

Response of the Everglades ridge and slough landscape to climate variability and 20th-century water management

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Abstract. The ridge and slough landscape of the Florida Everglades consists of a mosaic of linear sawgrass ridges separated by deeper-water sloughs with tree islands interspersed throughout the landscape. We used pollen assemblages from transects of sediment cores spanning sawgrass ridges, sloughs, and ridge–slough transition zones to determine the timing of ridge and slough formation and to evaluate the response of components of the ridge and slough landscape to climate variability and 20th-century water management. These pollen data indicate that sawgrass ridges and sloughs have been vegetationally distinct from one another since initiation of the Everglades wetland in mid-Holocene time. Although the position and community composition of sloughs have remained relatively stable throughout their history, modern sawgrass ridges formed on sites that originally were occupied by marshes. Ridge formation and maturation were initiated during intervals of drier climate (the Medieval Warm Period and the Little Ice Age) when the mean position of the Intertropical Convergence Zone shifted southward. During these drier intervals, marsh taxa were more common in sloughs, but they quickly receded when precipitation increased. Comparison with regional climate records suggests that slough vegetation is strongly influenced by North Atlantic Oscillation variability, even under 20th-century water management practices.

Key words: climate variability; Everglades; Florida, USA; late Holocene; paleoecology; pollen; wetlands.

INTRODUCTION

Restoration goals should incorporate knowledge of environmental response to disturbances and abrupt climate change (Mayer and Rietkerk 2004, Cronin and Walker 2006, Jentsch 2007) as well as the relative roles of allogenic changes vs. autogenic mechanisms in structuring ecosystems (Singer et al. 1996). Although historically documented trends in community composition typically have formed the primary basis for restoration targets, there is increasing acknowledgment of the importance of understanding the physical conditions that initially created the system (Harris et al. 2006). The Florida Everglades, USA, provides a unique opportunity to compare the relative influences of geology, hydrology, climate, and biology on wetland initiation, development, and differentiation with the impacts of human alteration of water flows and hydroperiods. Previous studies indicate the strong influence of interannual to centennial climate variability on the development of wetland and estuarine communities of the greater Everglades ecosystem (Gleason and Stone 1994, Winkler et al. 2001, Cronin et al. 2002, Chmura et al. 2006, Gaiser et al. 2006, Willard et al. 2006). This

new examination of long-term (10^1 – 10^3 yr) vegetation patterns in sawgrass ridges and sloughs expands our understanding of the external drivers of wetland plant communities in the region broadly known as the Everglades ridge and slough landscape (Fig. 1). Integration of paleoecological data from discrete vegetation types within the wider landscape (i.e., sawgrass ridges and sloughs) is critical to understanding the broadscale impacts of flow alteration and to identify the relative vulnerability and resilience of different components of the wetland to environmental and climatic stressors. Such a long-term perspective on ecosystem response to both a range of natural climate fluctuations and human alteration of the system is critical to forecasting likely responses to a range of management actions.

The ridge and slough landscape of the Florida Everglades comprises distinctive, linear flow-oriented sawgrass ridge and slough plant communities interspersed with tree islands. Sawgrass ridges are topographically higher and have shorter hydroperiods than adjacent sloughs, but their distribution does not appear to be tied to the bedrock highs that form the core of many elongate tree islands (Science Coordination Team 2003). The ridge and slough landscape originally extended from as far north as Lake Okeechobee to the termination of Shark River Slough at the Gulf of Mexico (Fig. 1), but it now is restricted to parts of Water Conservation Area 1 (WCA 1; also known as the Arthur R.

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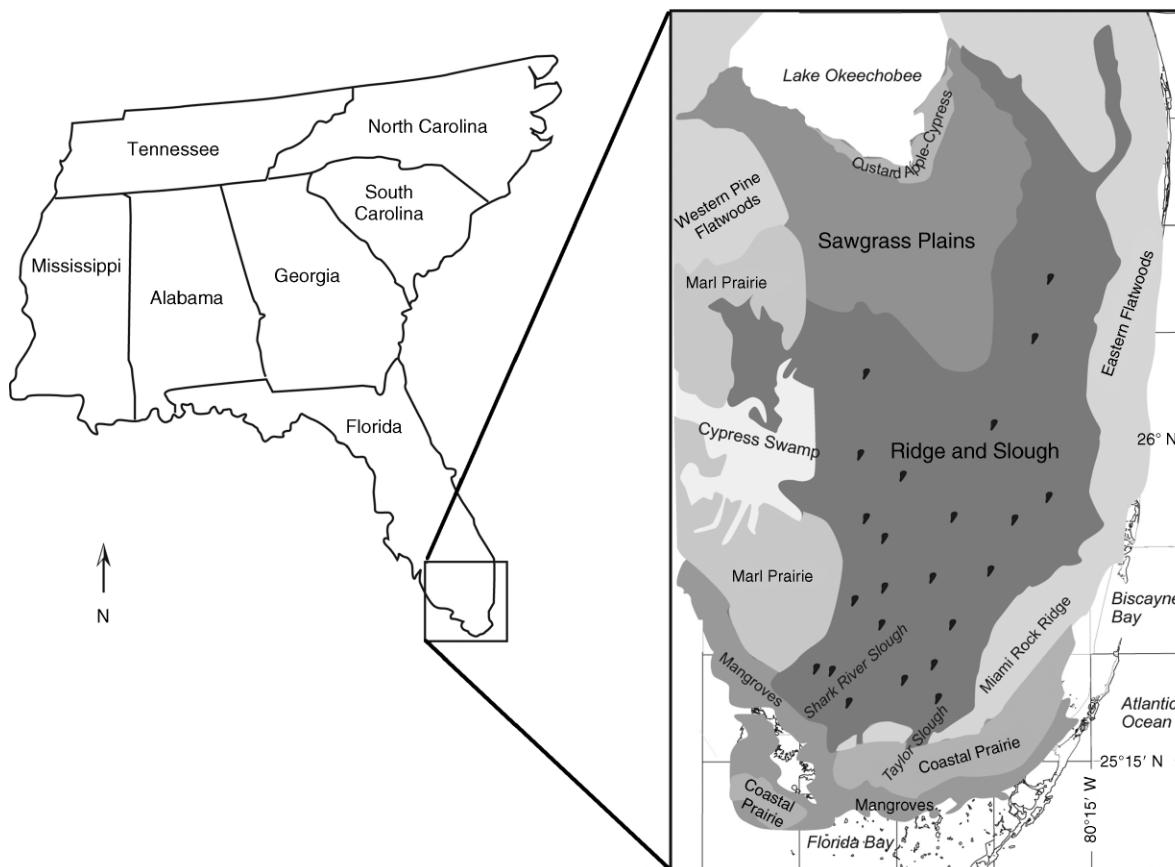


FIG. 1. Reconstructed pre-drainage distribution of habitat types in the greater Everglades ecosystem (modified from Lodge [2005]). The map shows the location of the Florida Everglades within the southeastern United States.

Marshall Loxahatchee National Wildlife Refuge), WCA 2, and Everglades National Park (Fig. 2; Lodge 2005). The reduction in its areal extent has been attributed to 20th-century anthropogenic alterations of the natural hydrologic regime for increased agricultural activities and urban populations. These changes have resulted in an expansion of sawgrass marshes into sloughs and a loss of the distinct ridge and slough structure (Science Coordination Team 2003). Much restoration planning has focused on factors necessary to restore and maintain the remaining sawgrass ridge and slough landscape, emphasizing the role of flow in structuring the landscape (Science Coordination Team 2003). Little is known about the long-term dynamics governing initiation of the linear ridge and slough pattern, the role of flow in structuring the landscape, or the pre-20th-century history and variability of the system.

Conceptual models and empirical studies of the origin and formation of the landscape point to randomly distributed clumps of sawgrass forming into linear flow-oriented sawgrass ridges through positive feedbacks such as greater soil stabilization and aeration, the focusing of floc deposition along ridge edges, alteration of flow, and increased peat accumulation (Larsen et al. 2007, Givnish et al. 2008). Climate usually has not been considered as a significant factor influencing the

formation of the ridge and slough landscape (see Ogden 2005 for a detailed description of 20th-century drivers and stressors). However, past climate variability, primarily prolonged dry periods associated with the Medieval Warm Period and the Little Ice Age in the Florida Peninsula, has been suggested as a driver of tree island development within the ridge and slough landscape (Willard et al. 2006). It is possible that such climate drivers also influenced formation and development of sawgrass ridges and sloughs within the broader landscape. Here we use paleoecological studies of ridge and slough sediments to examine the dynamics of sawgrass ridge and slough communities over decadal to millennial timescales in an effort to evaluate the validity of different hypotheses and models of sawgrass ridge and slough formation. Specifically, the study was designed to document the origins of sawgrass ridge and slough plant communities, their development and variability through time, and their response to changes in hydrology and climate. The critical points addressed are (1) the timing of ridge and slough formation; and (2) the response of components of the ridge and slough landscape to late Holocene climate variability and 20th-century water management. Given the intensive efforts devoted to Everglades restoration, such studies provide

perspectives on the long-term function and structure of wetland communities that are necessary to develop strategies for sustainable ecosystem restoration.

