Mid- to late-Holocene El Niño-Southern Oscillation dynamics reflected in the subtropical terrestrial realm

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High resolution pollen analysis of mid- to late-Holocene peat deposits from southwest Florida reveals a stepwise increase in wetland vegetation that points to an increased precipitation-driven fresh water flow during the past 5,000 years. The tight coupling between winter precipitation patterns in Florida and the strength of the El Niño-Southern Oscillation (ENSO) strongly suggests that the paleo-hydrology record reflects changes in ENSO intensity. A terrestrial subtropical record outside the Indo Pacific Warm Pool both documents ecosystem response to the known onset of modern-day ENSO periodicities, between ≈7,000 and 5,000 years B.P., and subsequent ENSO intensification after 3,500 years B.P. The observed increases in "wetness" are sustained by a gradual rise in relative sea level that prevents a return to drier vegetation through natural succession.

ENSO-teleconnections | Florida | paleoprecipitation | pollen

Intensification of the El Niño-Southern Oscillation (ENSO) in the mid-Holocene, between ≈7 and 5 thousand years (ka) B.P. (ages in calendar years unless stated otherwise) (1, 2), is thought to mark the onset of modern-day precipitation patterns in low-latitude regions. Proxy records of climate change indicate that the increased amplitude of ENSO variability had a clear impact on regional hydrological budgets of tropical parts of the Indo-Pacific region, South America, and Africa (3–5). Because the mode and intensity of ENSO varied with the orbital precession during the Holocene (6), the solar radiation budget is likely to have influenced global hydrological patterns. However, data on extra-tropical ENSO variability are still limited. Yet, the existent modern ENSO teleconnections imply that Holocene changes in precipitation must have had an impact on a much larger scale. As human-induced global warming progresses, it is crucial to understand to what extent the hydrological cycle has been altered by prominent climate systems such as ENSO. Here, we document the mid- to late-Holocene development in hydrological conditions in South Florida, a subtropical area characterized by a strong ENSO teleconnection, to recognize changing precipitation patterns that can be used as indicators of long-term ENSO dynamics outside the tropical Pacific.

The Florida peninsula is strongly influenced by ENSO variability, which particularly affects the winter precipitation (7–9). Precipitation-driven surface sheet flow across South Florida determines water availability during winter/spring, which largely controls the composition and growth conditions of the vegetation (10, 11). Because of the dependence of local plant growth on the ENSO system, identification of past changes in local wetland vegetation can elucidate past ENSO activity. This study presents a detailed record of vegetation change based on pollen analysis of a radiocarbon-dated peat core from a forested wetland in Southwest Florida.

Wetland areas extremely sensitive to hydrological perturbations have expanded vastly since ≈5 ka B.P. across subtropical South Florida (12). The expanse has partly been attributed to continuing relative sea level rise, which reduced the gradient from the Florida aquifer to the coast and, thus, caused wetter soil conditions toward the sea. However, peatland formation in slightly elevated inland areas has likely been caused by increased precipitation (12, 13). So far, vegetation and climate history studies in southern Florida have been restricted to the Lake Wales Ridge region in south-central Florida, the Everglades, and adjacent water conservation areas (14–18) (Fig. 1). Holocene Lake Wales Ridge pollen records display small centennial variations during the past 5,000 radiocarbon years (14, 19) and do not show a large response to ENSO forcing. However, these records are derived from a relatively dry upland area on permeable carbonate soil, which does not retain the winter precipitation (20). Thus, water is not stored and cannot influence plant growth during the growing season. In contrast, the organic wetland soils south of Lake Wales Ridge support vegetation adapted to continuous moist conditions, which is therefore strongly controlled by winter precipitation. Hence, South Florida wetlands provide an ideal setting for reconstructing past ENSO dynamics.

The Big Cypress Swamp ecosystem, an extended forested wetland in southwestern Florida, was selected as study area. A section of this wetland, the Fakahatchee Strand Preserve State Park (FSPSP, 25°95′N, 81°49′W, Fig. 1), contains an elongated, wide, and shallow dissolution structure (slough) underlain by the more impermeable, slightly elevated Tamiami Formation (16). The low-energy, moist conditions in the slough allow peat formation. The FSPSP present-day ecology has been well studied, and it has been demonstrated that the wetland vegetation is highly sensitive to hydrological changes (21). For this study, an undisturbed deposit from the FSPSP *Taxodium* (cypress) swamp has been subjected to palynological investigation (Fig. 1). A surface sample data set that covers environmental gradients (21, 22), water depth/hydroperiod, salinity, and bedrock type, is used here to interpret changes in the FSPSP pollen record.

The FSPSP record will clarify whether pronounced variation in winter rainfall occurred during the mid- to late-Holocene and help to further elucidate past ENSO variability and its impact on areas outside the tropical Pacific.

