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WETLAND ECOLOGY

A Hydrogeologic-Landscapes Framework for Depressional-Wetland Vegetation in the Southeastern Coastal Plain, USA

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Abstract

Numerous wetland depressions occur across the U.S. Atlantic Coastal Plain, a region of complex physiography spanning a landward-to-seaward elevation gradient. Coastal Plain depressional wetlands are noted for supporting a diversity of plant communities that provide important faunal habitats. Because these "isolated" wetlands are vulnerable to degradation and loss on private lands, protected and managed public lands have become important refugia for their conservation. A practical system of vegetation types and vegetation-dynamics models can aid in developing management or restoration strategies for these conserved wetlands. The concept of hydrogeologic landscapes provides a useful model framework because landform, soils, and topographic position can influence not only depression form and hydropattern, but also ecological drivers of vegetation change such as drought, fire, and land-use. In the Lower Coastal Plain of South Carolina, USA, a hydrogeologic-landscapes approach was used to examine relationships between wetland vegetation and depression attributes such as size, soil type, and hydroperiod. The Lower Coastal Plain data were also combined with a similar Upper Coastal Plain study to provide a synthetic analysis of region-wide patterns. These studies identified a consistent set of wetland vegetation types that differed in landscape-associated depression attributes. Wetland types also differed in occurrence across sub-regions, owing in part to contrasting histories of land-use and wetland disturbance. The findings were used to develop conceptual state-change models that link wetland vegetation to depression hydropatterns and other ecological drivers in different landscape settings.

Keywords Carolina bay · Coastal plain · Depressional wetland · Hydrogeologic landscape · Wetland vegetation

Introduction

The Atlantic and Gulf Coastal Plains represent one of several U.S. physiographic provinces with high numbers of "isolated" depressional wetlands, a hydrogeomorphic class (Brinson 1993) with ponding regimes that are driven by variation in rainfall inputs and some interactions with shallow groundwater (Tiner 2003). Coastal Plain depressions vary considerably in size, form, and origin across a large geographic and climatic range. They are notable for supporting a diversity of vegetation communities that provide critically important habitats for rare plants and wetland-dependent animals (reviews include Sharitz and Gresham 1998; Kirkman et al. 2012; Cartwright and Wolfe 2016). These wetlands have been especially vulnerable to degradation and loss from agriculture, forestry and urbanization, owing to their frequent small size, hydrologic variability, and lack of surface connections to other water bodies. Despite efforts over several decades, Coastal Plain depressional wetlands continue to lack regulatory protections on private lands (Christie and Hausmann 2003; De Steven and Lowrance 2011; Gardner and Okuno 2018). Consequently, public lands have become important refugia for this wetland class; for example, these wetlands are typically ranked as a special-interest ecosystem in management plans for federally-owned National Forests across the Southern U.S. (USDA Forest Service 2004, 2014, 2017).

Strategies for maintaining or restoring these important wetlands can be aided by conceptual models that link identifiable vegetation types to key depression attributes (e.g., hydropattern, size, soil type) and also to important environmental drivers of vegetation change. The concept of hydrogeologic settings or "landscapes" can be a useful framework for such models (Godwin et al. 2002), because the correlated properties of landform, soils, and topographic position influence hydrologic systems

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at coarse and fine scales (Winter 2001; Ator et al. 2005). For example, geomorphology-influenced hydrologic settings have been used to predict the potential vegetation of multiple wetland types across the Mississippi Alluvial Valley (Klimas et al. 2009), and relative topographic position has been shown to influence hydrologic regimes and vegetation locally in Gulf Coastal Plain depressional wetlands (Kirkman et al. 2000). Complex hydrogeologic landscapes occur in the South Carolina Coastal Plain, which spans several landward-to-seaward sub-regions that differ considerably in surficial geology and topography (Fairey 1977; Soller and Mills 1991). While the vegetation types of depressional wetlands in this region have been regarded as difficult to predict (e.g., Richardson and Gibbons 1993), understanding how vegetation-environment relationships vary across sub-regional hydrogeologic landscapes can aid in developing locally-based models for wetland conservation and management.

Botanical studies of depressional wetlands in the Carolinas have described numerous plant "communities" based on plot-scale data (e.g., 9–13 groups and 63 community-types in Nifong 1998; 18 alliances and 44 associations in NatureServe 2021), but such fine-scale classifications can be difficult to interpret or use in a management context. Wetland-level vegetation classifications offer a practical basis for managing depressions as functional units, especially if the dominant vegetation can be linked to definable wetland attributes and landscape settings. An early qualitative survey across four geographic sections of the South Carolina Coastal Plain (Bennett and Nelson 1991) classed wetland depressions into six to eight vegetation types with recognizable differences in distribution, dominant species, and relative canopy openness. Using a quantitative approach in the Upper Coastal Plain sub-region, De Steven and Toner (2004) identified six wetland types ranging from deepwater ponds to emergent marshes and closed forests. They found that these types differed in soil and hydrologic attributes that were, in turn, associated with differing hydrogeologic landscapes and land-use histories. Their results also suggested landscape-dependent patterns of vegetation dynamics, with implications for wetland management and restoration.

Here we report on a parallel study conducted in the South Carolina Lower Coastal Plain sub-region, where contrasting landforms, soils, and land-use histories could result in different vegetation types and environmental correlations. This paper addresses two objectives: 1) identify the principal Lower Coastal Plain wetland types and determine their relationships to depression attributes and hydrogeologic landscapes, and 2) synthesize results from the two studies to provide a conceptual framework for the important drivers of vegetation composition and dynamics across the Coastal Plain region.

Coastal Plain Landscapes and Study Areas

South Carolina's Coastal Plain region is divided into three physiographic sub-regions that vary in topography and surficial geology (Fairey 1977). The Tertiary-age Upper ("Inner") Coastal Plain (elevations > 76 m [250 ft] above sea level) has varied, dissected topography with moderate to high relief. A broad "Outer" Coastal Plain, representing a sequence of marine-origin coastal terraces, is subdivided into a Pliocene-age Middle Coastal Plain tableland (43–76 m elevation), and a Lower Coastal Plain of low-relief Pleistocene terraces descending from 43 m (140 ft) elevation to sea level. Forestry and agriculture are the primary regional land-uses, with agricultural lands found more commonly in the Upper and Middle Coastal Plains. Depressional wetlands of varying size and type occur across the region. The iconic "Carolina bays" — large, elliptical depressions on wide, level terrain with sandy sediments — are features of the Middle and Lower Coastal Plains (Soller and Mills 1991; Marlowe 2008), but smaller, rounded depressions of karstic origin co-occur in the same areas (unrecognized by Sutter and Kral 1994, but noted in Nelson 1986; Tiner 2003; Willoughby 2007). Similar depressions of possible clay-subsidence origin (variously termed high ponds, Grady ponds, or Citronelle ponds) predominate in the Upper Coastal Plain, where Carolina bays are uncommon (see De Steven and Toner 2004; Cartwright and Wolfe 2016).

The De Steven and Toner study in the western half of the South Carolina Upper Coastal Plain (Bennett and Nelson's NW section, in part) spanned a multi-county area focused on and around the U.S. Department of Energy's Savannah River Site (SRS), an 80,000-ha (198,000-ac) land reserve of managed pine and pine-hardwoods forests. Surrounding areas were typically managed or protected forests as well as agricultural lands. The study identified three hydrogeologic landscape settings containing depression wetlands: Sandhill (level to sloping uplands of deep, droughty sands), Loam Hill (dissected uplands with shallow-sand and sandy-loam soils), and River Terrace (relict alluvial terraces with clay soils and some deeper sands of possible colluvial origin). As defined in the study, the Sandhill landscape represents exposed or overlying strata of mid-Tertiary or Pliocene age (Prowell 1994) that are distinct from higher "Fall-Line Sandhills" which lie along the inner margin of the Coastal Plain. The Sandhill and Loam Hill landscapes are generally well-drained, whereas lower-elevation River Terraces may be poorly- to somewhat poorly-drained. Some large "Carolina bay"-like features are found mainly on deep-sand landscapes; other depressions of variable size and form occur in all landscape settings. (Note that earlier studies often refer to any depression as a Carolina bay, regardless of size or form).

The second study was conducted on the 105,000-ha (259,000 ac) Francis Marion National Forest (FMNF), located within the western half of the South Carolina Lower Coastal Plain (Bennett and Nelson's SW section). The FMNF encompasses managed and unmanaged pine and pine-hardwood forests, large expanses of lowland and river swamps, and coastal tidal marshes. Analogous to the Upper Coastal Plain, depressional wetlands occur in three Lower Coastal Plain hydrogeologic landscapes that differ in physiography, soils, and relict geological landforms (Table 1). Sand Ridges represent ancient coastal beach scarps and have deep-sand soils. Lower-lying Flats, with predominantly shallower loamy-sand soils, are nearly level and often poorly drained. Terrace landscapes have predominantly clay soils and represent a relict fluvial surface and an older coastal terrace, respectively.