REGIONAL OVERVIEW

Regional climate

The Florida Peninsula is characterized by seasonal precipitation, with most rain (70%) falling during the wet season from May through November (average 86 cm; range 58–135 cm), resulting in high Everglades water levels in the summer and fall (Duever et al. 1994). An average of 43 cm of rain (17–78 cm) falls during the remainder of the year (McPherson and Halley 1996). This seasonal precipitation pattern is driven by the Bermuda High (BH). In the wet season (summer–fall), the BH is located near Bermuda, and in the dry season, it is located near the Azores (Stahle and Cleaveland 1992). Interannual variability is influenced by the El Niño–Southern Oscillation, with heavy winter rainfall during large El Niño warm events and low winter precipitation during La Niñas (Kiladis and Diaz 1989, Beckage et al. 2003).

Vegetation of the Everglades ridge and slough landscape

The Everglades presently covers an area of ~6000 km² (Fig. 2) and is a phosphorus-limited, precipitation-driven, subtropical wetland system (Davis et al. 1994). The natural wetland covered an area of ~12000 km² (Fig. 1) and reflected the seasonal precipitation pattern. Water flowed southward during the wet season along a gentle slope of 3 cm/km (Kushlan 1990) from Lake Okeechobee toward Florida Bay and the Gulf of Mexico through Shark River Slough and, to a lesser extent, Taylor Slough. Water depth and hydroperiod were controlled by a combination of precipitation and substrate elevation. The latter is influenced by bedrock topography, sediment accumulation rates (which also are influenced by vegetation type), and sediment loss from exposure or fire. The distribution of Everglades wetland plant communities are controlled by water depth, hydroperiod, substrate type, and fire regime (Kushlan 1990). The ridge and slough landscape encompasses a mixture of long- to moderate-hydroperiod wetlands characterized by longitudinally oriented ridges of *Cladium* (sawgrass) and open-water sloughs dominated by *Nymphaea* (water lily) interspersed with tree islands (Fig. 3). Ridge vegetation consists almost entirely of *Cladium*, typically reaching ~2 m high. *Morella cerifera* (wax myrtle), *Cephalanthus occidentalis* (button bush), and ferns also are common locally in the ridge. The greatest peat thickness and shallowest water depths occur in sawgrass ridges. The transition between ridges and sloughs consists of sparse, short (<1 m) *Cladium*, *Sagittaria* (arrowhead), *Pontederia* (pickerel weed), and *Crinum* (white lily). Transition zone water depths are greater and the peats are slightly thinner than those in the ridges (Bernhardt et al. 2004). *Nymphaea* and *Utricularia* (bladderwort) dominate elongate open-water sloughs,

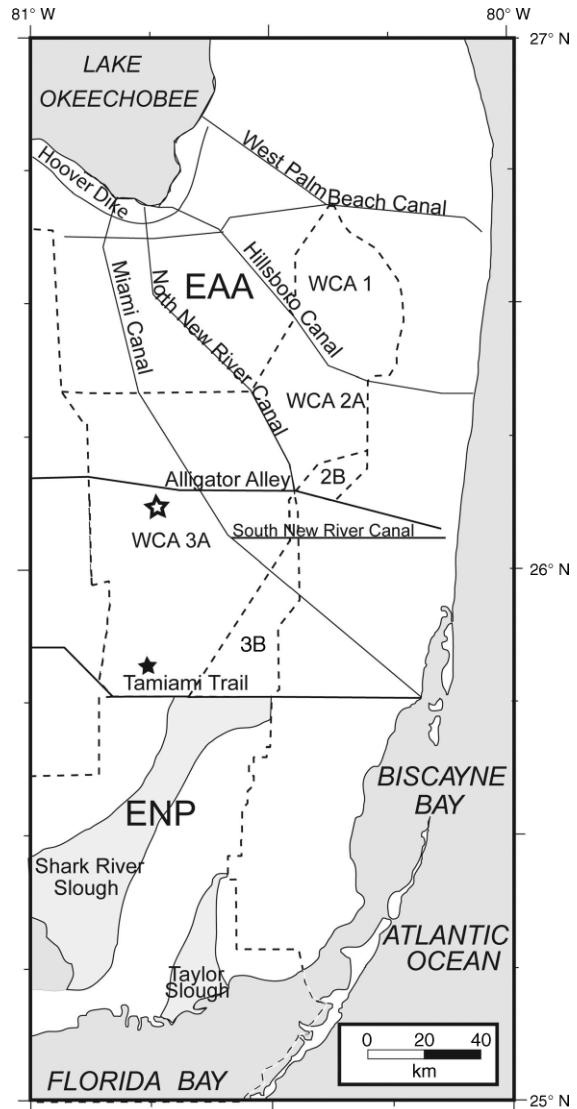


FIG. 2. Map of the Florida Everglades. The current extent of the Everglades wetland is restricted to parts of water conservation areas (WCAs) 1, 2, and 3 and Everglades National Park (ENP). Ridge and slough transects of sediment cores are noted with a solid star (discussed in text and Table 1) and an open star (see Appendices E and F). EAA indicates the Everglades Agricultural Area. The figure is modified from Willard et al. (2006).

where vegetation is sparse overall. Slough communities have the deepest water depths of the Everglades, and the underlying peats typically are thinner than in the ridge or transition zone. The patterning in the landscape described above is probably unrelated to changes in bedrock topography (Larsen et al. 2007).

20th-century water management in the Everglades

Drainage efforts to render parts of the Everglades usable for agricultural and urban development began in the late 19th century (Light and Dineen 1994). The first

major drainage phase began in the 1910s with excavation of four canals (North New River, Hillsboro, Miami, and West Palm Beach Canals) that linked Lake Okeechobee to the Atlantic Ocean (Fig. 2) and drained an area of 607 100 ha (Sklar and van der Valk 2002). Shortly thereafter, the east–west running Tamiami Trail, which blocks water flow north to south, was completed, and the Hoover Dike encircled Lake Okeechobee, greatly reducing freshwater flow across the wetland. The second drainage phase began in 1948 when Congress signed the “Central and Southern Florida Project for Flood Control and other Purposes” (C & SF Project) into law. The C & SF Project included an extensive system of levees, canals, and pump stations to ensure adequate water supply during droughts and to store large quantities of water to protect urban areas during unusually wet years. This construction effectively divided the Everglades into distinct compartments, resulting in different hydrologic conditions (i.e., hydroperiods) within each WCA. Since completion of the C & SF Project, a series of water regulation schedules have been enacted in attempts to create more natural hydroperiods and water depths and improve the ecological conditions in the remaining Everglades (Brandt 2006). Recent restoration efforts are part of the Comprehensive Everglades Restoration Plan (CERP), which aims to simultaneously restore, preserve, and protect the south Florida ecosystem and ensure adequate water supply and flood protection for the population (Water Resources Development Act 2000).

METHODS

Core collection, sampling, geochronology, and analysis of pollen assemblages

Transects of cores were collected across two relatively pristine, well-defined ridge and slough systems in water conservation area (WCA) 3A (Figs. 2 and 3). These transects consisted of a series of cores collected in the deepest, central slough, in the transition from slough to sawgrass ridge, and in the central ridge (Fig. 3). Cores were collected using a piston corer with a 10-cm barrel. The core barrel was pushed through the sediment until it reached the underlying limestone. After extruding sediments from the core barrel, we described sediment lithology and sampled cores for pollen in 1-cm increments for the upper 20 cm and in 2-cm increments for the remainder of the core. We dried samples in a 50°C oven.

The chronology of these cores is based on radiocarbon (^{14}C) and lead (^{210}Pb) dating and on pollen biostratigraphy (see Plate 1). Radiocarbon dates were obtained on bulk sediments by Beta Analytic (Miami, Florida, USA) and calibrated to calendar years using the Pretoria Calibration Procedure (Table 1; Talma and Vogel 1993, Stuiver et al. 1998). Radiocarbon dates in Table 1 are presented as calibrated years before sample collection (AD 2002; cal yr BP). This convention is used to minimize confusion as to what is meant by “present”

(see discussion by Rose 2007 and Wolff 2007) and to facilitate integration of radiocarbon dates and ^{210}Pb data into a single age model. Age models for the last century of deposition were based on ^{210}Pb analyses and, where applicable, the first occurrence of pollen of *Casuarina equisetifolia*, an exotic species introduced to south Florida ~AD 1900 (Langeland 1990). Pollen of *C. equisetifolia* first occurs in south Florida sediments at ~AD 1910 and is common only in sediments deposited after 1940 (Wingard et al. 2003). Age models are constructed using a weighted mixed-effect regression using the computer program R (Version 2.8.1; Heegaard et al. 2005). Accumulation rates were calculated from ^{210}Pb data using the assumptions of a constant initial excess ^{210}Pb concentration (the constant initial concentration [CIC] model; Bernhardt et al. 2004). Age models for all cores included in the analysis are provided in Appendix A.

