

## STRUCTURE OF EVERGLADES ALLIGATOR HOLES

Michelle L. Palmer and Frank J. Mazzotti<sup>1</sup>

*University of Florida*

*Department of Wildlife Ecology and Conservation*

*Fort Lauderdale Research and Education Center*

*3205 College Avenue*

*Davie, Florida, USA 33314*

*E-mail: fjma@mail.ifas.ufl.edu*

**Abstract:** Alligators create disturbance patches within the Everglades, but little is known about spatial and temporal variation in alligator holes throughout this ecosystem. Forty-eight alligator holes in Water Conservation Area 3 of the central Everglades were sampled to assess variation in morphology and vegetation and to identify landscape- and habitat-level features that correlate to alligator-hole variation. Field observations and plant community ordination suggested three distinct categories of alligator holes: holes containing shrub/tree species (shrub holes), holes surrounded by marsh (marsh holes), and holes dominated by cattails (cattail holes). Shrub holes were the most species-rich and diverse of the three types. All alligator holes except for cattail holes contained a greater richness of vascular plants than the surrounding marsh. Cattail holes were deeper than shrub or marsh holes, and all holes were deeper than surrounding marsh. Major landscape features that may influence structure of alligator holes seem to be distance from canals and surrounding marsh vegetation matrix. Alligator holes increase spatial heterogeneity, influence plant community composition and structure, and increase biological diversity. Restoration and management plans for the Everglades ecosystem should ensure that this landscape feature is perpetuated.

**Key Words:** Everglades, alligators, alligator holes, plant communities, biological diversity, ecosystem engineer

### INTRODUCTION

The American alligator (*Alligator mississippiensis* Daudin) is a keystone species in the Everglades ecosystem due to their creation and maintenance of small ponds called alligator holes (Mazzotti and Brandt 1994). Alligator holes provide a constant source of water for alligators and other aquatic organisms such as fish, aquatic invertebrates, reptiles, and amphibians when the surrounding marsh is periodically dry (Beard 1938, Kushlan 1972, Kushlan 1974, Kushlan and Kushlan 1980, Loftus and Eklund 1994). During the dry season, these ponds are important foraging sites for wading birds and mammals (Frederick and Spalding 1994, Hoffman et al. 1994). Alligator holes also influence Everglades' plant communities at a local scale. Alligators, in the process of creating and maintaining holes, remove vegetation from within and near the basin and push sediment onto banks of the new pond (McIlhenny 1935, Craighead 1968, 1971). Removal of vegetation and altering of soil properties through movement of soil allows for changes in plant community composition and structure that may be physically, chemically, and biologically distinct from

the surrounding undisturbed marsh. However, these changes in plant communities have not been quantified, and the manner in which alligator holes affect plant diversity has not been described.

The extent to which alligator holes serve as refugia for aquatic organisms to survive through a dry season and subsequently re-colonize the surrounding marsh is unknown. After finding dead fish in alligator holes where no depredation by wading birds occurred and fish surviving in holes when depredation occurred, Kushlan (1972) concluded that depredation by wading birds of aquatic organisms would thin the population of aquatic organisms to conserve oxygen. Mazzotti and Brandt (1994) hypothesized that the value of any particular alligator hole as an aquatic refugium varies both spatially and temporally. For example, only the deepest holes would have value as aquatic refugia during the driest years. However, we do not know how morphological variation of alligator holes might correlate with vegetation patterns.

Kushlan and Hunt (1979) described three types of alligator holes based on their location in the landscape. Ponds in cypress swamps are large, deep, and found in limestone depressions. Smaller, shallower ponds are found in depressions in wetlands with rock and marl

