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CAROLINA BAY WETLANDS: UNIQUE HABITATS OF THE SOUTHEASTERN UNITED STATES

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Abstract: Carolina bays, depression wetlands of the southeastern United States Coastal Plain, are ''islands'' of high species richness within the upland landscape and are the major breeding habitat for numerous amphibians. The 2001 Supreme Court decision that removes isolated wetlands from protection under the Clean Water Act has potential for great losses of these wetland ecosystems. Most Carolina bays are not naturally connected with stream drainages or other water bodies, and their hydrology is driven primarily by rainfall and evapotranspiration. Their potential interaction with shallow ground water is not well-understood. Water levels in these wetlands may vary seasonally and across years from inundated to dry, and organisms inhabiting Carolina bays must be adapted to fluctuating and often unpredictable hydrologic conditions. The ecological importance of these wetlands as habitats for species that require an aquatic environment for a part of their life cycle has been well-documented. Many Carolina bays have been drained and converted to agriculture or other uses, and many of the smaller bays have been poorly inventoried and mapped. If these wetlands are not protected in the future, a major source of biological diversity in the southeastern United States will be lost.

Key Words: depression wetlands, Carolina bays, Delmarva bays, variable hydrology, amphibian habitat

INTRODUCTION

Carolina bays are elliptical depressions that occur throughout the southeastern United States (U.S.) Coastal Plain, from New Jersey to northern Florida. They are most abundant in southeastern North Carolina and mid-coastal South Carolina, where they extend from the coast inward to the Fall Line, which separates the Coastal Plain from the Piedmont. They have a unique and characteristic geomorphic structure (shape, alignment, and surrounding sand rim, Figure 1), and their hydrology is dominated by precipitation inputs and evapotranspiration losses (Lide et al. 1995). Carolina bays range in size from greater than 3,600 hectares to less than a hectare, and their long axis is usually oriented in a northwest-southeast direction, with a sand rim to the southeast (Prouty 1952, Thom 1970, Savage 1982). Although estimates of the number of bays are as large as 500,000 (Prouty 1952), it is more likely that 10,000 to 20,000 currently exist (Richardson and Gibbons 1993). Large differences in estimates may be related to how ''Carolina bay'' is defined (Lide 1997); many small isolated depression wetlands within this geographic range may lack a sand rim, or the classic elliptical shape, especially if they have been disturbed. From an ecological perspective, a debate over how one defines Carolina bay may be a matter of semantics, and it is more appropriate to consider ''Carolina bays and similar wetland depressions'' (Lide et al. 1995). Additionally, the thousands of these depressions that occur on the Delmarva Peninsula in Delaware and Maryland are often called Delmarva bays.

Although the name ''bay'' implies presence of water, these shallow basins range from nearly permanently inundated to frequently dry. Water levels fluctuate seasonally and among years, depending on rainfall patterns. Carolina bays characteristically have no natural drainages into or from them, and overland surface flows are minimal; thus, their primary water source is direct precipitation. The extent to which they may be connected with shallow ground water has been poorly studied, although evidence suggests that some bays are influenced by subsurface lateral flows (Lide et al. 1995, Chmielewski 1996), and a few bays have artesian water sources (Wells and Boyce 1953, Newman and Schalles 1990). Evapotranspiration, especially during the warm growing season, can result in complete drying of the shallow basins. Many smaller Carolina bays are temporary or ephemeral aquatic habitats that may dry completely during periods of low precip-