We isolated pollen from both sediment cores and surface samples using standard palynological preparation techniques (Traverse 1988, Willard et al. 2001b). For each sample, one tablet with a known number of *Lycopodium* spores was added to 0.5–1.5 g of dry sediment for calculation of absolute pollen concentration (pollen/g). Samples were processed with HCl and HF to remove carbonates and silicates respectively, acetylated (one part sulfuric acid : nine parts acetic anhydride) in a boiling water bath for 10 min, neutralized, and treated with 10% KOH for 10 min in a water bath at 70°C. After neutralization, residues were sieved with 149- μm and 10- μm nylon mesh to remove the coarse and clay fractions, respectively. When necessary, samples were swirled in a watch glass to remove mineral matter. After staining with Bismarck Brown, palynomorph residues were mounted on microscope slides in glycerin jelly. At least 300 pollen grains and spores were counted from each sample to determine percentage abundance and concentration of palynomorphs. In the few samples with low pollen concentrations, minimum counts of 100 were considered acceptable. Identification was aided by slides from the USGS (Reston, Virginia, USA) reference collection and Willard et al. (2004). Pollen data are archived with the South Florida Information Access (SOFIA; *available online*)⁴ and the North American Pollen Database at the World Data Center for Paleoclimatology in Boulder, Colorado, USA (*available online*).⁵

Statistical analysis

Our reconstruction of past plant communities is based on statistical comparison of fossil and modern assemblages from different wetland communities throughout the Everglades (Willard et al. 2001b). Using the modern analogue technique (Overpeck et al. 1985), we calculated

⁴ (<http://sofia.usgs.gov>)

⁵ (<http://www.ngdc.noaa.gov/paleo/pollen.html>)

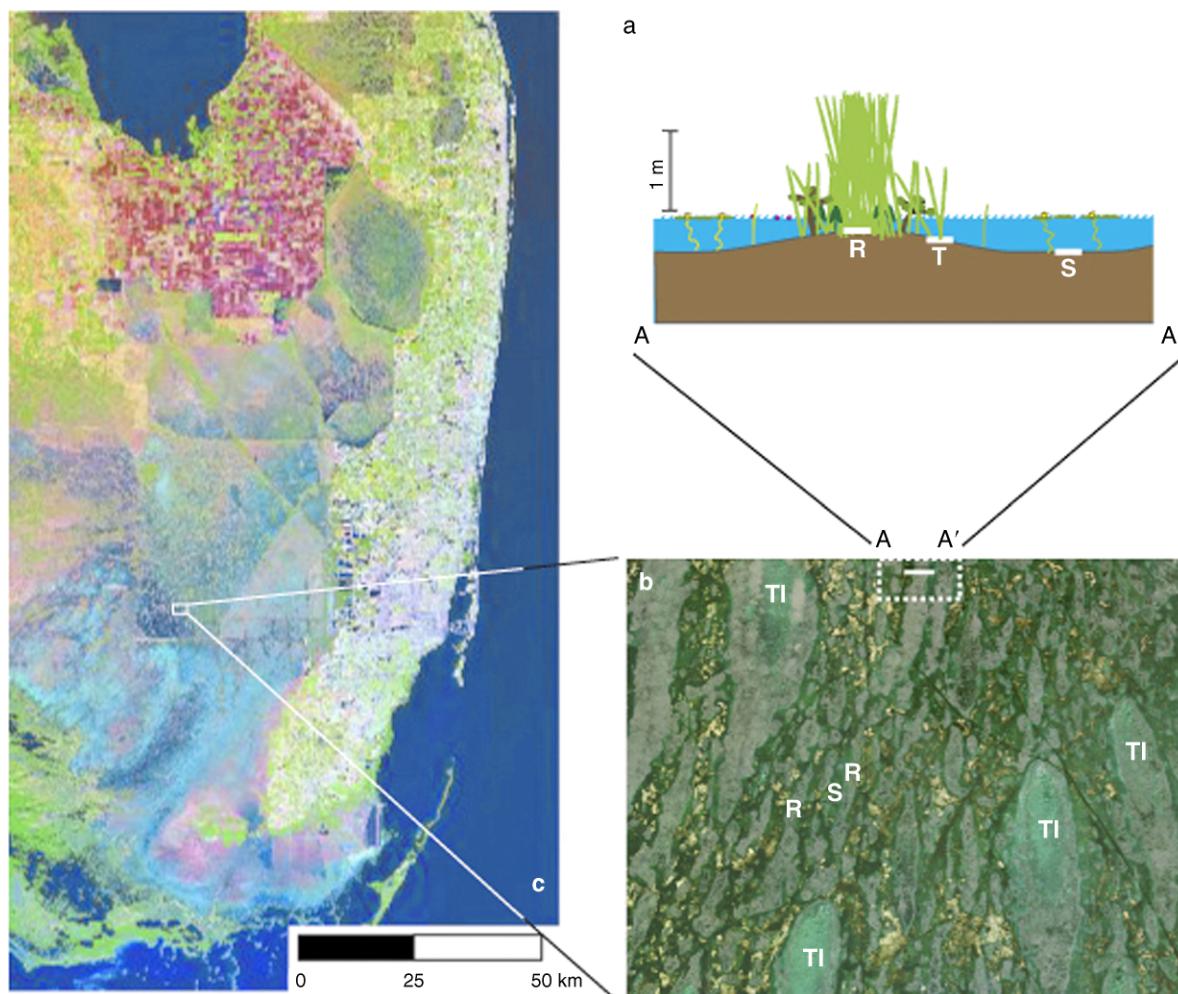


FIG. 3. Illustration of the sawgrass ridge and slough landscape. (a) An idealized cross section along transect A–A' of the ridge and slough landscape where R = ridge (core 02-05-21-2), T = transition zone (core 02-05-21-4), and S = slough (core 02-05-21-5). (b) Satellite image of linear ridge and slough landscape showing orientation of transect A–A' (TI, tree island; R, ridge; S, slough). (c) Satellite image of Florida Everglades showing the location of the transect. The satellite image in (b) was obtained from Google Earth. Satellite image (c) was cropped from a 2000 Landsat 7 image at 120-m resolution (http://fce.lternet.edu/data/GIS/interactive_map/).

squared-chord distance (SCD) between down-core pollen assemblages and surface samples collected throughout the Everglades (Willard et al. 2001*b*, 2006) to define the dissimilarity between each fossil and modern assemblage. SCD was chosen because it is robust and is not influenced by rare pollen taxa in the data set (Overpeck et al. 1985). Down-core samples with dissimilarity coefficients ≤ 0.15 (the critical value) are considered to share similar vegetation and environmental parameters with their modern analogue (Willard et al. 2001*b*). We divided cores into pollen zones based on a combination of ecological reasoning, modern analogues, and objective zonation using the program CONISS (Grimm 1992).

We used rarefaction analysis after Birks and Line (1992) as a measure of diversity. We standardized all

analyses to a count of 110 grains. The expected number of species encountered is a conservative estimate because 110 individuals represented the lowest pollen sum encountered during analysis. However, most counts averaged ~ 300 individuals, and species of plants with morphologically similar pollen are lumped either within a single genus or family during analysis.

We used detrended canonical correspondence analysis (DCCA) to calculate vegetation turnover through time (ter Braak 1986; methodology follows Birks 2007) using the computer program CANOCO 4.5 (ter Braak and Smilauer 2002). Chronology (in cal yr BP) was the sole environmental variable, and the amount of vegetation turnover (SD) was determined from the rescaled first DCCA axis score (Birks 2007). DCCA reports the amount of vegetation turnover in standard deviation

TABLE 1. Location and radiocarbon dates for cores collected in the Florida Everglades, USA.

Lab ID	Core ID	Location	Latitude (N)	Longitude (W)	Sample depth (cm)	$\delta^{13}C$	Conventional age (yr before 2002)
172255	02-05-21-2	ridge	25°49.76'	80°46.10'	20–22	–27.1	292
172256	02-05-21-2	ridge	25°49.76'	80°46.10'	38–40	–26.7	1232
172257	02-05-21-2	ridge	25°49.76'	80°46.10'	54–56	–25.8	2682
172261	02-05-21-4	transition	25°49.76'	80°46.08'	20–22	–26.8	442
172262	02-05-21-4	transition	25°49.76'	80°46.08'	36–38	–26.5	1432
172263	02-05-21-4	transition	25°49.76'	80°46.08'	52–54	–26.5	2852
172264	02-05-21-5	slough	25°49.75'	80°46.07'	20–22	–26.7	872
172265	02-05-21-5	slough	25°49.75'	80°46.07'	32–34	–27	1872
172266	02-05-21-5	slough	25°49.75'	80°46.07'	50–54	–25.8	3392
180443	02-05-20-14	ridge	26°06.17'	80°44.17'	20–22	–26.8	692
180444	02-05-20-14	ridge	26°06.17'	80°44.17'	35–39	–24.4	2692
180445	02-05-20-13	slough	26°06.13'	80°44.26'	20–22	–26	1352
180446	02-05-20-13	slough	26°06.13'	80°44.26'	30–32	–26.4	1862
180447	02-05-20-13	slough	26°06.13'	80°44.26'	36–40.5	–25.9	2582

Note: All dates were obtained on bulk peat samples and analyzed by Beta Analytic (Miami, Florida, USA) and are reported as years before 2002.