<sup>1</sup> Corresponding author

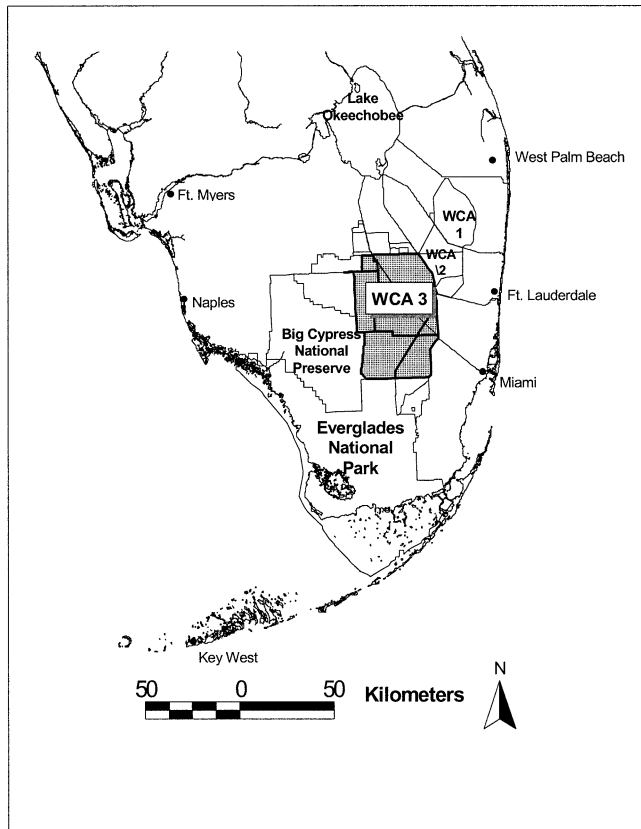


Figure 1. Location of study area (shaded) in South Florida. WCAs are Water Conservation.

substrates. Peatland ponds, found in central Everglades ridge and slough wetlands, are also smaller and shallower but are not associated with underlying depressions in the bedrock (Campbell 1999). Natural holes could be divided further into those with trees and shrubs and those without. In the central Everglades, Campbell and Mazzotti (2001) found natural and man-made ponds that were occupied and maintained by alligators.

As restoration of the greater Everglades ecosystem begins, the role of alligator holes as aquatic refugia has become an important component of system simulation models and criteria for restoration success. Yet, information about natural variation in shape and vegetation of alligator holes, critical to ecosystem modeling and monitoring efforts, is lacking. Objectives of this study were to determine variation in morphology (size and depth) and vegetation of alligator holes and to evaluate relationships among vegetation, morphology, habitat, and location of alligator holes.

## METHODS

### Study Area

Water Conservation Area Three (WCA 3) is a 2,442 km<sup>2</sup> area located in the center of the Everglades eco-

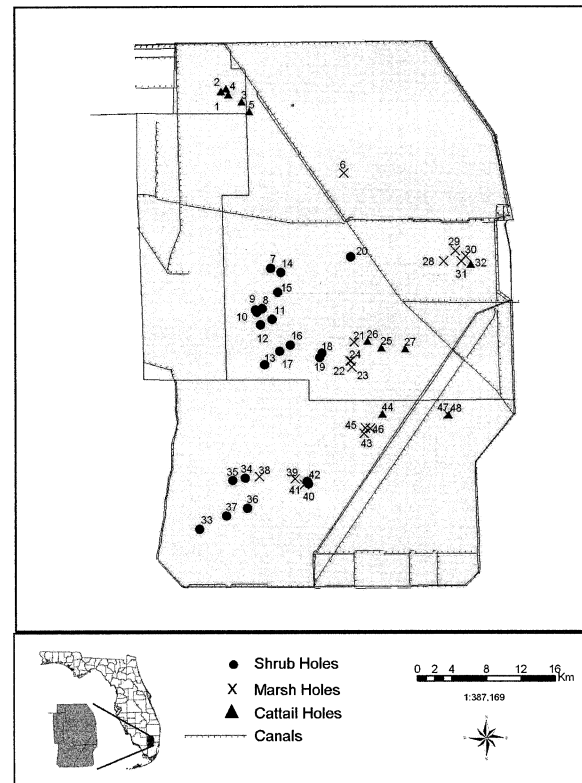


Figure 2. Location of Everglades alligator holes. Forty-eight holes classified as Shrub Holes, Marsh Holes, and Cattail Holes are shown.

system, which extends from Lake Okeechobee to Florida Bay (Figure 1) (Schomer and Drew 1982). Current vegetation communities in WCA 3 include sawgrass (*Cladium jamaicense* Crantz) marshes, wet prairies, sloughs, and tree islands (Loveless 1959, Lodge 1998). Sawgrass marshes lack vegetation diversity and are found in areas of shorter hydroperiod. Sloughs are deep marsh communities that are usually inundated year round and contain submerged and floating plants. Wet prairies, found in areas of longer hydroperiod, are the most diverse of the three major vegetation communities. Two major types of tree islands occur in WCA 3: willow heads and hardwood islands. Soils in WCA 3 are peat overlying limestone bedrock.

### Field Sampling

Six hundred and forty alligator holes were identified and mapped from 1:24,000 color infrared photographs taken in September 1994 (Campbell and Mazzotti 2001). WCA 3 was divided into nine blocks, and each block was subdivided into 20 plots. Two of the 20 plots in each block were selected randomly, and all of the holes in a plot (total of 48) were sampled (Figure 2). Alligator holes were located using a differentially

corrected Global Positioning System mounted on an airboat.

