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THE ECOLOGICAL BOUNDARIES OF SIX CAROLINA BAYS: COMMUNITY COMPOSITION AND ECOTONE DISTRIBUTION

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Abstract: Community and environmental gradients within the ecological boundaries of Carolina bay wetlands may provide important information on the interaction between Carolina bays and associated uplands, and may also provide guidance for improved management. We established twelve 30-m transects on the sloping rims of each of six Carolina bays in northeastern South Carolina to characterize the community gradient, as well as important environmental factors producing this gradient. Mid-points of the transects were placed on jurisdictional wetland boundaries. Hydrology, soil properties, and plant species composition were measured within these transects. On average, transects included an elevation change of 0.6 m that corresponded with gradients of hydrology, soil properties, and community characteristics. Decreasing surface soil moisture (i.e., fewer flood events) and decreasing soil nutrients were associated with a shift from shrub-bog vegetation with relatively low alpha diversity and prominence of evergreens to a relatively diverse and heterogeneous community characterized by grasses, herbs, low shrubs, and vines. Ecotones, identified by abrupt changes in community composition, were more frequently found outside jurisdictional wetland boundaries. Likewise, five near-endemic and endemic plant species were found outside the wetland boundaries. Our data reinforce the need for better understanding of how Carolina bays interact with adjacent landscape elements, and specifically how ecological boundaries are influenced by this interaction.

Key Words: buffer, elevation, endemic species, environmental gradient, fire, hydrology, jurisdictional wetland boundary, ordination, pocosin, transect, wetland boundary

INTRODUCTION

Ecological boundaries are defined as areas of relatively steep environmental or community gradients (Cadenasso et al. 2003). Because ecological boundaries of wetlands may regulate the flow of energy, materials, and organisms between wetlands and adjacent uplands, it is important to accurately characterize those boundaries with the goal of protecting or improving wetland integrity (Holland 1996). Efforts to characterize ecological boundaries associated with wetlands and other ecological systems have focused on identifying environmental gradients and detecting changes in community structure or composition (i.e., ecotones) within the context of spatially structured sampling (Walker et al. 2003). Ecotones associated with wetlands may or may not coincide with jurisdictional wetland boundaries (Carter et al. 1994, Kirkman et al. 1998), but they do define important characteristics of ecological boundaries and may be of importance in determining boundary location and width (Holland 1996).

The focus of our research was a well-defined ecological boundary described previously as a pocosin-sand rim ecotone (Bennett and Nelson 1991), a savanna/pocosin ecotone (LeBlond 2001), or more simply as the Carolina bay rim (Luken 2005a). This particular boundary may play an important role in speciation and conservation of the endemic flora of the Cape Fear Arch region of the Carolinas (Bennett and Nelson 1991, LeBlond 2001, Luken 2005b). More generally, this boundary may influence the seasonal habitat suitability of Carolina bays for reptiles and amphibians (Gibbons 2003), and may contribute to high biodiversity in areas of the

Atlantic Coastal Plain where Carolina bays exist within a matrix of pine savanna (Kirkman et al. 1999, Sorrie and Weakley 2001). These important functions of Carolina bay ecological boundaries have not been clearly placed in the spatial context of the wetland/upland continuum. However, such placement is necessary in order to better manage large landscapes where Carolina bays exist in a matrix of pine savanna. Our research used transects established across the ecological boundaries of Carolina bays in an effort to address the following questions: Do soil properties, hydrology, and plant communities vary within the boundary? Do ecotones exist within the ecological boundary and if so, are ecotones uniformly distributed within the ecological boundary? Are specific locations within the ecological boundary more likely to support high biodiversity? And finally, what factors might influence structuring of Carolina bay ecological boundaries?

METHODS

Study System and Research Site

Carolina bays are shallow, ellipsoid-shaped depression wetlands of unknown geologic origin that occur across the Southeastern Coastal Plain (Thom 1970). The ecological boundary of a Carolina bay is defined by a narrow, sloping rim (Luken 2005b). It is commonly assumed that Carolina bays receive water mainly by precipitation, with a few notable exceptions (Sharitz and Gibbons 1982, Richardson and Gibbons 1993). Some bays contain permanent water while others include ephemeral ponds and still others have no open water, existing as closed shrub bogs (Lide et al. 1995, Sharitz 2003). As Carolina bays lack obvious connections with navigable waters, they are now referred to as isolated wetlands, although there is considerable debate regarding this designation (Sharitz 2003, Winter and Lebaugh 2003). Variations in soil, hydrology, and landscape setting produce a wide range of plant communities within Carolina bays (Porcher 1962, Sharitz and Gibbons 1982, Kirkman and Sharitz 1994, Sharitz and Gresham 1998, Sharitz 2003, DeSteven and Toner 2004).