† Calibrated against the Intcal98 database, after Stuiver and van der Plicht (1998), Stuiver et al. (1998), and Talma and Vogel (1993).

‡ Upper and lower limits based on two sigma errors in calibration.

units (SD). The SD score serves as a useful tool to compare the degree of vegetation change during certain time intervals between cores in the ridge and slough landscape, as well as cores from other wetland types (Birks 2007, Birks and Birks 2008). Birks and Birks (2008) stated that the turnover (SD) calculated by DCCA is equivalent to beta diversity and therefore

illustrates the usefulness of the SD metric as an ecologically interpretable unit.

Calibration of pollen assemblages and source vegetation

Pollen assemblages from sawgrass ridges, the transition zone, and sloughs are readily distinguishable based primarily on the percentage abundance of *Cladium*,

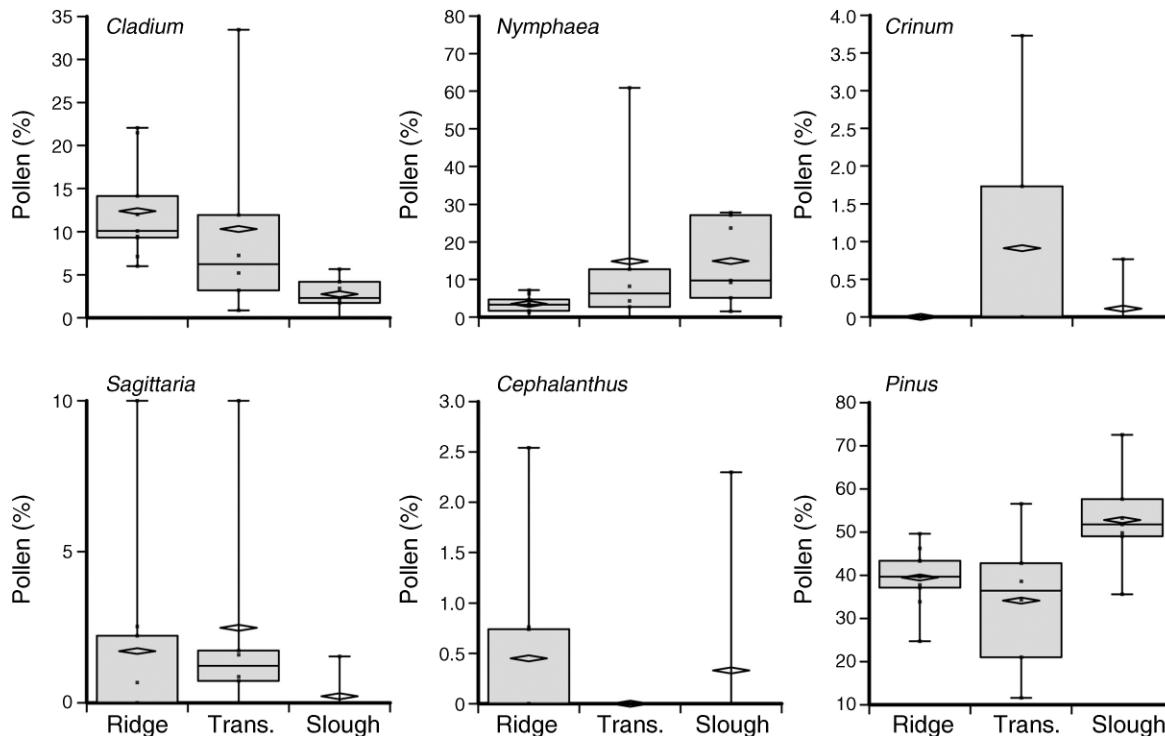


FIG. 4. Tukey box and whisker plots of percentage abundance of pollen of six genera from sawgrass ridge, slough, and transitional (Trans.) surface samples. Boxes capture the upper and lower median. Points indicate sample abundance, diamonds indicate mean, horizontal lines indicate median abundance, and error bars indicate maximum and minimum sample abundance.

TABLE 1. Extended.

1 σ counting error	Calibration intercept (yr before 2002) [†]	+2 σ (yr before 2002) [‡]	-2 σ (yr before 2002) [‡]
60	342	502	0
60	1122	1312	1012
70	2812	2912	2562
50	532	572	362
60	1342	1432	1232
70	2932	3132	2812
60	772	962	712
60	1782	1932	1632
70	3632	3772	3452
70	692	742	582
80	2807	2917	2537
60	1312	1362	1122
70	1772	1942	1602
80	2777	2827	2407

Nymphaea, and *Crinum* pollen (Bernhardt et al. 2004). In ridge surface samples, *Cladium* pollen typically comprises 9–14% of assemblages, compared to <5% in the adjacent sloughs. In contrast, *Nymphaea* pollen comprises <2% of the ridge surface sample assemblages and 5–30% in the slough surface samples. Within the transition zone, pollen assemblages are highly variable, but *Crinum* and its pollen are restricted to this zone (Fig. 4). No other taxa show distinctive patterns of pollen distribution within the ridge and slough system.

To more clearly understand general patterns of community response to altered hydrology, we grouped taxa into functional groups. Functional groupings of species facilitate a holistic interpretation of vegetation dynamics by including species traditionally omitted from pollen diagrams due to low abundance. The taxa in these groupings include only those taxa represented in pollen analyses. Functional groups organized by hydroperiod preference are determined by field observation of plant distribution within the ridge and slough habitat and habitat preference (Davis 1943, Loveless 1959, McPherson 1973, Kushlan 1990, Cronk and Fennessy 2001). Four functional groupings of pollen are defined (see Table 2): (1) deepwater slough assemblage dominated by *Nymphaea* but including other plants that prefer long hydroperiods and deep water (such as *Nuphar*, *Utricularia*, *Ludwigia*, *Myriophyllum*); (2) ridge–slough transition assemblage, consisting of pollen of *Sagittaria*, *Crinum*, *Justicia*, Poaceae, and Apiaceae,

representing communities such as those found in wet prairies and transition zones between sawgrass ridges and sloughs; (3) ridge assemblage, consisting of *Cladium* and to a lesser extent *Salix* and *Cephalanthus* (moderate hydroperiods and water depths); and (4) dry assemblage, comprising mainly Amaranthaceae, *Morella*, *Ilex*, Asteraceae, and Polygonaceae. This assemblage incorporates extra-local vegetation to a greater extent than other assemblages (see Table 2 for a complete list of taxa). Because our sites were not situated near canals or other nutrient-enriched sites, we assumed that the presence/absence of *Typha* in these locations is controlled by hydrology rather than nutrient loading.

RESULTS

We focused on the last 1500 years to illustrate the baseline variability of the system under a range of climate conditions and to maximize temporal resolution. Pollen assemblages in all cores are divisible into three assemblage zones representing common patterns of development: pre-1000 cal yr BP, ~1000–100 cal yr BP, and the 20th century (Figs. 5, 6, and 7). Our discussion focuses on wetland species and does not discuss trends in *Pinus* abundance because, even though it dominates many assemblages, it represents the regional pollen rain. Comparison of absolute pollen concentration and percentage abundance of *Pinus* indicates that percentage abundance patterns of other species are consistent (Appendices B–D). The transect of cores discussed here is representative of patterns of timing and vegetational composition observed in other ridge and slough sites (see Fig. 8 and Appendices E and F).

Basal zone 1 represents pollen assemblages from vegetation that occupied the sites before 1000 cal yr BP. In the ridge sites, assemblages from zone 1 are analogous to modern sloughs and sawgrass marshes with long to moderate hydroperiods. Assemblages are dominated by Amaranthaceae pollen (15–60%); *Nymphaea* pollen is subdominant, and *Cladium* pollen is common. Other taxa consistently present include Asteraceae, Poaceae, *Typha*, and *Sagittaria*. In the ridge–slough transition and slough sites, assemblages are analogous to modern sloughs with long hydroperiods. *Nymphaea* pollen is abundant, Amaranthaceae pollen is common, and pollen of Polygonaceae and Asteraceae are present in both sites (Figs. 5, 6, and 7).

TABLE 2. Functional groupings of pollen assemblages.

Functional group	Hydroperiod in days (average annual water depth in cm) [†]	Included taxa
Deepwater	363 (67)	<i>Nymphaea</i> , <i>Nuphar</i> , <i>Utricularia</i> , <i>Ludwigia</i> , <i>Myriophyllum</i>
Ridge–slough transition	361 (56)	Poaceae, Apiaceae, Euphorbiaceae, Cyperaceae, <i>Justicia</i> , <i>Crinum</i> , <i>Typha</i>
Ridge	357 (48)	<i>Cladium</i> , <i>Salix</i> , <i>Cephalanthus</i>
Dry	NA	Amaranthaceae, Asteraceae, Polygonaceae, <i>Quercus</i> , <i>Ilex</i> , <i>Morella</i>

Note: Pollen is grouped according to species' hydroperiod preferences.

[†] Measurements of hydroperiod and average water depths are from Givnish et al. (2008).

