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THE ECOLOGY, STATUS, AND CONSERVATION OF TWO NON-ALLUVIAL WETLAND COMMUNITIES IN THE SOUTH ATLANTIC AND EASTERN GULF COASTAL PLAIN, USA

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Abstract

The existence and integrity of the majority of southern Atlantic and eastern Gulf coastal plain non-alluvial wetlands (and the plant and animal species dependent on these communities) are critically threatened. Federal efforts and public interest have concentrated on the protection of coastal wetlands and riverine bottomlands, but many other coastal plain wetland communities are declining rapidly. Among these threatened natural communities are non-alluvial systems such as pond cypress Taxodium ascendens *savannas, karst ponds, coastal plain small depression ponds, longleaf pine* Pinus palustris *savannas, and pocosins. We estimate that more than a third of the rare plant species in the Southeast occur in these wetland communities. The threats to these isolated wetland communities are numerous, from local site specific threats including drainage and development to threats to the regional hydrology. In this paper we present an overview of the non-alluvial wetlands in the southern Atlantic and eastern Gulf coastal plain and focus on two of the most threatened non-alluvial wetland communities in the region, pond cypress savannas and karst ponds.*

Keywords: south-eastern USA coastal plain, non-alluvial wetlands, pond cypress savannas, karst ponds, Carolina bays.

INTRODUCTION

The southern Atlantic and eastern Gulf coastal plain, defined here as the coastal plain south from North Carolina to central Florida (as far south as Lake Okeechobee) and west to the Mississippi Embayment (Fig. 1), has a diverse set of non-alluvial wetland communities. Eighteen non-alluvial communities are recognized by Allard (1990*a*) in her classification of natural communities of the Southeastern United States. Two of the most threatened non-alluvial wetland communities in this region are the pond cypress *Taxodium ascendens* savannas and karst ponds, the latter often referred to as limestone pond complexes, dolines, or sinkhole lakes and ponds. Both systems are distinct floristically and are frequent to common systems within this region. They are characterized by a long hydroperiod (6–9 months a year) and non-peat soils, but have different sources of water.

The southern Atlantic and eastern Gulf coastal plain is defined geologically by a seaward-thickening wedge of alluvial and marine sediments over sloping Paleozoic and Precambrian rocks (Horton & Zullo, 1991). The coastal border has been influenced by processes of embayment, uplift, and delta formation resulting in a complex shoreline of submerged islands, barrier islands, and deltas. The inland border of the Atlantic coastal plain is distinct, being the fall line that marks the contact with the crystalline rocks of the piedmont. This boundary follows a northwest–southwest line that extends into southeastern Alabama, where the piedmont province pinches out east of Montgomery. The boundary from Alabama westward is more difficult to place, extending diagonally northwestward following the southern edge of the Appalachian physiographic province to northwestern Alabama, then following the western edge of the Cumberlands and the Interior Low Plateau and the northern border of the Mississippi Embayment in Tennessee, Kentucky, and Illinois. The physiography of the coastal plain is characterized by a level to gently sloping topography, a lengthy complex shoreline with numerous barrier or sea islands, the most diverse assemblages of freshwater wetlands in North America (Christensen, 1988), and an upland typically dominated by species of pine.

The vegetation assemblages and the distribution of plant species in this region are primarily controlled by gradients of soil and hydrology and the frequency and intensity of fire (Christensen, 1988). A generalized transect along a non-riverine, inland topographic gradient would include an evergreen shrub bog in peaty depressions, through a wet longleaf pine *Pinus palustris* savanna over a sandy-loam soil, to a longleaf pine–scrub oak