The vast majority of Carolina bays have been modified by ditching and draining and these converted systems exist in a landscape devoted largely to agriculture (Bennett and Nelson 1991, Sharitz 2003). However, government preserves and some private lands still harbor intact Carolina bays within a matrix of pinelands. These pinelands are now commonly the focus of efforts to restore species-rich savanna that was historically widespread throughout the Southeastern Coastal Plain (Glitzenstein et al. 2001).

Our study was conducted at Lewis Ocean Bay Heritage Preserve (LOBHP; latitude 33°47′N, longitude 78°52′W) near the northeast edge of Horry County, South Carolina, on the South Atlantic Coastal Plain. Climate is humid subtropical with mean annual temperature of 15.9°C and mean annual precipitation of 133 cm. The preserve is a 3,640-ha tract that includes 22 Carolina bays. The bays at LOBHP are embedded in a mosaic of non-bay depression wetlands and remnant pine plantations. The preserve is owned and managed by the state of South Carolina and prescribed burning of the uplands is attempted every 2–3 yrs.

Carolina bays at LOBHP do not typically have open-water habitats, but support low-density forests comprised of *Pinus serotina*, *Persea palustris*, *Gordonia lasianthus*, and *Magnolia virginica*. The understory is comprised of thickets of evergreen shrubs such as *Lyonia lucida*, *Ilex coriacea*, and *Ilex glabra* forming shrub-bog (or pocosin) of various heights. Moreover, Carolina bays dominated by evergreen shrubs occur mostly in the northeastern part of the state (Bennett and Nelson 1991). Vegetation of LOBHP bays differs from the aquatic and emergent vegetation surrounded by a forested rim as described by Schalles and Shure (1989) on the Upper Coastal Plain in South Carolina, or grass- and sedge-dominated communities noted by Tyndall et al. (1990) in Maryland, Kirkman and Sharitz (1994) and Mulhouse et al. (2005) in South Carolina, and Kirkman et al. (1998) in Georgia.

Upland soils at LOBHP are classified as Leon fine sand, Witherbee sand, or Echaw sand (USDA 1986). The texture of the A horizon typically ranges from sandy to sandy loam and is underlain by a sandy E horizon occasionally followed by a sandy or sandy loam B horizon. Soils of Carolina bay boundaries have sandy, loamy sand, sandy loam, or sandy clay loam A horizons occasionally overlaid by a thin organic layer. Often a sandy or sandy loam E horizon is present. Soils within Carolina bays are classified as Johnston loam (USDA 1986) and typically have an organic layer at least 10-cm thick underlain by a sandy clay or loam A horizon with a low chroma matrix. Occasionally, a sandy E horizon is visible.

Vegetation Sampling

Six ellipsoid-shaped Carolina bay wetlands within LOBHP were studied. Bays were selected based on access and presence of two well-defined axes. Bay areas averaged 15.2 ha and ranged from 4.1–73.0 ha. The long axes averaged 350 m and ranged from 129–445 m. The short axes averaged 234 m and ranged from 116–343 m. Two 30-m transects were established on the sloping rim of each bay, one on either the northeast or southwest side (hereafter referred to as the side transect), and one on the southeast end (hereafter referred to as the end transect). Coordinates from a geographic information system (GIS) were initially used to place transects at the middle of either the bay side or bay end. However, in some cases transects had to be shifted to avoid dirt roads or other disturbances. Transects extended from the bay, across the sloping bay rim, to the adjacent upland. The jurisdictional wetland boundary served as the midpoint of each transect and was determined based on the 1987 Army Corps of Engineers Wetlands Delineation Manual (USACOE 1987). Sandy hydric soil, a special and potentially problematic type of hydric soil, was identified with indicators listed by Tiner (1999). One-m^2 plots were placed every other meter along each transect to measure percent cover of plants comprising the ground layer and understory vegetation. This analysis included all plants with stems less than 2-cm diameter at breast height (dbh). Vegetation sampling was conducted from May to July 2005. Plant nomenclature followed Weakley (2004).

Topography, Hydrology, and Soil Sampling

Relative elevation of each plot along the 12 transects was measured using a transit level. These measurements enabled us to calculate total elevation change and topographic variation within each transect. Hydrology, water quality, and soil characteristics were measured at three positions on each transect with the assumption that these measurements represented environmental conditions of specific transect zones. One position (transect midpoint) was the jurisdictional wetland boundary. The other two positions were at opposite ends of the transects. Water wells were placed on the three transect positions and well depths ranged from 75–150 cm depending on relative elevation. Depth to the water table, conductivity, and pH were measured every two weeks or following rain storms that produced at least 2.54 cm of rain from May 24 to November 22, 2005. On each sampling day, all six bays were measured. Near each well, six soil subsamples to a depth of 20 cm were collected, composited, and analyzed at the Clemson University Agricultural Extension Service Laboratory for Mehlich-1 extractable phosphorus (P), potassium (K), calcium (Ca), as well as nitrate nitrogen, cation exchange capacity (CEC), organic matter, and soil pH.

