Remnants of the "Grande Savane?"
Insights from Soil Organic Matter at Two Sites
in the Deep River Triassic Basin of North Carolina

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ABSTRACT

Narrative accounts and floristics suggest a broader historical distribution of Piedmont upland savannas and woodlands with a prairie-affinity flora than today, although dates of emergence, spatiotemporal extent, and historical dynamics remain unclear. To help address the question whether remnant prairie-affinity patches in the state represent at least historical, if not ancient, grasslands, we analyzed stable carbon isotopes from soil organic matter from two well-known localities hosting prairie-affinity heliophytes, both within the boundaries of historically mapped "Grande Savane". Soil cores for $\delta^{13}C_{org}$ analysis and radiocarbon dating were collected from five sites, hosting different present-day plant communities and spanning three soil orders. Recovered $\delta^{13}C_{org}$ values suggest historical grasslands, likely savanna-type with some fluctuations in cover, were present at both localities essentially continuously over the past 2000 years until the more recent canopy closure over the past century. These findings are consistent with historical narrative accounts, although significant additional sampling is needed to determine its spatiotemporal extent. While the general trend at our localities transitions from open to closed systems, pronounced fluctuations are apparent in all profiles, particularly between 1254–1468 CE. Precipitation does not appear predominantly responsible, but available climatic reconstructions are from an adjacent basin. The timing of the pronounced vegetation class fluctuations is intriguingly coincidental to the timing of Siouan occupancy and intertribal movements, suggesting a need for more vigorous interdisciplinary investigations.

Key words: C_3/C_4, grasslands, heliophytes, "Piedmont prairie," soil organic matter (SOM)

INTRODUCTION

It is well established that the vegetation of the southeastern United States has dramatically changed since the last glacial maximum (LGM; e.g., Delcourt and Delcourt 1987). Supporting evidence comes primarily from pollen cores; however, as there are no natural lakes in the Piedmont, vegetation reconstruction for this physiographic province in particular has relied on extrapolation from mountain and Coastal Plain sites (Figure 1; Delcourt and Delcourt 1987). These generally demonstrate that since the LGM and except for a brief period during the Younger Dryas (~12,900–11,700 yrs BP), pine woodlands dominated the adjoining southeastern Coastal Plain, transitioning from jackpine to southern pines (e.g., *P. elliottii*, *P. palustris*, etc.) by at least 4,500 yrs BP (Watts 1980a). Even at 22,000 yrs BP, the non-tree pollen component is known to have been dominated by forbs of prairie and Sandhill affinity at Coastal Plain sites ranging from North Carolina to Florida, and west to Alabama and Tennessee (Watts 1980a). Suggested controls on vegetation distributions in the region are many (e.g., climate, fire, grazers, humans), and may be locally or temporally distinct. For example, fire is thought to have been an important component of vegetation dynamics throughout
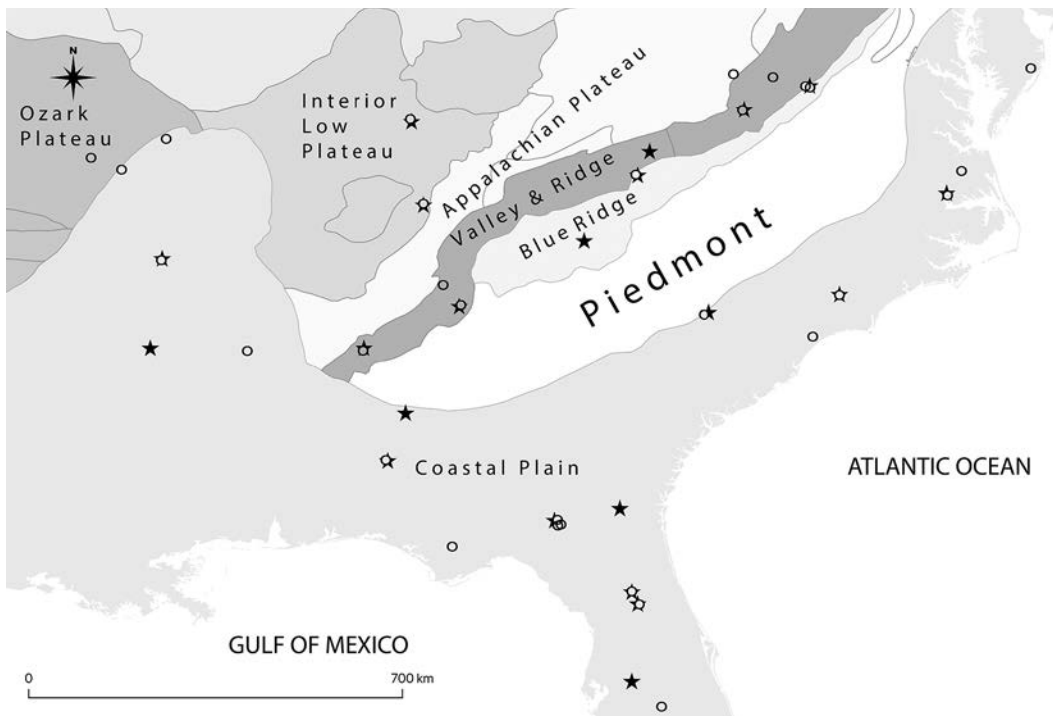
Figure 1. Paleoecological sites used in the reconstruction of late-Quaternary vegetation in the southeastern United States (Delcourt and and Delcourt 1987 [stars], and Prentice et al. 2001 and Harrison 2017 [circles]). Physiographic divisions follow Fenneman and Johnson (1946). Note the absence of paleoecological sites in the Piedmont in these reconstructions. Map created in QGIS (2019).

the Holocene (Delcourt and Delcourt 1997; Frost 2000; Fowler and Konopik 2007; Krause et al. 2018). Grazing was also likely an important contributing component, considering the presence of several species of mammoth, mastodon, and bison, until the catastrophic mega-herbivore extinctions around 11,000 yrs BP (Haynes 2002a) and the suspected much more recent arrival of *Bison bison* (Allen 1876; Rostlund 1960; Harington 1984; Belue 1996; but see Moore et al. 2016). The period of mass mega-herbivore extinction appears to coincide, at least in part, with suspected dates of Clovis arrival in the Southeast (Haynes 2002b), a hypothesized cosmic impact (Firestone et al. 2007), and a pronounced, though brief, reversal in the dominance of oaks and pines (Watts 1969, 1970, 1971, 1973, 1975a, 1975b, 1980b, 1980c; Whitehead 1964, 1973; Delcourt and Delcourt 1987). The Younger Dryas' short-lived reversion to glacial temperatures in an otherwise generally warming climate since the Wisconsin glaciation has been invoked to at least partially explain mega-herbivore extinctions, although the extent to which anthropogenic vs. other factors contributed remains unresolved (Haynes 2002a; Holliday et al. 2016; Wolbach et al. 2018a,b). The extinction of keystone mega herbivores and concurrent climatic transitions is hypothesized to have caused a cascade of ecological effects, ultimately resulting in increased levels of woody recruitment and invasion into various habitats ranging from wetlands to grasslands (Owen-Smith 1987; Newsom and Mihlbachler 2006).

It is unclear to what extent extra-provincial vegetation reconstructions can be extrapolated over the Piedmont, which is differentiated geologically from adjoining Coastal Plain and vegetatively, at least modern-day, from many vegetation associations of the adjoining provinces (Schafale and Weakley 1990; Schafale 2012). The region is also considerably heterogenous. For instance, in North Carolina alone, sites in the Piedmont exhibit ca. 305 mm (12 in.) differences in mean annual precipitation, 2–3-week differences in timing of frosts, substrates varying from felsic to mafic, upland soils varying

from acidic Ultisols to nearly circumneutral Mollisols, and an overall east-west elevation change of ca. 366 m (1,200 ft). Most present-day upland environments in the Piedmont are now dominated by closed-canopy pine or oak-hickory forests, wherever not modified to urban or agricultural land types (e.g., Leyk et al. 2020). However, some intriguing exceptions exist, particularly upland savannas and woodlands with a Midwest prairie-affinity, heliophytic flora. These are widely scattered in the south-eastern United States Piedmont along an arc beginning with the Black Belt prairies of Mississippi and Alabama (Webb et al. 1997; Leidolf and McDaniel 1998; Barone 2005; Barger et al. 2014), through Georgia (Echols and Zomlefer 2010), into the Carolinas and Virginia (Barden 1997; Fleming et al. 2001; Davis et al. 2002; Schmidt and Barnwell 2002; Tompkins et al. 2010a,b; Tompkins 2013; Stanley et al. 2019; Reed et al., in review), and northward into Maryland and southeastern Pennsylvania (Marye 1955 a,b,c). The constituent flora typically includes a component shared with the midwestern Prairie Peninsula, but also of broadly southern, as well as endemic species. These heliophytes continue to occur in a series of small, fragmented habitats (often powerline rights-of-way), and also in a very few sites of considerable acreage and quality. Many of these sites may have escaped plowing, as the underlying, high shrink-swell soils (typically Vertisols or Alfisols) are generally considered unsuitable for agriculture and development and thus avoided (Hardison and Long 1910; Moore 2007).

