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Palynological reconstruction of environmental changes in coastal wetlands of the Florida Everglades since the mid-Holocene

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ABSTRACT

Palynological, loss-on-ignition, and X-ray fluorescence data from a 5.25 m sediment core from a mangrove forest at the mouth of the Shark River Estuary in the southwestern Everglades National Park, Florida were used to reconstruct changes occurring in coastal wetlands since the mid-Holocene. This multi-proxy record contains the longest paleoecological history to date in the southwestern Everglades. The Shark River Estuary basin was formed ~5700 cal yr BP in response to increasing precipitation. Initial wetlands were frequently-burned short-hydroperiod prairies, which transitioned into long-hydroperiod prairies with sloughs in which peat deposits began to accumulate continuously about 5250 cal yr BP. Our data suggest that mangrove communities started to appear after ~3800 cal yr BP; declines in the abundance of charcoal suggested gradual replacement of fire-dominated wetlands by mangrove forest over the following 2650 yr. By ~ 1150 cal yr BP, a dense *Rhizophora mangle* dominated mangrove forest had formed at the mouth of the Shark River. The mangrove-dominated coastal ecosystem here was established at least 2000 yr later than has been previously estimated.

Introduction

Most coastal ecosystems around the world are influenced by changes in relative sea level (RSL). For example, tidal gauges from south Florida show that the average rate of RSL rise has increased to 3.8 mm/yr since 1930; this rate is 6 to 10 times higher than that of the past 3500 yr (0.4 mm/yr) and approaches the highest rate of RSL rise (>5 mm/yr) during the mid-Holocene Climate Optimum (Wanless et al, 1994). Studies predict that rapid RLS rise will continue during the 21st century (IPCC, 2014). Thus, an understanding of how coastal wetlands in regions like south Florida have changed in response to past RSL fluctuations may assist investigation of responses of coastal ecosystems to ongoing RSL rise (e.g., Wooller et al., 2004; Torrescano and Islebe, 2006; Monacci et al., 2009; Gonzalez et al., 2010).

Palynological studies have related changes in vegetation to hydrological and climatic changes. Some such studies have been conducted in south Florida (Donders et al., 2005; Willard and Bernhardt, 2011; van Soelen et al., 2012). These studies indicate that drier intervals have been influenced by southward shifts of the Inter-tropical Convergence Zone, and wetter intervals have been influenced by the positive phase of the North Atlantic Oscillation. Such climatic changes have been associated with shifts in hydroperiod and hence composition of wetland plant communities (Willard and Cronin, 2007; Bernhardt and Willard, 2009; Willard and Bernhardt, 2011). Similar vegetation shifts attributed to variation in climate have also been suggested by other studies in south Florida and the Caribbean region (Islebe et al., 1996; Donders et al., 2005; van Soelen et al., 2012).

Peat-accumulating ecosystems are among the coastal communities associated with rises in sea level. Previous studies have documented the initiation of peat accumulating wetlands (Scholl et al., 1969; Robbin, 1984) and formation of mangrove communities in south Florida from macrofossil records (Parkinson, 1989; Wanless et al., 1994). However, no pollen record from the Everglades is older than 5000 yr, and a detailed continuous chronology of Holocene changes in wetland vegetation in the now extensive mangrove region of South Florida remains lacking. Therefore a multi-proxy paleoecological record, focused on the mid-Holocene time of rapid RSL rise, should be useful in documenting changes and in generating hypotheses regarding processes involved in the formation of freshwater wetlands, their changes over time as RSL rise occurs, and their relationship to formation of coastal/estuarine mangrove forests.

In this study we present an estimated 5700 yr palynological record, retrieved from a mangrove-dominated estuarine wetland at the mouth of Shark River Estuary in Everglades National Park. We aim to: (1) document the origin and history of freshwater peat-accumulating wetlands, and determine when the modern brackish marsh/mangrove swamp was established at the Shark River Estuary; and (2) characterize the allogenic controls on the development of this important ecosystem.

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Study area

The largest contiguous mangrove swamp in the continental USA occurs in the Florida Everglades. Approximately 144,000 ha of dense mangrove forests extend along the modern coast from Naples to Florida Bay (Simard et al., 2006; Lodge, 2010). Our study was conducted at the western end of this region, at the mouth of the Shark River Estuary along the coast of southwestern Florida in the Everglades National Park (Monroe County). This region of the Florida peninsula is subtropical, having pronounced wet and dry seasons with 70–75% of the annual precipitation falling from June to September (Beckage et al., 2003). Water overflowing Lake Okeechobee and associated rainfall result in a southward sheet flow along a gentle slope of ~3 cm/km into Shark River Slough and to a lesser extent into Taylor Slough (Lodge, 2010; Rivera-Monroy et al., 2011; Castañeda-Moya et al., 2013). The water entering Shark River Estuary flows through long-hydroperiod prairie sloughs into a mangrove swamp at the river estuary and then into Whitewater Bay or the Gulf of Mexico along the southwestern coast of Florida. Our study site (25°21′10″N, 81°6′52″W) is located on the edge of Ponce de Leon Bay, at the mouths of Whitewater Bay and Shark River Estuary (Fig. 1). It is situated in a fringing mangrove forest, where *Laguncularia racemosa* (white mangrove) and *Rhizophora mangle* (red mangrove) are co-dominant species (Chen and Twilley, 1999a, 1999b), and *Avicennia germinans* (black mangrove) is also present. This location (Fig. 1) was strongly affected by Hurricane Wilma, resulting in 90% mortality for trees with diameters at breast height greater than 2.5 cm (Smith et al., 2009).