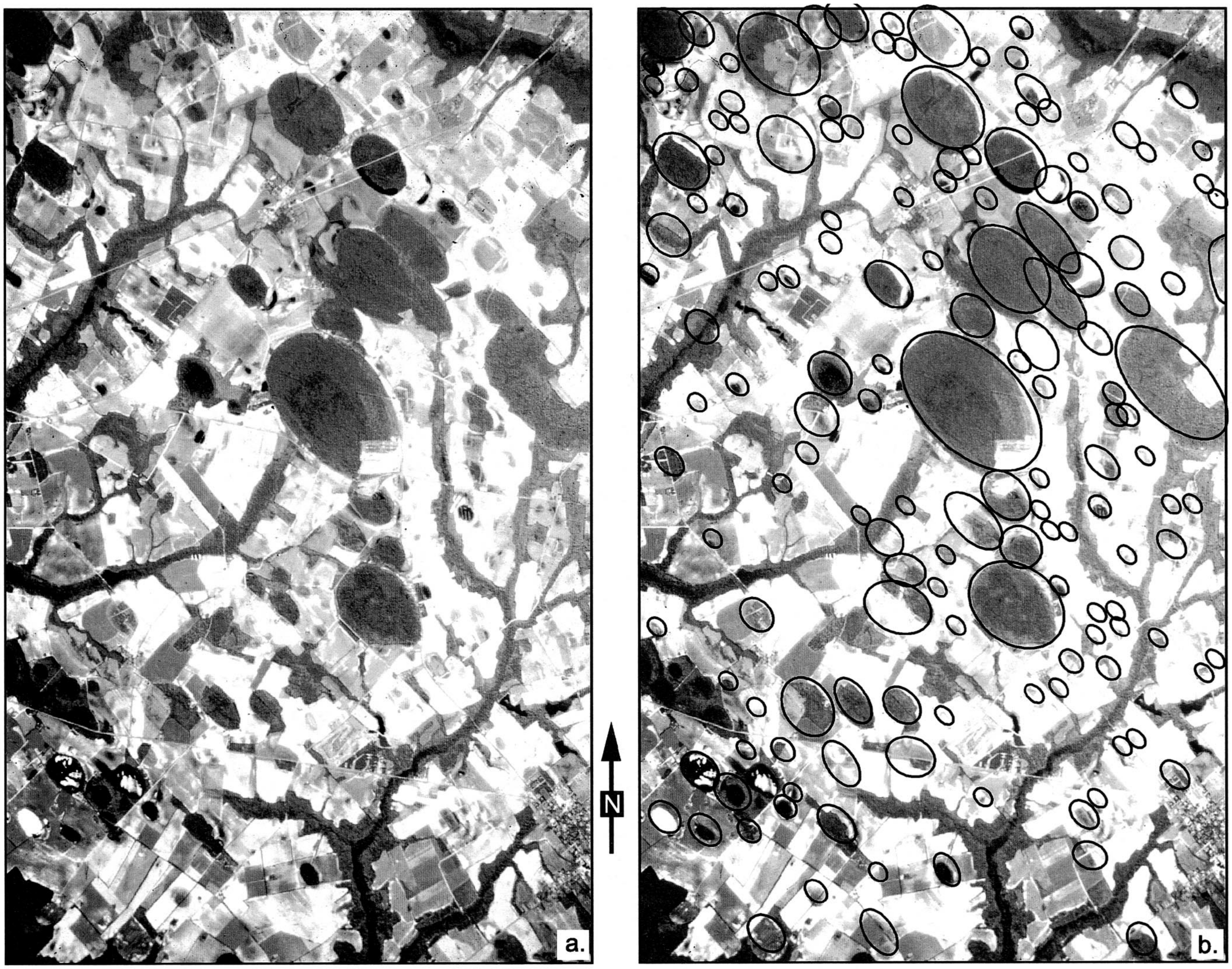

Figure 1. Aerial photograph of Carolina bays within a region of the upper Coastal Plain of South Carolina (scale: 1 cm = 1.5 km). a) Infrared image showing the pattern of intact and disturbed bays; b) The same image with bays (or former bays that have been disturbed by agriculture) outlined.

itation and high evapotranspiration and are referred to as ''dry-end'' wetlands (Whigham 1999).

It is often argued that dry-end wetlands are not as important as larger, more permanently inundated ecosystems, although there is no ecological basis for this conclusion (National Research Council 1995). As Whigham (1999) pointed out, small ephemeral wetlands may be more valuable than other types because of important landscape and biodiversity functions that they perform. Carolina bay depressions store surface water for short times during periods of heavy rainfall and may influence shallow ground-water tables (hydrologic functions), and they may occasionally retain and remove contaminants (biogeochemical functions); however, their most valuable ecological functions are providing habitat and food web support. Carolina bays support a diverse assemblage of species adapted to the fluctuating hydroperiods (Sharitz and Gibbons 1982). For example, the absence of predatory fish found in permanent aquatic habitats allows these ephemeral wetlands to support a rich fauna of aquatic invertebrates (Taylor et al. 1999) and to provide critical breeding sites for amphibians that require water during the early spring months for juvenile development (Semlitsch et al.1996). The variable hydrologic conditions that occur in these depressions also contribute to a large diversity of wetland plant communities across the southeastern Coastal Plain landscape and the presence of numerous rare species (Sutter and Kral 1994, Edwards and Weakley 2001). Furthermore, ecotones between these depression wetlands and uplands are used by many species of plants and animals (Burke and Gibbons 1995, Kirkman et al. 1998, Buhlmann and Gibbons 2001, Gibbons 2003). Thus, as habitats for numerous species that are well-adapted to the fluctuating hydroperiods and may even be dependent on their ''isolation'' from other aquatic systems, Carolina bays are a vital ecological resource.

Few unaltered Carolina bays remain, however (Bennett and Nelson 1991, Kirkman et al. 1996). Throughout the 1800s until the mid-1900s, landowners ditched and drained these wetlands in order to use the land for agricultural purposes (see Figure 1). Of 2,651 Carolina bays > 0.8 ha in South Carolina, 97% have been disturbed, chiefly by agriculture (71%), logging (34%), or both (Bennett and Nelson 1991). Although farming has historically been the predominant land use of bays, commercial and residential development now pose greater threats, as they do to wetland depressions in many parts of the country (Petrie et al. 2001).

The 2001 Supreme Court decision, *Solid Waste Agency of Northern Cook County v. U.S. Army Corps of Engineers, 531 U.S. 159* (''SWANCC''), stated that the Corps of Engineers had exceeded its statutory authority by asserting Clean Water Act (CWA) jurisdiction over isolated ponds that provide habitat for migratory birds. This ruling potentially removes most Carolina bay wetlands from federal protection through Section 404 of the CWA. For example, Petrie et al. (2001) estimated that 88% of the wetlands in the mid-Atlantic coastal area of Maryland, constituting 12% of the region's wetland area, could be excluded from CWA protection; they also concluded that small wetlands are at a disproportionately greater risk of being lost than larger ones. In South Carolina, 9–10% of the state's wetland area is considered at risk, and the most vulnerable sites are small Carolina bays (Southern Environmental Law Center 2003). The total potential effect of SWANCC on Carolina bays and similar wetland depressions throughout the Southeast has not been estimated, but the continued destruction of these dry-end wetlands will result in loss of biodiversity and a reduced ability of regional wetlands to provide important values, such as the movement of organisms and the exchange of energy across the landscape (Semlitsch and Bodie 1998).

The objectives of this paper are 1) to examine potential losses of Carolina bay wetlands under several interpretations of the SWANCC ruling and 2) to provide examples of the ecological importance of these wetlands and the significant functions that may be lost if they are not afforded protection. It is also necessary to describe the unique features of these wetland habitats as a context for understanding their ecological significance.

IMPACTS OF THE SWANCC DECISION ON CAROLINA BAYS

In the 2001 SWANCC decision, the Supreme Court ruled that under Section 404 of the CWA, which assigns the U.S. Army Corps of Engineers authority to issue permits for the discharge of dredge or fill material into waters of the U.S., jurisdiction is restricted to navigable waters, their tributaries, and wetlands that are adjacent to these navigable waterways and tributaries. Most Carolina bays do not have inlet or outlet streams or other natural surface-water drainages into navigable waters; thus, the SWANCC decision may have a great negative impact on this wetland resource. The potential extent of this impact is, however, very difficult to assess.

Some larger bays have been afforded a level of protection through state agencies or by The Nature Conservancy (e.g., Millington Wildlife Management Area in Maryland; Bladen Lake State Forest, Bushy Lake State Natural Area, Jones Lake State Park and the McIntire bay complex in North Carolina; Woods Bay State Park and Cathedral Bay Heritage Preserve in South Carolina). Smaller bays with seasonal hydroperiods (dry-end wetlands) are less likely to be protected; for example, only 13.3% of bay wetlands on the Delmarva Peninsula are located within currently protected areas (Olivero and Zankel 2001).