Data Analyses

Initial exploratory data analyses focused on plot-level trends within each transect to assess patterns of species distribution and to determine appropriate methods of multivariate community analysis (McCune and Grace 2002). Furthermore, total accumulated species richness and beta diversity were calculated for each transect. Beta diversity was assessed as beta turnover, β_T (Wilson and Shmida 1984), and as axis length in number of standard deviation units of species turnover (SD) derived from detrended correspondence analysis (DCA) in PC-ORD (McCune and Mefford 2006). These parameters were compared between side and end transects with a paired-sample t-test (SPSS 2002).

Non-metric multidimensional scaling (NMDS) and cluster analysis (Wards' Method) were done in PC-ORD Version 5 (McCune and Mefford 2006) and were used for examining relative similarities among transect zones and among transect plots. The NMDS used importance values, the Sorensen distance measure, and the autopilot mode. Minimal stress for NMDS was achieved by identifying and eliminating species that did not occur in more than three samples and by arcsine square root transformation of data. Transect zones (upper, middle and lower) were assessed by combining samples (i.e., plots 1–5, 6–10, 11–15) and by calculating importance values (i.e., relative coverage) based on total coverage of the individual species. This yielded 36 samples. Plots 6–10 included the jurisdictional wetland boundary. Cluster analysis was used to determine if transect zones represented identifiable communities. We also used NMDS and cluster analysis to examine the relationships among the 180, 1-m^2 community samples from the 12 transects.

Community and environmental parameters of the three transect zones were compared with analysis of variance (ANOVA) blocked by transect and followed by Tukey's test (SPSS 2002). The underlying assumptions of ANOVA were met by log transformation. In addition to the soil parameters, this analysis included species richness, diversity (H′), the weighted average index of hydrophytic vegetation (Tiner 1999), relative elevation, and an index of soil moisture based on number of times where water levels were within 15 cm of the soil surface. Weighted average vegetation indices < 2 are considered indicative of hydrophytic vegetation and weighted average indices > 4 are indicative of upland vegetation (Tiner 1999). These community

Table 1. Characteristics of 30-m transects established on the rims of six Carolina bays at Lewis Ocean Bay Heritage Preserve. In each bay, two transects were established, one on a side rim and one on an end rim. Means are presented ± standard error, n = 6. Superscript letters indicate no significant ($P \geq 0.05$) differences between side and end transects.

Position	Richness (S)	Beta Turnover ($ß_T$)	Axis Length (SD)	Elevation Change (m)
Side	18.7 ± 1.8^a	3.2 ± 0.3^a	4.0 ± 0.5^a	0.6 ± 0.2^a
End	21.8 ± 2.2^a	3.0 ± 0.3^a	4.3 ± 0.3^a	0.6 ± 0.1^a

and environmental parameters were also correlated with the NMDS axis scores for transect zones.

We used split moving window dissimilarity analysis (SMWDA) as a method of identifying relatively large changes in community composition within series of ordered samples (Ludwig and Cornelius 1987). We determined DCA axis 1 scores for samples within each transect. Then, we calculated the squared Euclidean differences of these scores for both two-plot and four-plot window widths. Ecotones were identified when the squared Euclidean difference was more than one standard deviation from the mean of squared Euclidean differences calculated for the entire transect.

Results of the cluster analysis and the assessment of ecotones provided guidance for three different sample group assessments. We used indicator species analysis (ISA) in PC-ORD (McCune and Mefford 2006) to determine if plant species were preferentially associated with a group. Significant indicator species were determined for: 1) a comparison of groups identified from cluster analysis of the transect zones, 2) a comparison of groups identified from cluster analysis of all plots measured among the 12 transects, and 3) a three-group comparison where group 1 included plots associated with ecotones identified by SMWDA, group 2 included remaining plots within the wetland, and group 3 included remaining plots outside the wetland. The level of significance for all parametric tests was $P \leq 0.05$.

RESULTS

General Site Characteristics

Fifty-six plant species were tallied within the 180 plots. Of these species, 29% were dicot herbs, 25% were evergreen trees or shrubs, 21% were deciduous trees or shrubs, 12% were grasses, rushes or sedges, 8% were vines, and 6% were ferns. The five most frequently tallied species were: *Lyonia lucida* (80%), *Ilex coriacea* (50%), *Smilax laurifolia* (32%), *Vaccinium crassifolium* (29%), and *Aronia arbutifolia* (22%). Four species listed as near endemic to the Carolina Coastal Plain (at least 75%, but less than 100%, of known county occurrences confined to the Carolina Coastal Plain) by LeBlond (2001) were found in the plots: *Aristida stricta, Carphephorus bellidifolius*, *Vaccinium crassifolium*, and *Zenobia pulverulenta*. One endemic species, *Dionaea muscipula,* was also found.

