listed rare plant species, including microendemics such as *Phemeranthus piedmontanus* (Piedmont fameflower), *Marshallia legrandii* (tall Barbara's-buttons), and *Dichanthelium harvillii* (Harvill's panic grass), state-listed rare species such as *Buchnera americana* (American bluehearts) and *Solidago rigida* var. *rigida* (stiff goldenrod), and the federally endangered *Echinacea laevigata* (smooth coneflower) and *Rhus michauxii* (Michaux's sumac) (Townsend and Ludwig 2020; Fleming and Patterson 2021; Townsend 2023).

Despite their endemic species richness and previous widespread distribution, southeastern grasslands, including those of Virginia's Piedmont, have lost an estimated 90% of their former range (Noss et al. 2021). Those that remain face continued habitat loss and fragmentation, the disruption of natural disturbance regimes, invasive species pressure, and changes in temperature and precipitation due to climate change (Tompkins 2019; Noss et al. 2021). For example, the Piedmont grasslands of Virginia have been nearly extirpated and persist largely as semi-natural communities maintained by human disturbance, such as grazing or mowing, that keep woody canopies from shading out heliophytic grassland species (Townsend and Ludwig 2020; Fleming and Patterson 2021). The only remaining examples of significant size (>2000 ha) are within the frequently burned military base training areas of Fort Barfoot and Quantico Marine Base (Fleming et al. 2001; Fleming and Patterson 2021).

To conserve the remaining Piedmont grasslands and to provide a target reference state for grassland restoration efforts, we need to determine the distribution of these grasslands and characterize grassland floristic groups. The Virginia Department of Conservation and Recreation currently classifies the grasslands of the Piedmont as a subtype of the Piedmont Oak-Hickory Woodlands, Savannas, and Grasslands Group, and this subtype description is based on just six open grassland locations and eleven savanna/woodland sites (Fleming and Patterson 2021). Fifty-four other woodland, bald, glade, and savanna sites have been surveyed by the Virginia Department of Conservation and Recreation, and an additional open woodland protected area in Halifax County has been shown to contain many rare plant species (Townsend and Ludwig 2020; Fleming and Patterson 2021; Szakacs et al. 2024). Aside from these limited studies, native grasslands, open woodlands, and savannas in the Virginia Piedmont have not been surveyed and their species compositions, distribution, and conservation statuses unknown.

To address these knowledge gaps, we located and surveyed high-quality grassland fragments across the northern and central Virginia Piedmont. We predicted that some sites would host diverse plant communities that included rare species. We also predicted that native plant communities would differ across various substrates based on field observations that suggested that soil factors, notably pH and base cation content, may be drivers of grassland persistence, diversity, and variability. Based on these predictions, we aimed to define general vegetation community groupings that can guide future floristic, conservation, and restoration work.

Study area

Our study was conducted within a 17-county region within the Piedmont physiographic province in northern and central Virginia (Figure 1). The Piedmont is characterized by its gently rolling topography and is bound by the Blue Ridge Mountains to the west and the Fall Line to the east. It extends from Virginia's northern border with Maryland to its southern border with North Carolina. It is underlain by a complex assemblage of metamorphic and igneous rock, which have been deeply weathered by the humid climate.

Methods

Site selection

We identified a pool of potential grassland fragments across the northern and central Virginia Piedmont through a combination of systematic inspections of satellite imagery, structured driving surveys, and consultations with regional botanical experts. From the grassland fragments initially identified, 132 species-rich sites with a predominance of native, helophytic species were selected for vegetation surveys (Figure 1). We chose to survey the highest-quality grassland fragments we could find to define a reference state to inform future grassland conservation and restoration efforts.

Most of the remaining grasslands on the Virginia Piedmont occur in areas with soils that are unsuitable for agriculture and histories of human management or disturbance that enable heliophytic species to persist. Therefore, many of our sites were located in powerline corridors, old fields (e.g. former pastures mowed every 1–3 years, historical battlefields maintained as parks), and roadside rights-of-ways. We did not sample actively hayed or grazed sites, sites known to be planted with native wildflower seed, or sites containing non-native species indicative of commercially available meadow seed mixes such as *Echinacea purpurea* (purple coneflower) or *Coreopsis tinctoria* (plains coreopsis).

Vegetation surveys

We sampled the vegetation at each site between June and November with modified Whittaker plots using a method adapted for sampling small, fragmented grasslands (Miller et al. 2015). We established one to three 100-m^2 study plots at each site based on their size, with more study plots in larger fragments to capture local community variability. All survey plots were placed so that there were no adult trees within the plot and minimal tree canopy cover. We iden-