Many of these smaller bay depressions are too small to be mapped readily and have been poorly inventoried. National Wetlands Inventory (NWI) maps have mapping units of 0.4–1.2 ha, but many bays are smaller. For example, on the Department of Energy's Savannah River Site (SRS) on the upper Coastal Plain of South Carolina, 46% of the 371 known Carolina bays or similar wetland depressions are 1.2 ha or less in size. Many bays fall below the size thresholds previously afforded protection by the Section 404 of the CWA or that pertain to Nationwide Permits and have already been disturbed or destroyed. In addition, dry-end wetlands with short annual hydroperiods may not meet the hydrology requirement necessary to be interpreted as jurisdictional wetlands.

Degree of Hydrologic Isolation

A few Carolina bays have small creeks flowing into them, and a few form the headwaters of perennial streams (Lide 1997). Lake Waccamaw, the largest Carolina bay, drains into the Waccamaw River and Big Creek in North Carolina, but most bays do not appear to be connected naturally to stream drainages (Figure 1). Because of the flatness of the Coastal Plain landscape and the high permeability of the sandy soils, substantial overland surface flow of water into bays or from bays to streams is infrequent and occurs only in periods of excessive rainfall, such as during hurricanes. Thus, natural direct surface connectivity of Carolina bays with navigable waters is uncommon. As an exception, a few bays in low-lying areas on the Del-

Table 1. Number of Carolina (or Delmarva) bays that would be at risk of loss of protection under Section 404 of the Clean Water Act under four different scenarios of ''adjacency'' to navigable waters or their tributaries. Data for bays in MD are taken from Petrie et al. (2001).

Region	Number of Depression Wetlands	% At Risk With No Buffer	% At Risk With 100-m Buffer	% At Risk With 500-m Buffer	% At Risk With 1000-m Buffer
SC (SRS)	371	92*	88	44	9
MD (Delmarva)	2170	88	81	41	11

* In the Savannah River Site (SRS) GIS analysis, a 50-m buffer was considered ''adjacent.''

marva Peninsula and the Eastern Shore of Virginia may be flooded under high tides and thus connected with waters of the Chesapeake Bay and Atlantic Ocean (Pettry et al. 1979).

The great majority of Carolina bays, especially those on the upper Coastal Plain, have drainage ditches. These ditches commonly lead to other bays at lower elevations, or to small streams, and many still function in moving water from bays to drainage systems. Bennett and Nelson (1991) found ditches in about 65% of the 2,651 bays in South Carolina that they examined. That such ditches may be functional connections to permanent water bodies was shown by Snodgrass et al. (1996), who in 1994 found fish populations in Carolina bay ponds that were completely dry during the drought of 1989–1990. Their study suggests that fish recolonization occurs either through ditches or by overland flow during periods of high water. It appears unlikely, however, that ditches to or from Carolina bays will be defined as tributaries of navigable waters.

Potential Losses

Since most bays do not have natural surface connections with other water bodies, the interpretation of ''adjacency'' in the post-SWANCC era becomes important in determining protection under Section 404 of the CWA. For example, adjacency could be defined narrowly as only those wetlands contiguous with a stream or more broadly as those within some wider floodplain (Petrie et al. 2001). In an estimate of potential losses to wetlands in several regions of the U.S., Petrie et al. (2001) used four scenarios of adjacency: contiguous with, or within 100 m, 500 m, or 1,000 m, of a navigable water body or tributary. These four scenarios were used to examine Carolina bays on the 780 km^2 SRS, where bays or similar depressions ranging in size from 0.22 ha (lower detection limit) to 78.2 ha have been identified and mapped (objective 1). Using existing geographic information system (GIS) data for the SRS, stream channels were buffered in an analysis similar to that proposed by Petrie et al. (2001). Assumptions were that all SRS streams are tributaries of navigable waters (although some are actually intermittent headwaters) and that a distance of 50 m (the lowest distance that could be reasonably determined in the GIS database) was an adequate surrogate for contiguous connection with the stream channel. The analysis revealed that with a 50-m stream buffer zone (considered contiguous), 92% of the bays were at risk of loss of protection under Section 404 of the CWA (Table 1). A 100-m buffer reduced risk to 88% and a 500-m buffer to 44%. Only with a 1,000-m definition of adjacency were most Carolina bays protected (Table 1, Figure 2).

It is not expected that the results of this analysis are representative of the situation for Carolina bays elsewhere in their range. The SRS is located on the very upper region of the Coastal Plain and is more dissected by small streams than is likely in regions of the middle or lower Coastal Plain; thus, proximity of bays to streams may be greater on the SRS than in other parts of their range. Also, a few bays on the lower Coastal Plain may be in contact with coastal waters, but none of the ones in this analysis were adjacent to estuaries. As a federal reservation, the SRS has been closed to public use and protected from agriculture and commercial development since 1950; thus, these depression wetlands have been largely protected for the last 50 years, and numerous small bays remain intact. The data set captures a range of bay sizes that is not available from NWI maps or that may not occur in more highly disturbed or recently disturbed landscapes. As such, it may be a ''best case'' estimate of Carolina bay wetland protection under various adjacency scenarios.

Interestingly, the analysis by Petrie et al. (2001) using NWI data to identify wetlands and the National Hydrological Dataset to identify navigable waterways and tributaries for eastern Maryland finds similar numbers of isolated wetlands at risk under the four adjacency scenarios (Table 1). In general, analyses using NWI maps may tend to underestimate the extent of isolated wetlands because of the scale and quality of the aerial photography used and the difficulty of identifying certain wetlands (Tiner et al. 2002). Thus, there is a problem in not including smaller, frequently dry wetlands, and it is difficult from NWI maps to determine cumulative impacts resulting from the losses of