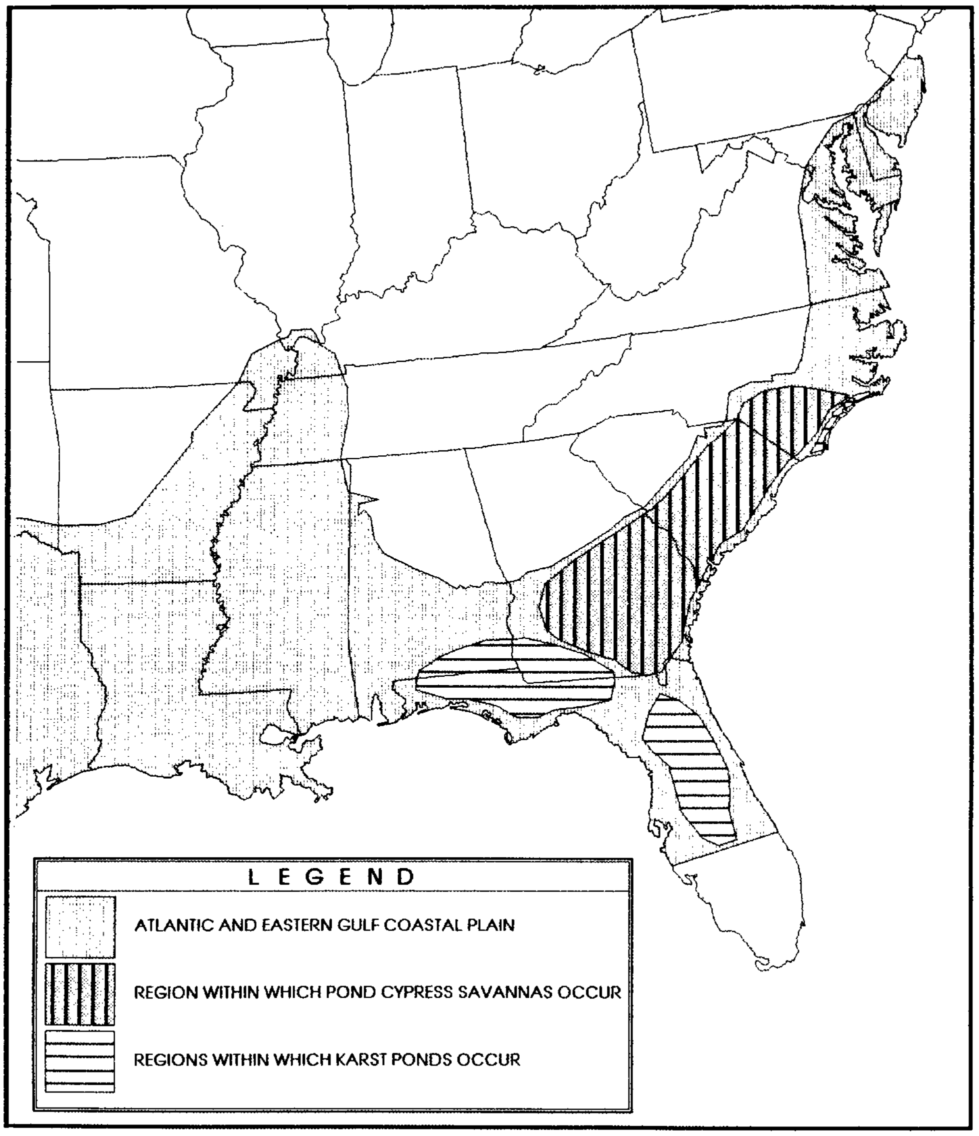

Fig. 1. Map of the Atlantic and eastern Gulf coastal plain with the regions in which pond cypress savannas and karst ponds occur.

community at the higher elevations over xeric sands. Fire is the dominant natural disturbance in the southeastern coastal plain, with the majority of natural communities being fire-maintained. Fire also plays a role in maintaining species richness and the sexual and vegetative reproduction of many species are tied to fire (Walker & Peet, 1983). There is no shortage of ignition sources in this region; the southeastern coastal plain has the highest frequency of lightning strikes in North America (Komarack, 1968).

Non-alluvial wetland communities in the southeastern coastal plain have received less attention than riverine and coastal wetlands. They are, however, significant features of the southeastern coastal plain, being common throughout the region. These non-alluvial wetlands range from some of the most species-rich in the region to some of the most species-poor. We estimate that over a third of the rare plant species in the southeast occur in these communities. They are also quite diverse, exhibiting a wide range of vegetation and soil types and hydrologic and basin characteristics. In general, non-alluvial wetlands are defined as wetland communities with variable hydroperiods occurring in basins or depressions, or on slopes, with no connection to above-ground stream or river systems. The four major environmental variables that control the vegetation in these communities are hydroperiod, fire frequency, the presence of organic matter, and the source of water (Ewel, 1990). The majority of these communities are nutrient-limited (Christensen, 1988), with the exception of karst ponds, having rainfall or shallow ground-water as the primary water source.

Allard (1990*a*) recognizes 18 non-alluvial wetland natural communities in the Southeast (Table 1). These can be distinquished by their canopy composition and structure, soil type, hydroperiod, water source, and fire frequency.

Four of the 18 communities are forested non-alluvial wetlands. Two of these, pond cypress pond forest and swamp tupelo pond forest, occur in basins with mineral to shallow organic soils. These two communities differ by the depth of organic matter, water depth and length of hydroperiod, and the frequency of fire. An increased frequency of fire and the consequent decrease in peat

Table 1. Summary of nonalluvial wetland communities of the southeastern United States
Community types are from Allard (1990*a*), information on community characteristics from Allard (1990*b*), Christensen (1988), Ewel (1990) and the authors.