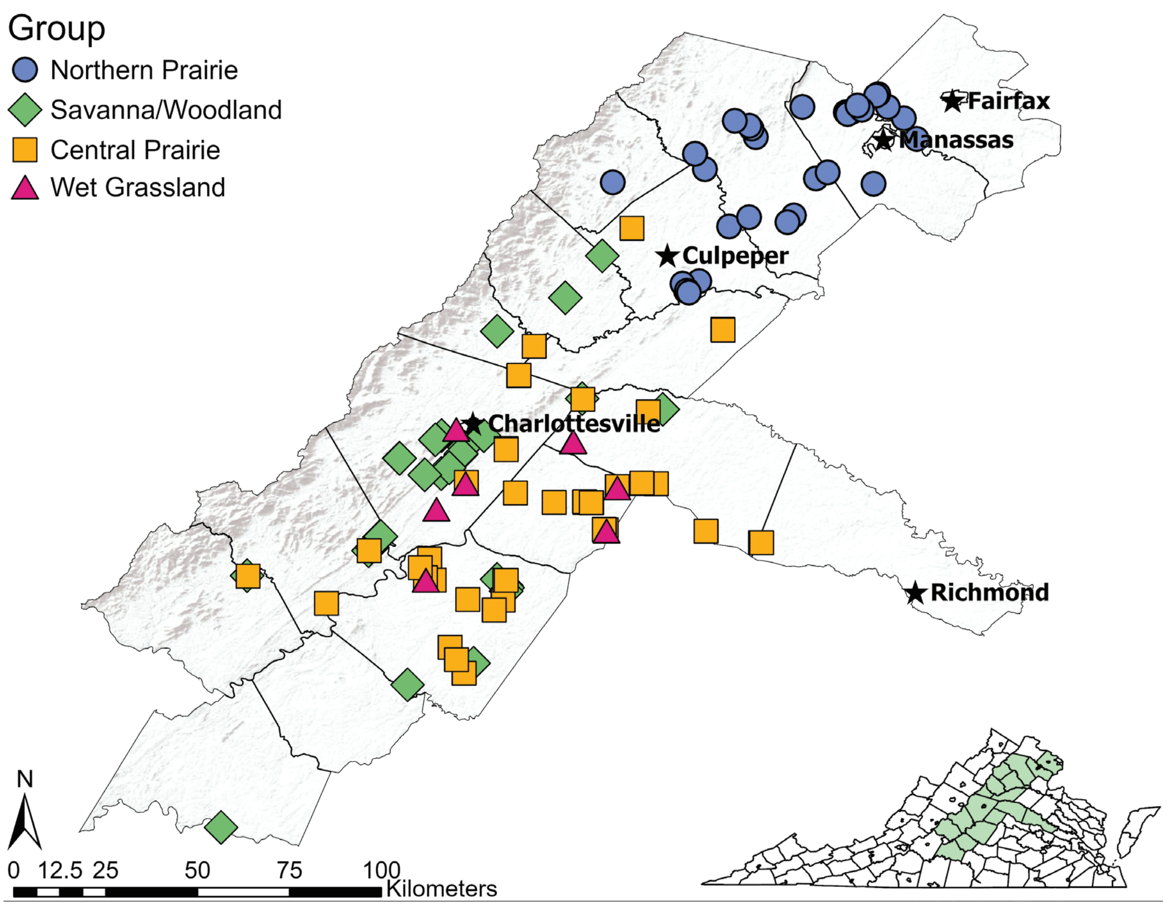

Figure 1. 129 of the 132 grassland sites surveyed in the northern and central Virginia Piedmont. Sites are colored according to their floristic community group as determined by this study. Three survey sites were excluded from analyses and are not included on the map.

tified all woody and herbaceous plants within each plot to the lowest taxonomic level possible using the dichotomous keys in the *Flora of Virginia* (Weakley et al. 2012). We collected voucher specimens of plants that could not be identified to the species level in the field for later identification.

For the first surveys conducted in the northern Piedmont in 2020, the survey plots were 2 × 50 m (100 m^2), and we estimated percent cover within five 1 m^2 quadrats evenly spaced every ten meters along the 50 m edge of the plot. Any species found within these plots but outside the quadrats were included in the plot species list. In subsequent surveys conducted in the Central Piedmont in 2021, the survey plots were modified to 4 × 25 m (100 m^2), and we estimated percent cover across the entire plot. To standardize the percent cover estimates from within quadrats in 2020 and across the entire plot in 2021, we calculated the average percent cover of each species across all five quadrats in the 2020 data. We converted percent cover into an ordinal cover class variable with ten possible values: 0 = absent, 1 < 0.1%, 2 = 0.1 to 1%, 3 = 1 to 2%, 4 = 2 to 5%, 5 = 5 to 10%, 6 = 10 to 25%, 7 = 25 to 50%, 8 = 50 to 75%, and 9 = 75 to 100%. This cover class scale follows methods used to determine formal floristic types in forests by the Virginia Department of Conservation and Recreation, though we adapted these methods to include a cover class of 0 in this study (Fleming 2007). Species found within the 100 m^2 plot but outside the quadrats in the 2020 surveys were assigned a cover class value of 1 in accordance with the treatment of incidental species recorded in surveys by the Virginia Department of Conservation and Recreation (Fleming 2007).

Soil sampling

To assess relationships between soil attributes and plant community composition, we aggregated at least five soil cores that were 15 cm deep and 5 cm in diameter. These cores were taken from locations distributed evenly throughout each study plot to create a single soil sample for each study site. We sent these soil samples to Brookside Laboratories, Inc. to analyze for pH, Mehlich III extractable micronutrients, total cation exchange capacity, percent organic matter, estimated nitrogen release, and bulk density (soil testing methods detailed in Suppl. material 1).

GIS data

We supplemented our field-collected data with soil unit characteristics and topographic information compiled from publicly available databases using the ArcGIS Pro Spatial Analyst package (Version 3.2.0, Esri Inc., Redlands, CA, US). We derived flood frequency and soil drainage class information from the dominant condition data for each soil unit underlying a site in the USDA Soil Survey Geographic Database (Soil Survey Staff 2022).

We obtained the elevation of each site in meters from the 30 m National Elevation Dataset (U.S. Geological Survey 2022). We calculated the slope of each site in degrees from the digital elevation model using the Spatial Analyst Slope tool. We calculated a simplified topographic position index for each site by subtracting the average elevation within a 10-cell circular radius of a site from the site's elevation (Weiss 2001). In the resulting index, positive values represent areas higher than their surroundings, like peaks, and negative values represent areas lower than their surroundings, like valleys.