Two perpendicular transects, used to measure alligator hole morphology and vegetation, were extended through the center of the alligator hole and 10 meters into the surrounding marsh. Water and sediment depths were measured at half-meter intervals. Water depth was measured to the surface of the sediment. Sediment depth was measured as the distance between sediment surface and underlying limestone bedrock. Plant composition and abundance were measured at half-meter intervals along each transect. For each half-meter interval, all vascular plants were identified to species, and the length each species occupied along the interval was measured.

Vegetation samples were assigned to one of three zones: pond, ecotone, or surrounding marsh. Ponds were defined by a sudden increase in water depth and were free of most emergent vegetation, although floating aquatic vegetation such as *Nuphar luteum* (L.) Sm. and *Nymphaea odorata* Sol. were common. The ecotone was defined as a transition in plant composition between the pond and the surrounding marsh, and marsh was defined as the dominant vegetation matrix surrounding each alligator hole. Marsh habitat was further classified as wet prairie, slough, sawgrass, or cattail based on dominant vegetation.

#### Data Analyses

**Morphology.** Surface area (size) of each pond was measured as an ellipse. Basin depth was determined by subtracting average marsh water depth from pond water depth.

**Vegetation.** Relative importance value (RIV) was computed by combining relative frequency and cover values, and species richness (number of species per sample) was tallied. These values were compared both within and between alligator hole types. Plant nomenclature follows Wunderlin (1998).

Vascular plant species were separated into five morphological groups: woody plants, emergent aquatics, floating and submerged aquatics, sawgrass, and cattails (*Typha* spp.). Sawgrass and cattails were placed into distinct groups because of their great abundance within the Everglades system and within alligator holes. In addition, presence of cattails may indicate greater nutrient levels (McCormack et al. 2002). Collectively, these five functional groups encompass all of vascular plants present in and around alligator holes, simplifying analysis of vegetation structure.

Samples were ordered using detrended correspondence analysis (DCA) (DECORANA; Hill 1979a) and classified using two-way indicator species analysis

(TWINSPAN; Hill 1979b) with PC-ORD (McCune and Mefford 1995). This analysis provided a dendrogram showing relationships among alligator holes. All species were included in the DCA ordination, and the downweight rare species option was selected to minimize influence of rare species.

Non-parametric statistical tests (Mann-Whitney U, Kruskal-Wallis, and Spearman's rank correlation) were used for all analyses (Daniel 1990).

## RESULTS

### Classification and Ordination

Relative importance values were summarized into a  $48 \times 44$  (sample  $\times$  species) table. Seven pseudospecies cut levels (0, 1, 2, 5, 10, 20, and 40, measured by their relative importance values) were designated for TWINSPAN analysis. The TWINSPAN dendrogram included three ecologically useful classes. The first division included 10 cattail holes, with pseudospecies abundance values above five. All but one of these holes contained at least 20% cattails. *Ludwigia peruviana* (L.) H. Hara was dominant in five of the ten holes, with pseudospecies abundance value above five.

The second division of the TWINSPAN classification produced two ecologically meaningful categories. The first contained 22 shrub holes and was dominated by *Salix caroliniana* Michx. and the smaller shrub *Cephalanthus occidentalis* L. Common understory plants in these alligator holes were *Polygonum densiflorum* Meisn., *Pontederia cordata* L., *Cladium jamaicense*, and *Panicum* spp. The second group of 16 marsh holes had no woody shrubs. Plants common to this division included sawgrass, *Pontederia cordata*, and *Sagittaria* spp.

The first DCA axis of the two-dimensional DCA model explained 50% of the variation in the data (Figure 3). There was a clear separation of the three TWINSPAN categories along this axis. Shrub holes dominated by woody species are located on the left side of the graph, marsh holes lacking woody species in the center, and cattail holes formed a cluster on the right side of the graph. The second and third axes explained little of the variation in alligator hole structure and were not considered further.

### Morphology

Considerable variation in alligator hole structural parameters was observed (Table 1). Pond area did not differ among the three types of holes (Kruskal-Wallis,  $H = 5.4$ , 2 d.f.,  $P = 0.07$ ). Alligator holes were deeper than surrounding marsh. Average pond water depth was  $110.8 \pm 30.2$  cm, while average marsh depth was