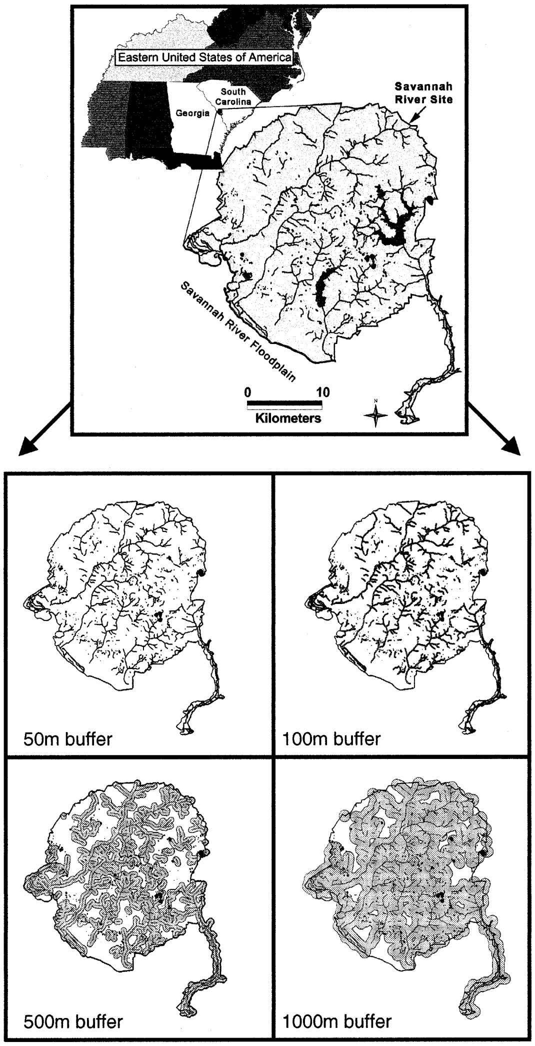

Figure 2. Maps of the Savannah River Site on the upper Coastal Plain of South Carolina, showing distribution of Carolina bays (dots) and their adjacency to streams under four scenarios: a) 50-m stream buffer, b) 100-m buffer, c) 500-m buffer and d) 1000-m buffer. It should be noted that if the active floodplain terrace of the Savannah River were buffered, the numbers would probably change little as few bays are found within 1000 m of the floodplain.

geographically isolated small Carolina bays or similar wetland depressions.

It also should be noted that ditches were not included in these analyses of connectivity to navigable waters. Ditches generally are too small to be detected from aerial imagery, and the effectiveness of ditches in connecting bays to other water bodies would have to be examined on an individual basis. If man-made ditches should be considered as connections to waters of the U.S., then it is an irony that it is those bays that have been hydrologically disturbed that would be protected, whereas the more pristine undisturbed systems would not be protected.

The SWANCC decision puts responsibility for protection of isolated wetlands back to the states. Within the range of Carolina bays, state wetland laws range from ''strong protection'' to ''weak protection'' as applied to isolated wetlands (Petrie et al. 2001); however, these laws may not pertain to small seasonally-inundated wetlands. Maryland now affords Delmarva bays special protection, but in Delaware, they are not protected. Several other states, including North Carolina and South Carolina, are moving forward with efforts to protect isolated wetlands, with varying success. For example, a bill, ''South Carolina Carolina Bays Protection Act'' introduced into the state senate in 2002 was not passed; however, the state's Department of Health and Environmental Control affirmed that all wetlands, isolated or not, are ''waters of the state'' and announced that it would undertake rulemaking to clarify the state's authority in the wake of the SWANCC decision (Southern Environmental Law Center 2003). Meanwhile, Carolina bay wetlands are being threatened by further losses through urban development as population growth in the southeastern Coastal Plain continues.

ECOLOGICAL SIGNIFICANCE OF CAROLINA BAY WETLANDS

Wetlands perform a broad array of ecosystem functions that provide value to human society. These can be classified as 1) hydrologic functions such as short-term water storage and maintenance of water tables; 2) biogeochemical functions, such as transformation and cycling of elements, and retention and removal of contaminants; and 3) habitat and food web support such as maintenance of plant and animal communities (National Research Council 1995). These ecological functions have to be considered in evaluating the effects of further losses of Carolina bays (objective 2).

The hydrologic and biogeochemical functions of Carolina bays are not well-characterized. They may store surface water during storm events and periods of heavy rainfall, thus reducing local flooding. Some bays may release surface water into shallow ground water, and bays that have been ditched to stream drainages also may provide slow release of water directly to these systems following storms. Bays that receive surface water contaminated with agricultural chemicals or other pollutants may serve a purification purpose, although such benefits have not been well-substantiated. On the Delmarva Peninsula, concentrations of nitrate, a major pollutant of concern in the regional ground water of the adjacent Chesapeake Bay, decrease in correlation with the presence of forested wetlands in bay depressions (Phillips et al. 1993).

In another example, Carolina bays in Horry County, South Carolina served as a pilot project to test the feasibility of using such systems to provide tertiary treatment of domestic wastewater (CH2M Hill 1994). In the first years of the project, significant assimilation of nutrients and metals occurred before the effluent recharged local ground water, and tree basal area and total plant diversity in the bays increased. Over time, however, changes occurred in plant species composition and productivity decreased; after 15 years, nitrogen concentrations in water leaving the wetlands were no longer significantly lower than those in the wastewater inputs.

The most significant ecological function of Carolina bays is providing habitat for a diverse and unusual flora and fauna (Sharitz and Gibbons 1982). The varied, and often unpredictable, hydrologic conditions of many bays exclude species requiring permanent water, while providing habitat for an abundance of species adapted to the fluctuating water levels. In addition, the combination of large and small depressions, wet and dry years, and long and short hydroperiods results in a far greater habitat diversity on the landscape than a single type of wetland would provide. The loss of these habitats may have serious consequences for rare plant species and for groups of animals, such as amphibians, that depend on temporary ponds as their primary breeding sites. To understand the potential consequences of the SWANCC decision on the habitat functions of Carolina bay wetlands, it is necessary to understand some of the physical and chemical features of these ecosystems.