Data preparation and transformation

We conducted all statistical analyses in R using RStudio (R Version 4.4.1 R Core Team 2024, RStudio Version 2024.09.0+375 Posit Team 2024). If a species could not consistently be identified to the subspecies or variety level in our surveys, all records of that species were reclassified to the species level. We created a matrix of the average cover class code for each species for each site. We used this species matrix to calculate the species richness, the inverse Simpson's Diversity Index, and the average cover classes of woody, graminoid, and forb taxa for each site. To reduce noise, we removed species that occurred at less than 1% of the 132 sites before conducting multivariate analyses (McCune et al. 2002). Removed species occurred in 75 of the 132 sites, only nine of which had more than five removed species, with a maximum of eight removed species at a single site. These removed species were included in the presented species lists and in the calculation of species richness and diversity values for all sites.

Three sites with an average Bray-Curtis dissimilarity from all other sites greater than 2.5 standard deviations from the mean were considered outliers and were removed prior to multivariate analysis to avoid distortions in the ordination (McCune et al. 2002). Plant species recorded at these outlying sites are included in Table 1 and Suppl. material 2, but these sites were not included in the cluster analysis, ordination, or indicator species analysis. Bray-Curtis dissimilarity was chosen to emulate the methods used to determine formal floristic types in forests by the Virginia Department of Conservation and Recreation (Fleming 2007). Bray-Curtis dissimilarity is widely used in vegetation studies due to the relatively equal weighting it gives to both dominant and rare species in analyses (Bray and Curtis 1957). The remaining 129 sites were used in the cluster analysis and non-metric multidimensional scaling (NMDS) ordination.

To prepare the ArcGIS data for analysis, we converted the categorical variable for soil drainage class to a numeric ordinal variable with higher values corresponding with increasingly poorer drainage. Flood frequency was similarly transformed, with higher values corresponding to more frequent flooding. These ordinal variables were converted to interval-scaled variables for analysis. The distributions of the continuous soil and geological variables were examined and transformed to linear distributions if necessary to correct for strong positive or negative skew. The variables estimated soil N release (#N/acre), soil bulk density (g/cm^3), and relative forb cover were squared. The variables slope, soil P content (mg/kg), soil K content (mg/kg), soil Mg content (mg/kg), soil Zn content (mg/kg), soil

Table 1. Species of conservation concern and the number of study sites at which they were recorded. A rank of S3 indicates that a species is uncommon in Virginia (20–50 sites state-wide), a rank of S2 indicates that a species is rare in Virginia (5–20 sites state-wide), while a rank of S1 indicates that a species is critically rare in Virginia (1–5 sites state-wide) (Townsend 2023).

Scientific Name	Common Name	State Rank	Global Rank	Number of Sites	Average Cover Class
Symphyotrichum ericoides var. *ericoides*	white heath aster	S3	G5T5	10	3.00
Pycnanthemum torreyi	Torrey's mountain-mint	S2	G2	6	3.00
Pycnanthemum clinopodioides	basil mountain-mint	S1	G1G2	3	4.33
Gymnopogon brevifolius	short-leaf beard grass	S3	G5	2	5.50
Agrostis scabra	rough bentgrass	S3?	G5	1	3.00
Asclepias purpurascens	purple milkweed	S3	G5?	1	1.00
Baptisia australis	blue wild indigo	S3	G5	1	3.00
Desmodium canadense	showy tick-trefoil	S1	G5	1	1.00
Dichanthelium annulum	ringed panicgrass	S3	G4	1	4.00
Dichanthelium ravenelii	Ravenel's rosette grass	S3	G5	1	2.00
Hexastylis lewisii	Lewis' Heartleaf	S3	G3	1	4.00
Solidago rigida var. *rigida*	stiff goldenrod	S2	G5T5	1	1.00
Tragia urticifolia	nettle-leaf noseburn	S3	G5	1	4.00

Mn content (mg/kg), and soil Ca content (mg/kg) were natural-log-adjusted. The variables relative woody cover and relative graminoid cover were square-root-adjusted. The variables elevation (m), soil pH, soil organic matter content (%), soil Al content (mg/kg), and total cation exchange capacity (meq/100g) were cube-root-adjusted. The variables soil Na content (mg/kg), soil Cu content (mg/kg), soil S content (ppm), soil Fe content (mg/kg), and soil B content (mg/kg) were arctangent adjusted.

Cluster analysis

To classify sites into plant community groups, we conducted a hierarchical, agglomerative cluster analysis using the R package cluster function agnes() using Bray-Curtis dissimilarity and a flexible linkage method using par.method = 0.625 (Maechler et al. 2023). This linkage method corresponds to a Lance-Williams flexible linkage formula with $\beta = -0.25$ by assigning $\alpha = 0.625$ and $\beta = 1 - (2 \times \alpha)$ to approximate Ward's linkage method, which is incompatible with Bray-Curtis dissimilarity (McCune et al. 2002). We pruned the resulting dendrogram at a height of 1.4 based on visual inspection to obtain smallest number of groups with the greatest between-group dissimilarity, resulting in four groups. We conducted permutational multivariate analysis of variance (PERMANOVA) of these groups using the R package vegan function adonis2() with a Bray-Curtis dissimilarity matrix and 9,999 permutations (Oksanen et al. 2024).

Indicator species analysis

Following cluster analysis, we conducted indicator species analysis to identify characteristic species within each grassland group. Analysis was run using the R package indicspecies function multipatt() with the IndVal.g test statistic based on the Indicator Value index of Dufrêne and Legendre (1997) and 999 permutations (De Cáceres and Legendre 2009). This analysis produces a list of species associated with each group ranked by an Indicator Value test statistic that is the product of a site specificity value, *A*, and a fidelity value, *B*. The specificity value measures the probability that a site containing the species is part of the group, with an *A* value of 1.0 indicating that a species is found only at sites within in the given group. The fidelity value measures the probability of finding a species across all sites in a group, with a *B* value of 1.0 indicating that a species is found at all sites within the group. Therefore, species with high Indicator Values are found in most of the sites within a given group but are uncommon in sites from other groups.