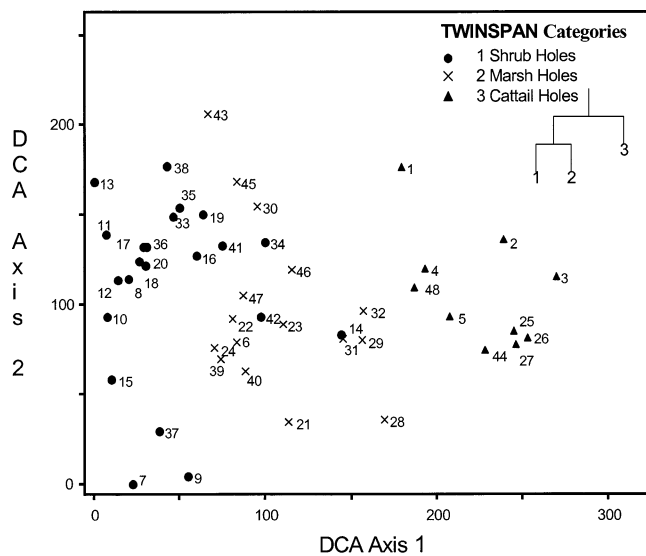


Figure 3. DECORANA ordination of 48 alligator holes from WCA 3. Small numbers are hole identifications; symbols and the corresponding dendrogram represent the TWINSpan-based community types detailed in Figure 4.

43.9 ± 18.8 (48.9) cm (Mann Whitney U, T = 3423.0, P < 0.001). Average basin depth (water depth difference between pond and surrounding marsh) was 67.3 ± 20.1 cm. Cattail holes had greater basin depths than shrub or marsh holes (Kruskall-Wallis, H = 8.1, 2 d.f., P = 0.02). Average hole muck depths did not vary with hole type (Kruskall-Wallis, H = 5.3, 2 d.f., P = 0.07). No significant relationships were detected between pond area and water depths; larger ponds were not necessarily deeper ponds.

Morphological characteristics also varied among marsh types (Table 2). Alligator holes located in sloughs had greater sediment depths than holes in wet or sawgrass prairies (Kruskall-Wallis, H = 15.2, 2 d.f., P < 0.001), and basin depth was greatest for holes within a sawgrass matrix (Kruskall-Wallis, H = 10.2, 2 d.f., P = 0.006). Alligator holes within wet prairie

marsh were largest (Kruskall-Wallis, H = 7.5, 2 d.f., P = 0.024).

### Vegetation

Vegetation present in alligator holes varied on both local and landscape scales. The most abundant plants within 10 meters of the pond boundary in order of importance (RIV) were *Pontederia cordata*, *Cladium jamaicense*, *Utricularia* spp., *Panicum* spp., *Salix caroliniana*, *Sagittaria* spp., *Cephalanthus occidentalis*, *Polygonum* spp., *Crinum americanum* L., and *Peltandra virginica* (L.) Schott & Endl.

These plants were found in disturbed soils surrounding alligator holes. Floating aquatics such as *Nuphar luteum*, *Nymphaea odorata* and *Utricularia* spp. were prevalent in ponds of alligator holes. Cattails were common in holes in deeper areas, especially those close to canals, and sawgrass was found in and around most alligator holes.

Emergent aquatic plants were the most abundant plants (31.7%) in alligator holes (Figure 4). Sawgrass (18.6%), woody vegetation (15.6%), cattail (13.5%), and floating aquatics (13.0%) were almost equally abundant in alligator holes. On average, open water occupied 7.6% of the transects. Overall, surrounding marshes had fewer emergent aquatics than shrub or marsh holes (Figure 4). Additionally, the marsh matrix contained more floating aquatics and sawgrass and had few woody species.

Plant composition varied among alligator hole types. Shrub holes had more coverage by woody plants than did other types of holes (Figure 4). Shrub holes also contained more emergent aquatic plants than other types of alligator holes. Marsh holes lacked woody plants (only 5% of the total plant abundance were plants in this functional group). These holes were dominated by sawgrass (30%). Cattails made up 43% of the total plants found in cattail holes, whereas cat-

Table 1. Morphological and vegetative characteristics of alligator holes.

Variable	All holes combined	Shrub Holes	Marsh Holes	Cattail Holes
Sample size	48	21	16	11
Diameter (m)	8.7 ± 2.7	9.4 ± 2.5	7.6 ± 2.5	9.0 ± 2.7
Surface area (m <sup>2</sup> )	63.9 ± 34.0	71.8 ± 29.7	49.8 ± 31.9	69.5 ± 40.8
Max. surface area (m <sup>2</sup> )	153.9	148.4	127.6	153.9
Min. surface area (m <sup>2</sup> )	19.6	28.3	19.6	23.7
Basin depth (cm)	67.3 ± 20.1	63.3 ± 15.0	62.7 ± 24.5	81.9 ± 16.0
Sediment depth (cm)	98.4 ± 32.5	90.0 ± 40.6	103.5 ± 21.3	107.1 ± 27.0
Species richness (N)	13.3 ± 5.0	17.3 ± 4.2	10.4 ± 2.8	9.8 ± 3.5
Max. richness (N)	26	26	15	16
Min. richness (N)	6	10	7	6

Table 2. Morphologic and vegetative properties of alligator holes within the three different marsh types. Values shown are mean  $\pm$  s.d. Different symbols within the same parameter demonstrate significant differences at a significance level of  $P < 0.05$  (Kruskall-Wallis test).