Depressional-wetland abundance within the FMNF administrative boundary was tabulated using 1:24,000 topographic maps and aerial photos (false-color infrared, orthomosaic quarter-quads) to locate all depressions ≥ 0.2 ha (0.5 ac) on representative areas of the three landscapes. This survey encompassed roughly 70% of total FMNF land area and most of the uplands. Wetland areas were digitized from the photography in a GIS coverage, which also included overlays of topographic and soil survey maps. The survey identified 166 depressional wetlands ranging from 0.2 ha to 103 ha, with 51% occurring on Sand Ridges, 27% on Flats, and 22% on Terraces. Larger depressions (> 4 ha) occurred only on Sand Ridges (cf. Table 1). Compared to a similar survey on the Upper Coastal Plain SRS (Lide 1994), the FMNF has relatively more small depressions < 1 ha, but also relatively more large depressions > 10 ha (Fig. 1). Smaller wetlands occur in all landscapes, but the largest Carolina bays (50–103 ha) were found only on FMNF Sand Ridges (with one exception in the SRS Sandhill landscape).

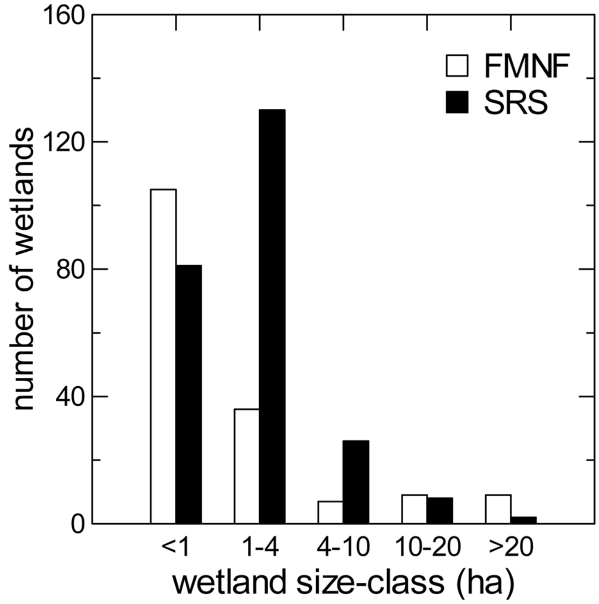

Fig. 1 Size distribution of depressional wetlands ≥ 0.2 ha on the Francis Marion National Forest in the Lower Coastal Plain (n = 166), and on the Savannah River Site in the Upper Coastal Plain (n = 247; data from Lide 1994)

Methods

From the GIS depressional-wetland coverage for the FMNF, we chose a restricted-random sample of 26 wetlands for intensive study, with constraints of location on National Forest land and accessibility from a road. Site selection was stratified by landscape and the three common size-classes (< 1 ha, 1–4 ha, and 4–10 ha), yielding a representative sample of 11 Sand Ridge wetlands (on the "Cainhoy ridge"; see Table 1 footnote), 8 Flat wetlands, and 7 Terrace wetlands. The selection did not include very large Carolina bays, which typically have distinctive pocosin (shrub-bog) vegetation that has been well-described in other studies (Porcher 1966; Bennett and Nelson 1991; Weakley and Schafale 1991). Following the methodologies in De Steven and Toner, we assembled data on key wetland attributes (e.g., size, soils, hydrology) and sampled plant species composition to identify and describe vegetation types.

Table 1 Features of three Lower Coastal Plain depressional-wetland landscapes on the Francis Marion National Forest, South Carolina

	Hydrogeologic Landscape		
Feature	Sand Ridge	Flat	Terrace
Pleistocene landform[a]	barrier beach	backbarrier/lagoon	riverine; high terrace
Pleistocene coastal terrace(s)[a]	Pamlico/Lower Talbot; Upper Talbot	Lower Talbot	Upper Talbot; Penholoway
Land relief and drainage class	flattened ridge, well- to moderately well-drained	level, moderately to somewhat poorly drained	level, moderately to somewhat poorly drained
Predominant soils (taxonomy)	Quartzipsamments and Alorthods	Paleudults and Paleaquults	Paleudults and Paleaquults
Predominant soil types	deep sands	shallow/loamy sands	clays
Sand depth to subsoil layer[b]	≥ 100 cm	50 cm	< 25 cm
Median (range) elevation, m[c]	12 (8–15)[d]	9 (6–11)	7 (5–9); 14 (9–17)
Mean (range) wetland size, ha	9 (0.2–103)	0.7 (0.2–4)	0.7 (0.2–3)

[a] Sources: Soil Survey Staff 1980, McCartan et al. 1985. Sand Ridge landscapes represent two scarps (Cainhoy; Bethera)

[b] Typical values for the soil types (Clemson Extension Service 2001)

[c] Meters above sea level, based on topographic elevations of all FMNF depressions

[d] Overall values; ranges for the Cainhoy and Bethera ridges, respectively, are 8–14 m and 11–15 m

Wetland Soils and Hydrology

The principal soil type of each study wetland was characterized with 2–3 soil profiles spaced along a transect from the center to a point mid-way to the wetland edge. Each profile (including horizons and textures) was described to a depth of 152 cm (60 inches) and assigned to soil series by a professional soil scientist; series taxonomy was also noted (Soil Survey Staff 1999). Based on South Carolina soil-series groups (Clemson Extension Service 2001), the profile data were used to class each wetland's soil type as either deep sand (group 1 or 2), shallow sand/sandy loam (group 3), or clay (group 4). Soil type was also quantified as the profile depth of sandy horizons ("sandy epipedon") over a clay-textured subsoil horizon; typical depths are 100–200 cm for deep sands, 50–75 cm for shallow sand/sandy loams, and ≤ 25 cm for clays. In 20 wetlands, the topsoil layer (0–15 cm) of the central profile was sampled for lab analysis of total organic carbon (multiplied by 1.7 to estimate % organic matter). Samples could not be obtained for 6 wetlands owing to logistical constraints. Association between wetland soil type and hydrogeologic landscape (Table 1) was tested with likelihood-ratio chi-square (df = 4).

The area's climate is humid subtropical; rainfall averages 1310 mm y^{-1} (51.6 inches), with 50–60% occurring in summer and autumn (June–October) (National Oceanic and Atmospheric Administration, climatological normals for 5 stations). The Atlantic hurricane season peaks in August to September and may bring heavy rain events in some years. In response to the seasonality of rainfall and evapotranspiration, water levels in Coastal Plain depressions typically rise during the winter months to maximum ponding depths in spring (March–April) and dry down to minimum (or zero) depths by the end of November. Starting in 2003, surface water depths (pond stage) were monitored with Type M staff gauges in an initial group of 19 study wetlands. One gauge was placed at the deep center of each wetland, with additional gauges placed at peripheral locations and calibrated to the center gauge. Water depth was recorded bi-weekly and translated to pond stage at the wetland center. Monitoring of gauged wetlands was conducted from April 2003 to April 2005, encompassing two annual cycles and three spring seasons. In the remaining 7 study wetlands, pond stage was measured bi-weekly to monthly at permanently marked deep-center points from February 2004 to February 2005 (one annual cycle). Local rainfall data for the study period were obtained from a weather station (Met25) maintained on the FMNF Santee Experimental Forest (USDA Forest Service, Southern Research Station). The year 2003 was extremely wet (1671 mm, 27% above normal), whereas 2004 was drier (962 mm, 26% below normal) but received a cluster of heavy rains from two hurricanes and a tropical storm in the month of August.

The monitoring data were used to calculate descriptive hydrologic metrics for each wetland, including growing-season hydroperiod (percent of dates ponded from April 1 to November 30), number of growing-season months with ponding, and "normal pool" depth (defined as the average maximum spring depth). All wetlands were nearly continuously ponded in the extreme wet year of 2003, thus the drier year of 2004 was more informative for characterizing differences among wetlands. We used the quantitative metrics to assign a ranked index of hydroperiod pattern to each wetland, where 4 = deep and semi-permanently ponded; 3 = moderately deep and seasonally ponded; 2 = shallow and seasonally ponded; and 1 = shallow and short-seasonal to temporarily ponded. The seven less-monitored wetlands were assigned index values based on their 2004 metrics plus pattern-matching with gauged wetlands. The hydroperiod index was strongly correlated with 2004 growing-season hydroperiod (Pearson $r = 0.90$, df = 24, $P < 0.001$), normal pool depth ($r = 0.93$, $P < 0.001$), and other quantitative metrics.

Vegetation Classification and Analyses

In late summer (July–August), we sampled plant composition at the whole-wetland scale using a modified line-intercept method (see De Steven & Toner). Briefly, in transects spanning the long axis and two perpendicular axes of each wetland interior, plant species presence was recorded in 1-m line segments at 10-m intervals (20-m intervals in one large 8-ha wetland). Presence was tabulated in three strata: canopy/overstory, mid-story, and shrub/ground layers. The percent of sample segments in which a plant species occurs (irrespective of stratum) provides an abundance metric ("frequency") that is proportional to its coverage (dominance) in each wetland. The full dataset containing 205 identified species was used to calculate descriptive traits for each wetland's vegetation, including species richness (number of species), percent and relative abundance of herbaceous and woody species, and percent canopy cover (percent of segments with an overstory stratum).