Transects positioned on sides and ends of Carolina bays were generally similar in terms of community metrics and elevation change (Table 1). Individual transects were not particularly species rich (i.e., alpha diversity), but more than one community (i.e., beta diversity) occupied bay rims (Table 1) along elevation gradients of 0.6 m.

Zones within our transects differed in terms of soil properties, community characteristics, and physical characteristics (Table 2). However, these differences were not uniform among variables. For example, species richness (S) was significantly different among lower, middle and upper zones with mean richness varying from 7.0 in the lower zone to 15.4 in the upper zone (Table 2). Diversity (H') was lowest in the lower zone, but was equivalent between middle and upper zones. The weighted average index of hydrophytic vegetation was lowest in the lower and middle zones and significantly higher in the upper zone (means ranged from 2.03–2.62). Soils of the lower zone relative to the upper zone soils had significantly lower pH, higher extractable potassium and calcium, and higher organic matter content, and relative to the middle and upper zones had higher extractable phosphorus (Table 2). This trend of higher soil nutrients in the lower zone was paralleled by trends in well water conductivity. Transects encompassed the topographic gradient of the bay rims. The relative elevation (compared to the middle of the transects) was, however, much greater in the upper zone as compared to the relative elevation of the lower zone. The three zones were significantly different in terms of number of times where the water level was within 15 cm of the soil surface (Table 2), with seven times occurring in the lower zone and one time in the upper zone.

Communities and Environment

Figure 1 shows the results of NMDS where samples represent composites of plots within tran-

Table 2. Soil properties and community characteristics within the ecological boundaries of Carolina bays at Lewis Ocean Bay Heritage Preserve. Samples represent lower, middle, and upper zones of 12 boundary transects. Means are presented ± standard error. Means with different letters indicate significant ($P \leq 0.05$) differences among transect zones.

Variable	Lower	Middle	Upper
Soil pH	3.80 ± 0.10[a]	3.92 ± 0.08[ab]	4.18 ± 0.10[b]
Extractable phosphorus (g/m^2)	0.79 ± 0.05[a]	0.42 ± 0.05[b]	0.57 ± 0.13[b]
Extractable potassium (g/m^2)	5.77 ± 0.64[a]	3.53 ± 1.38[b]	2.39 ± 0.61[b]
Extractable calcium (g/m^2)	29.93 ± 7.17[a]	20.36 ± 4.13[ab]	12.20 ± 1.31[b]
Nitrate nitrogen (ppm)	2.66 ± 0.22[a]	2.58 ± 0.23[a]	2.00 ± 0.12[a]
Organic matter (%)	20.36 ± 5.57[a]	3.78 ± 0.60[b]	4.22 ± 2.36[b]
Species richness (#)	7.0 ± 0.7[a]	11.2 ± 1.4[b]	15.4 ± 1.3[c]
Diversity (H′)	1.25 ± 0.13[a]	1.73 ± 0.13[b]	2.00 ± 0.09[b]
Hydrophytic vegetation index	2.03 ± 0.03[a]	2.20 ± 0.03[a]	2.63 ± 0.08[b]
Elevation (relative to plot 15)	0.67 ± 0.16[a]	1.09 ± 0.05[a]	2.20 ± 0.36[b]
Water level (# of times within 15 cm of the soil surface)	7.0 ± 1.2[a]	4.0 ± 1.3[b]	1.1 ± 0.5[c]
Conductivity (mV)	147.1 ± 7.0[a]	124.4 ± 10.1[b]	108.8 ± 5.4[b]

sect zones. The NMDS had a two-dimensional solution with a final stress of 16.9. Axes 1 and 2 represented 17.4% and 63.2% of the variation in the samples, respectively. Three groups were identified by cluster analysis. One group at the upper end of axis 1 included only samples from the upper transect zone. A second tightly clustered group at the lower end of axis 1 included mostly samples from the lower transect zone. A third group midway along axis 1 included samples from all three transect zones (Figure 1).