Ordination

To examine the separation of the grassland groups produced by the cluster analysis, we visualized the groups in multivariate space using non-metric multidimensional scaling (NMDS) ordinations of our species matrix. We created all NMDS ordinations with the R package vegan function metaMDS using Bray-Curtis dissimilarity and 100 random starts (Oksanen et al. 2024). To select an optimal solution that balances the need for a low stress value with the ability to visually interpret ordination results, we ran NMDS using 1 through 6 axes and built a scree plot of the number of axes run versus their stress values to determine the smallest number of axes needed to obtain a stress value less than 0.2 (Suppl. material 3: figure S3.1, McCune et al. 2002).

To assess which soil and environmental gradients correlated with the results of the NMDS ordination, we projected soil and environmental variable gradients onto our selected ordination using the R package vegan function envfit() with 100 permutations (Oksanen et al. 2024). We projected 23 variables: species richness, relative woody cover, relative graminoid cover, relative forb cover, elevation (m), slope (degrees), topographic position index, flood frequency class, drainage class, pH, soil organic matter content (%), estimated soil N release (#N/acre), soil P content (mg/kg), soil K content (mg/kg), soil Na content (mg/kg), soil Al content (mg/kg), soil Fe content (mg/kg), soil Mn content (mg/kg), soil Zn content (mg/kg), soil Cu content (mg/kg), soil B content (mg/kg), soil cation exchange capacity (meq/100g), and soil bulk density (g/cm^3). Species diversity, soil Ca content and soil Mg content, and soil S content had co-linearity values > 0.65 with species richness, soil cation exchange capacity, and soil Al content, respectively, so they were omitted from analysis. We removed 19 sites with missing data for at least one soil or environmental variable from all environmental variable analyses.

Results

Floristics

We identified 695 species, subspecies, and varieties of plants across all study sites (Suppl. material 2). Of these, 604 (86.9%) were native, 66 (9.5%) were introduced, 20 (2.9%) were invasive, and 5 (0.7%) were of uncertain status in Virginia (Weakley et al. 2012; Suppl. material 2). Only 23 taxa were found at 50% or more study sites while 518 taxa were found at 10% or fewer study sites, indicating that the communities varied greatly across our study region. The three most frequently recorded native taxa were *Rubus flagellaris* (northern dewberry), *Schizachyrium scoparium* var. *scoparium* (little bluestem), and *Dichanthelium acuminatum* (tapered rosette grass), all of which were found at 70% or more of our study sites. The most common non-native taxa, *Lonicera japonica* (Japanese honeysuckle) and *Kummerowia striata* (Japanese clover), were the only non-native taxa found at more than 50% of our study sites. Our surveys identified 13 state or globally rare species, including the globally critically imperiled mountain-mints *Pycnanthemum torreyi* (Torrey's mountain-mint) and *Pycnanthemum clinopodioides* (basil mountain-mint) (Table 1, NatureServe 2024; Townsend 2023). In addition, *Buchnera americana* (American bluehearts), which is rare to critically rare in Virginia, was found outside of the bounds of the 100 m^2 study plots at a site in the northern Piedmont and is therefore not reflected in our study results.

Compositional groups

Cluster analysis indicated four broad grassland community groups (PERMANOVA $P < 0.001$, $R^2 = 0.19$, Figure 2, Suppl. material 4). Based on our interpretation of the floristic composition, indicator species, and best-fitting environmental variables of these groups as detailed in the "Four Piedmont Grassland Groups" section below, we refer to these four groups as the Northern Prairies, Central Prairies, Savanna/Woodlands, and Wet Grasslands in all figures and tables. The number of sites in each group and the average species richness and relative cover classes of graminoids, forbs, and woody plants are listed in Table 2. An example site from each group is illustrated in Figure 2. Full species lists for each group can be found in Suppl. material 5.

Indicator species

The top five indicator species with the highest indicator values for each group are listed in Table 3. A full list of the statistically significant indicator species identified for each group and species associated with combinations of two and three groups can be found in Suppl. material 6.

Ordination and environmental variables

The selected NMDS solution was built on three axes (stress = 0.16, non-metric fit $R^2 = 0.98$, linear fit $R^2 = 0.87$; Figure 3 and Suppl. material 3: figure S3.2). The environmental and soil variables fit to this ordination, their average values for each grassland group, and their fit to the ordination are listed in Table 4. The fit of the soil and environmental variables with R^2 values greater than 0.25 and P values less than 0.05 to the NMDS ordination are illustrated in Figure 3; with the exceptions of slope (degrees) and soil P content (mg/kg) which nearly overlapped in the angle visualized in the figure with relative woody cover and soil organic matter content (%), respectively, to improve figure legibility. Plots that include all environmental and soil variables with P values less than 0.05,