The hydroperiod in the study site is influenced by both tidal cycles and freshwater discharge. A multi-year (2001–2004) monitoring study at a nearby location (SRS-6) (Fig. 1), ~4 km inland from the mouth of Shark River, showed that the mangrove forests are inundated by tides 90% of the year, with an average tidal range of 0.5 m (Castañeda-Moya et al., 2013). As a result of changes in hydrology along the Shark River, soil pore-water salinity inside the mangrove forests decreases

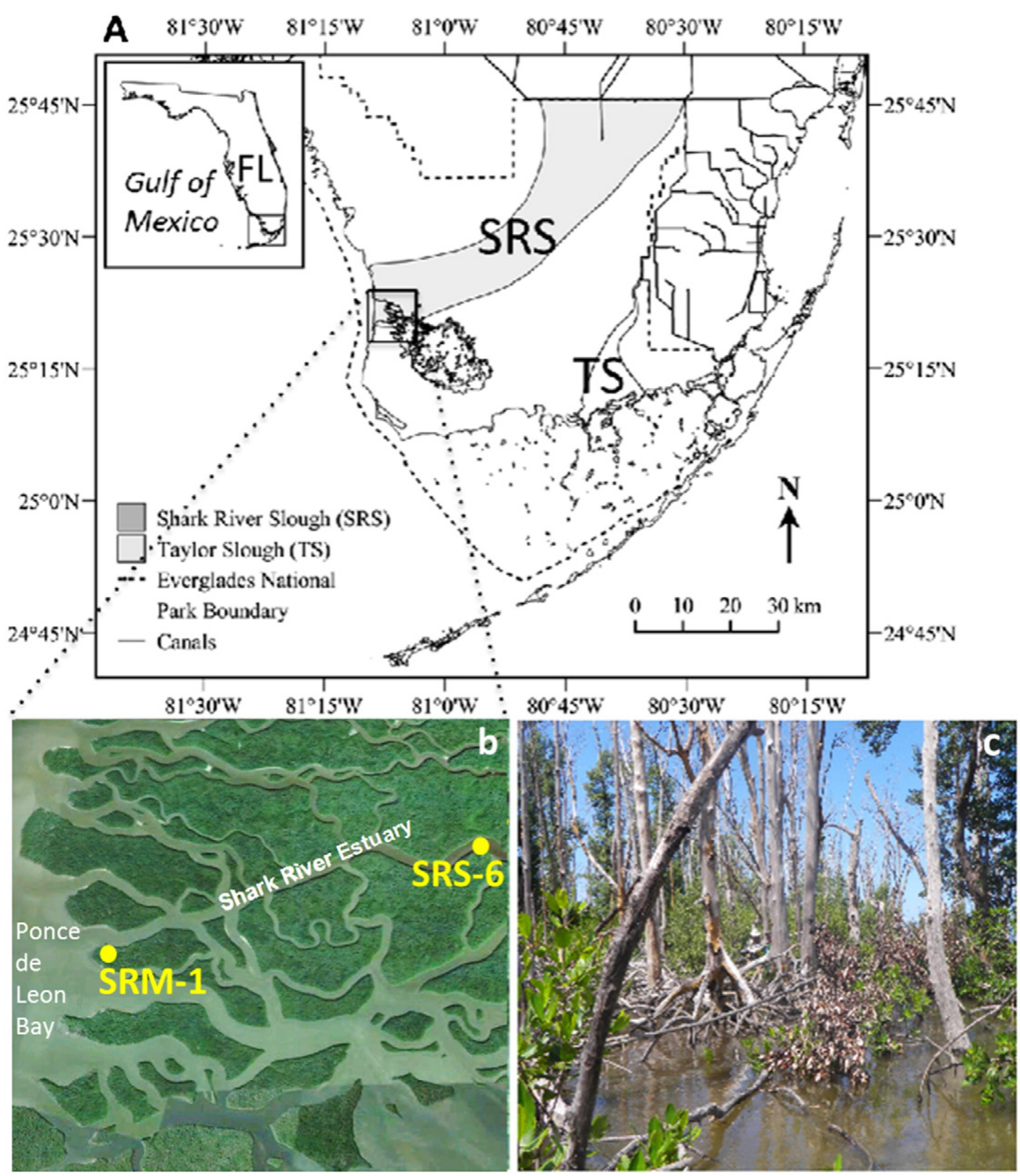

Figure 1. A) Location of the Shark River Slough (SRS) and Everglades National Park, South Florida (base map adapted from FCE LTER: http://fcelter.fiu.edu); B) Location of the Shark River Estuary, coring site (SRM) at the mouth of Shark River Estuary, and the SRS-6 site where hydroperiod and forest productivity has been monitored since 2002; C) Partial view of the SRM Mangrove forest impacted by Hurricane Wilma (crossed the study site in 2005); photo taken in 2010 when the cores were collected.

significantly from 27 ± 2.6 ppt close to the mouth (i.e. SRS-6) to 4.6 ± 1.1 ppt 20 km upstream (Castañeda-Moya et al., 2013). Since the early 20th century, land-use changes linked to anthropogenic activities (agriculture and urbanization) have dramatically reduced the seasonality of freshwater flow throughout the Everglades (Light and Dineen, 1994) and have affected surface and groundwater flows in this coastal region (Saha et al., 2012).

Regional paleoecological records

Much of the interior region north of the Everglades mangrove forests are marl prairies. A previous study indicates that short-hydroperiod or marl prairie is the oldest wetland type formed on the Everglades limestone platform and was established by ~ 12–13 ka during the last deglaciation (Kropp, 1976). These seasonal freshwater ecosystems, in which marl is deposited on a limestone terrain, often represent a transition between non-flooded ecosystems on subaerial limestone terrain and peat-accumulating wetlands (Gleason and Stone, 1994). Periphyton is a common component of marl prairies and is responsible for calcitic marl deposits underlying wide areas of wetland peat in the Everglades (Willard et al., 2001; Gaiser et al., 2011). Marl prairies currently occur along drainages in the northern Everglades to Shark River Slough, Whitewater Bay, Cape Sable, and Florida Bay, as well as the Long Pine Key region (Gleason and Stone, 1994; Lodge, 2010).

RSL has changed during the Holocene of south Florida. A sea-level record from south Florida shows that RSL rose at a rate of >5 mm/yr during 7500–6500 cal yr BP (Wanless et al., 1994). As a result of rapid RSL rise, the oldest freshwater peats on the Florida Platform started to accumulate on marl prairies in the southwest Everglades at ~ 6500 cal yr BP because of deeper water levels and longer hydroperiods (Scholl et al., 1969; Robbin, 1984). Microscopic studies of these peats have indicated that they were composed primarily of *Cladium* and *Sagittaria* (Willard and Bernhardt, 2011).

Rates of sea-level rise slowed during the mid-Holocene. Between 6500 and 3500 cal yr BP, the rate of RSL rise slowed to 2.3 mm/year (Wanless et al., 1994); still, moderate to long hydroperiod wetlands expanded on the south Florida platform during this period (Willard and Bernhardt, 2011). By 5000 cal yr BP, up to 165 cm of freshwater peat had accumulated on the Florida Platform from the Florida Keys to Lake Okeechobee (Gleason and Stone, 1994).