Community	Canopy dominants	Soil	Hydroperiod/ water source	Fire frequency
Forested wetlands in basins				
Pond cypress pond forest	*Taxodium ascendens*	Mineral to organic	6–12 months rainfall	Infrequent, 20–50 years
Swamp tupelo pond forest	*Nyssa biflora*	Organic to peat	6–12 months rainfall	Rare, one fire per century
Cypress dome	*Taxodium ascendens*	Peat	6–9 months rainfall	20+ years
Basin swamp forest	*Nyssa biflora*, *Acer rubrum*, *Liquidamber styraciflua*	Organic	6–9 months groundwater	Infrequent, 20–50 years
Wetland complexes (from forested to open water) in basins				
Limestone pond complex (karst ponds)		Mineral	Deep groundwater	1–10 years/yellow sand, 36–60 years/white sand
Coastal plain small depression pond		Mineral	Variable	Dependent on surrounding forests
Coastal plain lakeshore complex		Mineral	Variable	Rare, one fire per century
Okefenokee swamp wetland mosaic		Mineral–peat	Variable	Infrequent, 20–50 years
Woodlands and savannas on flat coastal terraces				
Slash pine flatwoods	*Pinus serotina*	Mineral	<3 months groundwater	3–10 years
Wet longleaf pine flatwoods	*Pinus palustris*	Mineral	<3 months groundwater	3–10 years
Wet longleaf pine–slash pine flatwoods	*Pinus palustris* and *Pinus serotina*	Mineral	<3 months groundwater	3–10 years
Longleaf pine savanna	*Pinus palustris*	Mineral	3–6 months groundwater	1–5 years
Coastal plain pitcher plant flat	A diversity of graminoid and herbaceous species including *Sarracenia* spp.	Mineral	6 months groundwater	1–5 years
Woodlands and savannas in basins				
Pond cypress savanna	*Taxodium ascendens*	Mineral	6–9 months rainfall	20+ years
Pond pine woodland	*Pinus serotina*, *Cyrilla racemiflora*	Shallow organics and peats	6–9 months rainfall	10–20 years
Evergreen shrub wetlands				
Low pocosin	*Pinus serotina*, *Cyrilla racemiflora*, *Zenobia pulverulenta*	Deep peat >0·5 m	6–9 months rainfall	15–30 years
High pocosin	*Pinus serotina*, *Cyrilla racemiflora*, *Lyonia lucida*	Shallow peat <0·5 m	6–9 months rainfall	15–30 years
Small depression pocosin	*Pinus serotina*, *Cyrilla racemiflora*, *Lyonia lucida*	Shallow peat <0·5 m	6–9 months rainfall	15–30 years

depth favors a pond cypress dominated canopy (Wharton, 1978; Landaal, 1991*b*). Wharton (1978) suggests that water fluctuations may be less in swamp tupelo ponds than in pond cypress ponds and swamp tupelo forests usually have deeper water (Landaal, 1991*b*). Both appear to be underlain by an impervious clay layer (Wharton, 1978). The two other forested communities occur in basins with greater depths of organic soil. Cypress domes, dominated by *Taxodium ascendens* with an understory of evergreen sclerophylls, have a long hydroperiod and a fire frequency averaging five per century (Christensen, 1988; Ewel, 1990). Basin swamp forests, with a deciduous overstory, have similar hydroperiods to cypress domes but are protected from fire (Ewel, 1990). Other differences and similarities of these communities are not well understood.

Several wetland complexes of uplands to permanently flooded basins have been recognized. These include limestone pond complex (which we call karst ponds), coastal plain small depression pond, coastal plain lakeshore complex, and Okefenokee swamp wetland mosaic. These communities are defined primarily by the type of lacustrine system present, with the surrounding vegetation dependent on soil type, soil pH, slope, basin size, fire frequency, and hydroperiod. With the exception of karst ponds, which are discussed below, these communities are too variable to summarize in this paper.

There are numerous recognized woodland/savanna non-alluvial wetlands on flat coastal terraces, including slash pine *Pinus elliotii* flatwoods, wet longleaf pine–slash pine flatwoods, wet longleaf pine flatwoods, and longleaf pine savanna. There are also two woodland/savanna wetlands in basins, pond cypress savanna and pond pine *Pinus serotina* woodland. The flatwoods and savannas on the flat outer-coastal plain terraces have high fire frequencies and generally occur on sandy soils. They are distinquished primarily on structural grounds (Christensen, 1988); flatwoods have moderately dense canopies over a dense shrub layer while savannas have a diverse graminoid understory beneath a sparse canopy. Longleaf pine savannas occur in wetter sites and have a higher fire frequency than flatwoods (one to three years for savannas and three to five years for flatwoods) (Allard, 1990*b*). Slash pine increases in abundance south and west in these communities, but its abundance may reflect a response to the logging of longleaf pine from these sites in the past (Clewell, 1981). One herbaceous wetland, coastal plain pitcher plant flat, also occurs on these flat coastal terraces. The vegetation of this community is quite variable through its range, but usually contains species of *Sarracenia* with a diverse assemblage of grasses and herbs.

Of the basin communities, pond cypress savanna have a pond cypress canopy over a diverse herbaceous understory. These sites have long hydroperiods (six to nine months), mineral soils, and a fire frequency of over 20 years (Wharton, 1978). Pond pine woodland have a scattering of pond pine over a very dense and tall shrub layer (Landaal, 1991*c*) occurring on acid, organic soils having a long hydroperiod. Fire is estimated to occur in this community every 10–20 years (Clewell, 1981).

Evergreen shrub wetlands on highly organic soils, known as pocosins, dominate much of the non-alluvial wetlands in the southeast, especially along the Atlantic coast (Richardson *et al.*, 1981; Sharitz & Gibbons, 1982; Christensen, 1988). Pocosins are dominated by a dense cover of evergreen and deciduous shrubs and a scattering of emergent trees (Christensen, 1988). These peatland communities are ombrotrophic, relying on rainfall and dryfall for nutrient input (Wilbur & Christensen, 1983). Thus pocosins are extremely nutrient-poor and acidic. Allard (1990*a*) recognizes three pocosin communities, low pocosin, high pocosin, and small depression pocosin. The first two types, which have similar species composition, are differentiated by peat depth and tree stature, with low pocosin occurring on the deeper peats (greater than 0.5 m) and having shorter stature pond pines. Small depression pocosin is differentiated from the other two by a smaller size and a hydrology influenced by shallow groundwater. Its vegetation and fire frequency are influenced by surrounding communities (Doyle, 1990). Fire frequency ranges from 15 to 30 years in these communities, and has a variable effect on species composition and richness, flowering, nutrient availability, and surface peat conditions (Christensen, 1988).