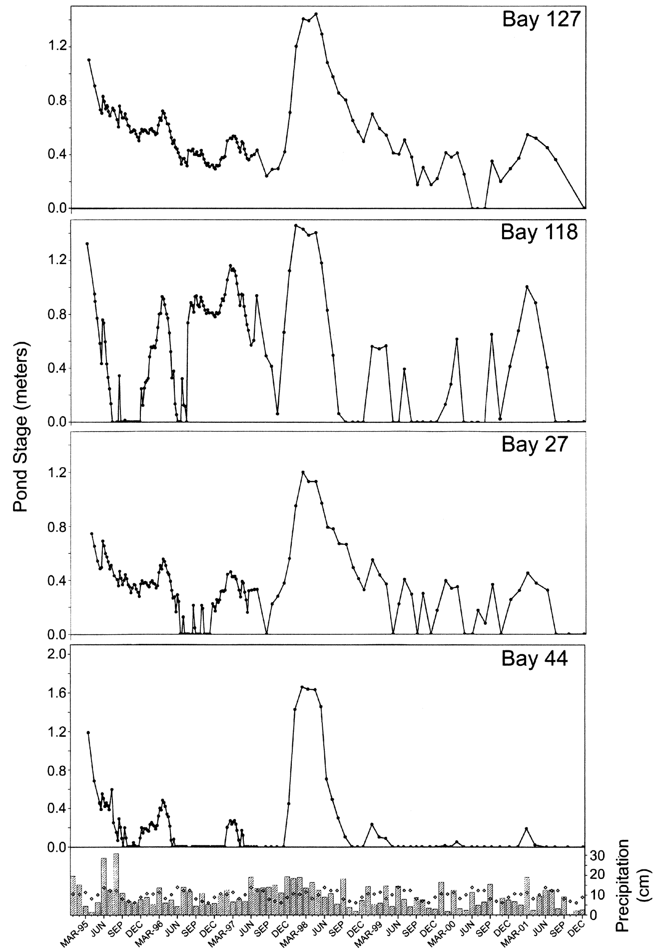

Figure 3. Hydrographs of four Carolina bays within 16 km of each other on the Savannah River Site on the upper Coastal Plain in South Carolina from January 1995–December 2001. Sizes of the depressions are: Bay 127 = 8.7 ha, Bay 118 = 2.5 ha, Bay 27 = 1.9 ha, and Bay 44 = 5.0 ha. Bars at the base of the figure indicate monthly regional precipitation, and diamonds indicate 30-year regional average precipitation. (Hydrograph data from R. F. Lide)

Features of the Carolina Bay Habitat

The distinctive shape and orientation of classic Carolina bays have been attributed to meteor impacts, substrate dissolution and subsidence, and a variety of other causes (e.g., Johnson 1942, Savage 1982, Ross 1987). The most generally accepted explanation of bay formation entails historic modification of shallow ponds through the action of waves generated by southwesterly winds (Thom 1970, Kaczorowski 1977, Grant et al. 1998). It remains uncertain whether some or all bays are of the same age. Radiocarbon dates from buried organic sediments in the basins range from > 48,000 years before present (YBP, Brooks et al. 2001b) to 16,000 YBP (Stolt and Rabenhorst 1987). Geochemical and diatom analyses of sediment cores from Lake Waccamaw suggest its age as 15,000 YBP or less (Stager and Cahoon 1987). In contrast, studies at Flamingo Bay on the SRS, using optically stimulated luminescence techniques, indicate formation of the basin about 109,000 YBP (Brooks et al. 2001a). More importantly, paleoenvironmental and archeological records suggest that bays have been dynamic systems, with changes driven by geologic and climatic processes as well as by human activity (Frey 1951a, Watts 1980, Brooks et al. 1996, Gaiser et al. 1998).

Climate and Soils. Carolina bays occur in areas of sandy surficial sediments across elevations ranging from several meters above sea level (ASL) near the coast to more than 200 m ASL on the extreme upper Coastal Plain. Temperatures throughout are mild, ranging from lows near freezing (-3.2° to 5.2° C) during January to highs of 31° to 33° C during July (Sharitz and Gresham 1998). Rainfall is greatest (1,335 mm) in the southeastern coastal region and is typically greater in the summer (July–September) and moderate in the winter and early spring (January–March, Figure 3).

Soils in the basins of Carolina bays that have not been disturbed by burning or land-management practices range from highly organic to predominantly mineral; most are underlain with sand alternating with impervious clay layers that retard vertical water movement and may result in a perched water table. In a study of 53 bays on the northern Delmarva Peninsula, Stolt and Rabenhorst (1987) discriminated between basins filled with predominantly sandy sediments and those containing substantial amounts of silty loam; more than 20% contained Histosols or had organic horizons up to 50 cm deep. Further south on the Virginia Eastern Shore, a survey of 40 bays described soils with mucky surfaces and high silt content, overlying sandy clay loam sediments (Bliley and Pettry 1979, Pettry et al. 1979). In North Carolina and South Carolina, bay basin soils are primarily Histosols or wet, fine-to-coarse textured mineral soils (Daniels et al. 1984). Bay soils in coastal areas generally have loam overlying loamy sand or sand; whereas bay soils in interior areas have loam over sandy clay loam, clay loam, or clay. Newman and Schalles (1990) surveyed 49 Carolina bays along transects from the upper Coastal Plain to the coast and reported surface peat depths ranging from < 1 cm to > 200 cm, with a tendency for thicker organic deposits in the bays closer to the coast. Some of the larger bays on the lower Coastal Plain in eastern North Carolina may have peat layers up to 4.5 m thick (Ingram and Otte 1981). A distinction is commonly drawn between ''peat-based'' bays of the lower Coastal Plain and ''clay-based'' bays of the upper Coastal Plain. Soils of bay rims are typically more sandy than those of basin interiors (Bliley and Pettry 1979, Stolt and Rabenhorst 1987, Lide et al. 1995).

The stratigraphy of Thunder Bay, a 7-ha bay on the upper Coastal Plain of South Carolina, has been studied in detail (Lide et al. 1995). The central, and frequently ponded, portion of the bay contains black mucky loam grading into a grayish loam (to a depth of 60 cm) overlying a layer of highly permeable white sand (up to 30 cm thick). Beneath these sediments is a sandy clay or sandy clay loam hardpan 4 m thick in the bay center and thinning to 1–2 m at the margins. The estimated hydraulic conductivity of the upper surface of the hardpan ranges from 3.6×10^{-9} to 1.1×10^{-6} m sec^{-1}, suggesting that it is moderately to slowly permeable (Lide et al. 1995). Similarly, De Steven and Toner (1997) reported depths of surficial sand above the clayey soil ranging from 38 to 97 cm in a survey of 57 bays on the upper Coastal Plain.

Spatial patterns of soil characteristics, especially within the shallow horizons, likely vary both among bays and across elevations within a bay. Reese and Moorhead (1996) described significant changes in soil properties, including clay content, organic carbon, and cation exchange capacity in the A horizon along a 1-m elevation change from the center to the rim of a 4.25-ha bay, but they did not find such gradients in the B horizon. They also reported significant differences among transects within the bay and proposed that the spatial variability in the A horizon reflects vegetation patterns and hydrology. Limited information is available on cations in Carolina bay soils, but exchangeable calcium (Ca), magnesium (Mg), and potassium (K) tend to be low (Schalles et al. 1989, Reese and Moorhead 1996). In general, Carolina bay soils are not unique compared with those of other regional wetlands, but the variability in soil characteristics among bays is influenced by numerous factors such as position on the Coastal Plain landscape, accrual of organic matter, hydrologic conditions, vegetation, and disturbance.