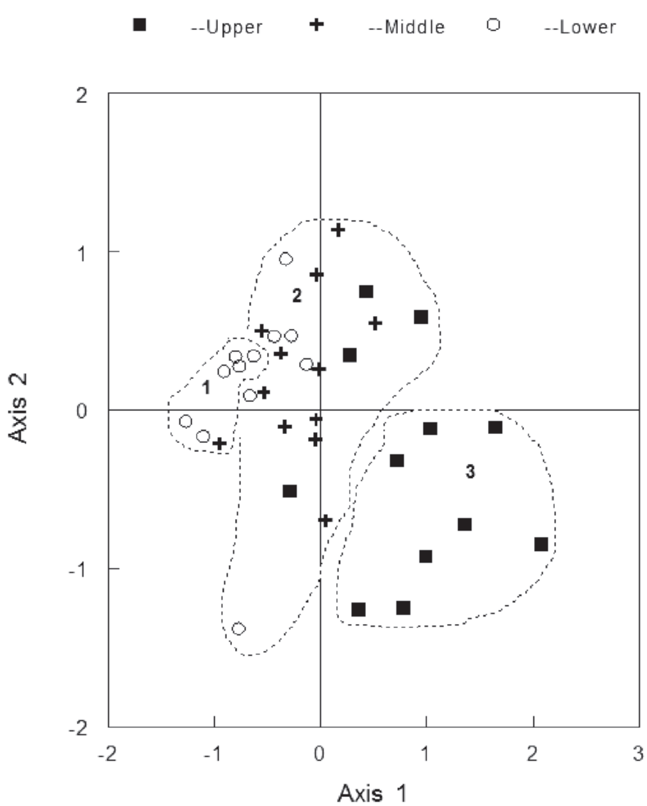

Figure 1. Non-metric multidimensional scaling (NMDS) of samples compiled from three transect zones (upper, middle, and lower) on the ecological boundaries of six Carolina bays. Lines encompass three groups as determined from cluster analysis.

Axis 1 and 2 scores derived from NMDS of transect zones were significantly correlated with various soil, community, and physical properties. Most importantly, Table 3 shows that axis 1 scores reflected the underlying moisture gradient as measured by water level events (Table 3). Axis 1 also reflected various community properties such as hydrophytic vegetation index, richness, and diversity. Generally, axis 1 scores were positively correlated with pH, but negatively correlated with soil phosphorus, soil potassium, organic matter, and conductivity (Table 3). Correlation of axis 2 scores with soil properties generally confirmed the existence of a vegetation gradient associated with a soil fertility gradient.

Figure 2 shows the results of NMDS where samples represent 1-m^2 plots from the 12 transects. The NMDS had a three-dimensional solution with a final stress of 17.3. Axes 1, 2, and 3 represented 29%, 32%, and 21% of the variation in the samples, respectively. Axes 1 and 2 of NMDS, when coupled with cluster analysis, provided an interpretable representation of plot variation and thus these axes were chosen for presentation (Figure 2). Thirty-two plots from upper transect zone formed a relatively well-defined group at the lower ends of axes 1 and 2. However, some plots from the upper transect zone were also placed by

Table 3. Pearson Correlation Coefficients (r) followed by associated P values in parentheses between NMDS Axis 1 and Axis 2 scores and various characteristics of soils and vegetation. The ordination of transect zones is presented in Figure 2.

Variable	Axis 1	Axis 2
Soil pH	0.435 (0.008)	−0.39 (0.019)
Extractable phosphorus (g/m^2)	−0.348 (0.038)	0.211 (0.218)
Extractable potassium (g/m^2)	−0.510 (0.001)	0.440 (0.007)
Extractable calcium (g/m^2)	−0.221 (0.195)	0.447 (0.006)
Nitrate nitrogen (ppm)	−0.270 (0.111)	0.446 (0.006)
Organic matter (%)	−0.333 (0.047)	0.269 (0.113)
Species richness (#)	0.632 (0.001)	−0.084 (0.625)
Diversity (H′)	0.568 (0.001)	−0.217 (0.203)
Hydrophytic vegetation index	0.853 (0.001)	−0.547 (0.001)
Elevation (relative to plot 15)	0.512 (0.001)	0.043 (0.324)
Water level (# of times within 15 cm of the soil surface)	−0.517 (0.001)	0.169 (0.324)
Conductivity (mV)	−0.522 (0.001)	0.345 (0.039)

cluster analysis in a group that included plots from the middle and lower transect zones (Figure 2). Generally, Figure 2 demonstrates the greater variation of community samples from upper transect zones while plots from middle and lower transect zones formed a more homogeneous group.