The existence and integrity of the majority of these southern Atlantic and Gulf coastal plain non-alluvial wetlands (and the plant and animal species dependent on these communities) are critically threatened. The plight of all wetlands in the Southeastern United States has been well documented. With 50% of the wetlands in the United States, it has experienced a 28% loss of wetlands since European settlement (Hefner & Brown, 1985). In the last 30 years, 84% of the wetland loss in the United States has been in the southeast (Hefner & Brown, 1985). Many of the smaller, non-alluvial wetland communities are declining at an equal or greater rate. Longleaf pine forests, within which are wetter longleaf savannas, have declined to less than 1% of their original extent (Ware *et al.*, 1993). Pocosins have declined to less than 60% of their presettlement area (Richardson *et al.*, 1981). The original extent of many of the non-alluvial communities is not known, due to their small size, isolated occurrences, and the absence of a recognized community classification, but herbarium records of species restricted to these communities suggest that there have been extensive declines. The threats to these isolated wetland communities are numerous, including drainage associated with agriculture, silviculture and grazing, changes in local or regional hydrology, and recreational/residential/industrial development. Fire suppression has been particularly damaging, with many non-alluvial communities succeeding to shrub thickets. In addition to being converted to other vegetation types, protected lands are not being managed to maintain these natural communities and their populations of common and rare species.

The remainder of this paper will focus on two of these non-alluvial wetland communities, pond cypress savannas and karst ponds. These are two of the most species-rich communities in the southeast.

POND CYPRESS SAVANNAS

Pond cypress savannas occur in shallow basins having moderately long hydroperiods (six to nine months) and a substrate with little or no peat, usually underlain by a clay hardpan. These communities are found primarily on the inner coastal plain from North Carolina south to Georgia (Wharton, 1978; Nelson, 1986; Schafale & Weakley, 1990; Landaal, 1991*a*), although similar sites occur elsewhere in the southeast including north Florida (Ewel, 1990).

Taxodium ascendens is the dominant and diagnostic species in this community, usually forming a open canopy over a diverse herbaceous-grass understory (Fig. 2). Other canopy species include *Nyssa biflora*, *Acer rubrum*, and *Diospyros virginiana*, and further south, *Persea palustris*. Shrub dominants include *Ilex myrtifolia* and *Cephalanthus occidentalis*. The herbaceous flora can change dramatically from year to year and differs greatly among sites. It is generally rich in sedges (*Rhynchospora filifolia*, *R. inundata*, *R. perplexa*, *R. pusilla*, *R. tracyi*, *Scleria ciliata*, *S. georgiana*, *S. pauciflora*, and *S. reticularis*), *Juncus* spp., grasses (numerous *Panicum* spp., *Andropogon* spp., *Erianthus giganteus*, *Leersia hexandra*) and wetland herbs (*Lachnanthes caroliniana*, *Pluchea rosea* and *P. foetida*, *Hypericum denticulatum*, *Boltonia asteroides*, *Ludwigia* spp., *Xyris* spp. and *Utricularia* spp.). A number of rare species are also present in these sites, including *Rhexia aristosa*, *Lobelia boykinii*, and *Oxypolis canbyi*. The first two species are candidates for listing by the US Fish and Wildlife Service, while the last is already listed as Threatened. Pond cypress savannas are perhaps one of the most floristically diverse community types in the southeastern coastal plain. Pond cypress savannas also offer excellent breeding habitat for amphibians.

The extent and position of a pond cypress savanna community within coastal plain basins vary. In basins

Fig. 2. Pond cypress savanna with overstory of pond cypress, standing water, and some emergent herbaceous vegetation.

having shallow, relatively flat basins, the pond cypress savanna nearly fills the entire basin, surrounded by a narrow band of non-alluvial swamp forest with *Acer rubrum*, *Liquidambar styraciflua* and *Liriodendron tulipifera* mixed in with *Taxodium ascendens* and *Nyssa biflora*, beyond which is the dryer sand rim. In more steeply sided basins, the pond cypress savanna community is limited to a zone between deeper zones with longer periods of inundation (and sometimes permanent ponds) and upper zones with dryer conditions. The extent of the community in these sites is dependent on the hydroperiod and slope and size of the basin.

The natural processes that control the vegetation in these pond cypress savannas appear to be the duration and magnitude of inundation and fire. The hydrologic characteristics of this natural community include an average annual inundation of six to nine months, but with dramatically fluctuating and unpredictable water levels (Ewel, 1990; Schalles *et al.*, 1989). The hydrology of pond cypress savannas depends primarily on rainfall, although some water movement from adjacent uplands and ground water is thought to be present (Schalles *et al.*, 1989). The hydrologic fluctuations provide an unpredictable environment for a mix of species, all of which must endure periods of flooding and drought. The hydrologic fluctuations are also important in eliminating water-intolerant upland species that, if present, could dominate the community and eventually reduce species richness.