Evidence from narrative accounts, paleoecology, and floristics (see citations above, as well as Morris 2005, Dobbs 2006) suggests a broader historical distribution of these communities in the Southeast than today, although dates of emergence, spatiotemporal extent, and historical dynamics are quite unclear. Early narrative accounts describe savanna-like conditions in the Piedmont at least as far back as the 1500s (Barden 1997). In North Carolina, these systems may have stretched at a minimum along the Piedmont Crescent (based on the location of remnant patches) to a maximum from the Fall Line to the foothills of the mountains. The latter is suggested by two intriguing maps placing Piedmont savannas in the state, those of Lederer (1670) and De L'Isle (1718). De L'Isle's map more closely follows mapping standards employed today (Figure 2), but unlike John Lederer, De L'Isle never visited North Carolina, instead using first-hand accounts (Dawson 2000). In his resulting map, he labeled a vast swath of central North Carolina as the "Grande Savane" (De L'Isle 1718). Thus, both the ecology of remnant heliophytes (Szakacs et al. 2022), as well as the intriguing narrative accounts of historical landscapes, naturally lead to the question of whether remnant prairie-affinity patches in North Carolina (if not the Southeast at-large) represent at least historical, if not ancient, old-growth grasslands.

Veldman et al. (2015) discussed the concept of ancient grasslands (i.e., formed over centuries or more), providing intrinsic characteristics in three functional categories: Ecosystem-level, Factors of Biodiversity Maintenance, and Taxon Life-History. Many of these characteristics are exhibited by the flora of remnant "Piedmont prairies," including species assemblages that do not occur in young, secondary grasslands, high herbaceous layer plant species diversity, elevated small-scale (e.g., 1 m^2) species richness[1] (Appendix A), transient seed banks (Walker 2009; although these are not unique to grasslands, see Whigham 2004), high ratio of herbaceous species to tree species (Szakacs 2020), open discontinuous tree canopies (Barden 1997; Cowell 1995), numerous species that are relatively long-lived and/or exhibit strong re-sprouting capacity (e.g., Howe 1994; Brudvig et al. 2007; VanderWeide and Hartnett 2015; Krings et al. 2020), fire-enhanced flowering or fruiting (NC PCP 2018; Szakacs 2020), and fire-tolerant or -dependent, thick-barked trees (e.g., *Pinus echinata* Mill., *Quercus marilandica* Münchh., *Q. stellata* Wangenh.; Burns and Honkala 1990). In addition, congruent with the criteria of Veldman et al. (2015), the systems are thought to be maintained by frequent surface fires and degraded by fire suppression (Frost 2000) (although this is not unique to upland grasslands, see Vandermast et al. 2004). However, in contrast to the criteria of Veldman et al. (2015),

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[1]Small-scale species richness is a challenging characteristic for comparison, given that in landscapes as impacted as North Carolina, species richness at this scale is highly dependent on management legacy and can fluctuate considerably even within sites, dependent on management interventions (or lack thereof).
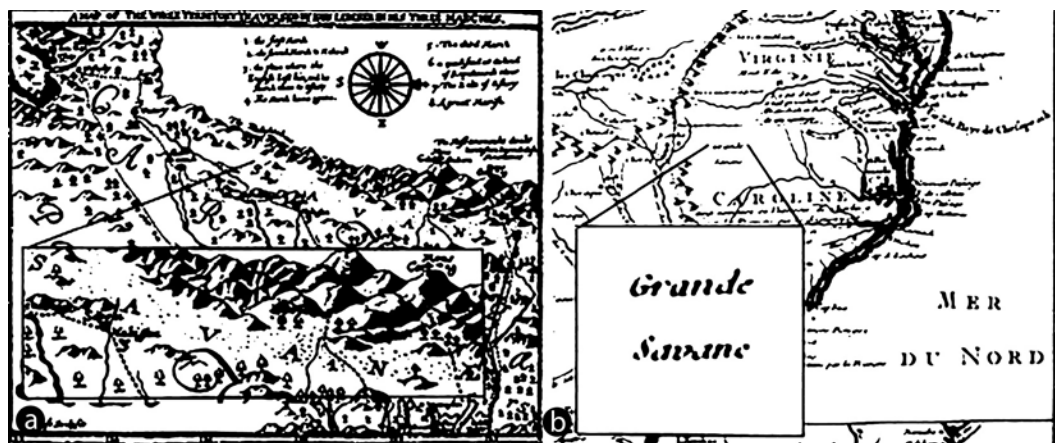
Figure 2. Historical maps suggesting widespread savanna vegetation in the Piedmont east of the Appalachians: a. Lederer (1670); b. De L'Isle (1718).

soils of the majority of "Piedmont prairie" remnants are not nutrient-poor. In fact, soils are predominantly nutrient-rich Alfisols or Vertisols (Oakley et al. 1995) with high base saturation and cation exchange capacity (Table 1). Alfisols in the area are predominantly derived from the weathering of igneous substrates, whereas Vertisols (especially in the Black Belt prairies of Alabama) are derived from ancient, calcium-rich marine deposits (Carr et al. 1905). In addition, the absolute number and percent of endemic species to the Piedmont physiographic region as a whole is quite small. Veldman et al. (2015) and Axelrod (1985) argued that a high number of endemics would be suggestive of an ancient ecosystem. In the southeastern Piedmont, only 69 taxa (spp., subspp., and vars., as well as five undescribed species; based on extraction from Weakley 2015, 2020) are endemic (Appendix B), compared to 1,600 taxa endemic to the adjoining Coastal Plain (Sorrie and Weakley 2001). Taxa endemic to the Piedmont represent only 2.8% of the Piedmont native flora (compared to 27% of taxa endemic in the Coastal Plain flora). In addition, among Piedmont endemic taxa, the largest group are endemics of granitic flatrocks and outcrops (40.6%; Appendix B). The percent of all Piedmont taxa endemic to Piedmont grasslands, including prairie-affinity patches, savannas, and woodlands is only 0.8% (Appendix B). Thus, remnant "Piedmont prairies" exhibit some, but not all criteria proposed for recognition of ancient grasslands.

Fortunately, it is well established that historical vegetation type in basic functional categories—such as C_4 grassland, C_3/C_4 semi-open woodland, C_3 forest—can be reconstructed based on stable carbon isotopes from soil organic matter (SOM; Tieszen and Archer 1990; Balesdent et al. 1993; Boutton et al. 1994; Archer 1995; Garten et al. 2000; Nordt et al. 2008; Cordova et al. 2011). Such reconstruction is possible because the plant C_4 photosynthetic pathway discriminates less against ^{13}C over ^{12}C in the initial stages of carboxylation, resulting in differential values of the ratio ^{13}C:^{12}C (commonly expressed as $\delta^{13}C$), depending on the type of vegetation (i.e., C_3 vs. C_4) dominant at the various time intervals represented in the soil profile (O'Leary 1981, 1988). Therefore, analysis of $\delta^{13}C$ of SOM has the potential to provide additional empirical data to address the question of whether present-day "Piedmont prairie" patches reflect former grasslands. We sought to apply such analyses, focusing specifically on two well-known localities hosting prairie-affinity heliophytes in the Deep River Triassic Basin of North Carolina, both within the boundaries of De L'Isle's (1718) "Grande Savane": Picture Creek Diabase Barrens (PCDB; Stanley et al. 2019) and Eno River Diabase Sill Preserve (ERDSP; Reed et al., in review). If these sites indeed represent remnants of historical, if not ancient, grasslands, one would expect to find $\delta^{13}C$ values reflective of open systems extending temporally more or less continuously through the soil profile. In contrast, if the sites represent a

Table 1. Soil characteristics from four cores at Picture Creek Diabase Barrens (PCDB) and one at Eno River Diabase Sill Preserve (ERDSP). Based on analyses by the Kansas State University Stable Isotope Lab ($\delta^{13}C$ [‰], %C, %N, $\delta^{15}N$ (Air)) and the NC Department of Agriculture and Consumer Services, Agronomic Services Division, Soil-testing Unit (BS%, CEC, pH). Bolded values indicate radiocarbon-dated increments (Table 2, Figure 7) *As discussed in text, profile mixing (likely from past agriculture) was detected in the PCDB-Ult core.