Hydrology and Water Chemistry. In response to seasonal rainfall and temperature, Carolina bays are often wetter in the winter and early spring when precipitation is moderate and evaporative water loss is low. They may gradually dry during the summer when evapotranspiration is high but be temporarily refilled by late summer rainfall events that are often associated with thunderstorms and hurricanes. Rainfall dominates the water input to most Carolina bays, and the characteristic sandy clay hardpan is often assumed to limit interactions between surface water and ground water and result in a perched water table. Other sources of water to some bays may include artesian wells (Wells and Boyce 1953, Wharton 1978), shallow ground water (Newman and Schalles 1990, Lide et al. 1995), inlet channels (Knight et al. 1989), and occasional surface runoff during periods of high rainfall. A small number of bays very close to the ocean may be influenced by coastal waters (Pettry et al. 1979).

Water loss is primarily by evapotranspiration, although seepage into shallow ground water may occur in some bays (Lide et al. 1995). A few Carolina bays have natural outlet channels, and many have drainage ditches. Although some bays contain permanent open water, many are semi-permanent ponds that dry during droughts, and others dry almost every year. In many bays, the net balance between inputs and losses results in a water table that fluctuates, often from 1–2 m above the soil surface (Schalles and Shure 1989, Lide et al. 1995) to 1 m or more below the surface (Knight et al. 1989). Timing and duration of ponding can differ greatly among bays, even those in close proximity that receive similar precipitation inputs (Figure 3). Furthermore, hydroperiod is not necessarily a function of size of the depression, although Snodgrass et al. (2000b) reported a significant, but very weak, relationship between bay size and duration of ponding in 86 bays on the SRS. Thus, fluctuating water levels, and the ephemeral nature of inundation in many small depressions, distinguish Carolina bays and similar depression wetlands from more permanent wetlands or aquatic habitats of the region.

There have been few detailed studies of potential surface-water and ground-water interactions in Carolina bays. Lide et al. (1995) reported that water levels in Thunder Bay were very responsive to climatic conditions, increasing with each rainstorm and gradually decreasing during rain-free periods. A simple water balance showed that net monthly change in pond stage was largely controlled by precipitation and evapotranspiration. Water-table profiles obtained from piezometers and wells, however, revealed seepage losses from the bay that resulted in water-table mounding beneath the basin during relatively dry conditions (Lide et al. 1995). There was also potential for ground-water inflow to the bay during unusually wet conditions and high water tables, although net ground-water outflow was dominant. Thus, Thunder Bay was not a hydrologically-perched wetland system. Somewhat similar results were reported by Chmielewski (1996), who examined pond stage records of nine bays, soils data, weather records, and data from a grid of water-table wells on the SRS to evaluate the likelihood of ground-water inputs. She found evidence of ground-water contributions to six of the bays.

Water chemistry in Carolina bays is influenced by various factors, including position on the Coastal Plain landscape and variation in shallow ground-water chemistry, weathering of underlying mineral substrates, paludification and associated accrual of organic substrates, and the degree to which precipitation versus surface runoff or shallow ground water dominate the hydrology. In their study of 49 bays in North Carolina and South Carolina (including five that are permanent lakes), Newman and Schalles (1990) found most to be ombrotrophic and acidic (median pH = 4.6, range = 3.4–6.7). Dissolved organic carbon was 17.2 mg L^{-1} (range = 2.1–70.0 mg L^{-1}) and represented 38% of the total anions. Waters were quite soft (median Ca = 1.69 mg L^{-1}; range 0.16–11.75 mg L^{-1}). Similar pH and Ca levels were reported by Gaiser (1997) and by Snodgrass et al. (2002a) in surveys of bays on the SRS. Newman and Schalles (1990) interpreted high (or ''excess'') sulfate (SO_4) concentrations in nine of the bays and four of the bay lakes to be an indication of ground-water enrichment (although anthropogenic additions could also be a factor). Although there was relatively large variation among bays for most chemical parameters, water chemistry values generally fell within the range of values found in other softwater, acidic systems including those on the southeastern Coastal Plain (pocosins, cypress domes, the Great Dismal Swamp, and the Okefenokee Swamp) and northern bogs (Newman and Schalles 1990).

Habitat Values of Carolina Bay Wetlands

Flora. A key to the high plant diversity in Carolina bays is the temporal and spatial variation in their hydrology. Studies of bays in North Carolina and South Carolina by Schafale and Weakley (1990), Bennett and Nelson (1991), and Weakley and Schafale (1991) have characterized at least 11 types, based largely on their vegetation associations (Table 2). Pocosin communities, pond cypress savannas, and pond cypress ponds are more abundant on the lower Coastal Plain; depression meadows occur mostly in the upper regions; and non-alluvial swamps occur throughout. Pond cypress savannas are likely the most floristically diverse of the bay communities (Bennett and Nelson 1991), with many sedge, grass, and forb species. Depression meadow communities are relatively rare and are sometimes considered to be a variant of the pond cypress savanna, lacking trees but with a similar herbaceous flora (Schafale and Weakley 1990). The Nature Conservancy has further classified 29 vegetation alliances found in southeastern depression wetlands (Weakley et al. 2000), although their listing includes Carolina bays as well as other types of wetland depressions.

There is much overlap of species among the vegetation types in Carolina bays, and several plant communities commonly occur within the same depression. De Steven and Toner (1997) related the vegetation in 57 relatively intact bays on the upper Coastal Plain in South Carolina primarily to position of the bay on the landscape (terrace, loam hills, sandhills) and to hydrology. In many Carolina bays, there may be a distinct zonal pattern of dominant species, with submerged and floating-leaved aquatic macrophytes in the center, followed by emergent graminoids (grasses, sedges, and rushes), and ringed by wetland shrubs and trees (e.g., Kelley and Batson 1955, Tyndall et al. 1990). Droughts or periods of unusually heavy rainfall (e.g., El Niño) cause shifts in these species zones, and fires and other disturbances result in changes in herbaceous species composition and dominance (Kirkman and Sharitz 1994, Kirkman 1995). Periodic fires may be especially important in Carolina bays with pocosin, cypress savanna, pond pine woodland, or bay forest vegetation, where they may reduce peat thickness (Wharton 1978, Schafale and Weakley 1990) and result in shifts in understory species composition (Sutter and Kral 1994).