The plant species dataset was used to class wetlands into vegetation types in PC-ORD (McCune and Mefford 2011). To reduce data noise from infrequent and erratic occurrences, we merged some ecologically-similar species to genus level and omitted taxa occurring in < 10% of wetlands, yielding a wetlands-by-species abundance matrix with 82 taxa. Cluster analysis used the flexible-beta method (cf. McCune and Grace 2002) with Sorenson dissimilarity and a beta value of -0.1, which produces results very similar to the group-average method but with less chaining. Two of 26 wetlands were atypical outliers that could not be assigned to a group. Indicator Species Analysis (Dufrene and Legendre method) of the 24 classified wetlands identified the species whose presence and abundance were strongly associated with specific vegetation types. Because ISA can produce spurious results for infrequent species and may only weakly detect association with more than one group, we limited the tests to 46 taxa occurring in at least 20% of wetlands and used a significance threshold of $P < 0.10$.

As in the Upper Coastal Plain study, we evaluated past disturbance and temporal change in vegetation cover by interpreting historical (black-and-white) aerial photography; in this case, the photos dated from 1934, shortly before the FMNF was established in 1937. For each wetland, the percentage of interior area in three visual categories (open/unwooded, sparsely-wooded, closed forest) was estimated. Intensity of wetland alteration (e.g., ditching, clearing, agricultural use) was scored with a disturbance index ranging from 0 (no apparent alterations) to 4 (major alterations of the interior) (details in De Steven and Toner). As a metric for land-use disturbance, we estimated the percentage of a 100 m-wide upland zone around each wetland that was open or sparse-wooded land (i.e., open-field or successional) versus closed forest. Wetlands were generally protected from significant disturbance after FMNF lands were placed into conservation and reforestation status. Currently, upland forest stands (particularly longleaf pine, *Pinus palustris*) are managed with prescribed fires, which may spread into wetlands when they are dry. This fire potential for each wetland was quantified as a burn-frequency index for the number of adjacent upland burns occurring in a 15-year period (1996–2005), where 1 = 0–2 burns, 2 = 3–4 burns, and 3 = 5 or more burns (data obtained from the FMNF). We also measured the distances of fire spread into nine study wetlands whose surrounding uplands were burned during the study period. Six of the nine wetlands were in Sand Ridge landscapes.

For the 24 classified wetlands, we tested for differences among five identified vegetation types in descriptive traits (species richness, percent herbaceous species, relative herb abundance), distribution among hydrogeologic landscapes, and wetland attributes (including depression area, soil properties, hydropattern, and historical disturbance). Categorical variables (landscape location, wetland soil type) were tested with likelihood-ratio chi-square (df = 8). Quantitative variables were tested with ANOVA (df = 4, 19). Data were transformed as needed to improve normality and variance homogeneity (log transformation for wetland area; square-root transformation for soil organic matter; arcsine square-root transformation for percentage variables). Specific post-hoc comparisons were tested with Scheffé contrasts (Zar 1999). Transformations did not change statistical conclusions compared to tests of untransformed variables. To assess vegetation stability or successional change over time, the historical state of each wetland was assigned as either open/herbaceous (< 30% forest cover), partially-forested (30–70% forest cover), or closed forest (> 70% forest cover). Historical state was cross-tabulated with contemporary vegetation type and tested by chi-square (df = 8), with a focus on successional transitions from open to forested cover. Statistical analyses were performed in SYSTAT® (SPSS, Inc., Chicago, IL).

Synthetic Analyses

Using the dataset-reduction procedures described above, the species data of both Coastal Plain studies were synthesized into a matrix with 83 wetlands (26 Lower, 57 Upper) and 96 plant taxa occurring in > 5% of sites. Wetlands were re-classed into vegetation types with the same flexible-beta method, which accurately reproduced the earlier Upper Coastal Plain classification based on a group-average method. Clustering identified six groups, with only three wetlands not aligning reliably to a group. A complementary Detrended Correspondence Analysis ordination (cf. McCune and Grace 2002) was used for visualizing the variation in species composition among types. The array of sites along ordination axes can reflect underlying environmental gradients and also shows compositional overlap between classified groups. While non-metric multi-dimensional scaling has been advocated as a preferred ordination method, DCA is useful for resolving heterogenous data with wide first-axis gradients (ter Braak 1995; cf. De Steven and Toner 2004).

Wetland attribute data were updated with minor corrections to the earlier dataset for consistency across the two studies. The same statistical procedures were used to test differences among the six vegetation types in their environmental, historical, and landscape attributes (df = 10 for chi-square tests, df = 5, 74 for ANOVAs). Overall patterns were summarized in a general table for the wetland types and their associated depression and landscape attributes.

Results

Soils and Hydrology of FMNF Depressions

In this Lower Coastal Plain area, the hydric soils of wetland depressions are strongly associated with hydrogeologic landscape (chi-square = 35.4, df = 4, $P < 0.001$). All wetlands on Sand Ridges had deep-sand soils (group 1; Alaquods and Humaquepts in Lynn Haven, Rutlege, and Pickney series), 63% of wetlands on Flats had shallow/loamy-sand soils (group 3; Typic Aquults in Paxville and Pantego series), and 71% of Terrace wetlands had clay soils (group 4; Typic Aquults in Coxville, Bladen, Byars, and Cape Fear series). This was a closer association between depression soils and upland landscapes than was found in the Upper Coastal Plain. No soil profiles in the Sand-Ridge depressions were "clay-based" (a regional term sometimes used for Carolina bays with mineral soils), but one karst depression excluded from the above analysis had a deep organic soil (Pungo muck, Typic Haplosaprist). Sixty-two percent of the wetland depressions had adjacent upland soil profiles exhibiting a water table at depths of 50–100 cm (20–40 inches).

Hydropatterns (spring maximum depths and ponding durations) varied between years and differed among wetlands. All wetlands had long growing-season hydroperiods (72–100% duration) in the extreme wet year of 2003, but exhibited a wider and more characteristic range of hydroperiods (28–100% duration) in the drier year of 2004. Growing-season hydroperiod in 2004 was positively correlated with normal pool depth, which reflects basin depth (Pearson $r = 0.79$, df = 24, $P < 0.001$). However, depth was not a simple function of depression area (correlation not significant); smaller wetlands ranged from shallow to deep (0.3 m to > 1 m), whereas the large Sand-Ridge wetlands were shallow (pool depths < 0.45 m). Landscape setting influenced hydropatterns indirectly, through relationships to soil type and depression size. Among 15 wetlands with shallow-sand and clay soils (on Flats and Terraces), the hydroperiod index averaged 3.3 and correlated positively with wetland area (Pearson $r = 0.72$, df = 13, $P < 0.01$). Among 11 wetlands with deep-sand soils (on Ridges), the hydroperiod index averaged lower (2.2) but trended inversely with area, in that values in smaller wetlands (< 3 ha) ranged from short to long (1–4) but were short (1–2) in the larger wetlands (3–8 ha).

Extreme rainfall events can alter seasonal hydropatterns, given the area's proximity to the Atlantic coast. The multiple hurricane/storm events in August 2004 produced almost 280 mm of rainfall (29% of the annual total). Nearly 70% of study wetlands had dried down by mid-June or earlier, but the concentrated rains caused re-ponding of dry wetlands and water-level rises in all wetlands, in some cases up to normal pool depths. On low-lying Flats, some adjacent uplands were also temporarily flooded. Post-storm ponding durations were proportional to pre-storm durations ($r = 0.83$, df = 24, $P < 0.001$), with about half the wetlands drying again by year's end.

Vegetation Types of FMNF Depressional Wetlands

Cluster analysis identified five vegetation groups, although some are variants of others owing to overlaps in species composition (Table 2, Appendix Table 6). Most wetlands (71%) were forested, averaging 82–96% canopy cover and 60–70% woody species. Two of three forested types were dominated by swamp tupelo/swamp blackgum (*Nyssa biflora*) but differed in co-dominant or associated species. Tupelo-cypress swamps have frequent co-occurrence of pondcypress (*Taxodium ascendens*) and sparse herbaceous cover, whereas tupelo-sedge swamps have slightly lower canopy density and greater herb cover, particularly the flood-tolerant peatland sedge (*Carex striata*) and a common fern species (Virginia chain-fern, *Woodwardia virginica*). The shrub shining-fetterbush (*Lyonia lucida*) is common to both types. In contrast, the mixed bottomland-hardwoods swamp was distinguished by additional tree species of floodplains and lowlands, including Carolina red maple (*Acer rubrum* var. *trilobum*), laurel and willow oaks (*Quercus* spp.), and sweetgum (*Liquidambar styraciflua*).