Variable	Sawgrass prairie N = 8	Wet prairie N = 16	Slough N = 24
Surface area (m) <sup>2</sup>	38.4 $\pm$ 17.8 <sup>a</sup>	72.9 $\pm$ 32.8 <sup>b</sup>	66.4 $\pm$ 35.7 <sup>b</sup>
Basin depth (cm)	76.8 $\pm$ 12.2 <sup>a</sup>	58.2 $\pm$ 13.0 <sup>b</sup>	70.3 $\pm$ 27.0 <sup>a</sup>
Sediment depth (cm)	96.0 $\pm$ 31.2	75.7 $\pm$ 25.9 <sup>a</sup>	114.4 $\pm$ 28.4 <sup>b</sup>
Richness (# of species)	12.1 $\pm$ 2.7	17.7 $\pm$ 4.6 <sup>a</sup>	10.7 $\pm$ 3.8 <sup>b</sup>

tails comprised only 2% and 9% of the transects for shrub and marsh holes, respectively (Figure 4).

There was a significant difference in species-richness among the three hole types (Kruskall-Wallis,  $H = 24.8$ , 2 d.f.  $P < 0.001$ ) (Table 1). Species-richness did not differ between marsh holes and cattail holes, but shrub holes were more species-rich than either marsh or cattail holes (Mann-Whitney U,  $P < 0.05$  for all pair wise comparisons). No relationship was found between size of the hole and richness (Spearman's rank correlation,  $r = 0.03$ ,  $P = 0.83$ ).

Species richness was greater in alligator holes than in the surrounding marsh. The ecotone had higher richness values than surrounding marsh for shrub holes, marsh holes, and all holes combined (Mann-Whitney U,  $P < 0.02$  for all tests). However, richness of cattail holes was not greater than in the surrounding marsh (Mann-Whitney U,  $P = 0.057$ ).

Vegetation richness also varied among holes surrounded by different marsh types (Table 2). Holes located in wet prairie had significantly higher richness values than alligator holes located in the other two marsh types (Table 2,  $H = 18.0$ , 2 d.f.  $P < 0.001$ ).

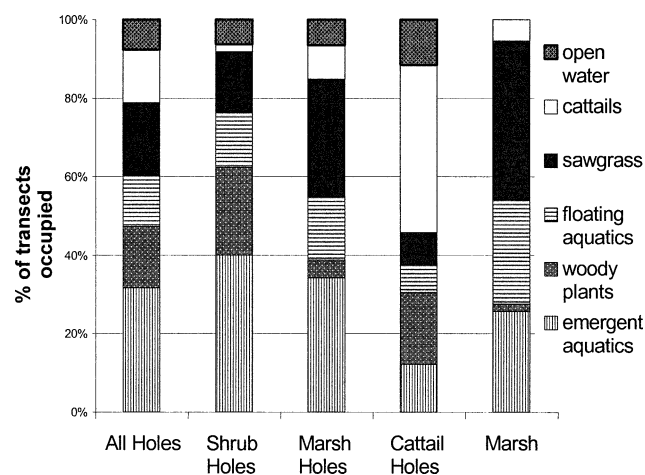


Figure 4. The percentage of the five plant functional groups plus open water found along the line transects for the surrounding marsh, all holes combined, and for the Shrub Holes, Marsh Holes, and Cattail Holes separately.

## Landscape and Habitat Linkages

Distance from alligator holes to canals explained much of the spatial variation of vascular plant species within alligator holes. DCA axis one was negatively correlated with distance to canal ( $r = -0.63$ ,  $P < 0.05$ ). Shrub holes were on average  $8467.4 \pm 2958.6$  m away from canals, marsh holes were  $5394.3 \pm 2780.0$  m, and cattail holes were  $3378.2 \pm 1474.7$  m from the nearest canal structure. Cattail holes were closest to canals (Kruskall-Wallis,  $H = 18.6$ , 2 d.f.,  $P < 0.0001$ ).

## DISCUSSION

Campbell and Mazzotti (2001) described two types of natural holes in central Everglades ridge and slough wetlands: those with woody plants and those without. We further divided holes without trees and shrubs into marsh holes with a mixed plant species assemblage around the hole and into holes dominated by cattails.