More recent sea level rise was slower. After 3500 cal yr BP, the rate of RSL rise slowed to 0.4 mm/year (Wanless et al., 1994). This resulted in more stabilized coastlines and establishment of mangrove forests along the southwest Florida coast (Robbin, 1984; Wanless et al., 1994). The oldest mangrove peats retrieved from southwest Florida are from the Ten Thousand Islands area and Whitewater Bay and were deposited between 3000 and 3500 cal yr BP (Scholl et al., 1969; Parkinson, 1989). By ~2200 cal yr BP, mangrove peats were found up to 20 km inland from the coastlines in southwest Florida (Willard and Bernhardt, 2011). Nonetheless, no pollen record has documented the earliest developmental phase of mangrove forest in these estuarine environments.

Since AD 1930, the rate of RSL rise has increased dramatically. Recent rates of sea level rise have increased to 3.8 mm/yr, a rate that is 6 to 10 times that of the past 3500 yr (Wanless et al, 1994). Inland replacement of freshwater marshes by mangrove wetlands has been observed in the ENP as a result of salt water intrusion and salinity changes in groundwater (Ross et al., 2000).

Materials and methods

A 5.25 m core (SRM-1) was retrieved at the study site in May 2010 using a Russian peat borer. The 50 cm core segments were measured, photographed, and wrapped in the field, and stored in a cold room (4°C) at the Global Change and Coastal Paleoecology Laboratory at Louisiana State University. The core was scanned using an X-ray fluorescence (XRF) analyzer at 2 cm intervals to measure elemental concentrations (ppm) of 32 chemical elements. XRF analysis is widely used in coastal studies and the behaviors of most key elements are well established through previous studies (Ramírez-Herrera et al., 2012; van Soelen et al., 2012). Loss-on-ignition (LOI) analyses were performed at contiguous 1 cm intervals to establish the ratio of organic versus inorganic sediment through the core (Dean, 1974).

Fourteen samples from core SRM-1 were used for AMS ^{14}C measurements. Ten samples consisting of leaf fragments and pieces of wood were selected under a dissecting microscope and sent to the NOSAMS Laboratory at Woods Hole Oceanographic Institution (Table 1, Fig. 2). In addition, approximately 10 g of sediments taken at 374 and 446 cm were submitted to Beta Analytic Inc., in Miami, Florida, for AMS ^{14}C measurements. At the dating facility these sediments were passed through a 180 μm sieve to separate the <180 μm fine organic fraction from the >180 μm coarse organic fraction. Both fractions were dated separately to compare dating results using different materials (Table 1). An age–depth model was developed by using BACON version 2.2 (Blaauw and Christen, 2013), a Bayesian age–depth modeling software using R as an interface. Priors were established using default settings or as suggested by BACON (acc.shape = 1.5, res = 5, mem.strength = 4, mem.mean = 0.7, and acc.mean = 10).

Sixty-five samples of 0.9 to 1.8 ml were taken at 5 to 10 cm intervals for palynological analysis. Samples were processed using standard procedures (Kiage and Liu, 2009; Liu et al., 2011). One commercial *Lycopodium* (L_c) tablet (~18,583 grains) was added to each sample as an exotic marker to calculate pollen concentration (grains/cm^3). Hydrofluoric acid treatment and acetolysis were omitted to minimize the degradation of microfossils during processing. The identification of pollen was based on McAndrews et al. (1973), Willard et al. (2004), and Chmura et al. (2006). Approximately 300 pollen grains and spores, including both terrestrial and aquatic taxa, were counted in most samples, and this pollen sum was used for the calculation of pollen percentages. Additional microfossils, including foraminifera linings, dinoflagellates tests, fungal spores, and charcoal fragments (>10 μm in size), were also counted. The pollen (and other) data will be archived with the Neotoma Paleoecology Database (http://www.neotomadb.org/).

Results

Stratigraphy and chronology

The stratigraphy and ^{14}C dating results of core SRM-1 are displayed in Figure 2. Core SRM-1 consisted of 4 sediment types. Homogeneous clay with very low contents of water, organics and carbonate occurred from 525 to 485 cm, and marl sediments were present from 485 to

Table 1
Radiocarbon dating results for core SRM-1. Dates in parentheses are rejected due to extreme age reversal.

Sample ID	Depth (cm)	Material	Conventional C^{14} age (^{14}C yr BP)	2-σ Calibrated range (cal yr BP)
OS-960a2	56	Leaf	145 ± 25	0–280
OS-83953	139	Leaf	1180 ± 30	990–1180
OS-90704	179	Leaf	1940 ± 30	1820–1970
OS-95704	243	leaf	2860 ± 30	2880–3070
OS-83943	246	Wood	155 ± 25	(Rejected)
OS-90685	246	Wood	>Modern	(Rejected)
OS-93264	260	Leaf	2240 ± 30	2150–2340
OS-96061	300	Bark	3540 ± 35	3700–3910
Beta-345774	374	Organic silt	4160 ± 30	4780–4830
Beta-346208	374	Roots	2940 ± 30	3000–3210
OS-96060	440	Leaf	1090 ± 20	(Rejected)
Beta-345775	446	Organic silt	5800 ± 30	6500–6670
Beta-346209	446	Roots	4060 ± 30	4760–4800
OS-84455	448	Plant debris	6620 ± 260	6940–7980