Fire is also thought to be important in these communities (Schalles *et al.*, 1989). Pond cypress savannas are usually located in what was once a matrix of fire-adapted natural communities dominated by longleaf pine. Fire probably entered the bays from the uplands during periods of drought. The long intervals between droughts obscure the importance of fire in these communities (Wharton, 1978). Fire would be important for the elimination of fire-sensitive species, thus maintaining an open canopy of pond cypress, and limiting peat accumulation (Schalles *et al.*, 1989). Wharton (1978) recognized two different fire cycles in coastal plain wetlands, short interval systems that burn every three to nine years and long interval systems that burn every 20-plus years. He placed pond cypress savannas in the latter category.

Table 2. Variation of herbaceous vegetation and water depth in Antioch Bay from 1989 to 1991

Data from one of 14, 10 × 10 m permanent plots established by The Nature Conservancy in 1989.

Species	1989 % cover	1990 % cover	1991 % cover
Boltonia asteroides	0–1	2–5	5–10
Diodia virginiana	0	0–1	Trace
Eleocharis tricostata	0–1	0–1	0–1
Eriocaulon sp.	0	0–1	0–1
Eupatorium recurvans	0–1	1–2	1–2
Euthamia minor	Trace	0	0
Hypericum denticulatum	0–1	0–1	0–1
Lobelia boykinii	0–1	0	0–1
Panicum longeligulatum	0	0	0–1
Panicum spretum	0	1–2	0
Panicum vericosum	0	1–2	0–1
Panicum wrightianum	0	0	50–75
Pluchea rosea	1–2	10–25	2–5
Polygala cymosa	0	0	0–1
Rhexia aristosa	Trace	0–1	0–1
Rhynchospora filifolia	0	0–1	0–1
Rhynchospora inundata	1–2	2–5	1–2
Scleria reticularis	0	0–1	0–1
Sclerolepus uniflora	0	0–1	0
Utricularia inflata	0–1	0	0
Water depth	53 cm	0 cm	1 cm

The herbaceous vegetation in pond cypress savannas varies greatly among years (Table 2), both in biomass and species composition, most likely in response to different water levels (Schalles *et al.*, 1989; Sutter & Boyer, in prep.). Several studies have shown that seed banks are important in the life history and survival of many species in similarly fluctuating environments (van der Walk & Davis, 1978; Keddy & Reznicek, 1982; McCarthy, 1987). A study to estimate the presence and extent of a persistent seed bank in pond cypress savannas (Sutter & Boyer, in prep.) found that a substantial seed bank was present and that the seed bank differed significantly between two sites (Table 3). One site had a seed bank consisting of 54 species with a range from 11,744 to 39,435 seeds/m^2. The other site had a seed bank with 41 species and a range of 4256 to 9590 seeds/m^2. While the two sites shared 56% of the species found in the seed bank, only 28% of the most abundant species were common to each. The most

Table 3. The most abundant species found in the seed bank by bay and by number of germinants across all treatments
Greenhouse treatments included inundated, inundated and drawdown, saturated, and moist (Sutter and Boyer, in prep.)

	Total number of germinants	Frequency[a] (%)
Antioch Church Bay		
Panicum spretum	825	86
Pluchea rosea	433	100
Utricularia subulata	153	29
Juncus sp.	146	57
Rhexia aristosa	134	100
Rhynchospora filifolia	130	100
Panicum sp.	128	14
Juncus elliotii	112	86
Rhyncospora pusilla	104	100
Panicum verrucosum	89	43
Ludwigia sp.[b]	77	86
Rhynchospora perplexa	70	100
Utricularia sp.	58[c]	29
Sclaria reticularis	35	100
Xyris sp.	33	86
Big Cypress Bay		
Sagittaria isoetiformis	138	100
Panicum spretum	83	80
Panicum verrucosum	79	60
Juncus sp.	47	60
Rhynchospora pusilla	44	80
Psilocarya nitens	44	40
Chamaesyce maculata	32	100
Rhynchospora perplexa	24	100
Rhynchospora inundata	24	60
Axonopus affinis	17	60
Rhexia aristosa	16	80

[a] Number of plots: Antioch Church Bay, 7; Big Cypress Bay, 5.
[b] Including both *Ludwigia liniaris* and *L. linifolia*, these species are difficult to differentiate vegetatively.
[c] Number of individual plants of this species was impossible to determine accurately; this number reflects number of flowering stems.

abundant species in the seed bank included *Panicum spretum*, *Pluchea rosea*, *Juncus* sp., *Utricularia subulata*, *Rhynchospora filifolia* and *Sagittaria isoetiformis*. *Panicum* was the most abundant genus represented in the seed bank, with between 25 and 33% of all germinants in each bay. Sedges, especially *Rhychospora* spp., were particularly common in the seed bank. Interestingly, two rare species in North Carolina, *Iva microcephala* and *Ludwigia linifolia*—never before seen in these well-inventoried sites—were found in the seed bank.