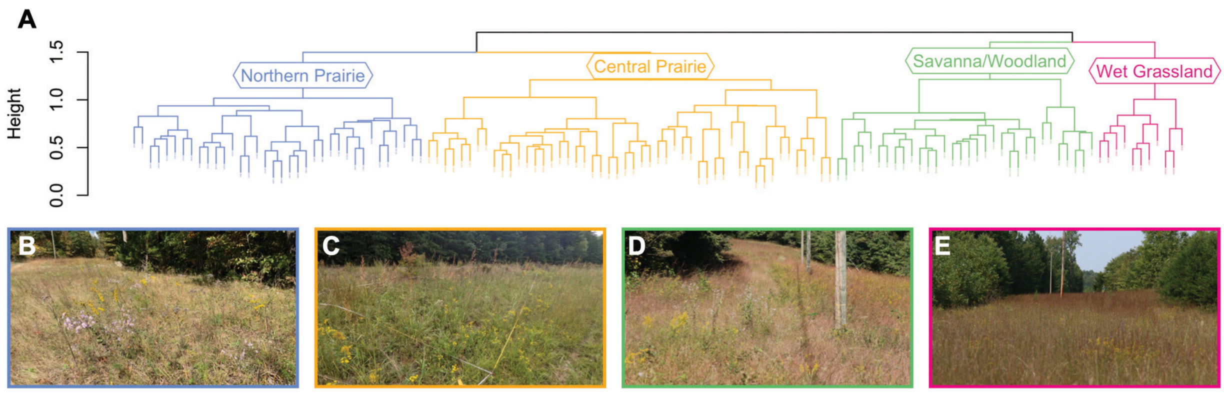

Figure 2. (A) Dendrogram of the four major grassland groups produced by the hierarchical agglomerative cluster analysis of 129 sites. The four major groups were supported by PERMANOVA (P < 0.001, R^2 = 0.19). (B) Northern Prairie site in Prince William County, VA photographed by JBCH. (C) Central Prairie site in Albemarle County, VA photographed by DF. (D) Savanna/Woodland site in Madison County, VA photographed by DC. (E) Wet Grassland site in Buckingham County, VA photographed by DC.

Table 2. Number of sites and average species richness and relative cover classes for each grassland group.

Group	Number of Sites	Average Species Richness ± Standard Error	Average Relative Graminoid Cover	Average Relative Forb Cover	Average Relative Woody Plant Cover
Northern Prairie	36	61.22 ± 2.18	0.31 ± 0.01	0.50 ± 0.01	0.19 ± 0.01
Central Prairie	50	67.49 ± 2.07	0.30 ± 0.01	0.53 ± 0.01	0.17 ± 0.01
Savanna/Woodland	32	74.25 ± 3.56	0.22 ± 0.01	0.47 ± 0.02	0.30 ± 0.02
Wet Grassland	11	67.55 ± 4.65	0.36 ± 0.02	0.46 ± 0.02	0.18 ± 0.03

Table 3. Top five indicator species for each grassland group.

Group	Scientific Name	Common Name	Specificity	Fidelity	Indicator Value	P Value
Northern Prairie	*Sorghastrum nutans*	Indiangrass	0.60	0.78	0.68	0.001
	Carex bushii	Bush's sedge	0.87	0.50	0.66	0.001
	Poa cuspidata	early bluegrass	0.85	0.44	0.62	0.001
	Chamaecrista fasciculata	partridge pea	0.74	0.39	0.54	0.002
	Strophostyles umbellata	pink fuzzybean	0.79	0.36	0.53	0.005
Central Prairie	*Carex glaucodea*	blue sedge	0.83	0.48	0.63	0.001
	Andropogon gyrans	Elliott's bluestem	0.68	0.52	0.59	0.002
	Andropogon ternarius	splitbeard bluestem	0.76	0.28	0.46	0.015
	Solidago pinetorum	Small's goldenrod	0.90	0.22	0.45	0.013
	Aristida dichotoma	churchmouse threeawn	0.89	0.20	0.42	0.016
Savanna/ Woodland	*Dichanthelium boscii*	Bosc's panicgrass	0.89	0.66	0.77	0.001
	Carya glabra	pignut hickory	0.80	0.66	0.73	0.001
	Prunus serotina var. *serotina*	black cherry	0.67	0.63	0.65	0.001
	Clitoria mariana var. *mariana*	butterfly pea	0.89	0.41	0.60	0.001
	Quercus velutina	black oak	0.66	0.53	0.59	0.004
Wet Grassland	*Eupatorium perfoliatum*	common boneset	0.93	1.00	0.96	0.001
	Dichanthelium microcarpon	branched panicgrass	0.83	0.91	0.87	0.001
	Juncus effusus	common rush	0.89	0.82	0.86	0.001
	Carex lurida	shallow sedge	1.00	0.73	0.85	0.001
	Persicaria sagittata	arrowleaf tearthumb	1.00	0.73	0.85	0.001

the locations of group centroids, and the positions of each species in ordination space can be found in Suppl. material 3: figure S3.2. The ordination indicates that the Central Prairie group has an intermediate species composition among the other three groups. The Northern Prairies diverge in a direction correlated with increased soil Mn content (mg/kg), the Savanna/Woodlands diverge in a direction correlated with increased soil organic matter content (%), higher elevation (m), and higher relative woody plant cover, and the Wet Grasslands diverge in a direction correlated with increased soil Fe content (mg/kg) and higher relative graminoid cover.

Four Piedmont grassland groups

The Northern Prairie group was named for its restriction to the northern Virginia Piedmont. In comparison to the other subgroups, Northern Prairie sites have somewhat more basic soils with notably higher Mn contents. The northern character of this group is reinforced by the presence of *Carex bushii* (Bush's sedge), a sedge that is most frequently found in Northern Virginia, as its second-strongest indicator species.

Likewise, the Central Prairie group was named for its restriction to the central Virginia Piedmont. Though there are indications that this subgroup could extend to the southern Virginia Piedmont as well, this will need to be confirmed by future studies. In contrast to the Northern Prairie group, the strongest indicator species for the Central Prairie group include species such as *Solidago pinetorum* (Small's goldenrod) and *Andropogon ternarius* (splitbeard bluestem) that are common in the central and southern Piedmont but infrequent in the northern Piedmont. Furthermore, the Central Piedmont sites were correlated with intermediate values for many soil and environmental variable gradients in our analyses in comparison to sites from the other three groups.