Carolina bays with a pronounced hydrologic cycle of flooding and drying may have a rich and persistent seed bank in the soil (Kirkman and Sharitz 1994, Sutter and Kral 1994, Poiani and Dixon 1995, Collins and

Table 2. Vegetation types and characteristic species in Carolina bays with different hydrologic and soil conditions (from Schafale and Weakley 1990, Bennett and Nelson 1991).

Carolina Bay Type	Hydrologic and Soil Conditions	Type of Vegetation and Characteristic Species
Lakes	permanently flooded; organic or mineral soils	zones of floating-leaved and emergent macrophytes (*Nymphaea odorata* Ait., *Nuphar lutea* (L.) Small, *Panicum hemitomon* J. A. Schultes, *Pontederia cordata* L., *Juncus effusus* L.) and shoreline shrubs (*Cephalanthus occidentalis* L., *Myrica cerifera* (L.) Small)
Small Depression Ponds	permanently flooded in center; sandy, clay or organic sediments	various submersed, floating-leaved and emergent macrophytes (*Utricularia* spp., *Nymphaea odorata, Nymphoides aquatica* (J.F. Gmel.) Kuntz, *Nuphar lutea, Panicum hemotomom, Eleocharis* spp.)
Vernal Pools	seasonally flooded; various soils	dense to sparse herbaceous vegetation of various species (*Leersia hexandra* Swartz, *Carex* spp., *Dicanthelium* spp., *Panicum* spp., *Centella asiatica* (L.) Urban, *Utricularia* spp., *Drosera* spp.)
Pond Cypress Ponds	semipermanently flooded; clay-based	pond cypress canopy (*Taxodium ascendens* Brongn.) with other trees and shrubs (*Nyssa sylvatica* Marsh., *Acer rubrum* L., *Ilex myrtifolia* Walt., *Lyonia lucida* (Lam.) K. Koch)
Non-alluvial Swamps	seasonally or frequently saturated or shallowly flooded; mucky mineral or organic soils	pond cypress (*Taxodium ascendens*), bald cypress (*T. distichum*) (L.) L. C. Rich, pond pine (*Pinus serotina* Michx.) and broad-leaved trees (*Nyssa biflora* Walt., *Acer rubrum, Liquidambar styraciflua* L., *Magnolia virginiana* L.)
Pond Cypress Savannas	seasonally to temporarily flooded; clay-based	pond cypress (*Taxodium ascendens*) and other trees including *Nyssa biflora*; shrubs (*Ilex amelanchier* M.A. Curtis ex Chapman, *Cyrilla racemiflora* L.); numerous graminoids (*Panicum hemitomom, Dicanthelium* spp., *Carex* spp., *Rhynchospora* spp.)
Depression Meadows	seasonally to temporarily flooded; clay-based	often distinct zones, rich herbaceous flora (*Panicum* spp., *Rhynchospora* spp., *Scleria reticularis* Michx., *Rhexia virginica* L., *Lachnanthes caroliniana* (Lam). Dandy, *Xyris* spp., and numerous others)
Low and High Pocosins	seasonally flooded or saturated; Histosols	evergreen shrubs and low trees (*Lyonia lucida, Cyrilla racemiflora* L., *Zenobia pulverulenta* (Bartr. ex Willd.) Pollard, *Ilex glabra* (L.) Gray) with *Smilax laurifolia* L.; stunted pond pine (*Pinus serotina*)
Small Depression Pocosins	seasonally or intermittently flooded; usually sandy soils	dense shrub layer (*Lyonia lucida, Cyrilla racemiflora, Ilex glabra* and others); sparse to dense canopy (*Pinus serotina, Acer rubrum, Persea palustris* (Raf.) Sarg.)
Pond Pine Woodlands	temporarily flooded or saturated; Histosols or oligotrophic mineral soils with organic surface layers	pond pine canopy (*Pinus serotina*); also evergreen shrubs and trees (*Gordonia lasianthus* (L.) Ellis, *Magnolia virginiana* L., *Pinus taeda* L., *Persea palustris*) and *Acer rubrum*; shrub layer of *Cyrilla racemiflora*, *Lyonia lucida* and other evergreen or semi-evergreen species
Bay Forests	seasonally saturated or flooded; Histosols or oligotrophic mineral soils with organic surface layers	predominantly evergreen trees (*Gordonia lasianthus, Magnolia virginiana, Persea palustris*); may include *Nyssa biflora* Walt., *Acer rubrum, Pinus serotina, Pinus taeda*; shrub layer with *Lyonia lucida, Cyrilla racemiflora,* and others

Battaglia 2001). In four depression-meadow bays on the SRS, Kirkman and Sharitz (1994) found the seed bank to be the most diverse of any reported in freshwater wetland habitats. Many of the species were not present in the above-ground vegetation when the bays were ponded but germinated during periods of drying and drought-related soil disturbances. Similarly, Collins and Battaglia (2001) found that the number of species germinating from the seed bank increased from pond-like bays to bays with more variable hydroperiods. Their study supports the hypothesis that hydrology strongly affects recruitment and plant species distribution in Carolina bays. Thus, a persistent seed bank may be considered an adaptation by plant species to survive under variable and unpredictable hydrologic conditions, and it serves to maintain a diverse community structure in an ecosystem that may undergo extreme environmental changes in short time periods.

Carolina bays contain an unknown number of rare and endemic plant species. Sutter and Kral (1994) estimate that more than a third of the rare plant species in the Southeast occur in non-alluvial wetlands, including Carolina bays as well as karst ponds and longleaf pine savannas. Of the 29 vegetation alliances of southeastern depression wetlands described by The Nature Conservancy (Weakley et al. 2000), 20 have rare plants (Edwards and Weakley 2001). Several of the alliances with the greatest concentrations of rare species are found in pond cypress savannas and depression meadow Carolina bays. Seed banks may be critical for the persistence of many rare plant species, yet seed bank information is available for less than 20% of the rare plants listed by Edwards and Weakley (2001). Furthermore, continued loss of small depression wetland habitats contributes to the increased rarity of these species.