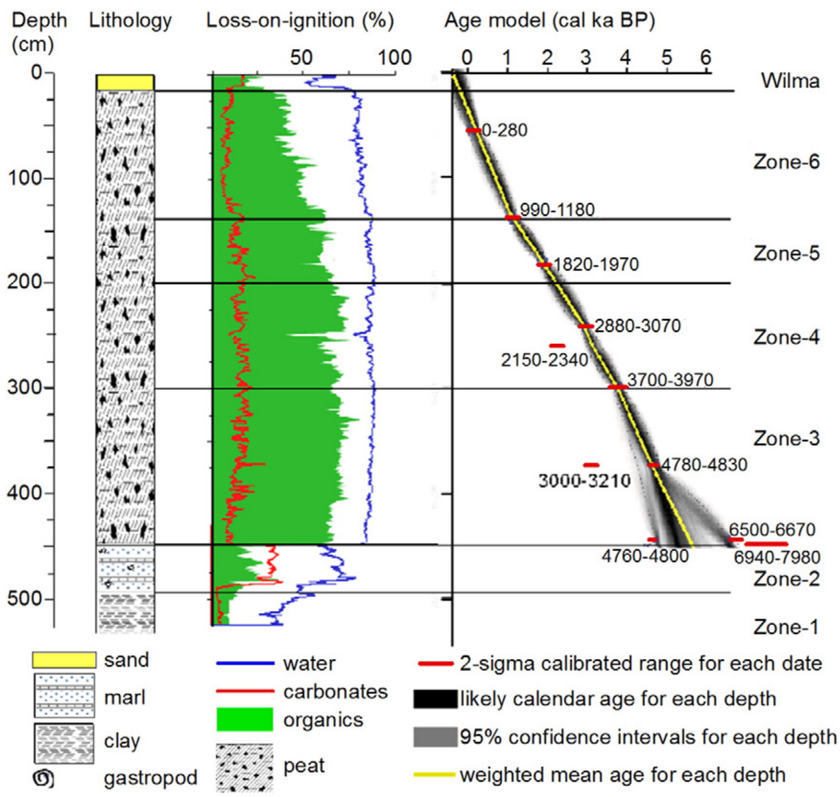

Figure 2. Lithology, loss-on-ignition diagram, and the age–depth model for the core. Loss-on-ignition diagram presents the % wet weight for water, and % dry weight for organics and carbonates. The age–depth model is developed by BACON and based on 11 calibrated C^{14} ages. The yellow curve shows the 'best' estimated age for each depth based on the weighted mean age. The surface (0 cm) of the core is assigned as −55 cal yr BP because it is identified as the Hurricane Wilma deposit. Further information about radiocarbon dates is shown in Table 1 and Supplementary information.

445 cm. This latter section contained shell hashes of the freshwater snail *Helisoma trivolvis* sp., and was low in water and organics and high in carbonates. Above the marl sediments were more than 4 m of continuous peat (445–10 cm) with very high contents of water and organic matter and relatively low concentration of carbonate. The top 10 cm of the core consisted of calcareous clastic sediments deposited by storm surges generated by Hurricane Wilma (Whelan et al., 2009; Castañeda-Moya et al., 2010; Barr et al., 2012).

Among the ten AMS ^{14}C dates obtained from NOSAMS, three anomalously young dates (OS-83943, OS-90685, and OS-96060) were rejected due to extreme stratigraphic reversal (Table. 1). The ^{14}C date from 448 cm (6940–7980 cal yr BP) may also be erroneous (i.e., too old) because it came from the base of the peat where it directly overlaid the marl, which increased the possibility of it being affected by carbonate error. For the two pairs of dates at 374 cm and 446 cm determined by Beta Analytic, the coarse organic fractions yielded much younger dates than the fine organic fractions by ~1200 to ~1800 yr (Table 1). We suspected that the coarse organic fraction might be contaminated, as visual inspection of sieve residues revealed intrusive (younger) rootlets (See Supplementary Information). All dates except for the three rejected ones (out of 14) were used to construct the age–depth model using BACON software (Fig. 2). The results indicate that the age–depth model (yellow curve, Fig. 2) based on the weighted mean age of each sample is very close to intercepting ^{14}C dates at 56 (178 cal yr BP), 139 (1138 cal yr BP), 179 (1872 cal yr BP), 243 (2947 cal yr BP), 300 (3777 cal yr BP), and 374 (4658 cal yr BP) cm, and the bottom date has great uncertainties ranging from 4760 to 7980 cal yr BP (95% confidence intervals) (Fig. 2). We used the "best" age–depth model based on the weighted mean age for each sample to construct the chronologies for all the proxy records discussed in this paper.

Pollen and XRF analyses

We divided core SRM-1 into six stratigraphic zones based on pollen composition, sediment stratigraphy, and chemical characteristics. Zone 3 was further subdivided into three subzones. The calcareous clastic sediments at the top of the core (Fig. 2) were included in Zone 6. The XRF, pollen percentage (%) and pollen influx (grains/cm^2/yr) results are given in Figures 3–5. Key features of each zone are described below.

Zone 1 (525–485 cm; >5700 cal yr BP)

XRF data show that the elemental concentrations of Zr, S, K, Ti, Fe, and most other heavy metals in Zone 1 are at least 5 to 10 times higher than values in the rest of the core (Fig. 5). Pollen is totally absent in samples from this zone (Figs. 3 and 4).

Zone 2 (485–450 cm; >5700 cal yr BP)

Palynological results show high influx values (1000–3000 grains/cm^2/yr) and abundant charcoal particles (20,000–60,000 fragments per cm^3) in Zone 2 (Fig. 4). The dominant taxon, *Salix*, accounts for > 50% of the pollen sum in some samples (Fig. 3). Subdominant taxa include Poaceae (20%), *Pinus* and *Quercus* (10–20%). Other major taxa (defined as those occurring at >5% in at least one level) include Amaranthaceae, *Sagittaria,* and *Typha*. XRF results reveal high concentrations of Ca (30,000–100,000 ppm) and Sr (150–400 ppm) (Fig. 5).

Zone 3 (450–300 cm; 5700–3800 cal yr BP)

Subzone 3a (~5700–5250 cal yr BP) are dominated by woody taxa (*Salix*, *Pinus*, *Morella*, and Rubiaceae), and some herbaceous taxa (*Typha*, Solanaceae, and Asteraceae) also commonly occur. A change in the pollen assemblage is notable in subzone 3b (~5250–4300 cal yr BP). The pollen assemblage records the concurrent decline of woody taxa, and Amaranthaceae increased markedly

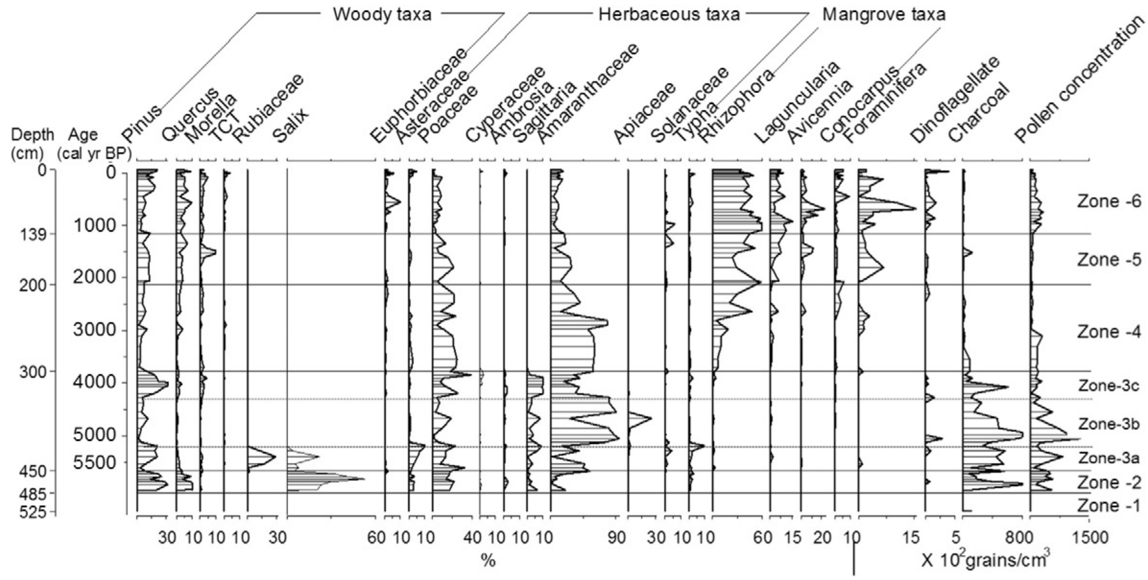

Figure 3. Pollen percentage diagram for core SRM-1. The concentration curves for marine planktons, charcoal, and pollen are added on the right to facilitate comparison. Dates on Y-axis are calibrated yr BP. TCT is the acronym for Taxodiaceae–Cupressaceae–Taxaceae.