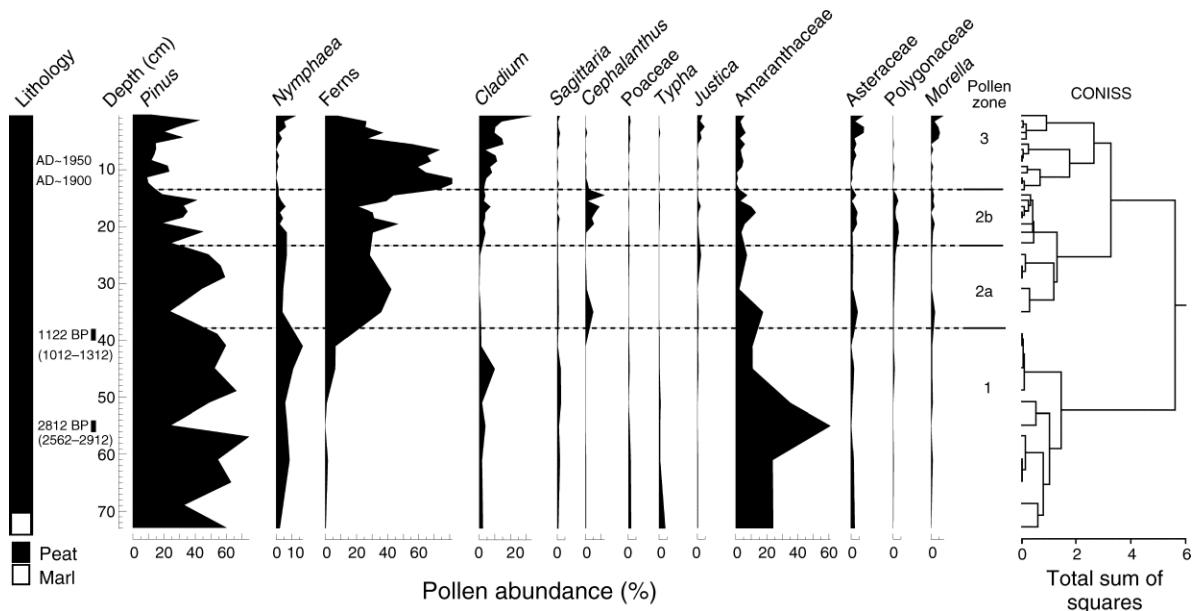


FIG. 5. Sawgrass ridge pollen assemblages from core 02-05-21-2. Pollen of diagnostic taxa are presented as percentage abundance. Radiocarbon dates are given as the intercept point and 2 sigma range as calibrated years before 2002 (cal yr BP; see Table 1). Dates within the 20th century were determined from ²¹⁰Pb analyses. Modern analogues for pollen zones are: 1, sawgrass marsh/slough; 2a, sawgrass marsh/transitional wetland; 2b, ridge/sawgrass marsh; and 3, ridge. Pollen zones were determined using the program CONISS (Grimm 1992).

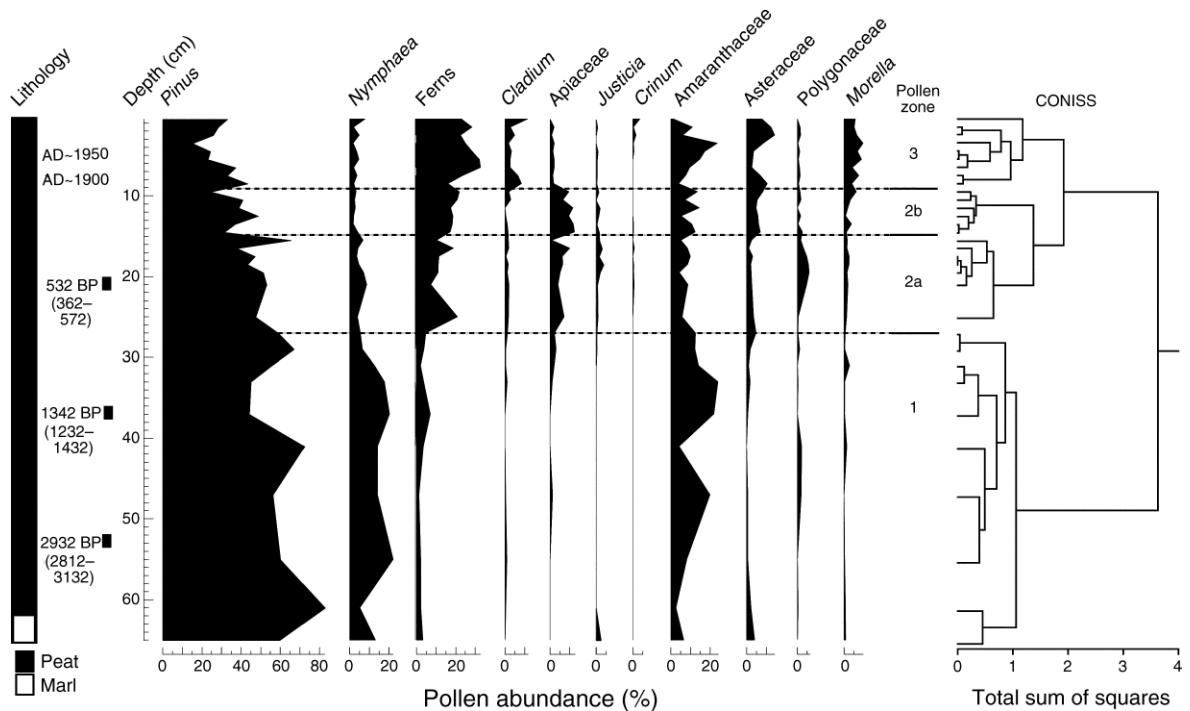


FIG. 6. Transition pollen assemblages from core 02-05-21-4. Pollen assemblages are shown from species with >2% abundance. Radiocarbon dates are given as the intercept point and 2 sigma range as calibrated years before 2002 (cal yr BP; see Table 1). Dates within the 20th century were determined from ²¹⁰Pb analyses. Modern analogues for pollen zones are: 1, slough; 2a, wet prairie/sawgrass marsh/slough; 2b, transition; and 3, ridge/transition.

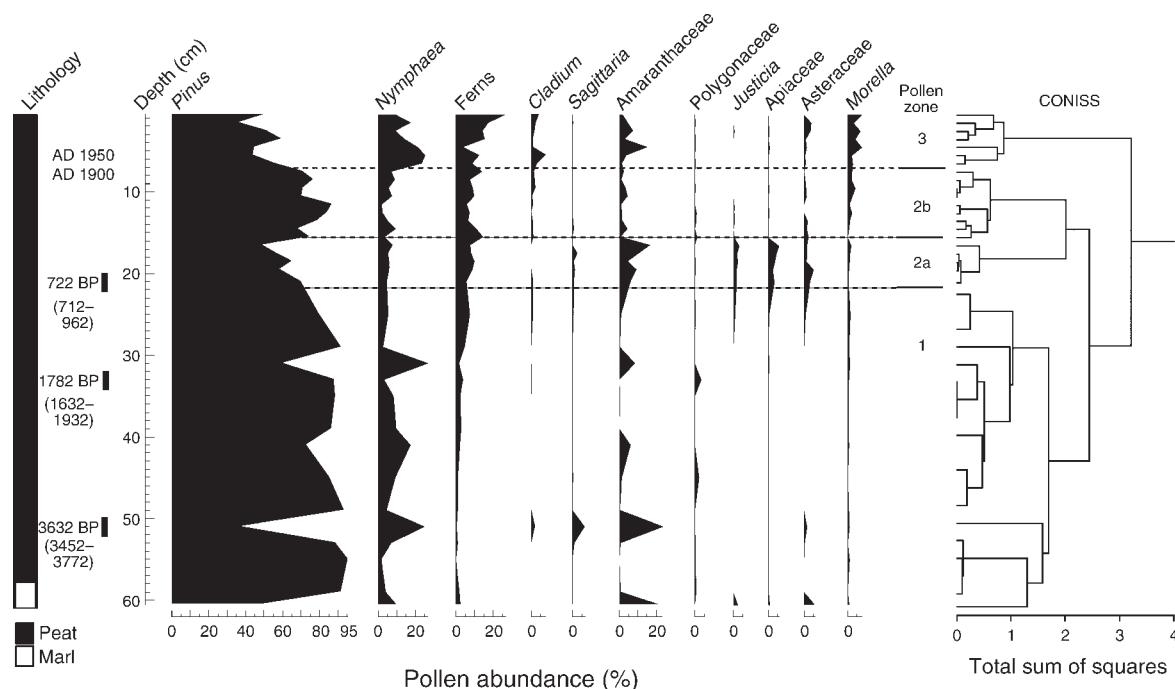


FIG. 7. Slough pollen assemblages from core 02-05-21-5. Pollen assemblages are shown from species with >2% abundance. Radiocarbon dates are given as the intercept point and 2 sigma range as calibrated years before 2002 (cal yr BP; see Table 1). Dates within the 20th century were determined from ²¹⁰Pb analyses. Modern analogues for pollen zones are: 1, slough; 2a, wet prairie/slough; 2b, wet prairie/slough; and 3, slough.