Craighead (1968) defined an alligator hole as a depression in the sediment, filled with water, and maintained by an alligator. This disturbance produces water depths greater than those of the surrounding marsh. Difference in water depths among alligator hole types may have significant impacts on the role of the alligator hole as a disturbance site. Deeper holes may provide the only open water during dry years.

Hydrology plays a key role in determining plant community composition in the Everglades landscape. Of special concern is the proliferation of cattails, which are replacing sawgrass marshes, especially near canals and inflow structures (Davis 1994, Newman et al. 1996). Cattails are well-adapted to deep water (over 1.2 m) and a long hydroperiod (Grace 1987, 1988). However, Newman et al. (1996) have demonstrated that cattails will not dominate over sawgrass solely in response to flooding. Competitive exclusion of cattails over sawgrass requires the interaction of disturbance, flooding, and increased nutrient levels, particularly phosphorus.

This phenomenon may explain why certain holes are dominated by cattail. In some cases, the deeper

water and greater nutrient inputs are associated with proximity to canals (Davis 1994). For example, Richardson et al. (1990) found that 90% of cattail were within 1000 meters of the canal within the Arthur R. Marshall Loxahatchee National Wildlife Refuge (WCA 1), with the remaining 10% occurring within the next 1000 meters. Vaithyanathan and Richardson (1999) also found dominance by cattails in phosphorous-enriched areas of Water Conservation Area 2 (WCA 2); cattail formed extensive stands near canals and inflow structures in both WCA 2 and WCA 3 (Davis 1994). Although cattail holes were closer to canals than other holes, they were not closer than 1000 m (Campbell 1999), where concentrations of nutrients are highest. In addition, the cattail matrix associated with proximity to canals did not surround the cattail-dominated alligator holes. Rather, six of ten cattail holes were found within a sawgrass prairie, and the remaining four cattail holes were found within a slough. Perhaps the combination of deeper water occurring within alligator holes (average of 81.9 cm deeper than the surrounding marsh) and a slight increase in nutrients due to enrichment by defecation and decomposition by alligators and other organisms seeking refugia in the alligator hole favors the proliferation of cattails at some locations.

Alligator holes are a small-scale disturbance in the Everglades ecosystem that plays an important role in structuring plant communities. Small changes in topography lead to significant variation in plant communities (Gunderson 1994), and experimental manipulations of microtopographic heterogeneity indicate clear differences in species preferences and varied community composition in sites differing by only a few centimeters (Vivian-Smith 1997). Disturbed soil of alligator holes may affect establishment and resilience of certain species by redistributing resources.

Shrub holes were the most species-rich and contained several woody and herbaceous plant species that were absent in the other types of holes. Shrub holes were found primarily in wet prairies. Wet prairie assemblages were more diverse than sawgrass marshes or sloughs (Jordan et al. 1997, Lodge 1998); the species pool that was available for colonizing these holes was greater than in other habitat types. Mounding of dead vegetation by alligators above the surrounding marsh within shrub holes also may explain why some plants, particularly woody species, can establish and persist on these holes.

Two patterns emerged from the ordination and classification procedures. Holes of the same type are found closer to each other than holes of different types, and cattail holes are found closest to canals and shrub holes the farthest from canals. Both hydrologic and nutrient gradients are a major determinant of plant communi-

ties located in alligator holes. These gradients are a cause of vegetation change across the Everglades ecosystem and have been discussed in detail elsewhere (Gunderson 1989 and 1994, Davis et al. 1994, White 1994, David 1996, Busch et al. 1998).

Neither pond area nor basin depth was related to position in the landscape or to proximity to canals. These morphologic properties are as likely a consequence of alligator biology, such as alligator size or duration of occupation, as they are to landscape features. However, sediment depth did vary with surrounding vegetation matrix, which may be due to differences in the underlying peat substrate of these three marsh types. Slough communities are found in the deepest peat overlying depressions in the bedrock (Gleason and Stone 1994), which is consistent with holes in the slough having the greatest sediment depths. Holes encompassed within sawgrass and slough matrices had very similar basin depths. The slough is the deepest marsh community, with the deepest sediment depths (Gunderson 1994); more sediment is available for excavation, and more water is then available to fill the resulting basin. This does not explain why cattail holes within the sawgrass matrix were deepest, as sawgrass prairies are typically drier than either slough or wet prairie (Gunderson 1994). Due to shorter hydroperiod and lower relative water table, alligators may need to create deeper holes in sawgrass prairies to obtain an adequate water source.