Two less common vegetation types (29% of wetlands) were wet savannas characterized by pondcypress as a dominant or an associated species, but a low occurrence of tupelo (Table 2). Pondcypress savanna is a woodland type with a semi-forested canopy and an understory of various herbs and shrubs (e.g., *Lyonia*). Grass-shrub savanna is an 'open' vegetation type (averaging < 40% canopy), with a species-rich grass-forb layer and a varying low-shrub component (principally inkberry, *Ilex glabra*). Apart from the difference in pondcypress presence, the two savanna types shared a similar ground flora of grasses (e.g., *Andropogon, Panicum, Amphicarpum),* sedges and rushes (e.g., *Rhynchospora*), forbs (e.g., *Iris* and *Lachnanthes),* and evergreen shrubs (e.g., *Ilex,* and *Persea*). Other herb taxa occurring at lower abundances included multiple species of witch-grass (*Dichanthelium*), meadow-beauty (*Rhexia*), water-primrose (*Ludwigia*), spikerush (*Eleocharis*), yellow-eyed grass (*Xyris*), and pipewort (*Eriocaulon*).

As in the Upper Coastal Plain, the FMNF wetlands had high floristic diversity at a landscape scale. Sampled richness averaged 30 species per wetland (range 12–80), while a cumulative total of 205 species was recorded across all wetlands. Savanna wetlands were significantly more species-rich (Scheffé contrast, F = 36.4, df = 1, 19, $P < 0.001$), particularly grass-shrub savannas with an average of 59 species (Table 2). One unclassified wetland, located on the innermost coastal terrace (Penholoway), had a distinctive species composition resembling an emergent-marsh type of the Upper Coastal Plain (see Synthesis, below).

Not included in the study sample, large pocosin depressions (up to 100 ha) are a sixth vegetation type on the FMNF, occurring on both Sand Ridges but typical of the older Bethera scarp (cf. Table 1; Porcher 1966). Pocosin vegetation is characterized by dense thickets of evergreen shrubs (e.g., fetterbushes, *Lyonia* spp.; gallberries, *Ilex* spp.; sweet pepperbush, *Clethra alnifolia*; huckleberries, *Gaylussacia* spp.), with small trees such as pond pine (*Pinus serotina*) and evergreen "bay" species (swamp bay, *Persea palustris*; sweetbay, *Magnolia virginiana*; and loblolly bay, *Gordonia lasianthus*). Typical soils are organic peats, a result of prolonged soil inundation (Richardson and Gibbons 1993). In South Carolina, pocosin depressional wetlands are more common in the eastern half of the Lower Coastal Plain (Bennett and Nelson's SE section).

Table 2 Vegetation characteristics of five wetland types in 24 Lower Coastal Plain depressional wetlands.

Wetland Type	Percent Canopy	Species Richness	Percent Herb Species	Percent Herb Abundance	Characteristic Dominants	Frequent Associated Species
Mixed BLH Swamp	91 (7)	22 (2)	31 (8)	19 (8)	*Acer rubrum, Quercus* spp.	*Liquidambar styraciflua, N. biflora, Pinus taeda, Carex glaucescens*
Tupelo-Cypress Swamp	96 (2)	23 (3)	41 (6)	18 (7)	*Nyssa biflora*	*Taxodium ascendens, Lyonia lucida*
Tupelo-Sedge Swamp	82 (5)	20 (4)	39 (4)	36 (4)	*Nyssa biflora, Carex striata*	*Woodwardia virginica, L. lucida*
Pondcypress Savanna	73 (5)	34 (2)	55 (2)	42 (6)	*Taxodium ascendens*	*L. lucida, Iris* spp., *Rhynchospora* spp., *N. biflora*
Grass-Shrub Savanna	31 (13)	59 (8)	71 (7)	68 (12)	*Iris* spp., *Ilex glabra, Panicum* spp.	*T. ascendens, Rhynchospora* spp., *Andropogon* spp., *Lachnanthes* sp.

BLH Bottomland hardwoods. Values are means (s.e. in parentheses); all traits differed significantly among types (ANOVA, all $P<0.01$). See Appendix Table 6 for species-abundance data

Vegetation–Environment Relationships and Change

The five FMNF wetland types occurred non-randomly across hydrogeologic landscapes (chi-square = 18.5, df = 8, $P<0.05$). All mixed-hardwood swamps were associated with Terraces, most tupelo swamps (85%) collectively were on Flats and Sand Ridges, and nearly all wet savannas (86%) were on Sand Ridges. Wetland attributes also differed among types (Table 3). The forested wetlands were generally smaller than savanna wetlands. As indicated by sandy epipedon depths, mixed-hardwood wetlands had clay soils, the tupelo swamps had shallow/loamy sand or deep-sand soils, and savanna types had deep-sand soils. The tupelo-cypress swamps were distinguished by very deep (≥ 1 m), semi-permanent hydroperiods and greater soil organic-matter accumulation. The tupelo-sedge and mixed-hardwood swamps were moderately deep (0.6–0.7 m) with seasonal hydroperiods (ponding 50–60% of the growing season). Savanna wetlands were distinguished by shallow ponding depths (< 0.4 m) and low hydroperiod index values (1–2), with the cypress savannas having somewhat longer-seasonal hydroperiods than the short-seasonal grass-shrub savannas (< 40% duration).

The study wetlands appeared relatively unaltered historically. Prior to FMNF establishment in 1937, lands within the current National Forest were sparsely-populated and had been logged extensively by large timber companies (Hester 2011). On average, 84% of upland area surrounding the study wetlands was historically open or sparse-wooded as a result of this logging (Table 3). Persistent wetness in the low-elevation landscapes also limited the conversion of inland areas to large-scale agriculture. Thus, wetland disturbance-index scores from the 1934 photo imagery were uniformly low, with little evidence of physical alterations such as ditching or agricultural clearing. Currently observable alterations are relatively minor, such as a culvert to prevent road flooding. The historical photo-interpretations suggest relatively stable vegetation structure since the 1930s (Table 4), as current and historic vegetation states are highly associated (chi-square = 25.9, df = 8, $P=0.001$). Of 17 currently forested wetlands (tupelo and mixed-hardwood swamps), 15 (88%) were also forested or semi-wooded historically, whereas the other 2 are small tupelo-sedge wetlands (< 1 ha) that had transitioned from a more open condition. All current savanna wetlands, of which 57% are large (3–8 ha), were likewise open or semi-wooded historically, although wooded cover has increased in some pondcypress savannas since that time. Present-day vegetation types differed in the historical percent of semi-wooded/forested wetland interior (ANOVA, F = 6.4, $P<0.01$), in parallel with their current differences in canopy cover (Table 4).

Uncontrolled fires were frequent in cut-over uplands prior to National Forest establishment, after which most fires were suppressed or managed as forests re-grew or were replanted (Hester 2011). Any historical fire effects on the wetlands are unknown. Contemporary differences in the upland burn-frequency index (Table 3) now reflect landscape-based management objectives. Savanna wetlands are exposed to greater fire potential because xeric Sand-Ridge uplands are frequently burned every three to five years to manage for longleaf pine forests (USDA Forest Service 2017). More mesic upland forests on low Flats or Terraces (e.g., loblolly pine [*P. taeda*] and pine-hardwoods) burn less often. However, fire effects are variable. In nine wetlands where adjacent uplands received mostly dormant-season burns during the study period, the observed fire spread averaged only about 10 m into the wetland periphery owing to saturated or ponded soils. Exceptions were a small tupelo-sedge wetland into which a low-impact summer burn spread completely, and a large savanna wetland that received a management burn to remove encroaching woody species (primarily loblolly pines).

Table 3 Mean values (s.e. in parentheses) for environmental attributes of Lower Coastal Plain depressional-wetland types.

Attribute	Mixed BLH Swamp	Tupelo-Cypress Swamp	Tupelo-Sedge Swamp	Pondcypress Savanna	Grass-Shrub Savanna
Depression area (ha)*	0.7 (0.2)	1.3 (0.3)	0.5 (0.2)	**3.2** (1.7)	**4.0** (1.7)
Sandy epipedon depth (cm)**	33 (8)	104 (16)	105 (17)	**118** (30)	**154** (1)
Soil organic matter, surface (%)*	11 (1)	**31** (9)	18 (3)	11 (1)	8 (3)
Normal pool depth (m)**	0.65 (0.09)	**0.98** (0.03)	0.68 (0.12)	0.33 (0.01)	0.20 (0.06)
Hydroperiod index**	2.4 (0.3)	**3.7** (0.2)	2.5 (0.4)	1.8 (0.2)	1.0 (0)
Growing-season hydroperiod (%), 2004**	50 (6)	**87** (7)	57 (5)	56 (8)	38 (3)
Growing-season months ponded, 2004**	4.5 (0.5)	**7.1** (0.4)	5.5 (0.3)	5.7 (0.3)	3.7 (0.2)
Wetland disturbance index	0 (0)	0.2 (0.1)	0 (0)	0.3 (0.3)	0 (0)
Historical open/sparse upland (%)[a]	77 (11)	72 (10)	100 (0)	98 (2)	94 (6)
Upland burn-frequency index*	1.5 (0.5)	1.7 (0.3)	1.0 (0)	**2.3** (0.7)	**2.8** (0.2)
Number of wetlands in type	4	9	4	3	4

Significant attributes are noted at *$P < 0.05$ or **$P < 0.01$, with contrasts noted for significantly high (boldface) or low (underlined) values

[a] Historical open/sparse upland represents cut-over timberland

Coastal Plain Synthesis

The combined cluster analysis largely confirmed the vegetation types of both studies, with minor shifts in group affiliation of a few wetlands. The complementary ordination analysis (Fig. 2) supported the classification of six vegetation groups region-wide, with the allied tupelo swamps ("gum swamps") and wet savannas, respectively, resolving into two broad types (Table 5). Sampled species richness averaged 20–22 species per wetland in all types except the wet savannas, which averaged 49 species. Not included in the analyses, a seventh regional vegetation group is represented by pocosins and closely-allied bay-tree forests (Bennett and Nelson 1991).