(often >50%, and up to 90%). In subzone 3c (~4300–3800 cal yr BP), Cyperaceae increased in abundance, while Amaranthaceae decreased precipitously in both percentage and influx values. Freshwater *Sagittaria* also increased, reaching its highest percentage (10%) in subzone 3c. Mangrove pollen first appeared in subzone 3a, but percentages were low throughout zone 3 (<5%). The XRF values were generally very low throughout Zones 3, 4 and 5 (Fig. 5).

Zone 4 (300–200 cm; 3800–2200 cal yr BP)

The overall pollen influx (<2000 grains/cm^2/yr) was low in Zone 4 (Fig. 4). At the beginning of the zone, the dominant pollen types were Amaranthaceae (>50%) and Poaceae (30%), but other herbaceous taxa (i.e., Apiaceae, Solanaceae, Asteraceae, *Typha*) were rare (<5%) or absent (*Ambrosia*, Cyperaceae, and *Sagittaria*). *Pinus* and *Quercus* were uncommon (<10%) throughout the zone. The abundance of mangrove pollen (especially *Rhizophora*) was low at the beginning of the zone, but increased towards the top of the layer (Fig. 3). Foraminifera linings made their first appearance in the upper part of the zone. Charcoal concentrations decreased from <10,000 fragments per cm^3 at the bottom of Zone 4 to insignificant levels at the top of the zone.

Zone 5 (200–139 cm; 2200–1150 cal yr BP)

Pollen influx values were very low (<1000 grains/cm^2/yr) in Zone 5 (Fig. 4). Mangrove pollen increased and eventually reached 50% of the pollen sum in the middle of the zone (Fig. 3). Dinoflagellates and foraminifera linings appeared at higher concentrations more consistently. Concentrations of charcoal fragments were generally insignificant in Zone 5.

Zone 6 (139–0 cm; 1150 cal yr BP–present)

Zone 6 is characterized by the total dominance of *Rhizophora* (>50%) and the highest influx values (2000–4000 grains/cm^2/yr) among all six zones. Other mangrove genera (*Laguncularia, Avicennia*, and *Conocarpus*) and dinoflagellate and foraminifera linings were also

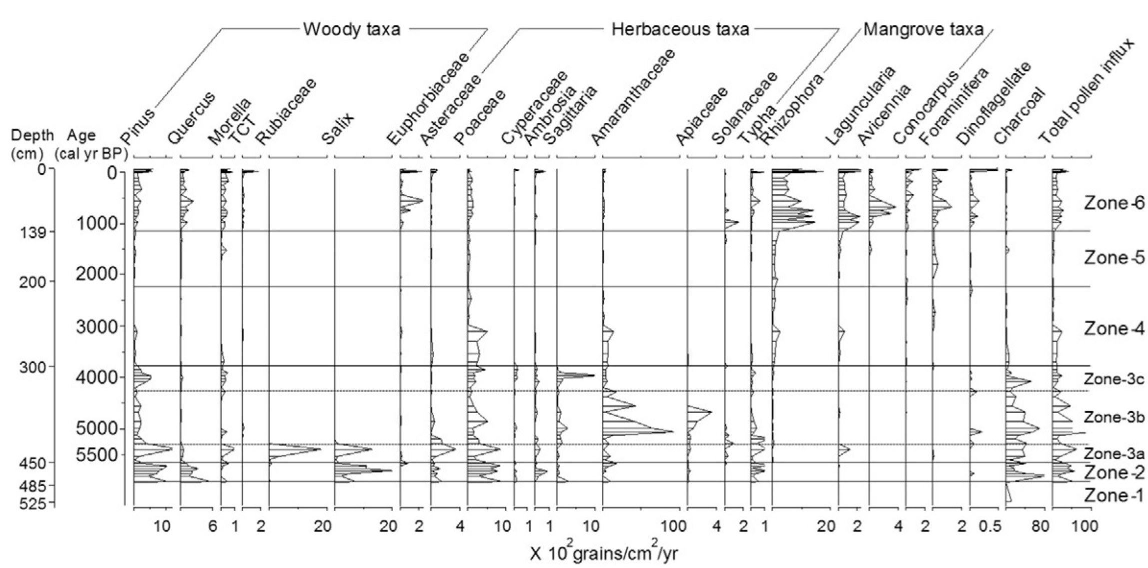

Figure 4. Pollen influx diagram for core SRM-1. The influx curves for marine plankton and charcoal are added on the right to facilitate comparison. Dates on Y-axis are calibrated yr BP. TCT is the acronym for Taxodiaceae–Cupressaceae–Taxaceae.

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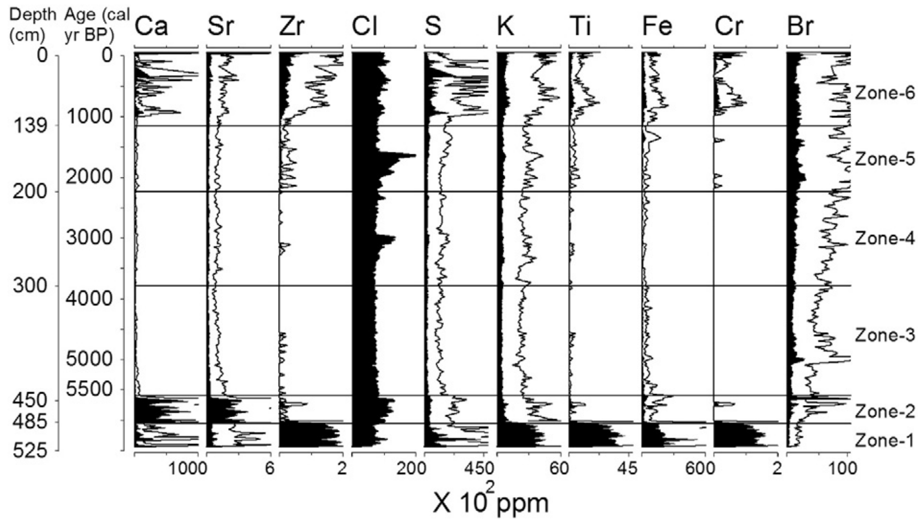

Figure 5. XRF results from core SRM-1. Dates on the Y-axis are calibrated yr BP. The black silhouettes represent the actual concentration of the elements, and the transparent curves represent 5X exaggerated values.

present in high concentrations. Charcoal fragments were absent in most samples in this zone. XRF results show a significant increase in the concentrations of Ca, Sr, Zr, S, Fe, and Ti (Fig. 5).