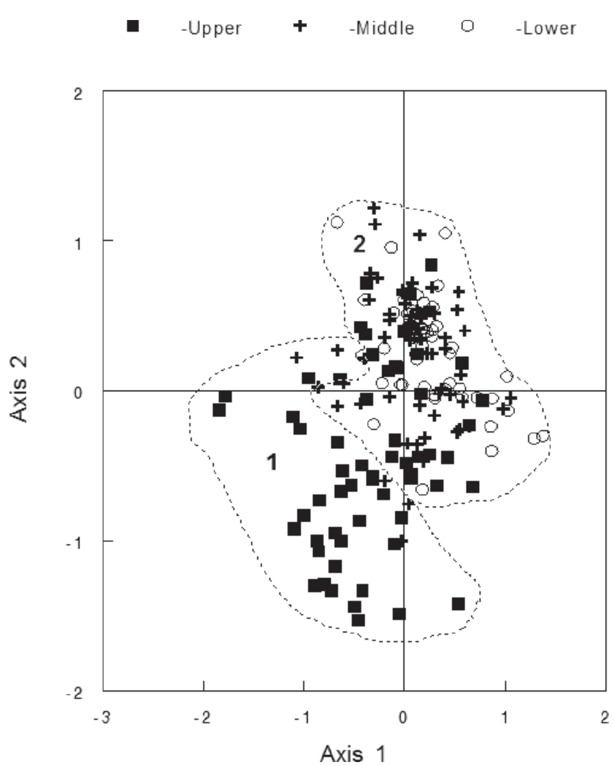

Figure 2. Non-metric multidimensional scaling (NMDS) of 180 1-m^2 plots assessed within three zones (upper, middle, and lower) of 12 boundary transects. Lines encompass two groups as determined from cluster analysis.

Ecotones

Split moving window dissimilarity analysis gave similar results with two- and four-window widths (Figure 3). Every transect had at least one ecotone and some transects had as many as three ecotones. Ecotones were not uniformly distributed within the transects, but instead increased in number from lower to upper transect zones (Figure 3).

Indicator Species

Groups identified from cluster analysis and graphically delineated in Figures 1 and 2 (i.e., comparisons 1 and 2) were generally associated with similar indicator species. For example, clusters that included samples from the upper transect zone were indicated by grasses such as *Andropogon virginicus*, *Aristida stricta,* and small shrubs and low-growing vines such as *Gaylussacia dumosa*, *Gelsemium sempervirens, Vaccinium crassifolium, and Vaccinium tenellum*. Clusters that included samples from middle and lower transect zones were indicated by taller evergreen shrubs (e.g., *Ilex coriacea, Lyonia lucida*) as well as the tangling vine *Smilax laurifolia.*

Comparison 3, based on plot position within the transect and plot placement in an ecotone, was influenced by the concentration of ecotones in upper transect zones. For example, indicators of wetland were generally the same as in comparison 2. However, the number of indicators of upper transect zones outside the wetland was reduced and we identified four species as indicators of ecotones. These ecotone indicators included *Andropogon virginicus, Gaylussacia dumosa, Rhexia alifanus,* and *Vaccinium tenellum* (Table 4).

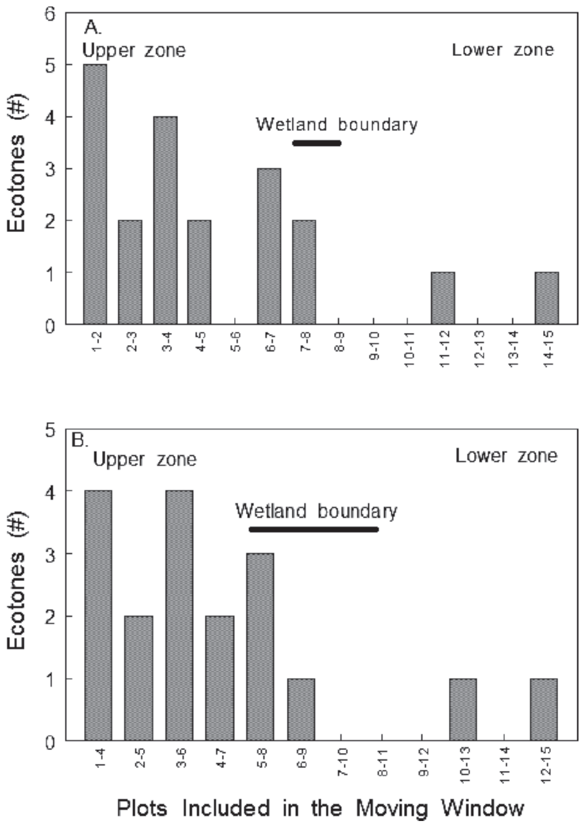

Figure 3. Distribution of ecotones within 12 transects established on the ecological boundaries of six Carolina bays. Ecotones were identified by split moving window dissimilarity analysis using both two-window (A) and four window (B) widths. Transect plot 8 represents the jurisdictional wetland boundary. Transect plots 1–7 are outside the wetland while transect plots 9–15 are within the wetland.

DISCUSSION

Environmental Gradients

Our research revealed two environmental gradients in Carolina bay boundaries over a relatively short distance: a moisture gradient and a soil fertility gradient. The moisture gradient, measured over seven months, was influenced primarily by subtle differences in elevation on our bay rim sites. Elevational gradients within other Carolina bays have previously been associated with gradients of soil moisture, soil nutrients, and plant communities (Sharitz and Gibbons 1982, Reese and Moorhead 1996, Collins and Battaglia 2001). Seasonal trends in soil moisture at LOBHP (Laliberte 2006) were similar to those measured by Lide et al. (1995) where water levels dropped gradually through the growing season but increased temporarily with increased rainfall. Although water levels were more frequently at or near the soil surface at lower transect zones, water levels did occasionally rise to the soil surface even at upper transect zones. Considering relative differences in organic matter content of the soils, and thus moisture holding capacity, it was likely that the moisture gradient also reflects a gradient in moisture extremes with areas in the middle and upper zones experiencing more frequent changes from flooded to drought conditions. A gradient of moisture extremes is obviously contingent on variation in precipitation (Lide et al. 1995).