The six vegetation types differed strongly in regional distribution as well as plant composition (Table 5, Appendix Table 7). Three distinctive Upper Coastal Plain types are mostly treeless, although swamp tupelo, pondcypress or the shrub buttonbush (*Cephalanthus occidentalis*) may be variably present at low densities. Semi-permanent, deepwater ponds are dominated by aquatic plants such as water-lily (*Nymphaea odorata*). Two moderately-deep emergent-wetland types are distinguished by different semi-aquatic clonal grasses: grass marsh by maidencane (*Panicum hemitomon*), a robust species which can form nearly monodominant cover, and wet depression-meadow by southern cutgrass (*Leersia hexandra*), a slender species which forms less-dense stands in combination with other graminoids and forbs. Only one example of these emergent types – a grass-marsh depression – was found in the FMNF. The mixed-hardwoods forest type also occurred primarily in the Upper Coastal Plain and is characterized by moderately flood-tolerant trees such as sweetgum and red maple, and by woody vines such as catbrier (*Smilax rotundifolia*) and trumpet creeper (*Campsis radicans*). The FMNF mixed-hardwoods swamps aligned with this group only loosely, owing to relatively higher presence of swamp tupelo and oaks and low woody-vine presence. Conversely, the semi-open to open wet savannas occurred almost entirely in the Lower Coastal Plain, apart from a single Middle Coastal Plain wetland (see De Steven and Toner 2004) that re-classed into this group. A few wet-savanna depressions may occur in the South Carolina Upper Coastal Plain (e.g., Zoellner 2007), but are apparently uncommon. The broad group of tupelo-cypress-sedge swamps is frequent in all Lower Coastal Plain landscapes, but also occurred on Upper Coastal Plain

Table 4 Transition matrix for state-changes between historical (1934) and current vegetation of depressional wetlands on the Francis Marion National Forest, where cell values are number of wetlands in each transition category. Vegetation types are ordered by increasing canopy cover (means shown below column totals)

Historical Vegetation Cover-Type	Current Vegetation Type					
	Grass-Shrub Savanna	Pondcypress Savanna	Tupelo-Sedge Swamp	Tupelo-Cypress Swamp	Mixed BLH Swamp	*Historical Totals*
Open (unwooded)	4	2	2	0	0	*8 (33%)*
Partially-forested	0	1	0	2	2	*5 (21%)*
Closed forest	0	0	2	7	2	*11 (46%)*
Vegetation Type Totals	*4*	*3*	*4*	*9*	*4*	*24*
Current % canopy	31	73	82	96	91	
Historical % partial and closed forest	14	28	52	82	80	

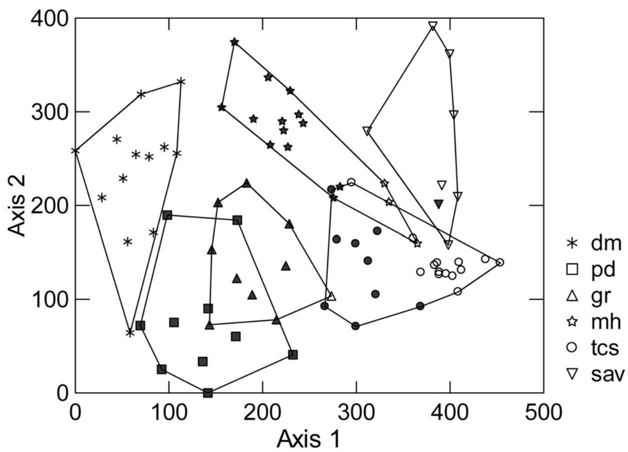

Fig. 2 Detrended Correspondence Analysis (DCA) ordination of 80 Upper and Lower Coastal Plain depressional wetlands. Convex hulls delineate six vegetation groups from cluster analysis (omitting 3 outlier sites). Legend shows symbol type for each group, where dm = wet depression-meadow, pd = open-water pond, gr = grass marsh, mh = mixed bottomland-hardwoods forest, tcs = tupelo-cypress-sedge swamps, sav = wet savannas. In the graph, open (unfilled) symbols represent Lower Coastal Plain wetlands

River Terraces (where some wetlands previously classed as "sedge marsh" were an open-canopy variant of this group). Pondcypress was present in 70% of Lower Coastal Plain wetlands but in only 23% of Upper Coastal Plain wetlands.

Wetland types differed in depression attributes and historical land-uses (Table 5). Open-water ponds and some savanna wetlands tended to be large, but they contrasted strongly in normal pool depths. Forested wetlands were relatively smaller. Depressions supporting ponds, grass marshes, and the tupelo swamps have longer hydroperiods irrespective of soil type, with both ponds and some tupelo swamps (tupelo-cypress variant; cf. Table 3) having deep (> 1 m) and nearly permanent growing-season ponding (7–8 months). Wet depression-meadows and savannas are both associated with sandy soils and are variably seasonal (ponded 3–7 months), but the former were moderately deep whereas the latter had distinctively shallow normal-pool depths (≤ 0.4 m). Mixed-hardwoods wetlands on clay soils had moderately deep ponding but short-seasonal hydroperiods (2–5 months). Finally, wetlands occurring mainly or exclusively on the Upper Coastal Plain (where historical aerial imagery dated to the early 1950s) were exposed to greater prior disturbance, including conversion of uplands to intensive farming and frequent evidence of past ditching in seasonally-ponded wetlands. Most Upper Coastal Plain wetlands maintained relatively stable vegetation after agricultural disturbance ceased, but small, mixed-hardwoods wetlands appeared to be a "re-growth" forest type from historic clearing and drainage (Bennett and Nelson 1991; De Steven and Toner 2004).

Discussion

These Coastal Plain studies suggest a practical system of wetland vegetation types that can be related to depression attributes at local and landscape scales. Apart from minor interpretive differences, the seven types described here (open-water pond, grass marsh, wet depression-meadow, tupelo-cypress swamps, mixed-hardwood swamps, wet savannas, and pocosins) are largely equivalent to the communities described in Bennett and Nelson's qualitative survey of more than 600 South Carolina depressions. Likewise, some North Carolina classifications (e.g., Nifong 1998; Schafale 2012) can be generalized into six to eight vegetation groups that approximately correlate to the South Carolina wetland types, though with somewhat different naming conventions. This classification has potentially wide application, as comparable vegetation types have been described in Gulf Coastal Plain depressional wetlands that include the limesinks of southwest Georgia (Kirkman et al. 2000) and the "cypress domes" and Citronelle ponds of northern Florida, Alabama, and Mississippi (Folkerts 1997; Ewel 1998).

Hydropattern and fire frequency are considered the two primary drivers of vegetation composition and dynamics in Coastal Plain depressional wetlands (e.g., Sutter and Kral 1994; Kirkman et al. 2000; De Steven and Toner 2004; Casey and Ewel 2006). Vegetation composition reflects, in part, the relative flood-tolerance of plant species over a spectrum of depression hydroperiods that contracts or expands in response to climate variability (Collins and Battaglia 2001; Stroh et al. 2008). Nearly all wetlands may be ponded for prolonged periods in very wet years, whereas the deepest and largest wetlands may dry down only during severe multi-year droughts. Early seasonal drawdowns can favor woody plant establishment and succession toward woodland or shrubland, unless counteracted by a return of deep ponding conditions or by the influence of fire. Fires can kill seedlings of pondcypress as well as tupelo and other hardwood trees, but the former is more fire-resistant when older if fires are not severe (Ewel 1998). Evergreen pocosin-shrubs can resprout after fire but are intolerant of deep ponding (Christensen 2000).

Additionally, through their influence on depression physical attributes and hydropatterns, landscape settings enable or constrain which vegetation types can be supported and their degree of susceptibility to the drivers of vegetation change. From the Lower to Upper Coastal Plain, there is a broad gradient of increasing land elevation, topographic relief, and depths to the surficial groundwater aquifer (Gellici and Lautier 2010). Sub-regional hydrogeologic landscapes represent gradients in soil type from deep permeable sands to poorly drained clays, which interact with depression morphology to influence wetland hydropatterns. Hydrogeologic landscapes also influence human land-uses that can alter hydropatterns and fire regimes. Contrasts in these environmental gradients have shaped wetland types and distribution at sub-regional scales.