Discussion

Environmental reconstruction

The early mid-Holocene dry upland landscape (>5700 cal yr BP)

The basal sections of the core (Zones 1 and 2) were deposited prior to ~5700 cal yr BP. At that time, the climate in south Florida was drier than today (Donders et al., 2005; Lodge, 2010; van Soelen et al., 2010). Zone 1 (486–525 cm) is composed of fine silicates (clastic clay) devoid of pollen. The very high concentrations of metals such as Ti, Fe, and Cr in these sediments of Zone 1 are most likely the result of acidic leaching; such sediments are commonly found in Florida (Hine and Belknap, 1986) and the Caribbean region underlying more recent mangrove peat (Macintyre et al., 2004; Wooller et al., 2007). Overall, the proxy record for Zone 1 indicates a terrestrial environment that was not inundated long enough to promote marl or peat accumulation and to preserve pollen. The absence of pollen precludes knowledge of the vegetation types present.

Short-hydroperiod prairie (>5700 cal yr BP)

Zone 2 (451–485 cm) consists of calcareous marl sediments that resemble those in marl prairies currently present in the Everglades. The formation of freshwater calcitic marl over subaerial substrate marks a transition from a dry and drained environment to a shallow seasonally flooded freshwater wetland environment (Gleason and Stone, 1994). Indeed, shell hashes of the freshwater snail *Helisoma trivolvis* found in Zone 2 are consistent with such environment. The record suggests a higher subsurface water table and increasing hydroperiod, but not yet wet enough to sustain peat accumulation.

The pollen assemblage of Zone 2 is dominated by a mixture of upland and wetland species. The composition of this pollen assemblage is consistent with a mixture of short-hydroperiod and longer-hydroperiod prairies, perhaps also with higher nonflooded areas (i.e., pine savannas) in the immediate vicinity. Such areas (e.g., Lostman's Pines and Raccoon Point regions of Big Cypress National Preserve; Long Pine Key in Everglades National Park) are present in the interior of the Everglades region of South Florida today (Doren et al., 1993; Willard et al., 2001; Schmitz et al., 2002; Bernhardt and Willard, 2009; Hanan et al., 2010). The freshwater marl-accumulating wetlands postulated as present in Zone 2 appear to have been subject to frequent fires. These habitats today have hydroperiods lasting less than 12 months and are thus dry seasonally, tending to burn more than once a decade, and even every 1–2 yr if located adjacent to pine savannas (Platt, 1999; Schmitz et al., 2002; Slocum et al., 2003; Platt et al., 2015). Such high fire frequency would be consistent with the abundance of charcoal particles in pollen samples. The occurrence of *Pinus*, *Quercus*, Poaceae, and Asteraceae in the pollen assemblage further suggests that upland habitats were in the vicinity.

We suggest that the study site was most likely a short-hydroperiod prairie containing longer-hydroperiod willow thickets as “islands” prior to ~5700 cal yr BP. These willow-dominated thickets may have been bounded by open water species like *Typha* and *Sagittaria*. These wetland habitats could have been surrounded by pine savanna dominated by pines, oaks and containing subtropical hammocks. Most importantly, the palynological data indicate not only that wetlands have been present for more than ~5700 yr in southwestern Florida, but also suggest that early wetland landscapes in interior southern Florida may have resembled the fire-maintained landscapes occurring today in Big Cypress National Preserve and Everglades National Park (DeCoster et al., 1999; Schmitz et al., 2002; Slocum et al., 2003, 2007).

Dynamic freshwater wetlands (~5700–3800 cal yr BP)

Zones 3, 4, and 5 consist of peat that dates back to ~5700 cal yr BP. Our study site in the southwestern region of the Everglades lies atop the permeable Tamiami limestone where the water table is very sensitive to changes in hydrological conditions (Gleason and Stone, 1994). The formation of peat instead of marl in Zone 3 (~5700–3800 cal yr BP) suggests deeper water levels and longer, 12-month hydroperiods in at least some local areas such as the coring site. Historically, water availability in the southern Everglades has been determined by local rainfall and drainage through sheet flow of water from Lake Okeechobee (Donders et al., 2005; Lodge, 2010; Michot et al., 2011; Saha et al., 2012). Some evidence indicates that intensification of the El Niño-Southern Oscillation (ENSO) during the mid-Holocene increased precipitation in south Florida (Donders et al., 2005). Therefore, formation of peat throughout Zone 3 is consistent with the hypothesis that the mid-Holocene intensification of ENSO might have marked the onset of more modern-day precipitation regimes in the Everglades (Rodbell et al, 1999; Koutavas et al, 2002).

Our study suggests that freshwater wetlands in south Everglades were dynamic and changing on time scales of millennia during the mid-Holocene. Between ~5700 and 5250 cal yr BP, at the onset of

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subzone 3a, numerous upland taxa (*Salix*, *Pinus*, Rubiaceae, *Quercus*, and *Morella*) and herbaceous taxa (Poaceae, *Typha*, Solanaceae, and Asteraceae) consistently appeared in the pollen assemblage (Figs. 3 and 4). This pollen assemblage, which persisted until ~5250 cal yr BP, suggests that 12-month hydroperiod sloughs dominated by *Salix* (willow) or perhaps *Cephalanthus* (buttonbush; Rubiaceae) and imbedded in long- or short-hydroperiod prairies dominated by grasses or sedges continued to persist after moisture levels increased over those associated with Zone 2 (Hanan et al., 2010).