The presence of a persistent seed bank has important implications for the conservation of this natural community and its rare species, which is obviously linked with the protection of the hydrology and the integrity of the soil. The seed bank and the germination requirements of many of the species are adapted to specific hydrologic conditions (Sutter & Boyer, in prep.) and data from the two pond cypress savannas suggest that subtle differences in hydrology and hydroperiods have a strong influence on the characteristics of the seed bank and the above-ground flora. The discoveries in the seed bank of new species to the site suggest that one-time inventories are not adequate to determine their flora. To compile a complete species list inventories will need to be done across a range of hydrologic conditions. For the protection of rare species, a seed bank may provide a buffer from extreme environmental variability and human disturbance, also from demographic stochasticity, and maintain a reservoir of genetic variability. The absence of a seed bank for some rare species may indicate that these species are more extinction prone.

While there are hundreds of basins containing pond cypress savanna natural communities dotting the inner coastal plain of North Carolina, South Carolina and Georgia, surveys in North and South Carolina have found few with undisturbed natural vegetation (Bennett & Nelson, 1991; NC Natural Heritage Program, pers. comm.). Many have been drained and converted to agricultural or silvicultural uses (Wharton, 1978). In South Carolina it is estimated that only 15–18% of the clay-based bays have less than 10% of their surface area disturbed (Bennett & Nelson, 1991). Even sites with intact natural vegetation have been ditched, grazed, cut, and burned (Peroni, 1988) and most have been heavily logged of their original timber (Wharton, 1978).

KARST PONDS

Karst ponds (dolines, limesink ponds, sinkhole ponds) present a physiographic, hydrologic, and floristic picture quite different from pond cypress savannas. These communities are characterized by being formed by subsidence, having water primarily supplied from underground sources, and having zones of vegetation from forest and shrub to sandy beaches dominated by grasses and sedges and open water (Fig. 3). The best examples of these are generally seaward from most of the clay-based ponds and are nestled in sandy uplands. These are mostly either yellow sands (inland) dominated by *Pinus palustris*, deciduous scrub oaks, hickories, and wiregrass *Aristida stricta*, or white sands (seaward) forested by *Pinus clausa*, evergreen scrub oaks, and numerous heaths. The regions in which karst ponds are best displayed are on the Florida peninsula, mostly on the Gulf side of the Paleozoic arch that underlies the peninsular Florida highlands, and west of the Suwannee in the Florida Panhandle and contiguous parts of southwest Georgia and southeastern Alabama (Cook & Mossom, 1929). The coastal plain ponds of southeastern North Carolina, in the vicinity of Wilmington, show a floristic correlation with those in western Florida, Georgia, and Alabama.

The presence of these karst ponds relates to underlying deep deposits of limestone which over time are being dissolved by underground, often artesian, water. The solution of limestone and formation of underground channels and caves results in a slumping or collapse under the weight of overlying sands. The amount of water replenished from below varies, as does the water chemistry. Sinks connected to an underground water source are crystal clear, well oxygenated and often of neutral pH. Those not or weakly connected to under-

Fig. 3. Karst pond at the Jones Ecological Research Center, Ichauway, Baker County, Georgia (photograph by Dr Katherine Kirkman).

ground water but with permanent water will become more acidic and dark, and build up substantial peat.

The steepness of the surrounding sandhills and proximity to underlying limestone determine the nature of the forest in the uplands as well as the pattern of concentric banding of vegetation around the pond. Thus a 'typical' karst pond will have a concentric system of vegetation belts from upland forest to open water (Fig. 3). The upper zones include (1) surrounding upland pine woodlands (see description above); (2) a girdle of forest that is predominantly of dicotyledonous evergreens including *Quercus virginiana*, *Taxodium ascendens* or *distichum*, and numerous *Ilex* and heath species; and (3) a zone of shrubs, mostly evergreen, with some tree invasion from zone (2). This latter zone is affected by the highest water levels.

In the next zone (4), the open sandy beaches dominated by grasses and sedges, the dynamics are often much more complex, driven by an unpredictable and variable hydroperiod. The soil in this zone has considerable exposures of bare sand and sand overlain with fine peat. This is the most dynamic, variable zone in karst ponds, with a set of zone-adapted species that have extreme variation in population sizes from year to year, including many *Rhynchospora* (*R. filiformis*, *R. fascicularis*, *R.pusilla*, *R. microcarpa*, *R. cephalantha*, *R. pleiantha*), *Fuirena* spp., *Scirpus* spp., *Scleria* spp., *Echinodorus parvulus*, *Eleocharis* spp., *Xyris* spp., *Eriocaulon lineare*, *Lachnocaulon minus*, *Sagittaria isoetiformis*, *Drosera filiformis* (disjunct by hundreds of kilometers from its nearest Atlantic coastal plain location), many *Ludwigia* spp. (especially *L. suffruticosa* and *L. sphaerocarpa*), *Utricularia*, *Sabatia brevifolia* and *S. grandiflora*, *Stylisma aquatica*, *Iva microcephala*, and *Eupatorium leptophyllum*. *Stylisma aquatica* often is a characteristic species of this zone (Lynch, 1986), which has the highest number of endemics and the species least understood taxonomically and floristically. While it is a grass-sedge dominated zone, in the Florida Panhandle it is marked by a distinctive myriandrous species, *Hypericum lissophloeus*, a tall and graceful, wand-branched shrub (Adams, 1962). The next zone inward (5) is one of tall emergents, again predominantly grasses and sedges, including *Panicum hemitomon*, *Eleocharis* spp., and *Polygonum* spp. and shallow water submergent and floating aquatics in the genera *Nymphoides*, *Nymphaea*, *Utricularia*, *Eleocharis*, and *Mayacca*. This grades finally into (6) deeper water submergents or open water. With the clarity of the water, *Mayacca*, *Najas*, and species in the Nymphaceae and Cyperaceae (i.e. *Websteria*) may inhabit substantial depths.