Table 5 General summary of six depressional-wetland types in the South Carolina Upper and Lower Coastal Plains (CP).

Trait	Open-water Pond	Grass Marsh	Depression Meadow	Cypress-Grass-Shrub Wet Savannas	Tupelo-Cypress-Sedge Swamps	Mixed BLH Forests
Characteristic/defining dominants	*Nymphaea odorata*	*Panicum hemitomon*	*Leersia hexandra*	*Taxodium ascendens,* various graminoids, *Ilex glabra, Iris*	*Nyssa biflora, T. ascendens, Carex striata*	*Liquidambar styraciflua, Acer rubrum*
Percent canopy	17	31	6	51	**80**	**85**
Percent herb abundance	**87**	**69**	**89**	**58**	34	26
Species richness	12–30	7–40	7–41	**30–80**	7–34	7–34
Percent of type in the Lower Coastal Plain (versus Upper)	0	10[a]	0	**88**[a]	**61**	19
Hydrogeologic landscapes[b]	SH, LH, UT	UT, LH, SH	SH, LH, UT	SR, (MCP, FL)	FL, SR, UT, LT	LH, UT, (LT)
Predominant soil types	clays or sands	clays or shallow sands	shallow or deep sands	deep sands	sands or clays	clays
Wetland area (ha)	**7.3**	3.7	3.4	3.9	1.8	2.6
Hydroperiod index	**3.7**	2.9	2.4	<u>1.4</u>	**3.2**	2.1
Typical normal pool depths (m)	**0.7–1.5**	0.6–0.8	0.4–0.8	<u>0.2–0.4</u>	**0.6–1.1**	0.6–0.7
Months ponded, growing-season	**7–8**	**4–8**	3–7	3–6	**5–8**	2–5
Percent of wetlands with past intensive ditching[c]	20	**50**	**54**	0	13	**69**
Percent of wetlands with agricultural upland historically[c]	**90**	**70**	**92**	12	39	**81**
Upland burn-frequency index	1.0	1.0	1.0	**2.4**	1.3	1.1
Number of wetlands in type	10	10	13	8	23	16

BLH Bottomland hardwoods. All traits differed among types at $P < 0.01$; notable contrasts are in boldface or underlined. For descriptive purposes, non-percent values are presented as averages or typical ranges. See Appendix Table 7 for species-abundance data

[a] Grass Marsh percent represents one wetland on a Lower CP terrace; Savannas percent does not include a wetland in the Middle CP (see text)

[b] In order of occurrence frequency. Landscape codes: SH, Sandhill; LH, Loam Hill; UT, Upper CP Terrace; SR, Sand Ridge; FL, Flat; LT, Lower CP Terrace; MCP, Middle CP

[c] All such wetlands are in the Upper CP or Middle CP; see De Steven and Toner 2004 for additional disturbance metrics

Depressional Wetlands of the South Carolina Lower Coastal Plain

In Lower Coastal Plain landscapes, the surficial water-table aquifer occurs at shallow depths and is responsive to large rainfall events, thus depressional wetland hydroperiods can be directly influenced by groundwater fluctuations (Callahan et al. 2017). On Flats and Terraces, depression water volumes are stored mostly above-ground owing to near-surface clayey (low-permeability) soil horizons and high water tables; consequently, ponding durations increase with greater basin size and depth. On the Sand Ridges, depression water volumes are partially contained within the deeper sands, which may have spodic horizons indicating water-table fluctuations in the soil profile (Weber 2011). Thus, although above-ground ponding durations are relatively short in shallow Sand-Ridge wetlands of varying size, the larger wetlands (with larger water volumes) may remain saturated below the surface for longer periods after water draw-down. Conversely, long hydroperiods in deep Sand-Ridge wetlands may result from more persistent connections to shallow groundwater. Nowicki et al. (2022) have discussed a similar pattern in Florida sandhill depressional wetlands.

Owing to this hydrologic environment and low levels of historical disturbance, the Lower Coastal Plain wetlands exhibit a relatively limited variety of vegetation types. The allied tupelo-cypress swamps are the prevalent type and share some tree species with mixed-hardwoods swamps. On the FMNF, these forested wetlands have been stable for over 70 years, having persisted through a historical period when fires were common (though perhaps patchy) in the cut-over uplands. Likewise, the wet-savanna types have persisted as open-herbaceous or sparse-canopy systems for many decades. This stability suggests two distinct types of pondcypress-containing wetlands that are differentiated by hydrogeologic landscape and depression morphology. Cypress savannas are shallow-depth communities of large, flat-bottomed Carolina bays and smaller shallow depressions on xeric Sand Ridge landscapes, where shorter hydroperiods allow for frequent fire to maintain their open character. Swamp tupelo may be present but limited by droughty, infertile soil conditions and/or sensitivity to fire. In contrast, longer-hydroperiod tupelo-cypress swamps predominate in the sandy-loam and clay depressions of low Flats and Terraces, but also occur in small deep-bottomed Sand-Ridge depressions. As both swamp tupelo and pondcypress are highly flood-tolerant, these swamps represent a natural vegetation type with lower fire susceptibility owing to prolonged wetness (in deep basins) or to location in poorly-drained landscapes that are less fire-prone. The pondcypress component may vary from low to high for various reasons, whether by chance or from removal in the distant past (cf. Bennett and Nelson 1991; Casey and Ewel 2006). Ewel (1998) also noted that swamp tupelo becomes more co-dominant with pondcypress in depressions that occur northward of southern Florida.

Depressional Wetlands of the South Carolina Upper Coastal Plain

The Upper Coastal Plain represents older and geologically re-worked ("erosional") surfaces (Soller and Mills 1991) with complex interbedding of sand and clay sediments, high topographic relief, and often greater depths to the surficial water table (Gellici and Lautier 2010). De Steven and Toner (2004) found that depressional wetland hydropatterns exhibited more complex relationships to hydrogeologic landscapes and local attributes. Wetlands at the higher Loam Hill and Sandhill elevations appear to have water volumes perched above the regional water table (based on Hiergesell and Jones 2003), whereas wetlands on low River Terraces or at lower Sandhill elevations may have intermittent interactions with groundwater (Lide et al. 1995; Chmielewski 1996). Most wetland soils were shallow sands or clays (i.e., having more near-surface water-volume storage), with large wetlands (> 8 ha) generally having the longest hydroperiods. Hydroperiods of smaller wetlands ranged from long to short depending upon localized factors of topographic position, soil type, or basin form.

With this greater hydrogeologic complexity, there is a greater range of wetland vegetation types that reflect a strong hydroperiod gradient, partial associations with landscape setting, and land-use history (De Steven and Toner 2004). Open-water ponds and grass marshes are allied through larger basin size and long hydroperiods; ponds may also develop if land changes (such as damming by beavers) result in elevated water depths. Wet depression-meadows are associated with deeper-sand landscapes and have more variable hydroperiods. Tupelo-cypress-sedge swamps predominate in smaller depressions on low River Terraces that are thought to be extensions of the Pliocene-aged Middle Coastal Plain surface ("Sunderland Terrace"). The mixed-hardwood type is associated with significant past disturbance in smaller, short-hydroperiod clay-soil depressions. Notably, many herbaceous wetlands have persisted by means of longer-duration hydrologic regimes rather than frequent fire. This may partly reflect a historical legacy, as uplands in this sub-region were widely converted to intensive agriculture by the early 1950s. Such land-uses suppressed fires, but also removed or reduced the presence of woody species that could colonize herbaceous wetlands during drought periods (see discussions in Kirkman et al. 2000; De Steven and Toner 2004). Reasons for the low presence of swamp tupelo and pondcypress in deeper wetlands are unclear; however, these two very flood-tolerant species do not occur in adjacent uplands and, if removed, have limited to no means of re-establishing by seed dispersal from other wetlands.

Conceptual Models and Applications

Observed vegetation-environment relationships and historical patterns of change can be summarized in conceptual models that: 1) define hydrogeologic "templates" for different wetland types based on depression attributes and landscape setting, and 2) predict possible successional change in response to important ecological drivers (De Steven and Toner 2004). Such models represent a reference-system that can be used for applications such as identifying the conditions favoring wetlands of conservation interest, informing wetland management approaches, and suggesting where restoration actions may be feasible. For Coastal Plain depressions, the templates represent intrinsic hydroperiod types in relation to hydrogeologic landscapes, which differ by sub-region owing to important changes across a large regional gradient.