Pollen assemblages from the first half of zone 2 (pollen zone 2a: 1000–550 cal yr BP) are characterized by increased abundance of fern spores and decreased abundance of *Nymphaea* pollen (generally decreased by half). Modern analogues for ridges, sloughs, and transition zones indicate shorter hydroperiods than those of zone 1. In the ridge, *Justicia* pollen increased slightly. *Crinum*, Asteraceae, *Justicia*, Polygonaceae,

and Apiaceae pollen all increased in the transition (Fig. 6).

Pollen assemblages from the latter half of zone 2 (pollen zone 2b: 400–100 cal yr BP) indicated fundamental changes in vegetation across the ridge and slough transects. In the ridge, *Cladium*, *Cephalanthus*, and Polygonaceae pollen increased in abundance by 5% to 10% (Fig. 5). In the transition zone, *Nymphaea* pollen

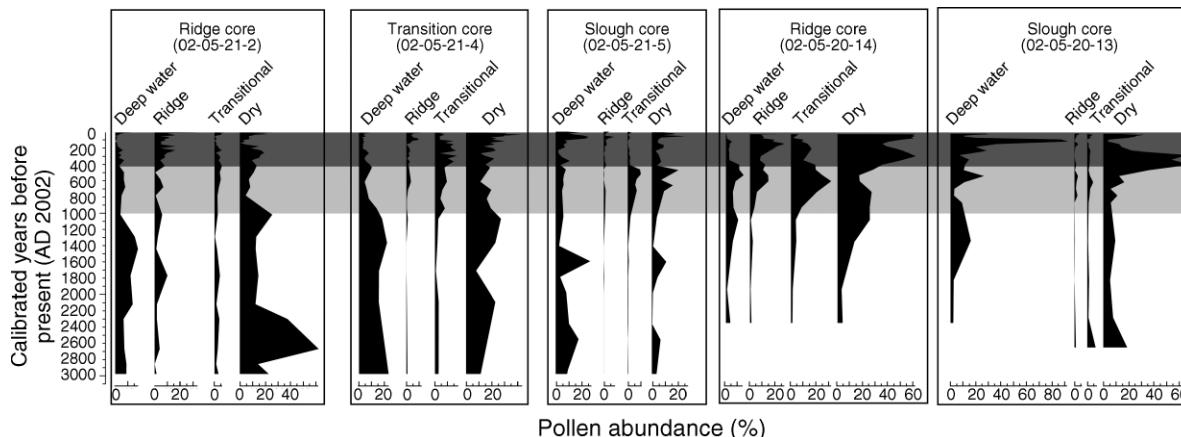


FIG. 8. Climate and vegetation response. Abundance of pollen of four functional groups (see Table 2) is plotted vs. age for cores in the sawgrass ridge (02-05-21-2), transition zone (02-05-21-4), and slough (02-05-21-5). Periods of regional drying, the Medieval Warm Period (~1000 cal yr BP), and the Little Ice Age (~300 cal yr BP) are marked by light and dark gray bands, respectively. The second ridge (02-05-20-14) and slough (02-05-20-13) cores represent a more northerly transect and are added to the figure to illustrate the regional nature of the changes observed.

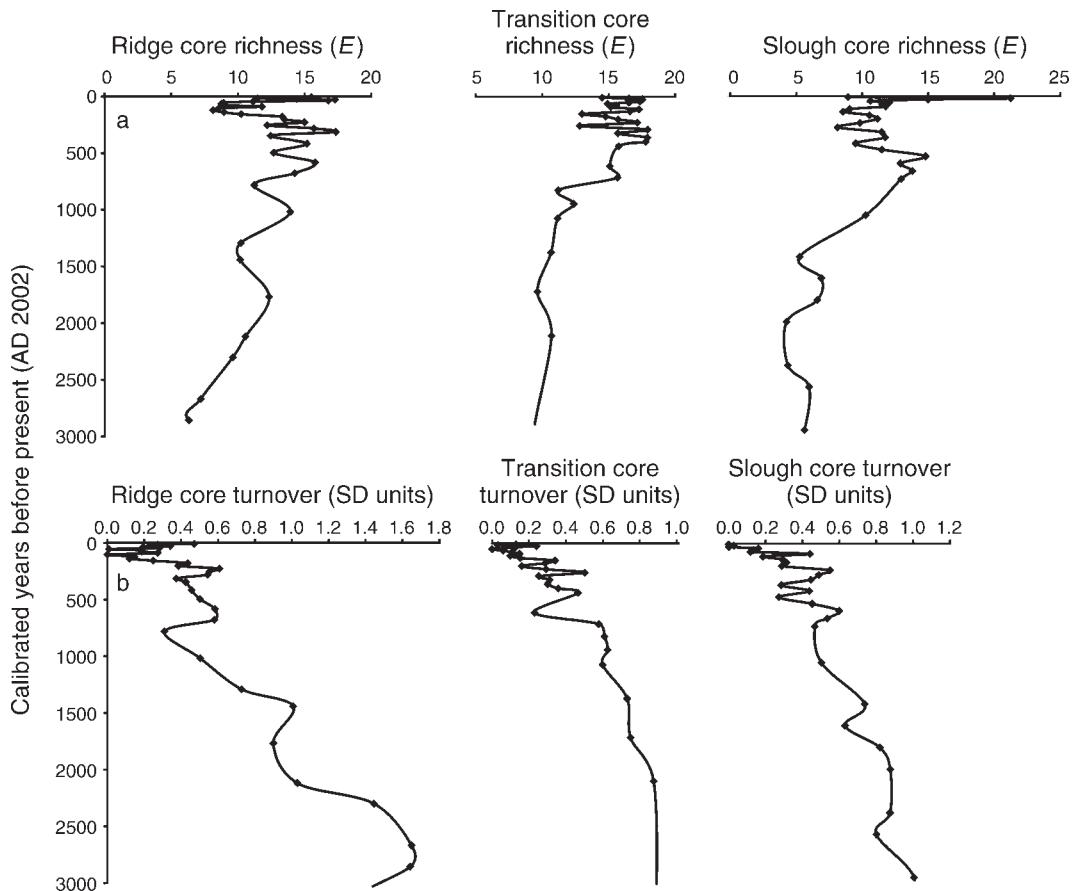


FIG. 9. Ecological statistics. (a) Palynological richness (E) vs. calibrated years before 2002. Calculations of E are based on a standardized sample size of 110 palynomorphs. (b) Amount of vegetation turnover (SD), calculated using detrended canonical correspondence analysis (DCCA), vs. calibrated years before 2002. Ridge core = 02-05-21-2; transition core = 02-05-21-4; slough core = 02-05-21-5.

abundance decreased, and abundance of fern spores and pollen of Asteraceae, *Justicia*, Polygonaceae, and Apiaceae continued to increase (Fig. 6). Slough assemblages are characterized by a decreased abundance of Amaranthaceae, *Justicia*, Apiaceae, and *Sagittaria* and a slightly increased abundance of *Cladium* and *Morella* pollen.

Pollen assemblages in zone 3 generally were deposited during the 20th century. In the ridge site, initially high abundance of fern spores shifted to greater abundance of *Cladium*, *Nymphaea*, *Morella*, *Justicia*, and Asteraceae in the upper 5 cm. In the transition, zone 3 was characterized by increased abundance of *Cladium* and *Morella* pollen and fern spores and significantly lower abundance of Apiaceae pollen; *Crinum* pollen occurred in the uppermost samples (~ 1 –2%). In the slough site, zone 3 was represented by much greater abundance of *Nymphaea* pollen, with lesser increases in *Cladium*, *Morella*, Amaranthaceae, and Asteraceae pollen.

Patterns in abundance of functional groups indicated rapid shifts in dominant communities at approximately 1000 cal yr BP and 400 cal yr BP. Documented in all cores was a concomitant decrease in deepwater taxa,

with a gradual increase in ridge and transitional wetland taxa after approximately 1000 cal yr BP (Fig. 8). This decreased abundance of deepwater taxa was less pronounced in the slough core than in the ridge and transition, but it was accompanied by an increase in abundance of transitional wetland taxa (i.e., *Justicia*, Apiaceae, and *Sagittaria*). We noted a second change at 400 cal yr BP, when abundance of ridge taxa increased. Droughts, resulting in sustained intervals of shorter hydroperiod, were indicated by greater than average abundance of dry taxa.

Palynological richness in all three cores increased ~ 1000 cal yr BP (Fig. 9), with the smallest increase occurring in the ridge core. The greatest variability in the number of species occurred during the last 500 yr BP. Within the slough core, species diversity doubled after 1000 cal yr BP but decreased after 500 cal yr BP. In general, the transition core had the highest number of expected species (17) during the last 1000 years BP. Vegetation turnover was highest before 1000 cal yr BP (Fig. 9). After this point, vegetation in all cores tended toward lower turnover, or vegetation similar to modern. The vegetation from near the base of the ridge core had

TABLE 3. Sedimentation rates recorded in cm/yr for cores 02-5-21-2, 02-5-21-4, and 02-5-21-5.