Because soil nutrients and conductivity were correlated with organic matter content, we suggest that long-term accumulation of organic matter in surface layers of Carolina bay soils is the primary factor for development of a fertility gradient in the ecological boundary. However, Sharitz and Gibbons (1982) concluded that even though organic matter represents a potential source of nutrients for plants, low pH and anaerobic conditions in wetland soils may constrain availability and uptake. Such conditions likely also exist in middle and upper zones of the transects but nutrient limitation may be even more extreme in the upper zones due to low organic matter content. Carolina bays are generally considered as ombrotrophic and it is likely that this designation can also be extended to the ecological boundary (Sharitz and Gresham 1998). Autecological studies of various plant species associated with the ecological boundaries of Carolina bays have concluded that these habitats are low in nutrients and alternate between flooded and drought conditions (Roberts and Oosting 1958, Kirkman et al. 1989, Luken 2005b).

Community Gradients

Alpha diversity within ecological boundaries at LOBHP was low in comparison to similar habitats (Kirkman et al. 1998) and in comparison to the numbers of plant species found in the Carolina Coastal Plain (Sorrie and Weakley 2001). Furthermore, the community gradient within the ecological boundaries was one of increasing richness and diversity from the lower zones to the upper zones, similar to that found by Kirkman et al. (1998) (but see Tyndall et al. (1990) for a reversed pattern within Carolina bays). This gradient also involved higher indices of hydrophytic vegetation; the mean values, however, did not exceed 4.0 reflecting the transitional status of our ecological boundaries (Tiner 1999). In contrast, beta diversity was relatively high considering the short lengths of the transects (Kirkman et al. 1998, Choesin and Boerner 2002).

Table 4. Significant ($P \leq 0.05$) indicator species for three group comparisons. Association of a species with a particular group is indicated by an asterisk. Comparison 1 (see Figure 1) includes three groups identified by cluster analysis when plot data were combined within upper (U), middle (M), and lower (L) transect zones; comparison 2 (see Figure 2) includes two groups, one comprised mostly of upper (U) plots and one comprised of upper, middle, and lower (UML) plots, identified by cluster analysis of all 180 individual samples; comparison 3 includes three groups identified by plot position outside the wetland (OW), in an ecotone (E) as shown in Figure 3, or within the wetland (W).

	Comparison 1			Comparison 2		Comparison 3		
Species	U	M	L	U	UML	OW	E	W
Andropogon virginicus	*	—	—	*	—	—	*	—
Aristida stricta	*	—	—	*	—	—	—	—
Cyrilla racemiflora	—	—	—	*	—	*	—	—
Gaylussacia dumosa	*	—	—	*	—	—	*	—
Gaylussacia frondosa	—	—	—	—	*	—	—	—
Gelsemium sempervirens	*	—	—	*	—	—	—	—
Ilex coriacea	—	*	—	—	*	—	—	*
Lyonia lucida	—	—	*	—	*	—	—	*
Morella cerifera	—	—	—	*	—	—	—	—
Osmunda cinnamomea	—	—	—	—	*	—	—	*
Quercus pumila	*	—	—	*	—	—	—	—
Rhexia alifanus	—	—	—	—	—	—	*	—
Smilax laurifolia	—	—	—	—	*	—	—	*
Vaccinium crassifolium	*	—	—	*	—	*	—	—
Vaccinium tenellum	*	—	—	*	—	—	*	—

Carolina bay boundaries at LOBHP include a distinct transition from shrub-bog vegetation dominated by a few evergreen shrubs and vines in the lower zone to a more diverse and heterogeneous community of low shrubs, herbs, grasses, and vines in the upper zone. The plant communities and most of the species found within these boundaries have also been observed in various depression wetlands of the southeastern USA and explanations for assembly of these communities acknowledged the roles of hydrology and fire (Kirkman et al. 2000, DeSteven and Toner 2004), wetland size, soil type, and disturbance history (DeSteven and Toner 2004), as well as characteristics of the surrounding landscape (Poiani and Dixon 1995). Generally, Carolina bays with accumulations of soil organic matter support evergreen shrub or pocosin-like vegetation (Richardson and Gibbons 1993) but the factors that start, maintain, or limit this type of vegetation are poorly understood (Sharitz and Gibbons 1982). Little research has been devoted to understanding environmental and community gradients within ecological boundaries of these wetlands (see Kirkman et al. 1998). However, our research did support the general idea that relatively high soil fertility coupled with the presence of potentially large and productive shrubs can produce wetland vegetation dominated by a few species (Wisheu and Keddy 1992).