Figure 3 presents a conceptual model for depressional wetlands in contrasting Lower Coastal Plain hydrogeologic landscapes. On xeric Sand-Ridge uplands that are managed for fire-dependent longleaf pine forests, tupelo-cypress swamp represents a stable vegetation maintained by semi-permanent ponding in deep depressions, because those attributes reduce sensitivity to drought or fire and would not support a savanna ground-layer vegetation. No moderately-deep long-seasonal Sand Ridge depressions were observed in the sample wetlands, but a tupelo-(cypress)-sedge type is hypothesized. Depending on basin size and hydroperiod, seasonally-ponded wet savannas in shallow depressions and Carolina bays will be more susceptible to drought effects and may depend on light- to moderate-intensity fires for their persistence. Absence of regular fire in drier basins could allow succession toward a pine-dominated savanna or woodland. In mesic low Flat and Terrace landscapes managed for loblolly pine or pine-hardwood forests, tupelo-cypress swamp will also be stable in larger depressions with deep, semi-permanent ponding. Moderately-deep, long-seasonal ponding favors a more open tupelo-(cypress)-sedge swamp with a herbaceous layer that could not persist in deeper water. Natural succession toward closed-canopy swamp may occur with time; fire effects are likely to be of low intensity but might help to maintain the sedge-marsh component. Mixed-hardwood swamps occur in somewhat deep to shallow clay-soil depressions, where shorter hydroperiods could allow the moderately flood-tolerant trees to regenerate and where low-intensity fire may not change composition substantially. Whether savanna vegetation could be established in low Flat/Terrace depressions is uncertain, as more intense management may be needed to counteract a natural trajectory toward forest in less fire-prone landscapes. Likewise, successional pathways toward pocosin vegetation are unclear, as competing mechanisms have been proposed (Christensen 2000; Cartwright and Wolfe 2016). Without fire, wet savannas might develop pocosin vegetation because the evergreen shrubs tolerate nutrient-poor sand soils and shallow ponding; slow litter decomposition could then promote peat development and greater soil saturation. Alternatively, longer-term change to pocosin could also occur in deep, permanently flooded tupelo-cypress depressions if peat soils were to build up over time and reduce ponding depth.

Figure 4 is a revised model for depressional wetlands in contrasting soil-landscapes that reflect the Upper Coastal Plain's more complex hydrogeologic settings. Differences from the Lower Coastal Plain include more herbaceous wetland types but a general absence of cypress-savanna and pocosin. Open-water ponds are maintained primarily by deep, semi-permanent ponding, usually in large depressions. Regional water tables have less influence in stabilizing hydropatterns, thus more wetland types

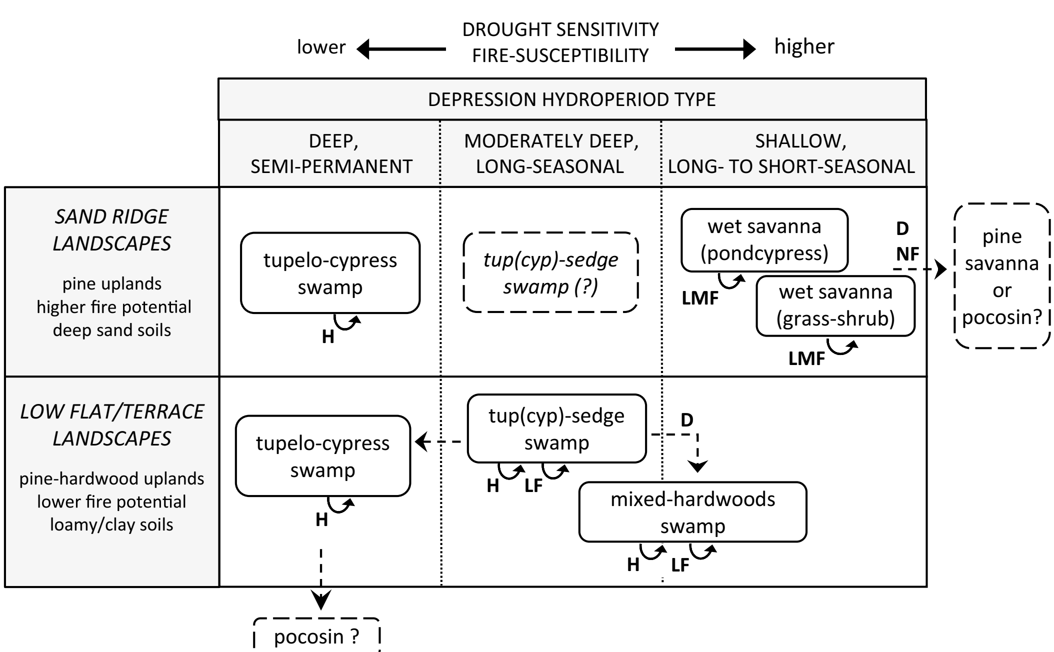

Fig. 3 Conceptual model of hydrogeologic templates for vegetation of depressional wetlands in Lower Coastal Plain landscapes. Potential vegetation differs by landscape setting and among hydroperiod types that vary in susceptibility to drought or fire effects. Solid curved arrows indicate factors that maintain stable vegetation under typical conditions (H=hydroperiod regime, LF and LMF=low-intensity to moderate-intensity fire). Dashed arrows indicate natural succession or other drivers that may shift vegetation toward a different state (NF=no/reduced fire frequency, D=dry years/drought). Vegetation states with dashed borders are hypothesized

are susceptible to vegetation shifts in response to drought. In xeric-soil (Sandhill) landscapes with pine-dominated uplands, deep ponds may shift reversibly toward depression-meadow vegetation but recover upon re-ponding. Depression-meadow wetlands may be colonized by flood-intolerant pines that can be killed by re-ponding or fire (Kirkman 1995; Stroh et al. 2008). However, prolonged drought can lead to woodland in short-seasonal depressions if pines become well-established and create drier conditions through increased evapotranspiration. In mesic-soil (Loam Hill, Terrace) landscapes where grass-marsh wetlands are more common, ponds may shift toward marsh during droughts, but the change may be less reversible because the dominant maidencane-grass can form expansive cover that survives deeper water (Holm and Sasser 2008). Depending on the timing, burning may not reverse this transition if the maidencane can re-sprout after fire (De Steven, pers. observ.). Maidencane marsh may eventually develop toward swamp forest, but perhaps more slowly because the denser grass cover and longer hydroperiods resist colonization by other species when compared to depression-meadows (Mulhouse et al. 2005). Tupelo-cypress swamps represent stable vegetation types in moderately deep wetlands, particularly on lower-lying Terraces. As in the Lower Coastal Plain, mixed-hardwood forests could occur naturally in shorter-hydroperiod wetlands (e.g., in Terrace landscapes); however, they also result from recovery after past forest removal and/or agricultural disturbances on more elevated uplands.

Hydrogeologic landscapes and relationships to vegetation have not been studied explicitly in South Carolina's Middle Coastal Plain. County-level soil surveys characterize the uplands of this weakly-dissected tableland as moderately to poorly-drained, often with high water tables; deep-sand and loamy-sand soils are common, but areas of clay soils occur, particularly on large-river terraces. Carolina bays attain sizes of 300–600 ha, and karst depressions may also range more widely in size. These features suggest hydrogeologic landscapes similar to the Lower Coastal Plain. However, as in the Upper Coastal Plain, extensive land areas were converted to agricultural use, sometimes through artificial drainage. Very large Carolina bays were often cleared and permanently drained for farming as well (e.g., Ewing et al. 2012). Those conditions would likely promote a wide range of vegetation types in less-disturbed wetlands. Consistent with this prediction, selected or non-randomized studies of Middle Coastal Plain depressions in both Carolinas have documented occurrences of deepwater pond, emergent marsh/meadow, and mixed-hardwood forests (Peroni 1988; Townsend 1995; Pyzoha 2003; Zoellner 2007; Altman-Goff 2016) in addition to tupelo-cypress swamp, pondcypress savanna, and pocosin (Nifong 1998). Some combination of the two conceptual models may be appropriate for management applications in this sub-region, depending on the depression attributes and the soil/landform setting for the sites of interest.

The conceptual models represent vegetation dynamics under typical conditions, thus the wetland templates can offer general guidance for specific habitat-management or restoration goals on conserved lands. For example, selective tree removal in forested depressional wetlands could increase the emergent-vegetation habitat needed by some pond-breeding amphibians (e.g., the Mississippi dusky gopher frog, *Rana sevosa*; Thurgate and Pechmann 2007); such management might be more successful in longer-hydroperiod wetlands, rather than in short-seasonal wetlands that are more likely to revert back to forest. An Upper Coastal Plain experiment found that attempts to convert short-hydroperiod mixed-hardwood wetlands to herbaceous wetlands (by ditch-plugging and forest removal) had a low success rate, partly because of small size and greater drought susceptibility that favored tree re-growth and re-colonization (De Steven et al. 2010; De Steven, pers. observ.). Conversely, intensive tree-removal treatments did restore herbaceous vegetation in hardwood-dominated Gulf Coastal Plain depressions when they occurred within a