The shift to an herbaceous-dominated landscape marks the onset of Zone-3b, between ~5250 and 4300 cal yr BP. The pollen assemblage records the concurrent decline in upland taxa (*Salix*, Rubiaceae, *Pinus*, *Morella*, and *Quercus*), and a marked increase in Amaranthaceae (Figs. 3 and 4). In addition, pollen percentages for *Sagittaria* and Apiaceae reach their maximum in Zone 3, suggesting widespread freshwater wetlands with 12-month hydroperiods near the coring site during this subzone.

Amaranthaceae abundance increases with disturbances. In present-day south Florida wetland habitats, such increases have been noted after natural lightning-ignited fires (Slocum et al., 2003, 2010) and hurricanes (Armentano et al., 1995), when open space is generated and colonized by species like *Amaranthus australis* (Schmitz et al., 2002). Increases of Amaranthaceae in other pollen diagrams have also been attributed to periods of drought (Willard et al, 2001; Willard and Cronin, 2007). Therefore the shift to an herbaceous community in this subzone suggests frequent major fires, perhaps in conjunction with periods of droughts; such intense fires have burned out willow thickets in the present-day Everglades (Beckage et al., 2003; Slocum et al., 2007). This interpretation is supported by the increase in micro-charcoal particles (Figs. 3 and 4). Such periodic droughts and intense fires may have characterized this subzone (~950 yr).

Subzone 3c (~4300–3800 cal yr BP) reflects the formation of open water sloughs. After 4300 cal yr BP, *Sagittaria* reaches its highest concentration throughout the core, and Cyperaceae reappears. At the same time, upland taxa reappear or increase, accompanied by a decrease in Amaranthaceae, suggesting that the long-hydroperiod prairies changed to open water and/or sedge-sloughs (perhaps dominated by *Eleocharis*) due to the rising water table. This change, which would have reduced fire frequency, is supported by the continuing decrease of charcoal fragments.

XRF results show no signs of marine influence in Zone 3 (Fig. 5), as common marine indicators (Ca, Sr, and Zr) are rare or absent (Miller, 1945; Ramírez-Herrera et al., 2012). During the mid-Holocene, sea level in southwestern Florida was at least 6 m lower than the present level (Parkinson, 1989), and the shoreline was probably 30 km seaward relative to today (Wanless et al., 1994), implying that marine influence was minimal or non-existent in the southwestern Everglades from ~5700 to 3800 cal yr BP.

Freshwater to marine transition (~3800–2200 cal yr BP)

Zone 4 (~3800–2200 cal yr BP) represents a transitional stage from freshwater to brackish marsh. At around 4000 cal yr BP, the sea level was at least 5 m lower than at present, with a regional sea level rise of ~0.6 mm/yr in southern Florida (Wanless et al., 1994). The resultant marine transgression gradually reduced the site-to-sea distance. This transition is clearly recorded by the palynological data (Fig. 3). Linings of foraminifera start to appear with greater regularity at the top of this zone, while mangrove taxa increase in abundance beginning at ~3800 cal yr BP, indicating increased seawater flooding (Scott et al., 2003; Sabatier et al., 2008; Gonzalez et al., 2010). Additionally, the abundance of Amaranthaceae and microscopic charcoal fragments diminishes, while *Sagittaria* and *Typha* pollen decline to trace values during this period, indicating a changing environment (less fresh water and fewer fires) with more marine influence (Willard et al., 2001; Willard and Cronin, 2007). These palynological data clearly show a period of marine transgression from ~3800 to 2200 cal yr BP. Similar environmental histories have been documented in southern Florida (Donders et al., 2005; van Soelen et al., 2010, 2012), suggesting that the freshwater marshes in the southwestern Everglades were receiving more and more marine influence during the late Holocene. Today, similar brackish marshes occur between mangrove forests and freshwater marshes in the Everglades, including the Shark River Estuary (Willard et al., 2001). Using these as a modern analog, it could be inferred that during ~3800–2200 cal yr BP, the Shark River Estuary was probably dominated by grasses and *Amaranthus*, with some scrub red mangroves and occasional black and white mangroves. Salt-intolerant species like *Sagittaria* were no longer present. The frequency of fire was probably much reduced due to lower fuel loads (less graminoids biomass) and a 12-month hydroperiod, but with low salinity.

The development of mangrove scrubs (~2200–1150 cal yr BP)

In Zone 5 (~2200–1150 cal yr BP), all mangrove species reach high percentages and gradually exceed the marsh pollen taxa. Previous palynological studies from mangrove areas have documented that 50% to 95% *Rhizophora* pollen in total pollen assemblages indicates a well-developed red mangrove forest (Chappell and Grindrod, 1985; Woodroffe et al., 1985; Behling et al., 2001; Ellison, 2008). Some studies have shown that the abundance of mangrove pollen production is positively correlated with canopy height (Gill and Tomlinson, 1977; Van Campo and Bengo, 2004; Versteegh et al., 2004; Scourse et al., 2005). Although *Rhizophora* exceeds 50% of the total pollen sum in most samples in Zone 5 (Fig. 3), we assume it represents low-stature *Rhizophora* scrubs, because the pollen influx values of *Rhizophora* remained low during this period. Thus, Zone 5 represents a transition from brackish marsh to mangrove forest. During this period, even though the shoreline was still undergoing transgression, the relatively stable sea level enabled mangroves to colonize the southern Everglades estuarine area (Parkinson, 1989; Wanless et al., 1994). The multi-proxy data from the beginning of Zone 3 to the end of Zone 5 thus show a multi-millennial transition from freshwater to marine influences at the site. Similar replacement of freshwater marshes by low-stature mangrove scrubs has been observed at some inland sites in the southeastern Everglades since AD 1930 (Ross et al., 2000; Castañeda-Moya et al., 2013). The significantly shorter transitional time span involved in the recent transitions can probably be attributed to the current rapid RSL rise rate of 3.8 mm/yr, compared with 2.3 to 0.4 mm/yr during the mid- to late-Holocene (Wanless et al., 1994; Ross et al., 2009). If the current rapid rate of RSL rise continues, present coastal zonation of the Everglades can be anticipated to be altered in similar ways, but much more rapidly than occurred during the late-Holocene.