Depth (cm)	PCDB-DBOHF ♣ Granville Co, NC Dry Basic Oak-Hickory Forest — Iredell series (Alfisol); IrB Fine, mixed, active, thermic Oxyaquic Vertic Hapludalf — 6.3 pH — BS% 92; CEC 16.3 meq/100 cm³ — 36.169211, -78.73736 +/-4.6 m (15 ft)				PCDB-XHF (Glade) ♠ Granville Co, NC Xeric Hardpan Forest — Iredell series (Alfisol); IrB Fine, mixed, active, thermic Oxyaquic Vertic Hapludalf — 6.5 pH — BS% 94; CEC 19.3 meq/100 cm³ — 36.16629, -78.73910 +/-6.7 m (22 ft)				PCDB-POW ♦ Granville Co, NC Powerline right-of-way — Picture series (Mollisol); PcA Fine, smectitic, thermic Vertic Argiaquoll — 6.4 pH — BS% 94; CEC 25.9 meq/100 cm³ — 36.16538, -78.73788 +/-9.7 m (32 ft)				PCDB-Ult* ♥ Granville Co, NC Dry Oak-Hickory Forest (Pd Subtype) — Creedmoor series (Ultisol); CrC Fine, mixed, semiactive, thermic aquic Hapludult — 4.5 pH — BS% 33; CEC 2.8 meq/100 cm³ — 36.16024, -78.74004 +/-14.9 m (49 ft)				ERDSP-XHF ● Durham Co, NC Xeric Hardpan Forest — Iredell series (Alfisol); IrB Fine, mixed, active, thermic Oxyaquic Vertic Hapludalf — 6.0 pH — BS% 91; CEC 15.4 meq/100 cm³ — 36.07588, -78.86246 +/-4.6 m (15 ft)			
	$\delta^{13}C$ (VPDB)	%C	%N	$\delta^{15}N$ (Air)	$\delta^{13}C$ (VPDB)	%C	%N	$\delta^{15}N$ (Air)	$\delta^{13}C$ (VPDB)	%C	%N	$\delta^{15}N$ (Air)	$\delta^{13}C$ (VPDB)	%C	%N	$\delta^{15}N$ (Air)	$\delta^{13}C$ (VPDB)	%C	%N	$\delta^{15}N$ (Air)
0–3	−29.14	36.8291	2.1017	−0.76	−26.18	3.8290	0.2329	2.31	−23.97	1.8265	0.1512	4.88	−26.98	1.1230	0.0952	1.70	−26.27	3.8509	0.2481	3.16
3–6	−28.10	19.0621	1.1067	1.26	−24.96	2.2341	0.1603	3.77	−23.24	1.0653	0.0949	6.38	−26.27	1.0291	0.0698	2.59	−25.08	2.0454	0.1647	3.89
6–9	−26.48	4.3670	0.3625	4.17	−23.21	1.1831	0.0961	6.44	−23.24	0.9116	0.0805	7.31	−25.76	0.5135	0.0446	3.65	−24.71	1.7671	0.1284	5.66
9–12	**−25.85**	3.8211	0.2782	5.16	−23.46	1.0786	0.0637	5.68	−23.33	0.7439	0.0725	7.52	−25.76	0.1277	0.0294	−7.42	−22.73	1.5227	0.1229	7.78
12–15	−25.24	2.0537	0.1909	5.54	−23.86	1.6838	0.1027	6.77	−22.33	0.5808	0.0557	7.58	−24.35	0.2486	0.0160	0.50	−20.70	1.0583	0.0867	8.23
15–18	**−23.68**	1.6568	0.1445	5.57	−22.17	1.0124	0.0770	6.35	**−21.34**	0.7050	0.0808	7.96	−23.77	0.1519	0.0330	11.14	−22.27	1.0764	0.0967	7.68
18–21	−23.11	1.2271	0.1065	6.29	−22.72	0.6525	0.0498	6.78	**−22.77**	0.4965	0.0504	6.82	−23.96	0.0926	0.0286	5.50	−21.67	0.6924	0.0643	6.14
21–24	−23.00	1.6976	0.1603	11.02	**−18.15**	0.3360	0.0422	9.83	−21.70	0.4595	0.0415	8.51	**−22.43**	0.0518	0.0219	2.19	−21.71	0.6687	0.0516	7.31
24–27	−22.22	1.1605	0.1753	7.53	−17.90	0.2976	0.0330	7.25	−27.26	10.6615	0.3766	2.66	−24.74	0.0348	0.0143	−0.11	−21.30	0.5233	0.0497	6.62
27–30	−19.80	0.9196	0.1513	11.14	−22.91	0.5103	0.0461	8.59					−25.33	0.0404	0.0190	1.77	−22.70	0.5874	0.0480	5.30
30–33	−20.90	0.6716	0.1669	11.59	−20.55	0.0649	0.0207	4.86					−24.39	0.0173	0.0244	7.55	−22.04	0.4718	0.0572	5.42
33–36	−19.45	0.8258	0.1493	9.14	−22.64	0.2259	0.0314	8.83					−24.31	0.1327	0.0314	4.12	−21.54	0.2787	0.0342	6.64
36–39	−18.18	0.3650	0.0617	10.09	−23.24	0.3279	0.0324	8.66					−22.95	0.1590	0.0282	3.45	**−24.12**	0.6045	0.0353	3.26
39–42	**−18.20**	0.2845	0.0741	16.75									**−25.58**	0.2103	0.0475	9.18	−20.72	0.2774	0.0361	3.81
42–45													−26.32	0.2745	0.0404	8.02	−20.38	0.2270	0.0332	6.62
45–48													−26.43	0.2343	0.0392	3.93				
48–51													−27.08	0.1965	0.0368	5.07				
51–54													−22.74	0.0041	0.0198	−0.18				
54–57													−23.45	0.0593	0.0249	4.96				

mixed history of alternating open and closed-canopy conditions, such should be reflected by alternating values representative of these conditions.

MATERIALS AND METHODS

Site Description

PCDB (Granville County) and ERDSP (Durham County) are located in the Deep River Basin, the largest of the Triassic basins in the North Carolina Piedmont (Olsen et al. 1991; Figure 3). The sites lie within ca. 16 km (10 mi) of one another and from the estimated route of a major Native American Trading Path (Dobbs 2006; Fecher 2008). Both sites are owned by the NC Department of Agriculture & Consumer Services (PCDB: Research Stations Division; ERDSP: NC Plant Conservation Program) and are currently managed, in part, for the numerous rare heliophyte taxa they host, including charismatic prairie species, such as *Baptisia aberrans* (Larisey) Weakley, *Echinacea laevigata* (C.L. Boynton & Beadle) S.F. Blake, *Liatris squarrulosa* Michx., *Lithospermum canescens* (Michx.) Lehm., *Silphium terebinthinaceum* Jacq., *Solidago rigida* L., and *Symphyotrichum depauperatum* (Fernald) G.L. Nesom (Stanley et al. 2019; Reed et al., in review). In the early 20th century, the sites were known to be considerably more open than today (Figure 4), but the majority of both sites is now forested, the heliophytes persisting in scattered areas of diffuse canopies (e.g., woodland glades) and open habitats created by humans (e.g., powerline right-of-way, roadsides, recent forest operations). Details on site history and land use can be found in Stanley et al. (2019) and Reed et al. (in review).

Sample Collection and Analysis

Soil cores for $\delta^{13}C_{org}$ analysis were collected from four sites at PCDB and one at ERDSP, spanning three soil orders: Alfisols, Mollisols, and Ultisols (Figure 5). At PCDB, these sites represented distinctly different present-day plant communities (following in part community concepts of Schafale, 2012), as mapped by Stanley et al. (2019): Dry Basic Oak-Hickory Forest (over Iredell series Alfisol [IrB]; ♣), Dry Oak-Hickory Forest (over Creedmoor series Ultisol [CrC]; ♥), powerline right-of-way (over Picture series Mollisol [PcA]; ♦), and Xeric Hardpan Forest (over Iredell series Alfisol [IrB]; ♠) (Figure 6). At ERDSP, a single core was collected from mapped Xeric Hardpan Forest (over Iredell series Alfisol; •) (Reed et al., in review).

Plastic (pvc) pipes (61 cm long [2 ft.], 5 cm inner diam. [2 in.]) were used to collect soil by pounding them into the ground and subsequently digging them out. Pipes were then sectioned in 3 cm increments using a bandsaw with a vacuum attachment (to prevent contamination by pvc shavings). Each cut increment was carefully cleaned to obtain a plug of soil representing the center of each increment. Samples of select soil plugs (5–10 grams) were sent to Beta Analytic (Miami, Florida) for accelerator mass spectrometry (AMS) radiocarbon dating of the alkali-insoluble organic fraction (employing an acid/alkali/acid pretreatment) and $\delta^{13}C_{org}$ analysis using isotope ratio mass spectrometry (IRMS). Beta Analytic employs an NEC accelerator mass spectrometer and Thermo DeltaV isotope ratio mass spectrometers. Prior to AMS, samples were crushed and dispersed in deionized water, then washed successively with (1) hot HCl acid to eliminate carbonates, (2) an alkali wash (NAOH) to remove secondary organic acids, and (3) an acid rinse to neutralize the solution before drying. Post analysis, radiocarbon age was calibrated to calendar years using the High Probability Density Range Method (HPD): INTCAL 13 (Ramsey 2009; Reimer et al. 2013). Reported results are accredited to ISO/IEC 17025:2005 Testing Accreditation PJLA #59423 standards. $\delta^{13}C_{org}$ analysis was also carried out at the Kansas State University Stable Isotope Mass Spec Lab (KSU SIMSL; Manhattan, Kansas). Preparation for $\delta^{13}C_{org}$ analysis was as follows: Portions of the soil plugs were placed into clean porcelain crucibles, covered with a loose lid (to prevent potential of airborne contamination), and allowed to dry in a warm area (e.g., a drying cabinet or drying room; time to dry was generally 2–5 days). Once dried, approximately 0.5 grams of material from each sample was placed into a labeled centrifuge tube and weighed. Samples were not sifted (to avoid introducing potential contamination from the use of sieves), but roots, rocks, or other unwanted
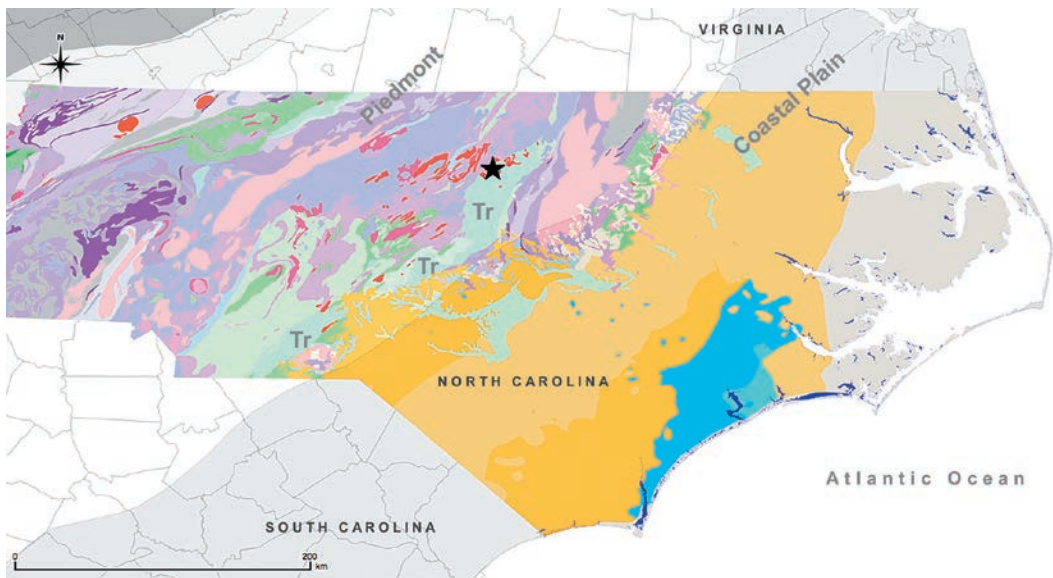
Figure 3. Location (starred) of the Picture Creek Diabase Barrens and Eno River Diabase Sill Preserve (the two are ca. 10 mi apart) in the Deep River Triassic Basin (Tr) in the North Carolina Piedmont. Physiographic provinces follow Fenneman and Johnson (1946). Geologic layer courtesy of USGS (2018). Tr=Triassic Basin. Map created in QGIS (2019).