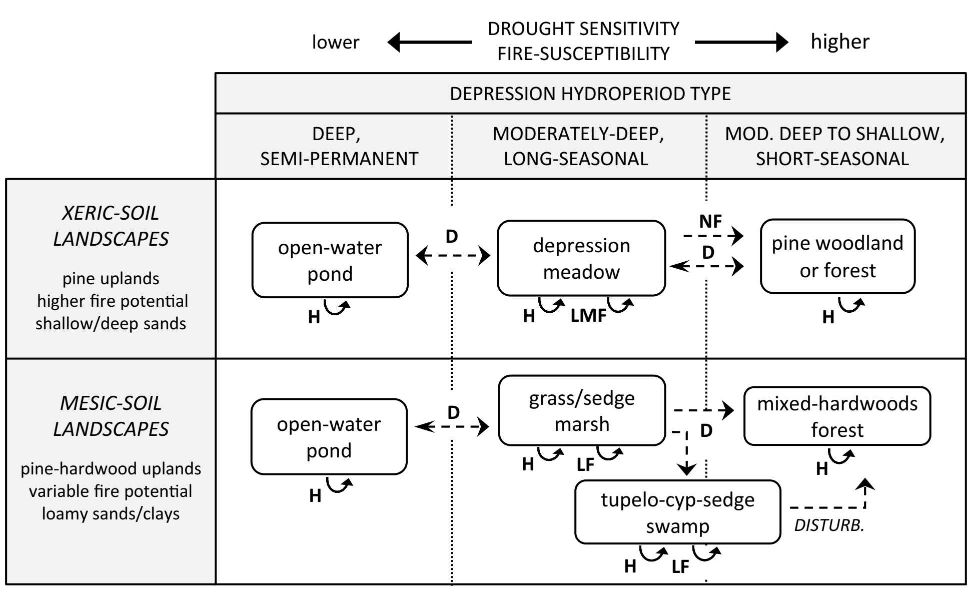

Fig. 4 Conceptual model of hydrogeologic templates for vegetation of depressional wetlands in Upper Coastal Plain landscapes (revised from De Steven and Toner 2004). Potential vegetation differs by landscape setting and among hydroperiod types that vary in susceptibility to drought or fire effects. Solid curved arrows indicate factors that maintain stable vegetation under typical conditions (H=hydroperiod regime, LF and LMF=low-intensity to moderate-intensity fire). Dashed arrows indicate natural succession or other drivers that may shift vegetation toward a different state (NF=no/reduced fire frequency, D=dry years/drought). Note that in non-forested types, drought-induced shifts may reverse when wet conditions return. *DISTURB.*=forest-removal disturbance

routinely fire-managed landscape that increased fire susceptibility (Martin and Kirkman 2009). De Steven and Toner (2004) discuss additional conservation and management implications, including possible effects of long-term climate change. For simplicity, the conceptual models do not predict the effects of catastrophic disturbance (e.g., destructive logging or severe uncontrolled fire) that would not be used in normal management; however, possible outcomes could be inferred based on the specific wetland type and hydrogeologic setting.

In summary, these Coastal Plain studies illustrate a general approach for assembling the geological, soils, and hydrologic information that can improve understanding of depressional-wetland vegetation composition and dynamics, particularly in forested ecoregions where plant communities are relatively persistent over time. How the approach may apply in other ecoregions is less certain. For example, in the semi-arid climates of the Northern American Central Plains, prairie-pothole wetlands exhibit dramatic temporal changes in water levels and herbaceous plant communities owing to high inter-annual rainfall variability. These wetlands occur in close spatial proximity within complex glacial deposits, such that their hydroperiods, groundwater inputs, and salinity are influenced locally by pothole topographic position and a potential for hydrological connectivity among wetlands. Under these conditions, wetland vegetation communities could differ more widely within a Plains sub-region over time than between sub-regions, requiring a different type of conceptual model for vegetation dynamics (see Euliss et al. 2004; Mushet et al. 2018).

Appendix

Table 6

Table 7

Table 6 Differentiated table of common species in five Lower Coastal Plain wetland types.

		Wetland Type				
Species[a]	Growth Form	Mixed BLH Forest	Tupelo-Sedge Swamp	Tupelo-Cypress Swamp	Pondcypress Wet Savanna	Grass-Shrub Wet Savanna
*Quercus laurifolia, phellos**	tree	**39**	m	m	–	–
Acer rubrum (var. *trilobum*)*	tree	**42**	8	14	6	5
*Liquidambar styraciflua**	tree	**18**	10	7	–	2
Pinus taeda	tree	32	6	6	9	11
Smilax rotundifolia	liana	30	–	m	1	3
*Carex glaucescens**	sedge	**20**	10	5	5	2
*Ilex myrtifolia**	shrub	**21**	–	m	3	m
Erianthus (3 + spp)*	grass	**16**	–	m	7	< 1
*Nyssa biflora**	tree	46	**74**	**86**	39	6
Carex striata	sedge	m	61	23	29	m
Lyonia lucida	shrub	m	36	35	33	m
Woodwardia virginica	fern	m	38	14	8	18
Vaccinium corymbosum	shrub	m	10	19	m	12
Clethra alnifolia	shrub	14	6	7	17	m
Panicum hemitomon	grass	–	12	m	1	8
*Taxodium ascendens**	tree	–	m	**42**	**58**	13
*Persea palustris**	shrub	m	m	5	**8**	**13**
*Ilex glabra**	shrub	6	10	–	7	**36**
*Iris tridentata, virginica**	forb	–	3	m	**17**	**45**
Rhynchospora (Diplostylae, 7 + spp)*	rush	8	m	m	**14**	**14**
Rhynchospora (*Haplostylae,* 2 spp)*	rush	m	–	m	**15**	**26**
Panicum (4 spp)*	grass	–	< 1	m	m	**28**
Andropogon (*virginicus*)*	grass	m	m	m	5	**16**
*Amphicarpum muhlenbergianum**	grass	–	–	–	8	**26**
*Lachnanthes caroliniana**	forb	–	–	–	m	**22**
Dichanthelium (9 spp)*	grass	m	–	1	m	**12**
*Aristida affinis, virgata**	grass	m	–	m	**7**	**8**
Number of wetlands in type		4	4	9	3	4

Values are mean % abundance in sites of occurrence; m = minor presence. * denotes a significant indicator species for one or more types, with defining abundances in boldface

[a] Nomenclature follows the usage in De Steven and Toner 2004

Table 7 Differentiated table of common species in six general Coastal Plain wetland types.

		Wetland Type					
Species[a]	Growth Form	Open-water Pond	Grass Marsh	Depression Meadow	Cypress-Grass-Shrub Wet Savannas	Tupelo-Cypress-Sedge Swamps	Mixed BLH Forest
*Nymphaea odorata**	aquatic	**58**	12	m	–	m	m
*Pontederia lanceolata, cordata**	aquatic	**37**	**20**	–	m	m	–
*Brasenia schreberi**	aquatic	**20**	7	**16**	–	m	–
Eleocharis (*Limnochloa,* 3 spp)*	rush	**16**	3	m	–	m	–
*Panicum hemitomon**	grass	25	**57**	24	5	11	–
*Leersia hexandra**	grass	18	**31**	**54**	m	m	m
*Cephalanthus occidentalis**	shrub	16	**23**	6	m	3	13
Pinus taeda	tree	6	26	7	10	7	19
*Eleocharis melanocarpa**	rush	5	m	**29**	m	m	m
Ludwigia (6 + spp)*	forb	9	5	**21**	7	m	m
*Diospyros virginiana**	tree	m	6	**21**	m	2	12
Panicum verrucosum	grass	7	16	23	13	m	20
Polygonum hydropiperoides	forb	1	7	17	m	m	14
Rhynchospora (*Diplostylae,* 14 + spp)*	rush	m	**21**	3	**14**	2	m
Rhynchospora (*Haplostylae,* 4 spp)*	rush	9	m	m	**23**	m	–
Andropogon (*virginicus*)*	grass	–	–	m	**10**	m	m
*Panicum longifolium, rigidulum**	grass	–	m	–	**18**	m	–
*Lachnanthes caroliniana**	forb	–	–	–	**22**	–	–
*Ilex glabra**	shrub	–	–	–	**24**	m	m
*Iris tridentata, virginica**	forb	m	m	–	**33**	m	–
*Taxodium ascendens**	tree	m	24	–	**35**	**43**	m
*Carex striata**	sedge	–	–	–	31	**51**	–
*Woodwardia virginica**	fern	–	5	–	**11**	**19**	m
*Lyonia lucida**	shrub	–	m	–	**28**	**35**	m
*Nyssa biflora**	tree	16	21	3	24	**67**	23
*Liquidambar styraciflua**	tree	4	16	11	2	13	**57**
Acer rubrum (var. *trilobum*)*	tree	5	8	m	5	13	**34**
*Quercus phellos, laurifolia, nigra**	tree	m	1	m	–	8	**22**
*Smilax rotundifolia**	liana	–	5	m	2	3	**18**
*Campsis radicans**	liana	m	m	m	–	m	**23**
Number of wetlands in type		10	10	13	8	23	16

Values are mean abundance (%) in sites of occurrence; m = minor presence. * denotes a significant indicator species for one or more types, with the defining abundances in boldface

[a] Nomenclature follows the usage in De Steven and Toner 2004

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Data Availability Datasets analyzed during the study are available from the corresponding author on reasonable request.

Declarations

Competing Interests None

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