The Savanna/Woodland group, the group with the highest average species richness of over 74 species per 100 m^2 study plot, was named for the prevalence of woodland and woody species in its indicator species list and the high average relative woody cover classes among its study sites. Though our study plots did not contain adult trees due to the routine mowing of the roadside rights-of-way, powerline corridors, and old fields that comprised the majority of our sites, the herbaceous and shrubby vegetation in these plots contain many species with affinities for woodland habitats despite the lack of woodland structure. Three of the top five indicator species for this group, *Carya glabra* (pignut hickory), *Prunus serotina* var. *serotina* (black cherry), and *Quercus velutina* (black oak) are trees, while another top indicator species, *Dichanthelium boscii* (Bosc's panicgrass), is often found in woodlands and forests. In addition to higher average relative woody cover classes, Woodland/Savanna study sites were correlated with higher elevations, steeper slopes, and had the highest average topographic position index value of 4.69 ± 1.20 among the four groups, indicating that the Woodland/Savanna group grasslands are associated with slopes and uplands.

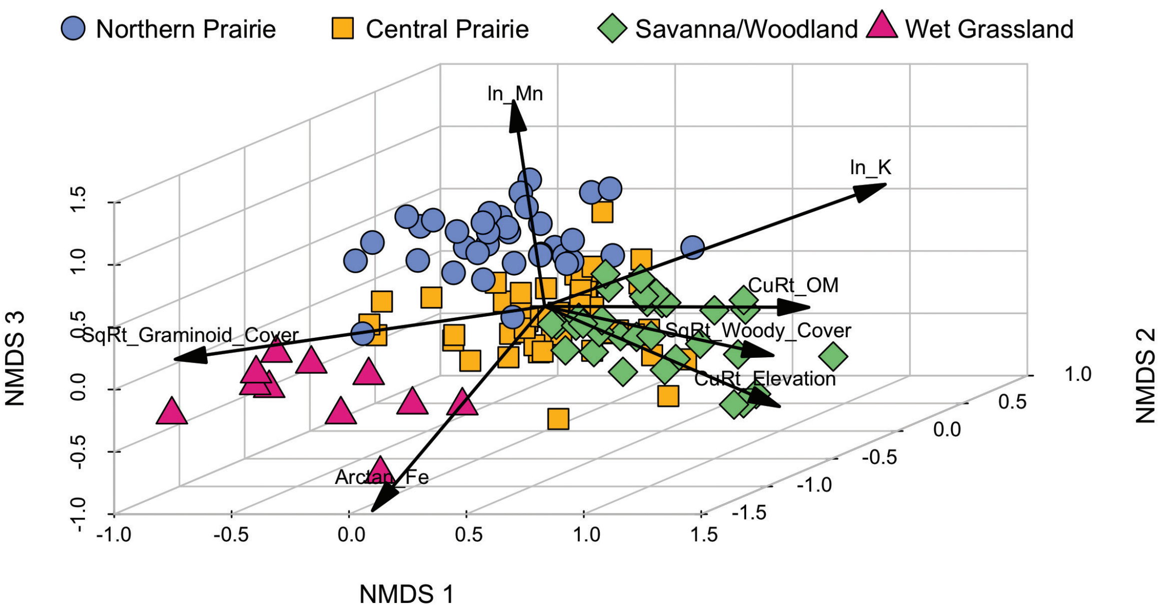

Figure 3. Scatterplot of the NMDS ordination in three dimensions (stress = 0.16, non-metric fit R^2 = 0.98, linear fit R^2 = 0.87). Point shapes and colors indicate the four groups: Northern Prairie, Central Prairie, Savanna/Woodland, and Wet Grassland. Overlaid arrows depict the environmental variables with R^2 values greater than 0.25 and P values less than 0.05, with the exceptions of slope (degrees) and soil P content (mg/kg), which nearly overlapped with relative woody cover and soil organic matter content (%), respectively, were removed for legibility (Table 4).

Table 4. Average values ± standard error and fit of each soil and environmental variable to the NMDS ordination. Group averages were calculated using untransformed data, while variable fitting to the NMDS was performed using transformed data.