Location (core ID)	Pre-MWP (>1500 cal yr BP)	MWP-LIA (1000–1500 cal yr BP)	LIA (400–100 cal yr BP)
Ridge (02-5-21-2)	0.018	0.025	0.06
Transition (02-5-21-4)	0.011	0.14	0.04
Slough (02-5-21-5)	0.011	0.013	0.01

Notes: Key to abbreviations: MWP, Medieval Warm Period; LIA, Little Ice Age; cal yr BP, calibrated years before sample collection (AD 2002).

the highest SD (1.7) and therefore, was considered to have the largest change in vegetational composition.

Peat accumulation rates varied among cores and through time (Table 3). In general, sediment accumulation rates were greatest on sawgrass ridges throughout the history of their formation. The greatest peat accumulation rates occurred from ~400–100 cal yr BP on the ridge (~0.06 cm/yr) and transition zone (~0.04 cm/yr). The most rapid peat accumulation in sloughs occurred between 1000 and 1500 cal yr BP (~0.013 cm/yr). Overall, there was no difference in slough accumulation rates compared to the two- to threefold increase in the ridge and transition between 400 and 100 cal yr BP.

DISCUSSION

Development of the ridge and slough landscape

Plant communities occupying modern ridge and slough sites have been distinct throughout the history of peat accumulation at these core locations. Vegetational reconstructions from modern analogues indicate that slough communities have occupied their present location throughout the history of peat accumulation, even during dry intervals (i.e., ~1000 cal yr BP) when the abundance of species characteristic of transitional wetland increased. In contrast, sites of modern sawgrass ridges were occupied by sawgrass marsh and/or wet prairie vegetation prior to ~1000 cal yr BP.

Vegetation changes associated with development into the modern sawgrass ridges and ridge–slough transition zones began during the Medieval Warm Period, ~1000 cal yr BP, when the abundance of deepwater species decreased and transitional wetland and dry species increased (Figs. 5, 6, and 8). During this interval, we also observed changes in vegetation composition turnover as well as a general increase in species diversity (Fig. 9). Modern ridge vegetation developed during the Little Ice Age, ~300–400 cal yr BP. It appears that the progressive changes leading to modern sawgrass ridge development resulted from hydrologic changes tied to regional climate variability of the late Holocene. The control that precipitation and hydroperiod exert on wetland plant communities is well documented (Loveless 1959, McPherson 1973, Kushlan 1990, David 1996, Jordan et al. 1997, Willard et al. 2001a, 2006). In addition, the timing and intensity of disturbance events, such as heavy precipitation, drought, and fire, affect

community composition and stability (Crawley 2004). We propose that changes in hydroperiod driven by regional and global climate patterns played a significant role in development of the Everglades ridge and slough landscape.

Major changes in pollen assemblages and shifts in abundance of plant functional groups appear to be centered on 1000 cal yr BP and 400 cal yr BP, intervals commonly referred to as the Medieval Warm Period (Hughes and Diaz 1994) and the Little Ice Age (Bradley and Jones 1993). Our data and previous work (Willard et al. 2001a, 2006) indicate that hydroperiods shortened throughout the greater Everglades between ~900 and 1100 cal yr BP (Fig. 8), which resulted in a persistent shift toward drier vegetation assemblages in sawgrass ridge sites (Fig. 8), tree islands, and other wetlands in the Everglades (Willard et al. 2001a, 2006). A second, drier interval ~400 cal yr BP (Little Ice Age) appears to have initiated the shift to modern sawgrass ridge communities and the expansion of transition zones into sloughs, also indicated by greater abundance of *Justicia* and *Crinum*. Development of modern ridge communities corresponds to intervals of greatest sediment accumulation rates in sawgrass ridges and transition zones, probably due to accumulation of greater biomass from the denser, taller stands of *Cladium* in the ridges (Table 3).

The dry intervals that influenced plant communities on Everglades sawgrass ridges correspond to arid periods documented in proxy records from other sites in the circum-Caribbean region (Hodell et al. 1995, 2001, 2005, Haug et al. 2001, Peterson et al. 2006). These periods of aridity have been attributed to changes in the position of the Intertropical Convergence Zone (ITCZ; Hodell et al. 1995, 2001, 2005). Intervals of ridge expansion correlate to times of southward displacement of the ITCZ, as reconstructed from titanium records from cores collected in the Cariaco Basin. The ITCZ represents a zone of convergence of northern and southern trade winds, forming a band of high precipitation. Mean southward shifts result in decreased precipitation in the circum-Caribbean. Three major precipitation minima are documented during the Little Ice Age, and highly variable precipitation occurred during the Medieval Warm Period when there was a mean southward annual migration of the ITCZ (Haug et al. 2001, Peterson and Haug 2006). This interpretation is supported by the occurrence of asynchronous events in the southern hemisphere, such as greater precipitation in

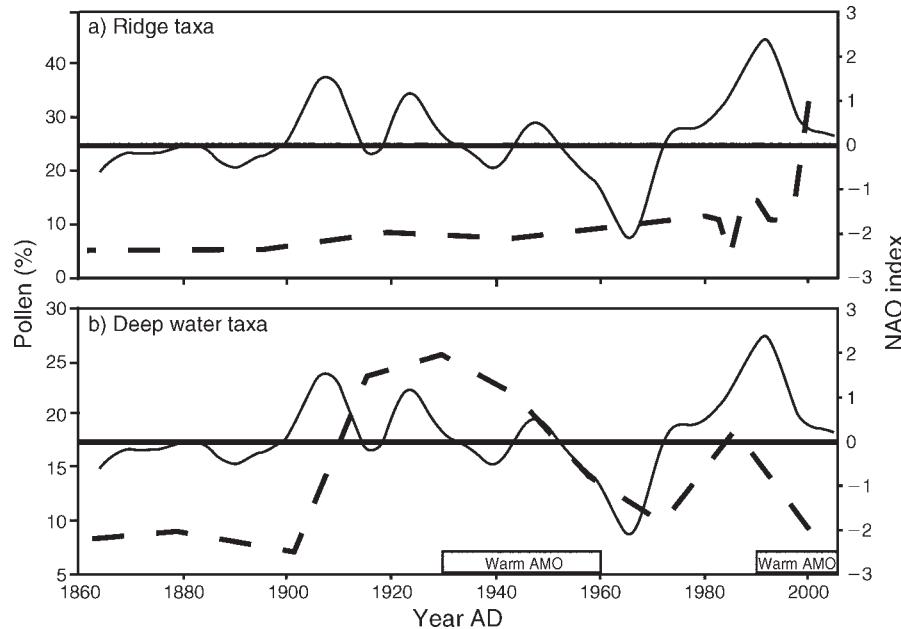


FIG. 10. Ridge and slough taxa vs. North Atlantic Oscillation (NAO). (a) Ridge development (dashed line) and (b) open-water slough vegetation response (dashed line) are plotted against the NAO record on the right-hand axis (Hurrell 1995). Periods of warm Atlantic Multidecadal Oscillation (AMO; McCabe et al. 2004) are denoted by rectangles along the x-axis. Pollen abundances are calculated from the functional groups for the ridge and slough, respectively. See Appendix A for error in the age model.

Lake Titicaca during the Little Ice Age (Baker et al. 2001). Increased precipitation variability during the Little Ice Age and Medieval Warm Period is also recorded in tree ring records of the southern United States (Stahle and Cleaveland 1994) and has been associated with periods of tree island formation (Willard et al. 2006).

While regional-scale dry conditions influence ridge development, slough vegetation appears to fluctuate in phase with the North Atlantic Oscillation (NAO) for at least the last 100 years. The NAO is the dominant pattern of atmospheric circulation variability in the North Atlantic region and is calculated as the surface pressure difference between the Subtropical High and the Subpolar Low (Hurrell et al. 2006). The positive phase of the NAO is thought to be indicative of greater winter precipitation in southern Florida (Swart et al. 1996). Pollen evidence from Everglades sloughs indicates increased abundance of deepwater vegetation during the positive phase of the NAO, independent of water management practices. In contrast, ridge vegetation shows no correspondence to changes in the NAO (Fig. 10). Additionally, a warm phase of the Atlantic Multidecadal Oscillation (AMO) occurred from 1930–1960 during a positive NAO phase. Warm phases of the AMO correspond to wetter conditions in south Florida (McCabe et al. 2004); during this time period, the annual inflow to Lake Okeechobee was more than double, and precipitation was also significantly higher (Enfield et al. 2001). Collectively, these data indicate that climate and precipitation are the primary influences

on slough vegetation, regardless of the presence of canals, levees, and the water conservation areas (WCAs) and associated impacts on water flows and hydroperiod.