The establishment of coastal mangrove forests (~1150 cal yr BP–present)

The multi-proxy record of Zone 6 (~1150 cal yr BP–present) suggests an established coastal environment with predominately marine influences. Marine microfossils (foraminifera and dinoflagellates) are found in most levels in this zone. Indeed, high concentrations of Ca, Sr, Zr, and S characterize a coastal environment with increased allochthonous sediment input in this period (Miller, 1945; Davison, 1988; Ramírez-Herrera et al., 2012). Moreover, Zr, the main constituent for Florida beach sand (Miller, 1945), starts to consistently appear at ~1150 cal yr BP (Fig. 6). Because tides (and episodic storms) are the only source that consistently carries marine sediments into the fringing wetlands, this chemical signature suggests that the coring site started to receive sand through tidal exchange at that time. Concurrently, the pollen influx diagram shows a significant increase in all mangrove species (Fig. 6). This relative shift in pollen dominance suggests that a mixed mangrove forest similar to today's in structure and composition was established at the mouth of the Shark River Estuary around 1150 cal yr BP. Because mangroves are generally found within the inter-tidal zones (Behling et al., 2001; Ellison, 2008; Monacci et al., 2009; Urrego et al., 2009), we propose that the modern coastal mangrove ecosystem was formed at approximately the same time. Previous studies suggest

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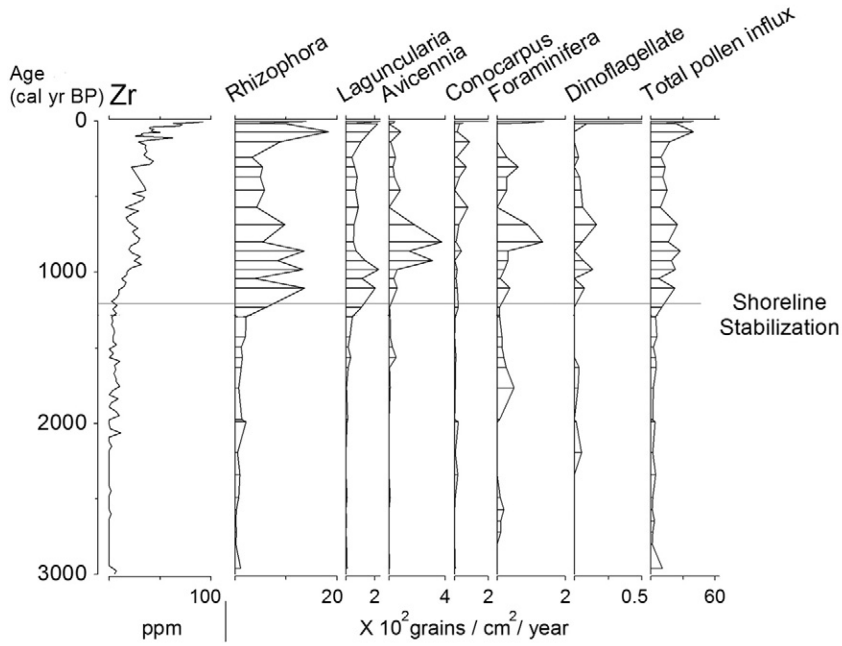

Figure 6. Zr concentration and influx values of selected microfossils for core SRM-1. The influx values of all mangrove species increase simultaneously with the concentration of Zr, indicating the establishment of mangrove forest and shoreline stabilization.

that the modern coastal mangrove ecosystem in southwestern Florida was established about 3500 to 3000 cal yr BP (Parkinson, 1989; Gleason and Stone, 1994; Wanless et al., 1994). Our pollen and XRF data suggest a different mangrove development and history. Although *Rhizophora* is the first to arrive at the study site, *Avicennia* and *Laguncularia* are always present locally or in the vicinity in the last 3000 yr (Fig. 6). At approximately 1150 cal yr BP, the tidal zone reached its modern position, and the modern shoreline dominated by mixed mangrove forest was formed at the mouth of the Shark River Estuary (Fig. 6).

Conclusions

Our multi-proxy record from the southwestern Everglades has yielded arguably the oldest basal peat date and longest paleoecological record for the region. We have five major conclusions regarding paleoecological changes occurring in wetlands that should be especially applicable to ongoing changes in the Everglades resulting from RSL rise.

(1) Palynological data indicate that wetlands have been present in the southwestern Everglades since the mid-Holocene. Initial wetland habitats most likely resembled present-day short-hydroperiod graminoids-dominated marl prairies in the interior of the Everglades and were subject to frequent fire. We note that because of the current overwhelming presence of human ecosystems in areas most likely to become wetlands, most wetlands formed from RSL rise will not resemble short- and long-hydroperiod prairies, nor will fire be a major environmental process unless management efforts are made to restore historical fire regimes.

(2) Our study site became part of the Shark River Estuary basin, with a continuous deposition of peat, around 5700 cal yr BP. Initially, once peat began accumulating, a mosaic landscape consisting of short- and long-hydroperiod prairies with embedded sloughs and surrounded by uplands prevailed. Between ~5250 and 4300 cal yr BP, these habitats were replaced by herb-dominated long-hydroperiod prairies. From 4300 to 3800 cal yr BP, as a response to increasing precipitation, long-hydroperiod prairies changed to open water and/or sedge-sloughs. These data suggest that freshwater wetlands in the southwestern Everglades date back to the mid-Holocene and were dynamic, changing almost continuously on millennial timescales.

(3) The multi-proxy data show a clear transition from a freshwater to a coastal/estuarine environment, as well as shoreline transgression beginning around 4000 cal yr BP due to RSL rise. From ~3800 to 2200 cal yr BP, plant communities at the Shark River Estuary shifted to brackish wetlands as marine influence (e.g., tidal inundation) increased. Over the next 1050 yr, relatively stable sea levels allowed the colonization of mangroves, causing a shift to mangrove-dominated forest in the southwestern Everglades. These changes occurred as the shoreline was still going through a transgression process.

(4) At around 1150 cal yr BP, a mixed mangrove forest similar in structure and composition to that present today was established at the present-day Shark River Estuary. This result suggests that the modern mangrove-dominated shoreline at the mouth of the Shark River is more than 2000 yr *younger* than previously estimated (Parkinson, 1989; Gleason and Stone, 1994; Wanless et al., 1994; Lodge, 2010). Because Shark River Slough is the largest freshwater outlet in the Everglades, its unique hydrological and ecological settings might have caused the inconsistency relative to other mangrove timelines proposed for other sites (e.g., Wanless et al., 1994; Lodge, 2010). Therefore more regional paleoenvironmental works are needed to verify the mangrove development history along the diverse southwest Florida coastlines.

(5) The pollen and XRF results from this study suggest little evidence of marine influence during the period from ~5700 to 3800 cal yr BP, therefore, increased precipitation was primarily responsible for the rising water table and initial formation of freshwater wetlands at the Shark River Estuary. However, after ~3800 cal yr BP, as increasing marine influence was observed in the pollen and XRF records, RSL rise directly resulted in shoreline transgression, hence the development of mangrove shorelines at the Shark River Estuary.

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