Variable	Northern Prairie	Central Prairie	Savanna/Woodland	Wet Grassland	R^2	P Value
Organic Matter Content (%)	4.47 ± 0.27	4.4 ± 0.17	7.57 ± 0.55	5.03 ± 0.96	0.48	0.01
Relative Woody Cover	0.19 ± 0.01	0.17 ± 0.01	0.3 ± 0.02	0.18 ± 0.03	0.46	0.01
Elevation (m)	116.08 ± 9.55	136.98 ± 4.29	176.71 ± 9.21	138.35 ± 7.26	0.44	0.01
Relative Graminoid Cover	0.31 ± 0.01	0.30 ± 0.01	0.22 ± 0.01	0.36 ± 0.02	0.42	0.01
Fe (mg/kg)	139.43 ± 7.96	186.02 ± 10.87	176.91 ± 9.22	367.73 ± 35.67	0.37	0.01
K (mg/kg)	61.43 ± 7.27	69.65 ± 6.51	78.88 ± 6.73	42.45 ± 10.68	0.33	0.01
P (mg/kg)	9.14 ± 2.14	8.04 ± 0.66	14.61 ± 3.17	8.36 ± 1.70	0.32	0.01
Slope (degrees)	2.37 ± 0.38	2.32 ± 0.19	6.49 ± 0.84	3.21 ± 0.59	0.31	0.01
Mn (mg/kg)	129 ± 21.45	65.45 ± 8.72	81.66 ± 12.37	39.73 ± 8.05	0.27	0.01
Bulk Density (g/cm^3)	1.05 ± 0.02	1.00 ± 0.01	0.90 ± 0.02	0.85 ± 0.05	0.24	0.01
Topographic Position Index	1.11 ± 0.53	1.70 ± 0.63	4.69 ± 1.20	-3.26 ± 0.87	0.23	0.01
Al (mg/kg)	709.00 ± 31.10	784.43 ± 29.68	854.22 ± 53.34	605.64 ± 71.01	0.22	0.01
Relative Forb Cover	0.50 ± 0.01	0.53 ± 0.01	0.47 ± 0.02	0.46 ± 0.02	0.21	0.01
Drainage Class	4.47 ± 0.22	3.22 ± 0.09	3.03 ± 0.12	3.30 ± 0.50	0.20	0.01
B (mg/kg)	0.27 ± 0.02	0.35 ± 0.03	0.37 ± 0.03	0.52 ± 0.04	0.19	0.01
Cu (mg/kg)	1.82 ± 0.19	1.33 ± 0.17	1.47 ± 0.20	2.97 ± 1.43	0.19	0.01
pH	5.65 ± 0.11	5.22 ± 0.06	5.26 ± 0.12	5.17 ± 0.10	0.18	0.01
Na (mg/kg)	24.29 ± 3.70	13.37 ± 0.66	13.34 ± 0.9	55.91 ± 36.02	0.13	0.01
Cation Exchange Capacity (meq/100g)	10.73 ± 1.51	7.54 ± 0.56	9.26 ± 0.57	5.94 ± 1.33	0.11	0.02
Flood Frequency Class	1.31 ± 0.15	1.06 ± 0.03	1.09 ± 0.09	1.20 ± 0.20	0.08	0.02
Zn (mg/kg)	4.14 ± 2.27	6.51 ± 1.18	4.30 ± 0.56	16.08 ± 11.06	0.03	0.31
Species Richness	61.22 ± 2.18	67.49 ± 2.07	74.25 ± 3.56	67.55 ± 4.65	0.03	0.42
Estimated N Release (#N/acre)	92.71 ± 2.58	88.22 ± 3.17	91.06 ± 7.22	92.73 ± 4.87	0.02	0.45

Finally, the Wet Grassland group was named for both the prevalence of wet-soil tolerant species in its indicator species list and for the correlation of its sites with characteristics indicative of wet habitats along the soil and environmental variable gradients. All five of its top indicator species are frequently found in or restricted to wet habitats such as floodplains, swamps, wet meadows, and other low habitats. The Wet Grassland group has the only negative average topographic position index of -3.26 ± 0.87, indicating that its sites are found in low-lying areas such as seeps and depressions. Wet Grassland sites also had notably higher soil Fe and Zn content than sites from the other three subgroups.

Discussion

Our study provides an initial synopsis of the floristic composition and variability of Virginia's most diverse and least studied ecological community. In our surveys of grassland fragments across the northern and central Virginia Piedmont, we have documented 604 native taxa in 132 survey sites. Many of these sites have notably high species richness: six of our study sites have 100 species or more within a single 100 m^2 plot, with a maximum of 114 species. We have distinguished four major community groups among our study sites, which we refer to as the Northern Prairies, the Central Prairies, the Savanna/Woodlands, and the Wet Grasslands. Each group has distinctive species composition and edaphic characteristics that should be considered in future conservation and restoration efforts in these threatened habitats.

Piedmont grasslands harbor high species richness

We documented 695 taxa across our study sites, which represent over 21% of the 3,164 species documented in the *Flora of Virginia* (Weakley et al. 2012). This high species richness was present despite the small size and fragmentary nature of our study sites. The severity of human impact on Virginia's grasslands and the lack of documented disturbance history makes it difficult to distinguish the origins or antiquity of many of our grassland sites. However, our observations of repeated patterns in plant community composition across this highly fragmented landscape suggest that some of our study sites were connected in grassland-savanna mosaics in the past. Semi-natural, managed, temperate grasslands in the Czech Republic hold the world record for the highest species richness values at small spatial grains, demonstrating that even small fragments of semi-natural grassland can have high biodiversity value (Wilson et al. 2012). Therefore, it is important to document the floristic variety represented by fragmented grassland communities and recognize their importance for conservation.

Six of our study sites had survey plots containing over 100 species, making these plots some of the most species-rich 100 m^2 plots recorded in the state of Virginia. Furthermore, our six plots may be among the most species-rich 100 m^2 plots recorded across the entire United States: of the 4,773 100 m^2 plots from the United States with publicly available data on VegBank at the time of writing, only six plots contained over 100 species, with a maximum of 129 species (Peet et al. 2013). We found a maximum value of 114 species in a Savanna/Woodland plot in Albemarle County, which had 103 native species. In addition to high native species richness, we have documented populations of 13 state-imperiled species across our study sites, including three potentially new Virginia populations of the globally rare *Pycnanthemum clinopodioides*, which was previously known from fewer than 30 extant populations worldwide (NatureServe 2024).

With their high species richness and the presence of threatened endemic species, our study sites are pockets of biodiversity threatened by a changing climate and landscape (Noss et al. 2021). The value of such fragments to biodiversity conservation are being recognized across the Southeast, and scientific study and conservation efforts in these fragments are increasing. For example, the Southeastern Grasslands Institute, a collaborative biodiversity conservation organization led by Austin Peay State University, has initiated surveys of grassland fragments in roadsides in partnership with the Tennessee Department of Conservation and surveys of powerline rights-of-ways in collaboration with Tennessee Valley Authority, the Electric Power Research Institute, and the Mississippi Entomological Museum (Southeastern Grasslands Institute and Austin Peay State University 2024a). The Piedmont Prairie Partnership, a group of non-profit, state, and federal agencies within the Southeastern Grasslands Institute, is building an interactive map of publicly accessible Piedmont grassland fragments across the Southeast to encourage public awareness and appreciation of native grasslands (Southeastern Grasslands Institute and Austin Peay State University 2024b). Our work in the northern and central Virginia Piedmont is complementary to these research efforts, expanding the area of study into the northern range of the historic Southeastern grassland region.