Karst ponds have a significant rare and endemic flora including *Rhexia salicifolia* (Kral & Bostick, 1969), *Hypericum lissophleus*, *Xyris scabrifolia* and *X. longisepala* (Kral, 1966). These ponds are also very important habitat for amphibians (Lynch, 1986). The absence of fish in these ephemeral ponds results in a diverse fauna of frogs and salamanders, including the flatwoods salamander *Amblystoma cingulatum* and gopher frog *Rana areolata*. The open water and marsh provide habitat for a number of bird and mammal species.

The natural process that primarily controls species distribution in this community, especially in zone (4), is the extent and length of hydroperiod. Water for these systems come from underground sources and is not sensitive to local rainfall. Water levels change over decades rather than seasonally, and are thus not seasonally predictable. Adjacent sinks often respond differently to regional rainfall, with one increasing its water level while another may dry out. The variation in hydroperiod results in numerous scenarios as species invade the inner zones. Fire is not important in inner zones, although very important in outer zones. With the water in these communities being well-oxygenated, decomposition is rapid and there is little peat formation.

Karst ponds are under increasing threats. The connection of this natural community to a regional water source ties the protection of these sites in with regional water quality and quantity. The water quality of one sink on peninsular Florida was contaminated by coliform bacteria from a city 64 km away. Many areas surrounding these ponds are being developed for residential communities. Development is also taking place on public lands. Two publicly owned sites in southern Alabama have had their beaches developed with areas cleared of vegetation and sand 'filled', periphery mowed and seeded with exotic stoloniferous grasses, shoreline developed for more fishing access, and waters fertilized and stocked with catfish. These actions have eliminated most of the shoreline endemics, altered the emergent vegetation, and darkened the water from crystal clear to grass-green.

DISCUSSION

These two diverse systems represent a range of conservation challenges. They both share a need for additional study. More needs to be known about the distribution and status of these non-alluvial communities. In contrast to coastal and riverine wetlands, their size and scattered distribution makes them difficult to survey. There is incomplete knowledge of the number of undisturbed pond cypress savannas and karst ponds or the number of extant populations of the rare species found primarily in these systems. To determine which sites to protect, more knowledge is needed on the floristic variability of each of these natural communities. Pond cypress savannas, while appearing similar in dominant species, have very different species compositions (Sutter & Boyer, unpublished data). If the goal of conservation is to conserve biological diversity, then the species diversity of pond cypress savannas and karst ponds can only be conserved by protecting a range of sites of each community type. An accurate regional community classification is needed to provide a common language to discuss, compare, and protect these communities. The various names used to describe pond cypress savannas provide an example. They are included in pine savannah and wet pine savannah in Mississippi, savanna in Alabama, wet flatwoods in Florida, and coastal plain bog/seep forest and Carolina bay in Georgia (Allard, 1990*a*). Additional community studies are needed of these non-alluvial communities.

In order adequately to preserve these sites, the dynamics of their natural processes need to be understood. This information is important at every level of conservation, from development of a preserve design and acquisition plan to a management plan and preservation strategy. Some of the questions that need to be addressed include: What is the primary water source for these wetlands? How much surrounding upland needs to be conserved to protect the water quality and the natural hydrologic variation? If disturbed, how can a non-alluvial wetland be restored? What was the frequency and seasonality of natural fire events? What role do seed banks play in the maintenance of rare plant populations? How much buffer of adjacent uplands and wetlands needs to be protected for migrating invertebrates?

One of the most important questions concerns the hydrology of non-alluvial wetlands. The two communities we have focused on represent extremes along a continuum, from a localized hydrology dependent primarily on rainfall to a regional hydrology dependent on an extensive aquifer system. Pond cypress savannas most likely can be conserved using traditional protection methods, acquisition of the critical area (the pond cypress savanna natural community) and appropriate buffer area. Karst ponds, however, represent a need for a more extensive protection strategy, one that protects critical areas by acquisition but includes and requires the protection of an ecological system (an aquifer) that encompasses a large area. This landscape/ecosystem protection will involve conservation agencies in regional water quality and land use issues. Thus, the protection of these sites will only occur through partnerships with local communities and state and federal agencies.

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REFERENCES

Adams, P. (1962). Studies in the Guttiferae, I. A synopsis of *Hypericum* sect. Myriandra. *Contrib. Grey Herb. Harvard Univ.*, No. 184, 1–51.

Allard, D.J. (1990*a*). *Southeastern United States Ecological Community Classification, Interim Report, Version 1.2.* The Nature Conservancy, Southeast Regional Office, Chapel Hill, NC.

Allard, D.J. (1990*b*). Community Characterization Abstract, wet longleaf pine flatwood. The Nature Conservancy, Southeast Regional Office, Chapel Hill, NC.

Bennett, S.H. & Nelson, J.B. (1991). *Distribution and Status of Carolina Bays in South Carolina.* South Carolina Wildlife and Marine Resources Department, Columbia, SC.