Conceptual model of the ridge and slough landscape response to natural hydrologic variability

The proposition that climate controlled formation of the ridge and slough landscape is consistent with findings from other paleoecological studies, including tree islands located within the ridge and slough landscape (Willard et al. 2006). The interpretation of these data within the perspective of regional climate variability also provides support for conceptual models proposed for ridge formation. In general, the gradual directional succession of a sawgrass marsh toward a linear flow-oriented sawgrass ridge can be explained by a series of positive feedbacks. Our data indicate origination of sawgrass ridges from sparse sawgrass marshes, with shallower water and slightly higher substrate elevations than adjacent sloughs. These marshes can be interpreted as “bumps” in the landscape (after Givnish et al. 2008), in which gradual increases in substrate elevation result from the feedback of litter decomposition and production. Elevation increases also may result from reduced flow velocity by sawgrass, which causes sediment deposition on the lee side of sawgrass patches (Larsen et al. 2007). Climate-related reductions in flow or hydroperiod may amplify these feedbacks, primarily by providing more favorable conditions for sawgrass establishment (Lorenzen et al. 2000). Our sediment cores support this hypothesis by documenting an increase

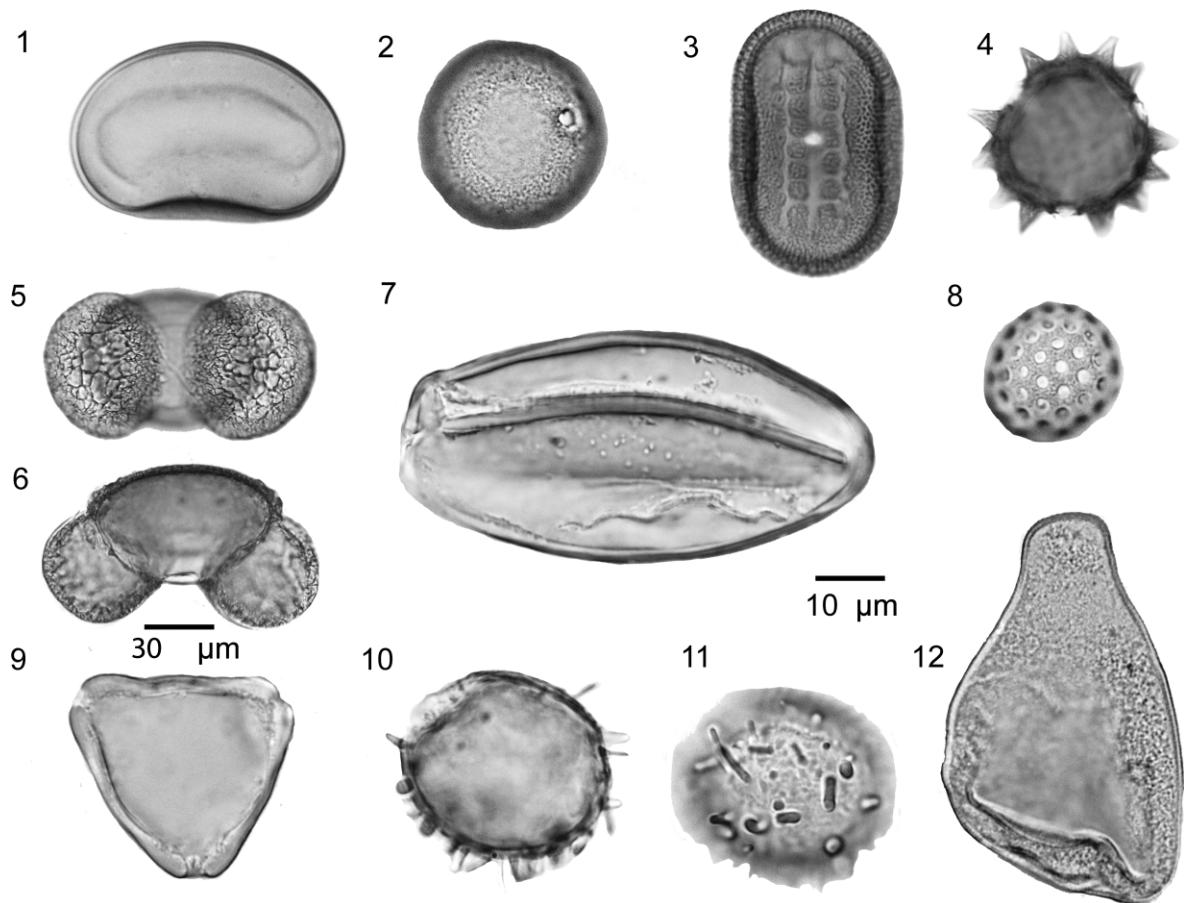


PLATE 1. Major pollen types observed in ridge and slough sediments. Photographs are at 1000 \times magnification with the exception of *Pinus*, which is at 400 \times . (1) Monolete fern spore; (2) *Andropogon* sp. (Poaceae); (3) *Justicia americana* (Acanthaceae); (4) *Pluchea* sp. (Asteraceae); (5–6) *Pinus* sp. (Pinaceae); (7) *Crinum americanum* (Liliaceae); (8) *Amaranthus australis* (Amaranthaceae); (9) *Morella cerifera* (Myricaceae); (10–11) *Nymphaea odorata* (Nymphaeaceae); (12) *Cladium mariscus* ssp. *jamaicense* (Cyperaceae). Photo credits: C. E. Bernhardt.

both in abundance of ridge species and in sedimentation rates during periods of regional drying. The sawgrass ridges were self-assembling through positive feedback factors, including climate variability. The role of nutrient content in the feedback loop was not addressed in this study and would require direct measurement of nutrient content in the sediments. Future research including such analyses would allow evaluation of the hypothesis that nutrient increases during droughts could have stimulated formation of the ridge community as well as increased peat accumulation and stimulated the formation of the modern ridge (Ross et al. 2006).

Slough vegetation remained stable throughout long-term fluctuations in climate-driven hydroperiod. During periods of dry climate, transitional wetland vegetation expanded into sloughs, receding rapidly after resumption of wetter conditions. Such fluctuation of ridge width is consistent with positive feedback. Slough communities appear to be driven by regional climate variability, whereas ridge communities, although re-

sponsive to climate fluctuations, are driven primarily by local feedback mechanisms.

Impacts of 20th-century water management practices

Pollen evidence from all sites in the transect indicate that the impoundment of water and the diversion of flow due to the construction of the WCAs and other water control structures altered the distribution of communities in the sawgrass ridge and slough landscape. Increased abundance of *Cladium* pollen on ridges and transition zones indicates progressive dominance of sawgrass on the ridges after 20th-century diversion and disruption of historic patterns of sheet flow. These changes are not mirrored in records from the sloughs, which appear to respond primarily to changes in regional climate, specifically the NAO and AMO, rather than to water management practices (Fig. 10). These patterns are consistent in our study area, which are located in areas where the general structure of the ridge and slough landscape remains intact. Because ridge and

slough communities in WCA 2A and 2B lack a strong linear structure and consist of relatively monotonous expanses of sawgrass (Science Coordination Team 2003), future work should include analysis of core transects collected across these apparently degraded portions of the ridge and slough landscape.

Implications for management and restoration

These long-term records documenting the response of the ridge and slough plant communities to climate variability merit strong consideration when making policies to maintain and restore the landscape. Millar and Woolfenden (1999) pointed out that goals of restoration in other plant communities are commonly keyed to a time that was climatically different from today, such as the Little Ice Age. Not only do past climate conditions have to be accounted for, but the Intergovernmental Panel on Climate Change (IPCC) has predicted that increased global and regional temperatures and decreased precipitation will characterize the region in the future (Meehl et al. 2007). Accurate prediction of the Everglades plant community response to such an altered climate requires a clear understanding of the impacts of a range of climate scenarios. Such evidence is contained within the paleoecological record of the last few millennia. These data provide evidence for the timing and magnitude of community response to hydrologic changes and indicate that ridge and slough communities may respond independently of one another both to patterns of climate variability (NAO and AMO) and to water management. The integration of such long-term records with "snapshots" of pre-drainage landscapes and monitoring records of the last few decades provides the broad temporal and spatial perspective necessary for the development of sustainable restoration strategies.

CONCLUSIONS

This research demonstrates that the modern ridge and slough plant communities have been distinct throughout the history of peat-accumulating Everglades. Regional periods of aridity, such as the Medieval Warm Period and the Little Ice Age, facilitated the positive feedbacks shown to force sawgrass ridge development, highlighting the important role of regional climate variability in shaping of the ridge and slough landscape. Although 20th-century alteration to flow and hydroperiod has affected plant community assemblages, components of the system still are responsive to large-scale climate phenomena such as the North Atlantic Oscillation.

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APPENDIX A

Age models (*Ecological Archives* A019-070-A1).

APPENDIX B

Sawgrass ridge pollen assemblages from core 02-05-21-2 (*Ecological Archives* A019-070-A2).

APPENDIX C

Transition pollen assemblages from core 02-05-21-4 (*Ecological Archives* A019-070-A3).

APPENDIX D

Slough pollen assemblages from core 02-05-21-5 (*Ecological Archives* A019-070-A4).

APPENDIX E

Slough pollen assemblages from core 02-05-20-13 (*Ecological Archives* A019-070-A5).

APPENDIX F

Sawgrass ridge pollen assemblages from core 02-05-20-14 (*Ecological Archives* A019-070-A6).