Grassland groups to inform conservation and restoration

The current community type description for the Piedmont Oak-Hickory Woodlands, Savannas, and Grasslands defined by the Virginia Department of Conservation and Recreation describes the herb layer of these habitats as "highly variable in both density and composition" and notes the presence of *Schizachyrium scoparium* var. *scoparium* (little bluestem), *Sorghastrum* spp. (indiangrasses), *Andropogon* spp. (broomsedges), *Danthonia spicata* (poverty oatgrass), *Desmodium* spp. (tick-trefoils), *Lespedeza* spp. (bush-clovers), *Eupatorium* spp. (thuroughworts), and *Solidago* spp. (goldenrods), particularly *Solidago nemoralis* var. *nemoralis* (gray goldenrod) and *S. juncea* (early goldenrod) (Fleming and Patterson 2021). Our results corroborate this description, listing *Schizachyrium scoparium* var. *scoparium* (little bluestem), *Solidago nemoralis* var. *nemoralis* (gray goldenrod), *S. juncea* (early goldenrod), and *Danthonia spicata* (poverty oatgrass) among the top 10 most common species found across our study sites, and our species list includes four *Andropogon* species, 12 *Desmodium* species, 10 *Lespedeza* species, 16 *Solidago* species, and 13 *Eupatorium* species (Suppl. material 2). However, some species highlighted in the formal description, such as *Erianthus alopecuroides* (silver plumegrass) and *Agalinis purpurea* (purple false foxglove), were found at ten or fewer of our sites, indicating that there is variety in Virginia's grasslands that is not represented by the current community type description.

Our evidence suggests that there are at least four broad grassland community groups in the northern and central

Virginia Piedmont. This expands the current description of Piedmont grasslands as a subtype of the Piedmont Oak-Hickory Woodlands, Savannas, and Grasslands Group defined by the Virginia Department of Conservation and Recreation, whose ability to survey the powerline, roadside, and battlefield sites that comprise the majority of our study has been limited by their designation as Semi-natural/Modified landscapes under the U.S. National Vegetation Classification (Fleming and Patterson 2021). The need to expand the current community type description to include more community groups is supported by the recent characterization of 12 new heliophytic Piedmont community types in southern Virginia and the Carolinas (Szakacs et al. 2024). Once formal vegetation surveys have been conducted across the entire Virginia Piedmont, our general grassland community groups can be further refined into formal community type descriptions based on underlying geology, soil chemistry, and moisture regimes using methods like those used by the Virginia Department of Conservation and Recreation to determine forest community types (Fleming 2007; Fleming and Patterson 2021).

By defining the floristic and environmental variation, our study can provide more accurate guidelines and define more detailed community composition and species richness goals to guide conservationists and restoration practitioners who manage native grasslands across Virginia. In the time since we have conducted our surveys, we have witnessed the degradation of several of our study sites. A population of the state-rare *Solidago rigida* var. *rigida* (stiff goldenrod) was sprayed with herbicide in a powerline clearing in Prince William County, and a population of the globally imperiled *Pycnanthemum torreyi* (Torrey's mountain-mint) was eliminated by the construction of a sidewalk in Albemarle County. These incidents exemplify the threats of habitat loss and degradation faced by grasslands across the Southeast. With habitat loss and destruction rates of 90–100% across their historic range, improving the management of known high quality Southeastern grasslands is an urgent priority (Noss et al. 1995, 2021; Noss 2013). Our experiences in our study sites indicate that limiting herbicide use by utility companies, treating non-native plant invasions, and preventing the conversion of grasslands to other land uses can prevent future losses at a fragment-level scale. Such small-scale efforts led by public land stewards and private landowners, in combination with the efforts of larger conservation organizations across greater Southeastern region such as Southeastern Grasslands Institute to raise public awareness and scientific study of these ecosystems, will be critical to the survival of Southeastern grassland biodiversity.

Conclusion

The native grasslands of the Southeastern United States are among the most diverse and threatened habitats in the country, yet they are understudied and largely unprotected. We need to increase recognition of their ecological value to encourage their conservation and restoration. Through our surveys of species-rich grassland fragments in the northern and central Virginia Piedmont, we have found evidence of at least four grassland community groups in need of further description and documentation. By defining these groups, we can promote the conservation of their endemic biodiversity and create more nuanced reference models for the ecological restoration of degraded Piedmont grassland landscapes.

Data availability

The data and code used in the preparation of this manuscript (with site locations expunged for the protection of rare species) are openly available in the Virginia Tech Data Repository (http://data.lib.vt.edu/) at DOI https://doi.org/10.7294/25267117.

Author contributions

J.B.C.H., D.F., J.L.R., and J.T.C. designed the study; all authors collected field data. J.T.C. compiled supplementary GIS data, conducted analyses, and wrote the first draft of the manuscript. All authors edited the manuscript.

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Supplementary material

Supplementary material 1
Soil analysis methods. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl1

Supplementary material 2
Species list for all study sites. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl2

Supplementary material 3
Scree, stress, and scatter plots for the selected NMDS solution. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl3

Supplementary material 4
Full PERMANOVA results. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl4

Supplementary material 5
Species lists for each of the four grassland types. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl5

Supplementary material 6
Full indicator species analysis results. (*.pdf)
Link: https://doi.org/10.3897/VCS.126066.suppl6