materials were removed from each sample using forceps and visual inspection under a dissecting scope before placing them into the tube. A metal bead was added to each tube before loading them into a Retsch MM400 mixer for grinding. Tubes were shaken at maximum frequency for 1.5-minute intervals until reduced to fine powder. The metal bead was then removed from each tube using a magnet and forceps. Labeled sample tubes were sent to KSU SIMSL for $\delta^{13}C_{org}$ analysis. KSU SIMSL employs an Elementar Pyrocube Elemental Analyzer (EA) and an Elementar GiovisION isotope ratio mass spectrometer. Samples were not pre-treated prior to analysis. Post-run data were calibrated using standards run at the same time (e.g., wheat flour, oak leaves, grass leaves).

In addition to the cores, small soil samples were taken at 10–20 cm depths from the same locations for analysis by the NC Department of Agriculture and Consumer Services, Agronomic Services Division, Soil-testing Unit (Raleigh) of basic characteristics, such as pH, base saturation (BS%), and cation exchange capacity (CEC).

Endmember Reconstruction

To provide context for comparison of $\delta^{13}C_{org}$ values obtained from our samples, we estimated $\delta^{13}C$ endmember values for vegetation classes (i.e., pure C_3, pure C_4) over time, by calculating $\delta^{13}C$ values for spatiotemporally pertinent mean annual precipitation (MAP) regimes and then adjusting for temporal differences in $\delta^{13}C_{atm}$, as described below. Such adjustments are necessary given that plants differentially incorporate carbon based on variations in MAP, and that the carbon isotopes ratio of the atmosphere has changed over time (Passey et al. 2009; Diefendorf et al. 2010; Kohn 2010; Tipple et al. 2010). Accordingly, we used data from Stahle et al. (1988) and NOAA (2010) to identify time periods over the period of 372 AD to present for which precipitation differed statistically (i.e., 2 standard deviations) from the adjusted long-term mean. As the SPI (Standard Precipitation Index) is the number of standard deviations that an observed value deviates from the long-term mean, we then assigned each temporal interval derived from the previous step to one of the three classes 2+ SPI, 0 SPI, or 2- SPI. We then calculated regionally appropriate MAP values (mm/yr) representing these three classes based on NOAA (2010). To obtain endmember values for pure C_3 for each temporal interval, we averaged $\delta^{13}C$ values for C_3 plants growing within similar
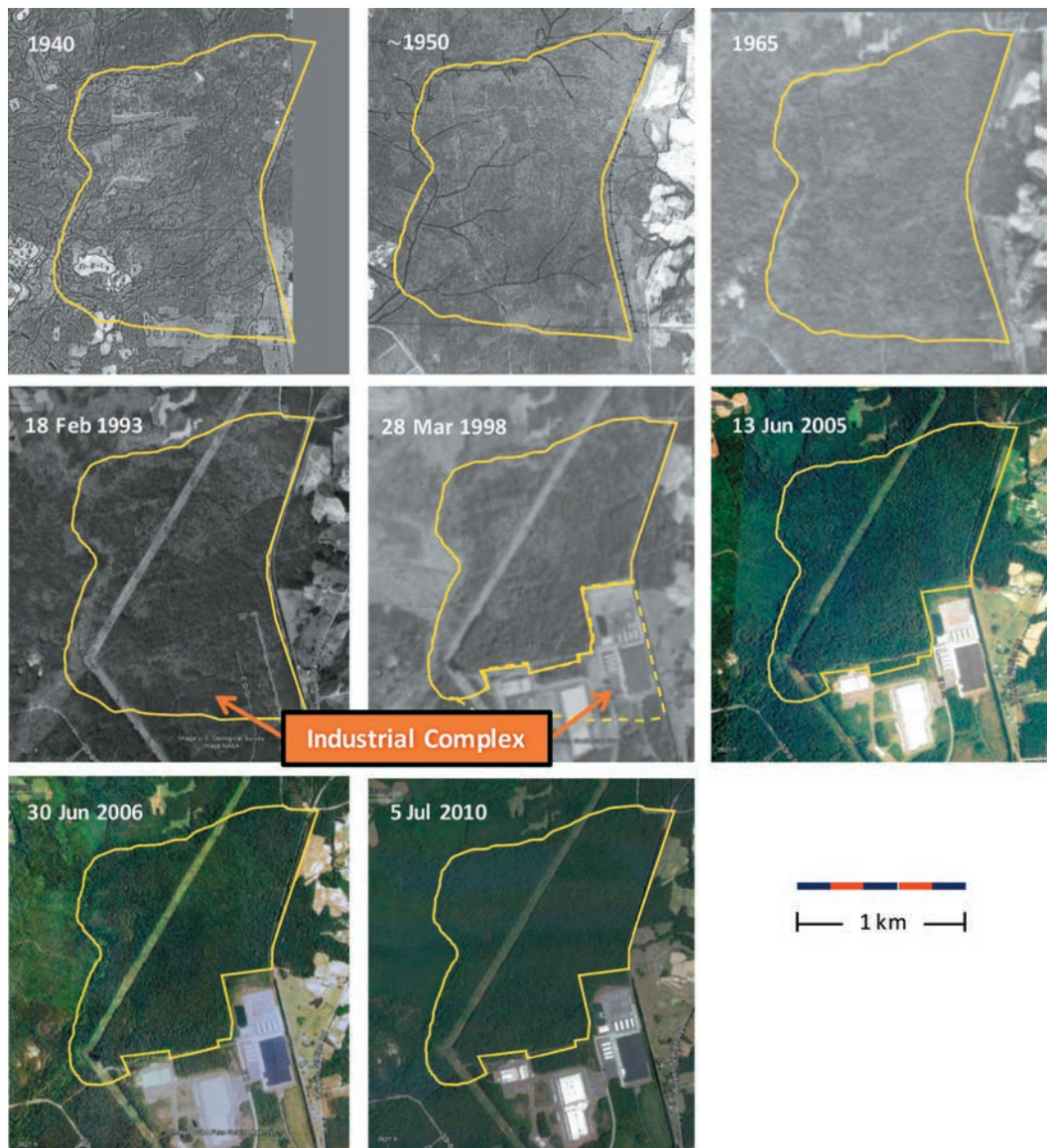
Figure 4. Aerial photographs of Picture Creek Diabase Barrens showing increasing forest cover since 1940. From: Stanley et al. (2019).

precipitation ranges as given in Diefendorf et al. (2010). These $\delta^{13}C$ values were then adjusted for each temporal interval for any difference in $\delta^{13}C_{atm}$ from modern values, using data from Friedli et al. (1984, 1986). $\delta^{13}C$ values were additionally adjusted from the values for a pure C_3 endmember by 14‰ for the pure C_4 endmember (e.g., Hyland et al. 2018).