Fauna. Some components of the fauna (e.g., zooplankton, aquatic invertebrates, amphibians and reptiles) have been studied extensively in a few Carolina bays, but thorough surveys across the range of bay habitats have not been conducted. Rich zooplankton communities have been found; for example, Mahoney et al. (1990) reported 44 species of cladocerans and seven species of calanoid copepods in bays on the SRS (including a new species endemic to the bays; DeBiase and Taylor 1997). A great variety of aquatic and semiaquatic insects live in bays (Taylor et al. 1999); a single wetland may support more than 100 species (Leeper and Taylor 1998), and well over 300 species have been collected. Larvae of dipterans, mainly chironomids, dominate the insect assemblages; at one bay on the SRS, 79 dipteran taxa, including 65 chironomids, were collected (Leeper and Taylor 1998). There are striking differences between the aquatic invertebrate assemblages of Carolina bays and nearby permanent ponds and reservoirs, probably due to the seasonal hydrology of bays that excludes fish predators (Taylor et al. 1999).

Although some Carolina bay lakes support permanent populations of fish, the majority of bays do not. Lake Waccamaw, a 3,200-ha bay lake, has 25 fish species (Frey 1951b), of which three may be endemic. Of 63 bays sampled on the SRS in 1994, only 13 contained fish (1–6 species/bay, 12 species total); presence or absence of fish was related to frequency of drying and proximity of the bays to permanent aquatic habitats that could serve as sources for recolonization following droughts (Snodgrass et al. 1996).

The absence of predatory fish allows semiaquatic vertebrates with aquatic larval stages to become extremely abundant in some Carolina bays. In a one-year study of two 1-ha bays, Gibbons and Semlitsch (1981) captured more than 72,000 amphibians moving to or from the water, including nine species of salamanders and 16 species of frogs. Out of 34 amphibian species that occur in bays on the SRS, 16 depend entirely on these seasonal wetlands for breeding (Gibbons and Semlitsch 1991). Long-term census data for amphibian species breeding in Rainbow Bay, a 1-ha depression, showed fluctuations of substantial magnitude in both the size of the breeding populations and in recruitment of juveniles (Pechmann et al. 1991), and hydroperiod was the primary driver of variation in community structure (Semlitsch et al. 1996). In a related study of 22 bays ranging in size from < 1 ha to > 80 ha on the SRS, Snodgrass et al. (2000b) found a relationship between amphibian species richness and hydroperiod length but not between species richness and wetland size. Furthermore, the species in the small bays were not a subset of those in the large ones (Snodgrass et al. 2000b). Semlitsch and Bodie (1998) also noted that many pond-breeding salamanders are philopatric, returning as adults to their natal ponds for breeding; thus, preservation of these smaller wetlands is essential to maintaining amphibian populations.

Other vertebrate species are also common users of Carolina bays; Gibbons and Semlitsch (1981) captured six species of turtles, nine of lizards, 19 of snakes, and 13 species of small mammals in their one-year study. There are no known endangered or rare vertebrate species that rely exclusively on Carolina bays, although the most northern and inland colony of the federally endangered wood stork (*Mycteria americana* L.) nests in a forested bay wetland in Georgia (Hodgson et al. 1988). Wood storks forage extensively in Carolina bays and other shallow wetlands of the region. The federally threatened flatwoods salamander (*Ambystoma cingulatum* Cope) breeds in small, shallow depressions, including Carolina bays, that frequently dry completely and lack predatory fish. Similarly, gopher frogs (*Rana capito* LeConte), designated as federally endangered in the western part of their range (Alabama, Mississippi, and Louisiana), breed in shallow temporary ponds and bays surrounded by upland longleaf pine habitat.

Terrestrial areas adjacent to Carolina bays are also critical habitats for many animal species (Gibbons 2003). Adult pond-breeding salamanders and newly metamorphosed juveniles use surrounding uplands throughout most of the year (Scott 1994, Semlitsch 1998). Mole salamander (*Ambystoma talpoideum* Holbrook) adults migrated on average 178 m (range 13–287 m), and juveniles migrated 47 m (range 14–204) from the edge of a bay wetland (Semlitsch 1981). Similarly, some aquatic turtles may spend more time in adjacent terrestrial habitats than in wetlands; Burke and Gibbons (1995) and Buhlmann and Gibbons (2001) have shown that almost all nesting and refugia sites for aquatic turtles of Carolina bays lie outside the jurisdictional boundaries of the wetlands. Excluding these terrestrial areas from protection would likely reduce both adult survival and recruitment of juveniles into the populations of these animal species (Semlitsch 1998).

Bays may play an important role in the metapopulation dynamics of wetland-dependent animal species (Semlitsch and Bodie 1998, Buhlmann and Gibbons 2001, Gibbons 2003) and serve as source populations to other wetlands where such species become extinct because of natural environmental conditions (drying) or through disturbance. Semlitsch and Bodie (1998) argue convincingly that small wetlands are extremely valuable for maintaining biodiversity and that their loss will cause a direct reduction in the connectance among remaining species populations. Thus, protection strategies should be directed toward clusters of bays in order to maintain the source-sink dynamics of many populations. Furthermore, bays may also serve as source populations to other wetland habitats, and movements of animals between bays and other aquatic ecosystems (Buhlmann and Gibbons 2001) link wetlands across the landscape.

CONCLUSIONS

Carolina bay wetlands are unique to the southeastern U.S. Coastal Plain. Numerous studies have documented their ecological significance as critical habitat for certain plant and animal species, and their importance to maintaining species diversity. The very fact that many bays lack permanent connections to other water bodies, coupled with periodic drying, enhances their habitat value for organisms such as aquatic invertebrates or pond-breeding amphibians that are preyed upon by fish in permanent aquatic habitats. Small bays and those that typically dry during the growing season have received little federal or state protection from destruction in the past, and many have been highly disturbed or completely obliterated. Since most Carolina bays do not have natural surface connections to navigable waters (although many are ditched), the 2001 SWANCC ruling has the potential for removing most of these depression wetlands from federal protection through the CWA. An analysis of a set of bays occurring on the upper Coastal Plain of South Carolina suggests that 92% of these wetlands may be at risk. Carolina bays are integrated into the southeastern landscape and are vital in maintaining the regional diversity of habitats and species. Although these wetlands may have the appearance of being *geographically isolated* from other wetlands, they are not necessarily *hydrologically isolated*, and they are certainly not *functionally isolated* from other wetlands.

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