## CONCLUSION

One major objective of the Everglades restoration effort is to restore habitat diversity and spatial heterogeneity. Alligator holes are a natural source of habitat heterogeneity for this ecosystem. Alligators, by creating and maintaining depressions, increase variation in topography and nutrients for vegetation establishment and a dry season refuge for aquatic organisms, with benefits that extend up the marsh food chain. The most species-rich alligator holes occur in wet prairie and slough habitats and are furthest from canals. In addition, these holes often are surrounded by woody vegetation that can have numerous environmental benefits, including nesting and roosting sites for wading birds, nesting locations for alligators, and cover for wildlife such as deer. In addition, holes in close proximity to canals are more likely to be monotypic stands of cattail and may actually reduce natural diversity of the Everglades system. By removing canals in the conservation areas, alligator holes may revert to more naturally diverse communities. Alligator holes can be a model for exploring the interaction of small-scale processes, such as the influence of deeper water and edaphic factors, on broader scale issues such as pro-

liferation of cattail in the Everglades. Information gained from this study may be useful in accomplishing the goal of increased habitat diversity.

#### ACKNOWLEDGMENTS

We dedicate this paper to the memory of Dr. Peter Rosendahl. We are indebted to Dr. Rosendahl for initiating this project, his constant support and encouragement, and his vision of a restored Everglades ecosystem. A Challenge Grant from the Everglades Agricultural Area Environmental Protection District and the National Fish and Wildlife Foundation supported this project. The Florida Cooperative Fish and Wildlife Research Unit, University of Florida provided logistical support, including the use of airboats and vehicles. We are grateful for the help of Mark Campbell, Matthew Chopp, Marina Rivecchio, and Julie Pennington, who provided invaluable assistance in the field. Laura Brandt, Mike Cherkiss, Geoff Cook, Jocie Graham, and Franklin Percival commented on the manuscript. This is a contribution of the Florida Agricultural Experimental Station Journal Series, Journal Series Number R-08459.