<div align="center">

RESULTS

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The subsurface soil samples from the locations mapped as Iredell (♣♠•; Alfisol) and Picture (♦; Mollisol) exhibited pH values in the range of 6.0–6.5 and percent base saturation of 91–94%, consistent with description of the respective soil orders (Table 1). CEC in these cores ranged from
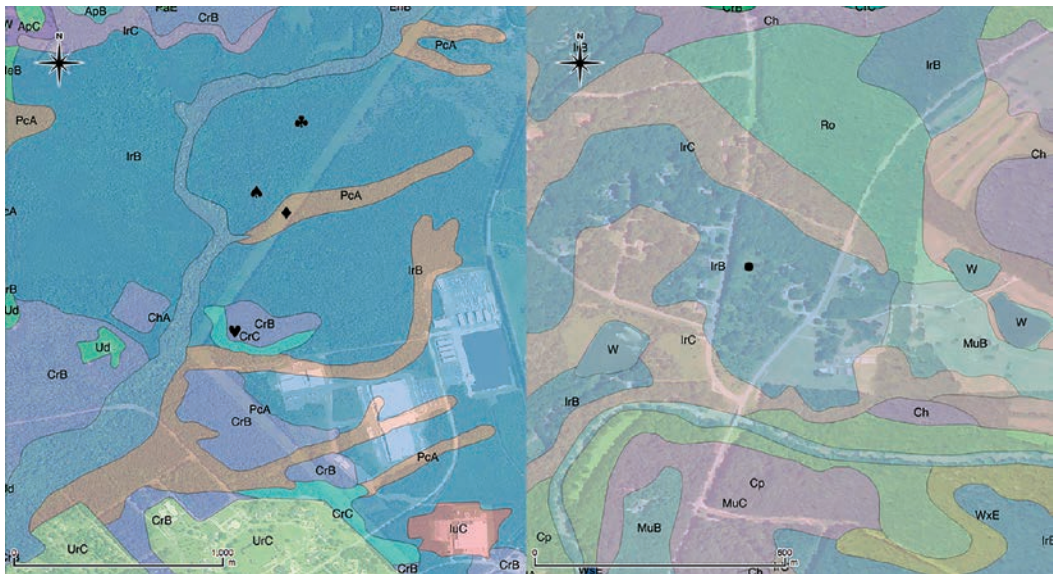
Figure 5. Location of cored soils (symbology follows Table 1) in context of mapped soil series at Picture Creek Diabase Barrens (left) and Eno River Diabase Sill Preserve (right). CrC = Creedmoor (Ultisol); IrB = Iredell (Alfisol); PcA = Picture (Mollisol). ♣ = PCBD-DBOHF; ♠ = PCDB-XHF (Glade); ♦ = PCDB-POW; ♥ = PCDB-Ult; • = ERDSP-XHF. Soil layer courtesy of USDA Web Soil Survey (SSS-NRCS-USDA 2022). Aerial imagery (NAIP) courtesy of USGS Earth Explorer (2022). Map created in QGIS (2019).

15.4–25.9 meq/100 cm^3. The subsurface soil sample from the single Ultisol in the study, mapped as Creedmoor (♥), exhibited a pH value of 4.5, percent base saturation of 33%, CEC of 2.8 meq/100 cm^3, consistent with description of the order (Table 1).

$\delta^{13}C_{org}$ values from the locations mapped as Iredell (♣♠•; Alfisol) and Picture (♦; Mollisol) ranged from −29.1‰ to −17.9‰ (‰ indicates parts per thousand; Table 1). Only two cores exhibited increment values of $\delta^{13}C$ below −20‰: PCDB-DBOHF (♣) and PCDB-XHF (♠). Values of $\delta^{13}C_{org}$ from the single Ultisol in the study (PCDB-Ult; ♥) ranged from −27.1‰ to −22.7‰ (Table 1). Although KSU SIMSL, unlike Beta Analytic, did not remove carbonates prior to $\delta^{13}C_{org}$ analysis, the recovered values did not differ substantially between the two labs for the dated increments (Table 2). Given that the dated increments were distributed at various profile depths and site locations, our results thus suggest it unlikely for carbonates to have affected the measurements from any of the increments (this would have been rather unusual given that the soils are not parented on carbonate [very low detrital CaCO$_3$] and conditions are too wet and humid to form authigenic carbonates). We also note that while organic input into upper profiles (e.g., O horizons) can lead to distinct $\delta^{13}C$ values, the only core exhibiting >10% organic carbon in the upper profile is PCDB-DBOHF and then only for the uppermost two samples (0–3 and 3–6 cm depth; see Table 1). Even without these samples, the trends in $\delta^{13}C_{org}$ we report are robust for all cores.

The estimated date ranges of radiocarbon-dated soil increments are provided in Table 2. The oldest estimate came from 36–39 cm in the ERDSP core (•; 133–264 CE). Radiocarbon dating suggested soil mixing in PCDB-Ult (♥), recovering a younger date (505–610 CE) at a deeper depth (i.e., 39–42 cm) than an older date (321–422 CE; 21–24 cm). The finding is consistent with deep furrows seen on site. In light of the mixing, this core is not further considered in our analyses. $\delta^{13}C$ values from the two analytical labs were consistent within a range of 0.06–1.72‰.

We found no evidence of similar vertical mixing in the other cores, nor of obvious furrows in the landscape. Based on current knowledge (i.e., lack of obvious furrows, anecdotal reports of old
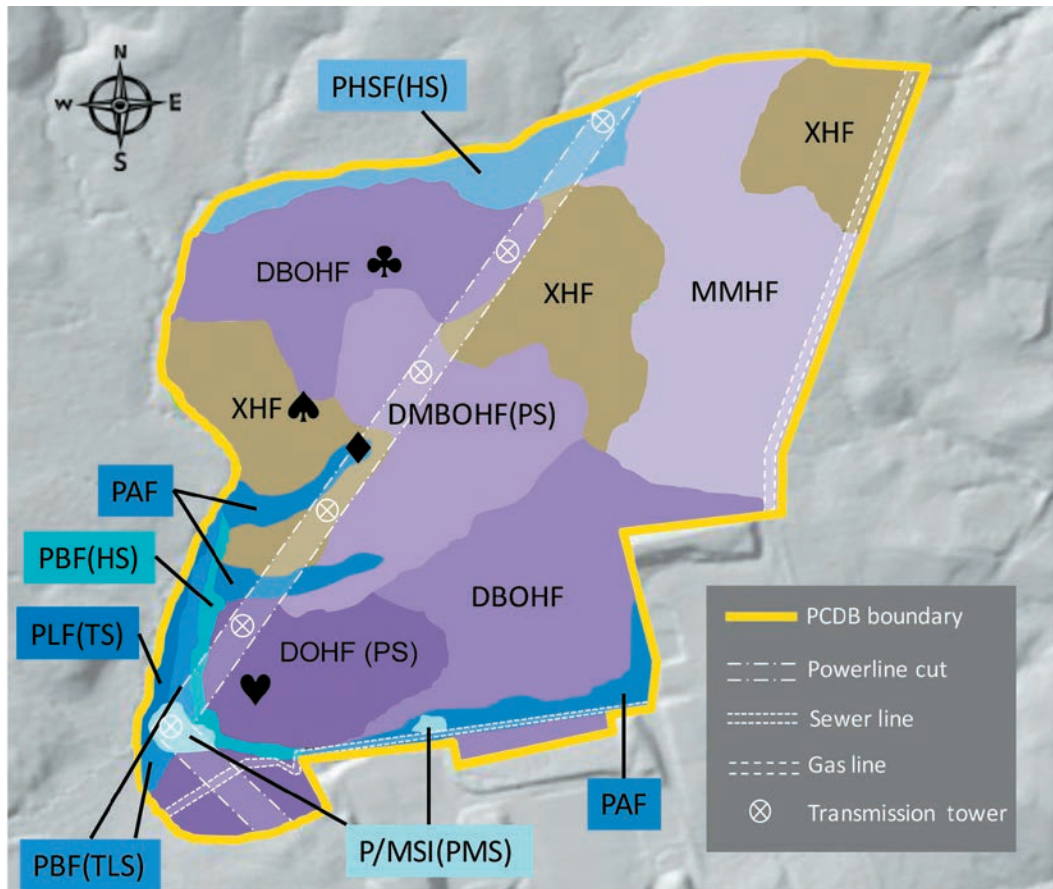
Figure 6. Location of cored soils (symbology follows Table 1) in context of natural community types at Picture Creek Diabase Barrens (sensu Schafale 2012, from Stanley et al. 2019). DBOHF = Dry Basic Oak-Hickory Forest; DMBOHF(PS) = Dry-Mesic Basic Oak-Hickory Forest (Piedmont subtype); DOHF(PS) = Dry Oak-Hickory Forest (Piedmont subtype); MMHF = Mixed Moisture Hardpan Forest; PAF = Piedmont Alluvial Forest; PBF(HS) = Piedmont Bottomland Forest (High subtype); PBF(TLS) = Piedmont Bottomland Forest (Typic Low subtype); PHSF(HS) = Piedmont Headwater Stream Forest (Hardpan subtype); PLF(TS) = Piedmont Levee Forest (Typic subtype); P/MSI(PMS) = Piedmont/Mountain Semipermanent Impoundment (Piedmont Marsh subtype); XHF= Xeric Hardpan Forest. ♣ = PCBD-DBOHF; ♠ = PCDB-XHF (Glade); ♦ = PCDB-POW; ♥ = PCDB-Ult.

cowbells from land managers suggesting a woodland grazing not plowing history, limited site history as discussed in Stanley et al. 2019, and active dissuasion of the plowing of Iredell by the Soil Conservation Service since at least the early 1900s [Hardison and Long 1910]), we have no reason to believe our other cores were placed in land once plowed. Nonetheless, since not all increments were dated, the resulting patterns naturally must be treated cautiously as hypotheses to be supported or refuted in future work.

As only select soil increments were radiocarbon dated, Figure 7 presents results based on sampling depth rather than age, where vegetation classes are simplified to linearly-delimited zones, the bounds of which represent minimum and maximum $\delta^{13}C$ values defined for each vegetation class. In the absence of a fully-dated profile, we suggest this provides a reasonable approximation at a coarse scale regarding the vegetation classes potentially associated with each depth. $\delta^{13}C$-based estimates of vegetation endmembers in the region over the period 375 CE to present are provided in Supplemental

Table 2. Radiocarbon dating of soil increments at Picture Creek Diabase Barrens (PCDB) and Eno River Diabase Sill Preserve (ERDSP) (Beta Analytic, Inc.; Miami, Fla.). $\delta^{13}C_{org}$ values (‰) provided both from analyses by Beta Analytic and Kansas State University Stable Isotope Lab (KSU).