Carolina bays are highly variable in terms of their communities (Sharitz and Gibbons 1982, Bennett and Nelson 1991, Battaglia and Collins 2006), but may share ecological boundaries with steep environmental gradients. From the perspective of boundary function, a steep gradient of hydrology within a matrix of sandy soils brings wetland vegetation and wetland conditions into close proximity with upland grass-dominated vegetation prone to frequent fire. Susceptibility to fire is likely the driving force that creates greater compositional variation within upper transect zones. The upper zone of the ecological boundary is also where we found highest richness, a result observed in the ecological boundaries of some ponds and lakes (Schneider 1994, Keddy and Fraser 2000) and found in experimental bay conditions (Battaglia and Collins 2006). In contrast, Kirkman et al. (1998) found greatest compositional variation in wetland plots relative to upland plots, however, their wetland plots were dominated by grasses, sedges and forbs, and the wetland had a complex disturbance history characterized by drought and flooding. The upper and middle transect zones are also where one finds a suite of relatively rare, endemic species, most of which are small or cryptic and some of which are carnivorous (LeBlond 2001, Luken 2005a and 2005b), suggesting that competition here is relaxed (Wisheu and Keddy 1992).

Ecotones Within Boundaries

Ecotones have historically contributed to community theory (Kent et al. 1997), to development of new concepts in landscape ecology (Cadenasso et al. 2003), and to the emergence of wetland delineation methods (Tiner 1996). Although ecotones have been variously defined depending on system and scale, recent definitions focus on relative change in community composition within a series of spatially ordered samples (Walker et al. 2003). Split moving window dissimilarity analysis has been widely used to detect points of high relative change (Cornelius and Reynolds 1991), although significance testing of ecotones identified by SMWDA is problematic for various reasons (Körmöczi 2005). Some researchers have developed significance tests specifically for the scale of the research approach (Walker et al. 2003, Hennenberg et al. 2005), while others have simply presented figures showing trends of dissimilarity values (Kirkman et al. 1998, Choesin and Boerner 2002). Our approach of identifying dissimilarity outliers within individual replicate transects, while not a significance test, is still consistent with other methods developed for identifying ecotones in spatially ordered data (Cornelius and Reynolds 1991).

Our results indicated that every transect included at least one ecotone and in some cases three ecotones; most of these were beyond the jurisdictional wetland boundary. Ecotones reflect small-scale heterogeneity in the plant community and may actually provide habitats for some species (Luken 2005b). While the origin of these ecotones is unknown, systems subject to frequent fires often have community and substrate heterogeneity generated by variations in fire extent and intensity (Menges and Hawkes 1998). Thus, a critical factor in structuring the ecological boundary of Carolina bays is likely the interaction between hydrology and the movement of fires from uplands into the bays (Wells and Whitford 1976).

Managing Carolina Bays for Biodiversity

The five endemic and near endemic species found in this study occurred outside the jurisdictional wetland boundary. As indicated by their wetland status, these species can occur in wetlands but are presumably limited in the ecological boundary by development of evergreen shrub vegetation. One of these plants, *Dionaea muscipula*, has a G3 rank for endangerment and is dependent on the small-scale community heterogeneity found in the areas outside the jurisdictional wetland boundary (Luken 2005b). If the areas immediately outside the Carolina bay wetlands were developed, 52% of all species found in our plots would be lost, including *Dionaea muscipula* and two of the near endemics. These results indicate the need for preservation not just of wetlands but also for preservation of ecological boundaries associated with wetlands (Pearsall and Mulamoottil 1996). Our research was based on relatively short transects so we cannot make specific recommendations other than that a 15-m buffer around the Carolina bays will preserve more plant diversity than preserving wetlands alone. Buffers will also likely benefit animals that use Carolina bays on a seasonal basis (Semlitsch and Bodie 2003).

Typically, management recommendations for protecting wetland function are based on the conclusion that ecological processes occurring outside wetlands influence wetland function (Houlahan et al. 2006, Riffell et al. 2006). However, in the case of Carolina bays supporting shrub-bog vegetation, wetland function likely extends beyond the jurisdictional boundary where there exists a tension zone for the interaction of hydrology and fire. If indeed this tension zone is an important habitat for plant speciation as suggested by LeBlond (2001) and for maintenance of plant diversity (this research), then management recommendations for areas surrounding Carolina bays should focus on actions that affect the fire regimen (Glitzenstein et al. 2003) and more specifically, how fires burn up to and into Carolina bays. Due to the nature of fire ecology, such actions will inevitably entail preservation or restoration of fire-prone savanna surrounding Carolina bays (Glitzenstein et al. 2001) as well as factors that contribute to the characteristic hydrology of Carolina bays (Lide et al. 1995).

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