Christensen, N. (1988). The vegetation of the coastal plain of the Southeastern United States. In *North American terrestrial vegetation*, ed. M.G. Barbour & W.D. Billings. Cambridge University Press, New York, pp. 317–63.

Clewell, A.F. (1981). *Natural Setting and Vegetation of the Florida Panhandle: An Account of the Environments and Plant Communities of Northern Florida West of the Suwannee River.* US Army Corps of Engineers, Mobile, AL.

Cook, C.W. & S. Mossom. (1929). Geology of Florida. *Florida State Geologic Survey Annual Report*, 20th, 29–228.

Doyle, K. (1990). Community Characterization Abstract, small depression pocosin. The Nature Conservancy, Southeast Regional Office, Chapel Hill, NC.

Ewel, K.C. (1990). Swamps. In *Ecosystems of Florida*, ed. R.L. Myers & J.J. Ewel. University of Central Florida Press, Orlando, Florida. pp. 281–323.

Fenneman, N.M. (1938). *Physiography of Eastern United States.* McGraw Hill Book Company, New York.

Hefner, J.M. & Brown, J.D. (1985). Wetland trends in the southeastern United States. *Wetlands*, **4**, 1–11.

Horton, J.W., Jr & Zullo, V.A. (eds) (1991). An introduction to the geology of the Carolinas. In *The Geology of the Carolinas.* The University of Tennessee Press, Knoxville.

Keddy, P.A. & Reznicek, A.A. (1982). The role of seed banks in the persistence of Ontario's coastal plain flora. *Amer. J. Bot.*, **69**, 13–22.

Komarack, E.V., Sr. (1968). Lightning and lightning fires as ecological forces. *Proceedings of the Annual Tall Timbers Fire Ecology Conference*, **9**, 169–97.

Kral, R. (1966). *Xyris* (Xyridaceae) of the continental United States and Canada. *Sida*, **2**, 177–260.

Kral, R. & Bostick, P.G. (1969). The genus *Rhexia* (Melastomaceae). *Sida*, **3**, 387–440.

Landaal, S. (1991*a*). Community Characterization Abstract, pond cypress savanna. The Nature Conservancy, Southeast Regional Office, Chapel Hill, NC.

Landaal, S. (1991*b*). Community Characterization Abstract, pond pine woodland. The Nature Conservancy, Southeast Regional Office, Chapel Hill, NC.

Landaal, S. (1991*c*). Community Characterization Abstract, swamp tupelo pond forest. The Nature Conservancy, Southeast Regional Office, Chapel Hill, NC.

Lynch, M. (1986). Classification of the natural communities of Ichaway Plantation, Baker County, Georgia. Nature Conservancy, Southeast Regional Office, Chapel Hill, NC (unpublished report).

McCarthy, K.A. (1987). Spatial and temporal distributions of species in two intermittent ponds in Atlantic County, New Jersey. MS thesis, Rutgers University, Piscataway, NJ.

Nelson, J.B. (1986). *The Natural Communities of South Carolina: Initial Classification and Description.* South Carolina Wildlife and Marine Resources Department, Columbia, SC.

Peroni, P.A. (1988). A vegetation history of the North Carolina Nature Conservancy clay-based Carolina bay preserve with recommendations for future research. The Nature Conservancy, North Carolina Field Office, Carrboro, NC.

Richardson, C.J., Evans, R. & Carr, D. (1981). Pocosins: An ecosystem in transition. In *Pocosin wetlands*, ed. C.J. Richardson. Hutchinson Ross Publishing Co., Stroudsburg, PA. pp. 3–19.

Schafale, M.P. & Weakley, A.S. (1990). *Classification of the Natural Communities of North Carolina, Third Approximation.* North Carolina Department of Enviroment, Health, and Natural Resources, Raleigh, NC.

Schalles, J.F., Sharitz, R.R., Gibbons, J.W., Leversee, G.J. & Knox, J.N. (1989). Carolina bays of the Savannah River plant. Savannah River Plant National Environmental Research Park Program, Aiken, SC.

Sharitz, R.R. & Gibbons, J.W. (1982). *The Ecology of Southeastern Shrub Bogs (Pocosins) and Carolina Bays: A Community Profile.* US Fish and Wildlife Service, USDI, Atlanta, GA.

Smith, C. & Hall, S. (1990). Preserve designs for pond cypress savannas. The Nature Conservancy, North Carolina Field Office, Carrboro, NC (unpublished report).

van der Walk, A.G. & Davis, C.B. (1978). The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology **59**, 322–35.

Ware, S., Frost, C.C. & Doerr, P. (1993). Southern mixed hardwood forest (the former longleaf pine forest). In *Biotic Communities of the Southeastern United States, Vol 1, Terrestrial Communities*, ed. W.H. Martin. John Wiley & Sons, New York, pp. 447–93.

Walker, J. & Peet, R.K. (1983). Composition and species diversity of pine–wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio*, **55**, 163–79.

Wharton, C.H. (1978). *The Natural Environments of Georgia.* Geologic and Water Resources Division and Georgia Department of Natural Resources, Atlanta, GA.

Wilbur, R.B. & Christensen, N.L. (1983). Effects of fire on nutrient availability in a North Carolina coastal plain pocosin. *Amer. Midl. Nat.*, **110**, 54–61.