Core	Depth (cm)	Beta lab number	Prob.	Age range	Conventional radiocarbon age	Beta δ^{13}C	KSU δ^{13}C
PCDB-DBOHF ♣	9–12	500456	69.1% 26.3%	1807–1928 CE 1684–1732 CE	90 ± 30 BP	−25.20	−25.85
PCDB-DBOHF ♣	15–18	493991	90.5% 4.9%	1246–1302 CE 1366–1383 CE	720 ± 30 BP	−25.10	−23.68
PCDB-DBOHF ♣	39–42	492138	95.4%	602–674 CE	1390 ± 30 BP	−18.70	−18.20
PCDB-XFH ♠	18–21	586588	95.4%	1488–1650 CE	310 ± 30 BP	−23.0	−22.72
PCDB-XFH ♠	21–24	523583	95.4%	1412–1468 CE	460 ± 30 BP	−19.10	−18.15
PCDB-POW ♦	15–18	586589	85.0% 6.6% 3.8%	1254–1302 CE 1228–1246 CE 1369–1378 CE	730 ± 30 BP	−21.4	−21.34
PCDB-POW ♦	18–21	586590	95.4%	382–542 CE	1630 ± 30 BP	−23.0	−22.77
PCDB-Ult ♥	21–24	551989	85.2% 10.2%	321–422 CE 258–296 CE	1680 ± 30 BP	−24.1	−22.43
PCDB-Ult ♥	39–42	554327	65.6% 29.8%	505–610 CE 428–498 CE	1520 ± 30 BP	−24.90	−25.58
ERDSP-XHF •	12–15	546608	51.9% 43.5%	1343–1394 CE 1280–1326 CE	650 ± 30 BP	−21.4	−20.70
ERDSP-XHF •	36–39	546609	68.5% 26.9%	133–264 CE 274–330 CE	1790 ± 30 BP	−22.4	−24.12

Figure 1. This model provides context for $\delta^{13}C_{org}$ values recovered from our soil increments and is thus also incorporated into Figures 7 and 8.

The general vegetation trend over the sampled Iredell and Picture series soils over the past ca. 2000 years appears to record a transition from open C_3 or C_3/C_4 mix to increasingly closed C_3 (Figure 7). C_4 grasslands do not appear to have been an ecosystem component of any sample sites over the past 2000 years. While the general trajectory appears to be one from open to closed systems, pronounced fluctuations are apparent in all profiles. A particularly marked fluctuation from an open C_3 to C_3/C_4 mix is seen in PCDB-XHF (♠) at 1412–1468 CE. Similar, though less extreme, fluctuations toward C_3/C_4 mix are apparent as well in PCDB-POW (1254–1302 CE; ♦) and ERDSP-XHF (1343–1394 CE; •). The three fluctuations are thus estimated within the combined time frame of 1254–1468 CE. Prior and subsequent to these fluctuations, vegetation classes in the three cores appear to have been predominantly open C_3, with exceptions at depth 42 cm and below in ERDSP-XHF (•). Vegetation class fluctuations are less pronounced in PCDB-DBOHF (♣), the general trajectory being primarily one of C_3/C_4 mix at 607–674 CE to canopy closure (present-day). This profile exhibits a minor (undated) fluctuation at depth 27–30 cm and another even less pronounced one at 1246–1302 CE. The latter takes place in the same interval of shifts toward mixed C_3/C_4 ecosystems as described above over the period 1254–1468 CE.

DISCUSSION

As we recovered no dates older than ca. 2000 years, we unfortunately cannot comment on whether PCDB or ERDSP represent remnants of ancient grasslands which may have existed during or after the LGM, except to note that our data do not contradict such. Evidence from the $\delta^{13}C_{org}$ values of our soil increments certainly does suggest that historical grasslands, likely savanna-type with some
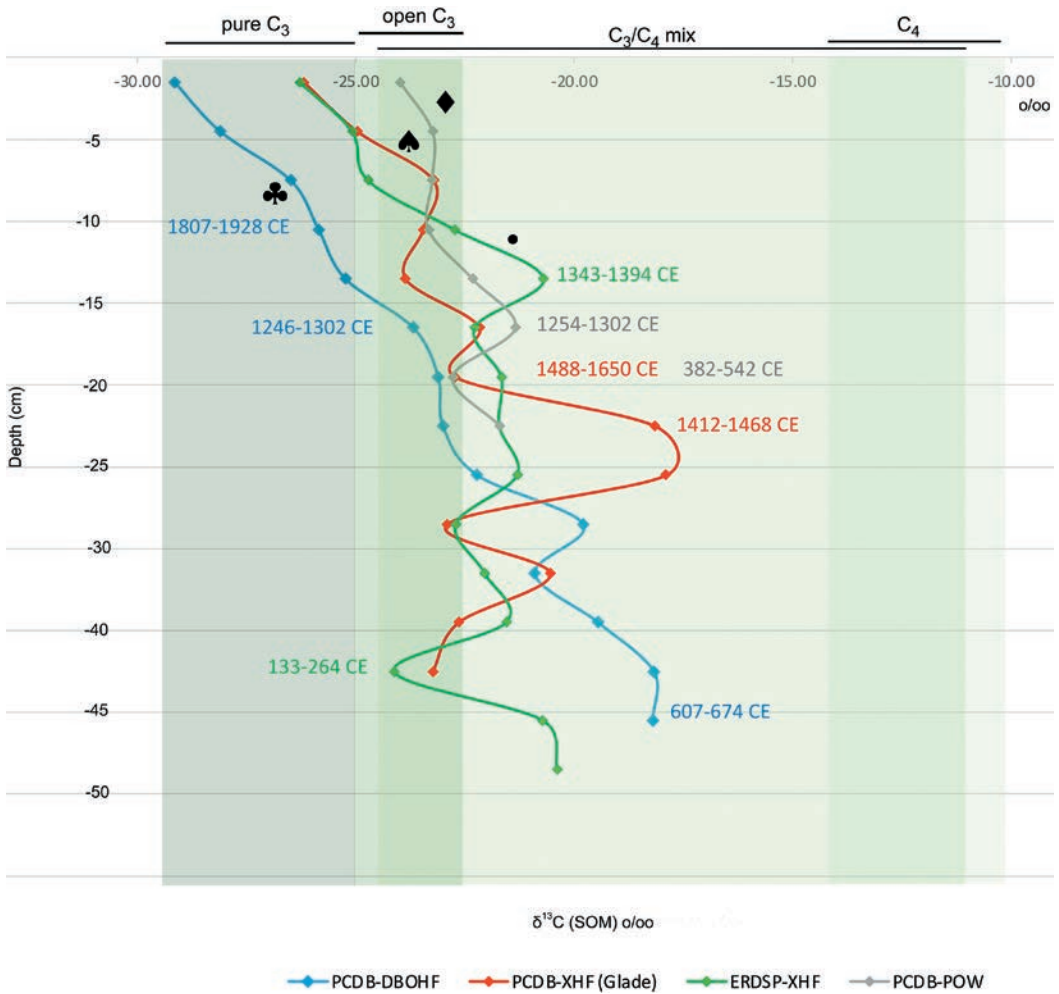
Figure 7. Estimated vegetation history at Picture Creek Diabase Barrens (♣♠♦; PCDB) and Eno River Diabase Sill Preserve (•; ERDSP) based on analysis of $\delta^{13}C$ in soil increments (small diamonds) in four cores (Table 1, Figures 5–6). Minimum and maximum bounds of vegetation classes based on Supplemental Figure 1. Symbology and abbreviations of present-day plant communities follow Table 1 (DBOHF = Dry Basic Oak-Hickory Forest; POW = powerline cut; XHF= Xeric Hardpan Forest; ♣ = PCBD-DBOHF; ♠ = PCDB-XHF (Glade); ♦ = PCDB-POW; • = ERDSP-XHF).

fluctuations in cover (open C_3 and C_3/C_4 mix), were present at both sites essentially continuously over the past 2000 years until the more recent canopy closure seen especially starkly over the past century (Figure 4). These findings are consistent with historical narrative accounts and do not contradict the concept of a "Grande Savane" as mapped by De L'Isle (1718). However, additional vegetation reconstructions, preferably multi-proxy, are needed, including from more common Ultisols, to broaden our understanding of any cohesiveness of savanna vegetation beyond our spatially near but edaphically isolated sites.