#### LITERATURE CITED

- Beard, D. B. 1938. Everglades National Park Project: Wildlife Reconnaissance. U. S. Department of Interior, National Park Service, Washington, DC, USA.
- Busch, D. E., W. F. Loftus, and O. L. Bass, Jr. 1998. Long-term hydrologic effects on marsh plant community structure in the southern Everglades. *Wetlands* 18:230–241.
- Campbell, M. R. 1999. Everglades alligator holes: distribution and ecology. M.S. Thesis. University of Florida, Gainesville, FL, USA.
- Campbell, M. R. and F. J. Mazzotti. 2001. Mapping Everglades alligator holes using color infrared photographs. *Florida Scientist* 64:148–158.
- Craighead, F. C. 1968. The role of the alligator in shaping plant communities and maintaining wildlife in the southern Everglades. *Florida Naturalist* 21:2–7,68–74,94.
- Craighead, F. C. 1971. *The Trees of South Florida, Vol. 1, The Natural Environments and Their Succession*. University of Miami Press, Coral Gables, FL, USA.
- Daniel, W. W. 1990. *Applied Nonparametric Statistics*. Wadsworth Publishing Company, Belmont, CA, USA.
- David, P. G. 1996. Changes in plant communities relative to hydrologic conditions of the Florida Everglades. *Wetlands* 15:15–23.
- Davis, S. M. 1994. Phosphorus inputs and vegetation sensitivity in the Everglades. p. 357–378. *In* S. M. Davis and J. C. Ogden (eds.) *Everglades: the Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- Davis, S. M., L. H. Gunderson, W. A. Park, J. R. Richardson, and J. E. Mattson. 1994. Landscape dimensions, composition, and function in a changing Everglades ecosystem. p. 769–789. *In* S. M. Davis and J. C. Ogden (eds.) *Everglades: the Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- Davis, S. M. and J. C. Ogden. 1994. Everglades: the Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, USA.
- Frederick, P. C. and M. G. Spalding. 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. p. 659–691. *In* S. M. Davis and J. C. Ogden (eds.) *Everglades: the Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- Gleason, P. J. and P. Stone. 1994. Age, origin, and landscape evolution of the Everglades peatland. p. 149–197. *In* S. M. Davis and J. C. Ogden (eds.) *Everglades: the Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- Grace, J. B. 1987. The impacts of preemption on the zonation of two *Typha* species along lakeshores. *Ecological Monographs* 57:283–303.
- Grace, J. B. 1988. The effects of nutrient additions on mixtures of *Typha latifolia* L. and *Typha domingensis* Pers. along a water depth gradient. *American Journal of Botany* 31:762–768.
- Gunderson, L. H. 1989. Historical hydropatterns in wetland communities in Everglades National Park. p. 1099–1111. *In* R. R. Sharitz and J. W. Gibbons (eds.) *Freshwater Wetlands and Wildlife*. U.S. Department of Energy, Oak Ridge, TN, USA.
- Gunderson, L. H. 1994. Vegetation in the Everglades: Determinants of community composition. p. 323–340. *In* S. M. Davis and J. C. Ogden (eds.) *Everglades: the Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- Hill, M. O. 1979a. DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Department of Ecology and Systematics, Ithaca, NY, USA.
- Hill, M. O. 1979b. TWINSpan: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Department of Ecology and Systematics, Ithaca, NY, USA.
- Hoffman, W., G. T. Bancroft, and R. J. Sawicki. 1994. Foraging habitat of wading birds in the Water Conservation Areas of the Everglades. p. 585–614. *In* S. M. Davis and J. C. Ogden (eds.) *Everglades: the Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- Jordan, F., H. L. Jelks, and W. M. Kitchens. 1997. Habitat structure and plant community composition in a northern Everglades landscape. *Wetlands* 17:275–283.
- Kushlan, J. A. 1972. An ecological study of an alligator pond in the Big Cypress swamp of southern Florida. M.S. Thesis. University of Miami, Miami, FL, USA.
- Kushlan, J. A. 1974. Observations of the role of the American Alligator (*Alligator mississippiensis*) in the southern Florida wetlands. *Copeia* 1974:993–996.
- Kushlan, J. A. and B. Hunt. 1979. Limnology of an alligator pond in South Florida. *Florida Scientist* 42:66–84.
- Kushlan, J. A. and M. S. Kushlan. 1980. Everglades alligator nests: Nesting sites for marsh reptiles. *Copeia* 1980:1930–1932.
- Lodge, T. E. 1998. *The Everglades Handbook: Understanding the Ecosystem*. St. Lucie Press, Boca Raton, FL, USA.
- Loftus, W. F. and A. M. Eklund. 1994. Long-term dynamics of an Everglades small-fish assemblage. p. 461–482. *In* S. M. Davis and J. C. Ogden (eds.) *Everglades: the Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- Loveless, C. M. 1959. A study of the vegetation in the Florida Everglades. *Ecology* 40:1–9.
- Mazzotti, F. J. and L. A. Brandt. 1994. Ecology of the American alligator in a seasonally fluctuating environment. p. 485–505. *In* S. M. Davis and J. C. Ogden (eds.) *Everglades: the Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- McCormack, P. V., S. Newman, S. Miao, D. E. Gawlik, D. Marley, K. R. Reddy, and T. D. Fontaine. 2002. Effects of anthropogenic phosphorus inputs on the Everglades. p. 83–126. *In* J. W. Porter and K. G. Porter (eds.) *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: an Ecosystem Sourcebook*. CRC Press, Boca Raton, FL, USA.
- McCune, B. and M. J. Mefford. 1995. PC-ORD. Multivariate Analysis of Ecological Data, Version 2.0. MjM Software Design, Gleneden Beach, OR, USA.
- McIlhenny, E. A. 1935. *The Alligators Life History*. The Christopher Publishing House, Boston, MA, USA.
- Newman, S., J. B. Grace, and J. W. Koebel. 1996. Effects of nutrients and hydroperiod on *Typha*, *Cladium*, and *Eleocharis*: Implications for Everglades restoration. *Ecological Applications* 6:774–783.

- Richardson, J. R., W. L. Bryant, W. M. Kitchens, J. E. Mattson, and K. R. Pope. 1990. An evaluation of refuge habitats and relationship to water quality, quantity and hydroperiod. Final Report to Arthur R. Marshall Loxahatchee National Wildlife Refuge, Boynton Beach, FL, USA.
- Schomer, N. S. and R. D. Drew. 1982. An ecological characterization of the lower Everglades, Florida Bay and the Florida Keys. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC, USA.
- Shannon, C. E. and W. Weaver. 1949. The Mathematical Theory of Communication. University of Illinois, Urbana, IL, USA.
- Vaithyanathan, P. and C. J. Richardson. 1999. Macrophyte species changes in the Everglades: Examination along a eutrophication gradient. *Journal of Environmental Quality* 28:1347–1358.
- Vivian-Smith, G. 1997. Microtopographic heterogeneity and floristic diversity in experimental wetland communities. *Journal of Ecology* 85:71–82.
- White, P. S. 1994. Synthesis: vegetation pattern and process in the Everglades ecosystem. p. 445–458. *In* S. M. Davis and J. C. Ogden (eds.) *Everglades: the Ecosystem and Its Restoration*. St. Lucie Press, Delray Beach, FL, USA.
- Wunderlin, R. P. 1998. *Guide to the Vascular Plants of Florida*. University Press of Florida, Gainesville, FL, USA.

Manuscript received 22 October 2001; revisions received 3 October 2002; 2 September 2003, and 31 October 2003; accepted 19 November 2003.