Examining our data in more detail, the fluctuations noted over the period 1254–1468 CE (Figure 7) are intriguing, because reconstructions of precipitation over the past 2000 years in North Carolina and the southeastern United States do not appear to provide evidence of correlated events (Stahle et al. 1988; Stahle and Cleaveland 1992, 1994; Krause et al. 2018). Long-term precipitation patterns have been identified in North Carolina and the Southeast, such as century-scale increases
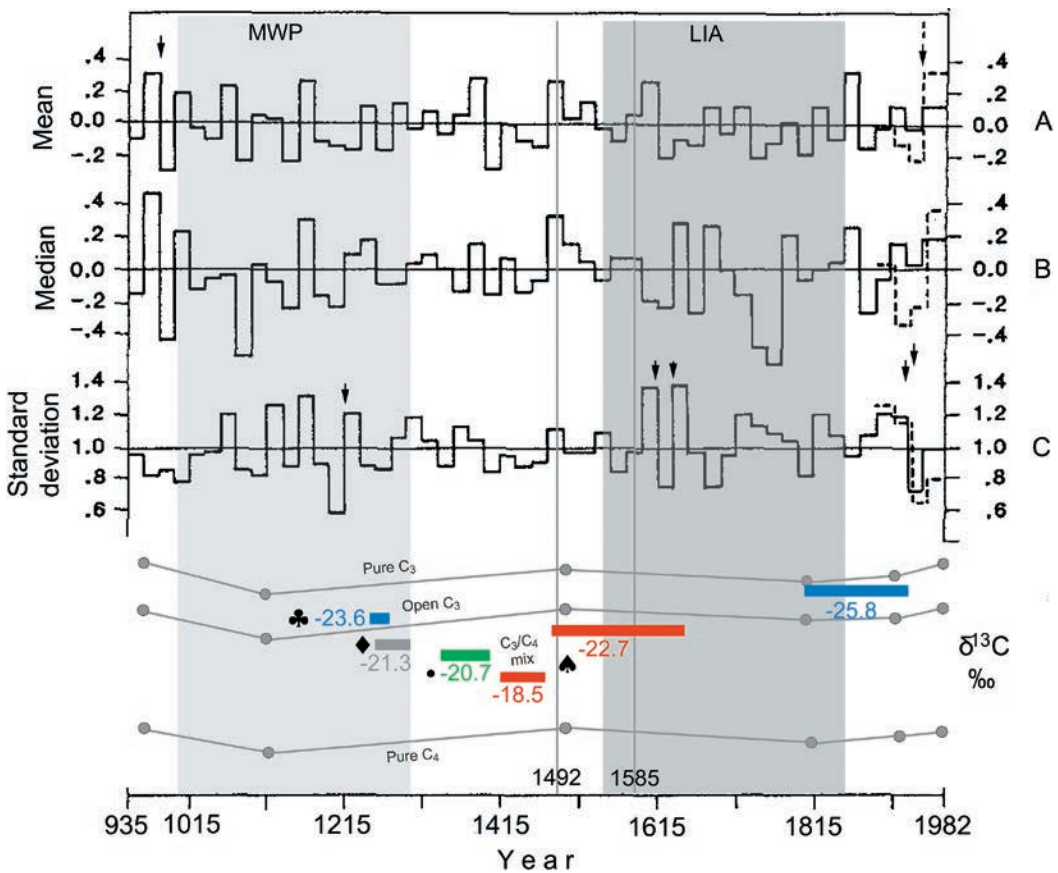
Figure 8. Estimated radiocarbon date ranges (Table 2) and δ^{13}C values (Table 1) of soil increments from Picture Creek Diabase Barrens and Eno River Diabase Sill Preserve overlaid on vegetation reconstruction (from Supplemental Figure 1) and graph from Stahle and Cleaveland (1994, reprinted with permission from Springer Nature) showing mean (A), median (B), and standard deviation (C) of tree-ring-reconstructed spring rainfall in the southeastern US, calculated for non-overlapping 20-yr periods from 935–1982 CE. Dashed lines indicate instrumental data. Arrows indicate statistically significant differences between adjacent 20-yr periods (see Stahle & Cleaveland 1994 for detail). MWP = Medieval Warm Period; LIA = Little Ice Age. 1492: Columbus reaches New World; 1585: Roanoke Colony founded in Dare Co., North Carolina (1st attempt at permanent English settlement in North America). Symbology follows Table 1.

in spring rainfall and associated decreases in summer rainfall, as have decadal-scale regimes of spring drought and wetness (Stahle and Cleaveland 1992). The latter, shorter duration events of drought and wetness (in the 20–30 yr range) appear to have been particularly well-developed during the Medieval Warm Period in North Carolina (MWP; ca. 1000–1300 CE; Stahle et al. 1988; Figure 8). However, over the past 1000 yrs, 20-yr intervals of precipitation levels statistically significant from adjacent intervals pertinent to our study were reconstructed only at 1215 CE, 1615 CE, and 1625 CE (arrowed in Figure 8; Stahle and Cleaveland 1994). Considering that these fall outside the temporal boundaries of the vegetation class fluctuations we observed (Figure 7), it does not appear likely that they are solely or predominantly responsible for the observed vegetation class fluctuations at PCDB and ERDSP. Climatic events, however, cannot be completely ruled out because the North Carolina components of the reconstructions of Stahle et al. (1988) and Stahle and Cleaveland (1992, 1994) are based solely on bald cypress (*Taxodium distichum* (L.) Rich.) from the Black River. Considering that the latter locality is outside of the watershed of PCDB and ERDSP, it may

not be reflective of conditions faced at these sites, especially if we consider within-state differences in precipitation patterns as likely in the past as today. To this end, it would be beneficial to reconstruct precipitation patterns based on dendrochronologies from the Neuse River Basin and other regions in the Piedmont, which may show distinct climate.

If drought or precipitation are not likely responsible for the observed fluctuations in vegetation class, how else may these be explained? Bison are known to disperse viable diaspores of numerous forbs and graminoids in their dung and matted fur (Rosas et al. 2008) and influence composition of local vegetation (Knapp et al. 1999; Fahnestock et al. 2003), but the extent of bison occurrence at least in the Carolinas and Virginia remains controversial. Historically, several species of bison are known from the southeastern United States—*Bison antiquus*, *B. bison*, and *B. latifrons*—but only *B. bison* is known from recent times, largely suspected to be a rather recent arrival within the past 300–500 years ("bison" hereafter refers strictly to *B. bison*; Allen 1876; Rostlund 1960; Harington 1984). That bison were abundant in some parts of the Southeast is supported by numerous narrative accounts well into the 18th century describing them as "abundant," "plentiful," and "very numerous" (Rostlund 1960), as well as, perhaps, the several hundred place names throughout the region that include the word "Buffalo". Rostlund (1960) thought the animals did not arrive in the East prior to ca. 1500 CE. They were recorded by surveyors in the vicinity of our project sites in westward-neighboring Orange County in 1737 (Morris 2005). However, no physical remains of bison have been recovered from the nearby Siouan settlements in the Hillsborough Archeological District, about 16 km (10 mi) west of ERDSP (Dickens et al. 1984, 1987; Ward and Davis 1993; Wells 2016)— or from anywhere else in North Carolina, for that matter. Thus, any role of bison in the observed vegetation class fluctuations remains inferential at best.

Understanding the interplay of succession, fire, and humans in the region is no doubt key to understanding spatiotemporal patterns of vegetation in our area. Succession, fire, and fire-suppression effects have been well-studied in North Carolina and the eastern United States (Oosting 1942; Keever 1950; Connell and Slatyer 1977; Wade and Lunsford 1989; Harrod et al. 2000; Fowler and Konopik 2007; Ostertag & Robertson 2007; Phillips et al. 2012; Palmquist et al. 2014; Gray et al. 2016). It is well-established that open conditions are maintained primarily by fire, not climate, in the southeastern United States and fire has become an important tool in the management of savanna and glade vegetation (Abrams 1992; Stritch 1990; Frost 2000; Caspary and Affolter 2012). Natural fire frequency is known to vary, with the highest densities of present-day lightning strikes in North Carolina occurring in the southeastern Coastal Plain (CP; roughly comparable to those in Arkansas, Illinois, Missouri) and the next highest densities in the middle CP and Piedmont (roughly equivalent to those in southern Wisconsin; MacGorman et al. 1984; Huffines & Orville 1999). The scope and severity of fire effects are a function of localized climatic conditions, fuel availability, and burn-compartment size (Wade and Lunsford 1989). Frost (2000) approximated fire return intervals in the Piedmont in the range of 4–6 yrs, but associated citations were exclusively extralimital. Despite the documented importance of fire in pre-settlement Piedmont (e.g., Cowell 1995), we are unaware of any empirical reconstructions of fire-return intervals in the physiographic province. Based on observations at PCDB, we suggest a shorter return interval may be necessary to keep hardwoods at bay and maintain the reconstructed "open" environments. Nonetheless, if we assume that natural, lightning-ignited fire occurred regularly prior to suppression efforts (as demonstrated in Virginia by Aldrich et al. 2014), then we would expect only relatively minor temporal fluctuations in vegetation, correlated with temporally-limited variations in precipitation. However, we suggest that the vegetation shifts observed in our data over the period 1254–1468 CE (Figure 7) appear too large and too temporally isolated to be caused by such "background" natural burning alone. Instead, we suggest a closer look at transient human activity. Changes in fire regime associated with influx or departure of Native Americans, as well as culture transitions (e.g., Archaic to Woodland, etc.) have been documented (or implicated) in various regions throughout the US, both pre- and post-European contact (Kilgore and Taylor 1979; Guyette and Cutter 1991; Fesenmyer and Christensen 2010), including the southern Appalachians (Delcourt and Delcourt 1997) and the

southeastern Coastal Plain (Krause et al. 2018). In the Coastal Plain, for example, multi-proxy recon-structions strongly suggest anthropogenic activity as causal, failing to establish, at least to date, any climatic basis for (1) the apparent relatively recent advent of frequent, low-intensity fire regimes (beginning ca. 1200 yr BP), (2) the distinct differences in the amount of charcoal at given mid to late Holocene periods from spatially proximate sites, and (3) the earlier, spatiotemporal heterogeneity in oak to pine transition during the early to mid-Holocene, ranging from as early as ca. 9000 yr BP in some areas to ca. 4000 yr BP in others (Taylor et al. 2011; Spencer et al. 2017; Krause et al. 2018; Lane et al 2018). It is thus not implausible that anthropogenic forces are at play in the Piedmont, as well.

PCDB and ERDSP lie within a few kilometers of a significant former Native American trading path more or less over or along which the major highway corridor I-85 from Charlotte to Durham now runs (Dobbs 2006). Ca. 16 km (10 mi) to the west of ERDSP lies the Hillsborough Archeological District, which includes several Siouan linguistic-branch settlements, dated to the Woodland period (Dickens et al. 1984, 1987; Ward and Davis 1993). In the northern NC Piedmont (i.e., in our project area), the Woodland period is thought to extend from ca. 1000 BCE to the time of European contact, with Mississippian influence thought to extend only into the southern Piedmont. Sites in the Hillsborough Archeological District (i.e., Frederick, Hogue, Jenrette, Wall sites) have been asso-ciated with at least the Occaneechi and Shakori, but a number of additional tribes are known from the northern Piedmont, including the Eno, Saponi, and Sissipahaw (Davis and Ward 1991; Ward and Davis 1993). Site occupancy is thought to have been temporally limited to a few decades at best and ceramic evidence suggests that at least some early Hillsboro phase populations (1400–1600 CE) moved into the area from elsewhere (Davis and Ward 1991; Ward and Davis 1993). Importantly, it has been demonstrated that subsistence activities emphasized disturbed habitats (Gremillion 1989) and that fire was the primary Amerindian tool to effect disturbance (Fowler and Konopik 2007). Any spatiotemporal, site-occupational shifts in pre-European contact Native Americans likely would have been accompanied by concomitant shifts in land-use. Influx into an area thus likely would have been accompanied by an increase in burning and abandonment–whether through semi-nomadic activity or intertribal conflict–with decreases. We suggest that the timing of the pronounced vegetation class fluctuations is so intriguingly coincidental to the timing of Siouan occupancy and intertribal movements, that it be pursued more vigorously through an interdisciplinary approach involving additional sites in the region. Any such future investigations would also benefit from corroboration and refinement of the $\delta^{13}C$ chronology through additional radiocarbon dating, as well as alternate lines of evidence for shifts in vegetation, such as phytoliths (e.g., McInerney et al. 2011).

AUTHOR CONTRIBUTIONS

AK co-conceived and directed the project, conducted field and lab work, analyzed and interpreted data, took the lead in manuscript preparation. ADS co-conceived the project, conducted field and lab work, wrote portions of the methodology, contributed to data analysis and interpretation, edited the manuscript. EGH wrote portions of the methodology, provided endmember reconstruction, contributed to data analysis and interpretation, edited the manuscript.

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APPENDIX A

Small-scale Species Richness Comparisons

Table A1. Mean 1 m²-plot plant species richness values by physiographic province out of 1470 plots in Fridley et al. (2005).

Province	Mean plot 1 m² spp. richness	Number of plots
CP	9.5	754
Pd	5.0	52
Mt	6.9	664

Table A2. Plots with highest mean 1 m² plant species richness values by province out of 1470 plots in Fridley et al. (2005).

Province	Mean plot 1 m² spp. richness	Plot ID	County
CP	39.5	003-04-0103	Brunswick
Pd	16.3	004-01-0151	Montgomery
Mt	21.8	033-0L-02-3	Macon

Table A3. Lowest and highest 1 m² subplot species richness and mean plot 1 m² plant species richness at Picture Diabase Barrens (PCDB; Granville Co., NC) and Eno River Diabase Sill Preserve (ERDSP; Durham Co., NC). As a comparison, mean plot 1 m² species richness in pine and hardwood forests over Ultisols in nearby Duke Forest (Durham Co., NC) was less than 9 in a study by Israel (2011).

Site	Lowest subplot 1 m² spp. richness	Highest subplot 1 m² spp. richness	Mean plot 1 m² spp. richness	sub-plots per plot	Plot ID	Soil order
ERDSP	7	31	18.1	8	CVS 129-05-1504 (2011)	Alfisol
PCDB-POW	16	19	17.3	4	CVS 129-04-1502 (2011)	Alfisol
PCDB-POW	15	24	21	4	CVS 129-04-1502 (2017)	Alfisol
PCDB-XHF	1	4	2.5	10	PCG04 (1993)	Alfisol
PCDB-XHF	3	12	7.9	10	PCG04 (2001)	Alfisol
PCDB-XHF	5	12	7.9	10	PCG04 (2018)	Alfisol
PCDB-XHF	8	19	13.6	9	PCG05 (1993; pre-burn)	Alfisol
PCDB-XHF	7	22	15.7	10	PCG05 (1994; post-burn)	Alfisol
PCDB-XHF	6	27	19.9	10	PCG05 (2001)	Alfisol
PCDB-XHF	4	23	17	10	PCG05 (2018)	Alfisol
			14.1	85		

APPENDIX B

Plant Species Richness and Endemism in the Piedmont

Based on species distributions in Weakley (2015), 2505 taxa (spp., subsp. and var.) are native to the Piedmont physiographic province of eastern North America. Sixty-nine (2.8%) of these are endemic to the Piedmont (Tables B1 and B2 below). Among Piedmont endemic taxa, the largest group are endemics of granitic flatrocks and outcrops (40.6%; Table B1 below). The percent of all Piedmont taxa that are endemic to Piedmont grasslands, including prairie-affinity patches, savannas, and woodlands is 0.8% (Table B1 below).

Table B1. Habitat classes for taxa (sp., subsp., var.) endemic or nearly endemic to the Piedmont physiographic province.

Habitat class	Number of taxa	Percentage of all Piedmont endemics	Percentage of all Piedmont taxa
1. Shallow soils of flatrocks or domes (usually granitic or sandstone, rarely diabase)	28	40.6	1.1
2. Bottomland forests, streambanks, river shoals, mesic forests	20	29.0	0.8
3. Barrens, glades, rocky or dry woodlands and forests	21	30.4	0.8
	69		

Table B2. List of taxa (sp., subsp., var.) endemic or nearly endemic to the Piedmont physiographic province by habitat class (based on extraction from Weakley 2015, 2020).

Shallow soils of flatrocks or domes (usually granitic or sandstone, rarely diabase)	Bottomland forests, streambanks, river shoals, river scour, mesic forests	Barrens, glades, rocky or dry woodlands and forests
Allium speculae Ownbey & Aase	*Cardamine micranthera* Rollins	*Acmispon helleri* (Britton) A. Heller
Allium keeverae D.B. Poind., Weakley & P.J. Williams	*Collinsonia* L. sp. 1	*Amorpha schwerinii* C.K. Schneid.
Cyperus granitophilus McVaugh	*Eurybia jonesiae* (Lamboy) G.L. Nesom	*Baptisia aberrans* (Larisey) Weakley
Diamorpha smallii Britton ex Small	*Eurybia mirabilis* (Torr. & A. Gray) G.L. Nesom	*Baptisia bracteata* Muhl. ex Elliott
Euphorbia georgiana Mayfield	*Geum lobatum* (Baldwin) Smedmark	*Clinopodium* L. sp. 1
Eurybia avita (Alexander) G.L. Nesom	*Hexastylis lewisii* (Fernald) H.L. Blomq. & Oosting	*Clinopodium talladeganum* B.R. Keener & Floden
Fimbristylis brevivaginata Kral	*Hexastylis minor* (Ashe) H.L. Blomq.	*Crataegus aemula* Beadle
Gratiola amphiantha D. Estes & R.L. Small	*Hexastylis naniflora* H.L. Blomq.	*Crataegus brittonii* Eggl.
Gratiola graniticola D. Estes	*Hymenocallis coronaria* (J. Le Conte) Kunth	*Crataegus buckleyi* Beadle
Helianthus porter (A. Gray) Pruski	*Ilex cuthbertii* Small	*Cuscuta harperi* Small
Hypericum radfordiorum Weakley ex J.R. Allison	*Magnolia acuminata* (L.) L. var. *subcordata* (Spach) Dandy	*Dichanthelium harvilii* J.C. Ludwig & LeBlond
Isoetes piedmontana (N. Pfeiff.) C.F. Reed	*Phacelia maculate* Alph. Wood	*Echinacea laevigata* (C.L. Boynton & Beadle) S.F. Blake
Isoetes L. sp. 4	*Rhododendron eastmanii* Kron & Creel	*Eutrochium purpureum* (L.) E.E. Lamont var. *carolinianum* Sorrie
Isoetes L. sp. 5	*Smilax leptanthera* Pennell	*Helianthus laevigatus* Torr. & A. Gray
Isoetes L. sp. 6	*Solidago plumosa* Small	*Helianthus schweinitzii* Torr. & A. Gray
Isoetes tegetiformans Rury	*Stachys matthewsii* G.P. Fleming, J.B. Nelson & J.F. Townsend	*Heuchera caroliniana* (Rosend., Butters & Lakela) E.F. Wells
Isoetes virginica N. Pfeiff.	*Trillium catesbaei* Elliott	*Marshallia legrandii* Weakley
Isoetes melanospora Engelm.	*Trillium discolor* T. Wray & Hook.	*Pediomelum piedmontanum* J.R. Allison, M.W. Morris & A.N. Egan
Juncus georgianus Coville	*Trillium oostingii* Gaddy	*Quercus georgiana* M.A. Curtis
Micranthes petiolaris (Raf.) Bush var. *shealyi* P.D. McMillan & L. Cushman	*Trillium reliquum* J.D. Freeman	*Solidago pallescens* C. Mohr.
Mononeuria uniflora (Walter) Dillenb. & Kadereit		*Symphyotrichum depauperatum* (Fernald) G.L. Nesom
Phacelia dubia (L. Trel.) var. *georgiana* McVaugh		
Phemeranthus mengesii (W. Wolf) Kiger		
Phemeranthus piedmontanus S. Ware		
Portulaca coronata Small		
Portulaca smallii P. Wilson		
Rhynchospora saxicola Small		
Sedum pusillum Michx		