Materials and Methods

The FSPSP consists of a forested *Taxodium distichum* (bald cypress) swamp with a long hydroperiod, surrounded by more seasonally inundated hardwood-hammock and wet-prairie vegetation. The peat deposit located in the main slough of the FSPSP was cored in the winter of 1998 with a modified Livingstone corer (Fig. 1). The lowermost 5 cm of the 195-cm sequence consists of coarse sand containing some peat fragments, gradually becoming sandy peat and finally dark, organic rich, homogenous fine peat. The top ≈25 cm was not consolidated and contained identifiable plant remains. The core sections were subsampled every 4 cm for both pollen analysis and Loss-On-Ignition. Pollen samples were prepared by following standard palynological peat processing techniques (23). Pollen and spore
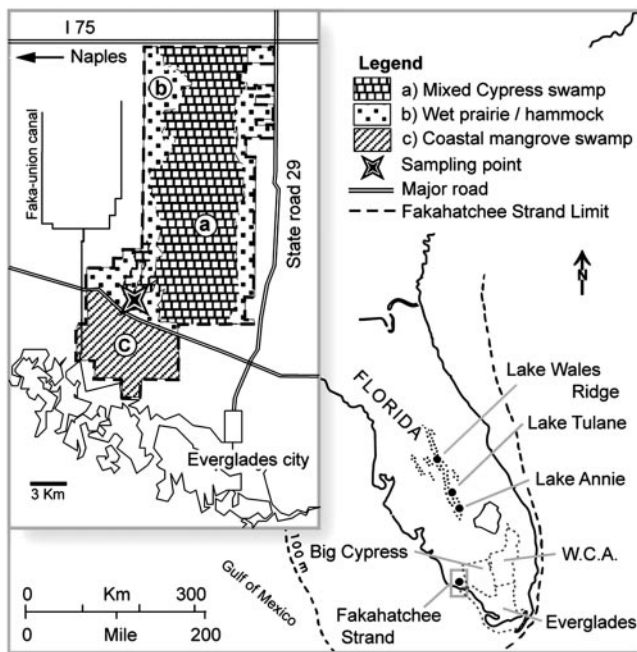
Fig. 1. Location of the Fakahatchee Strand State Preserve Park (FSPSP, *Inset*) in southwest Florida. Main vegetation units and coring location are indicated in relation to previously studied sites in Florida.

Fig. 2. Age-depth relationship and Loss-On-Ignition (LOI) results for the FSPSP sediments. Arrows indicate where different models were applied. ▲, radiocarbon ages used in model I; ■, ages in model II; ● age in model III. Date at 80 cm depth (in gray) has been excluded from models (see Table 1).

identification (≈300 grains per sample with a maximum of five slides) was based on the reference collections of the U.S. Geological Survey (Reston, VA), and the Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands, and refs. 24–26.

Peat material from 14 horizons was radiocarbon dated by accelerator mass spectrometry. To assess possible contamination by younger rootlets, one horizon (at 9 cm depth) was accelerator mass spectrometry radiocarbon dated by using both bulk peat and macro leaf remains (Table 1). Radiocarbon data were
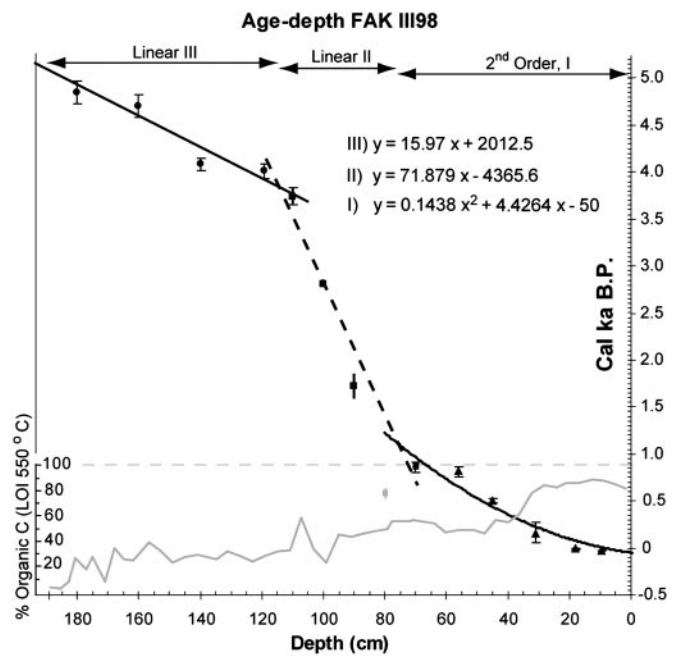
Table 1. Accelerator mass spectrometer ^{14}C-dated horizons in FAK III98, FSPSP, FL

UtC no.	Depth, cm	δ ^{13}C, %	^{14}C age ± 1σ, year B.P.	Cal age ± 1σ, year B.P.
12258	9.5 a	−30	−1729 ± 29	−29.5 ± 6*
12257	9.5 b	−28.1	−1703 ± 29	Excluded
12256	18	−28.4	−1062 ± 30	−10.5 ± 6*
12255	31	−27.9	104 ± 33	150 ± 120
12254	45	−28.3	447 ± 31	502 ± 20
12253	56	−29	936 ± 33	805 ± 65
12252	70	−28.2	850 ± 35	860 ± 50
12251	80	−27.8	650 ± 35	608 ± 48†
12250	90	−28.2	1,792 ± 45	1,720 ± 100
12249	100	−28	2,729 ± 37	2,813 ± 38
12248	110	−27.8	3,468 ± 37	3,740 ± 90
12109	119	−28.5	3,719 ± 36	4,010 ± 80
12247	140	−28.1	3,719 ± 38	4,085 ± 65
12246	160	−28.4	4,169 ± 38	4,700 ± 120
12110	180	−28	4,290 ± 60	4,850 ± 120

All samples are bulk peat, except sample 9.5 a (*Taxodium* sp. leaflet), to assess the reservoir effect between peat and macrofossils. Calibration performed with OXCAL 3.9 with prior assumption of chronologically ordered samples. UtC, R. J. Van de Graaff laboratory, Utrecht University.
*Samples calibrated with 20th century bomb carbon anomaly (27).
†Considered to be an outlier, excluded from age-depth model.

calibrated with OXCAL 3.9 calibration software (28, 29), which uses the INTCAL98 calibration curve (30) and provides output as a probability density function (PDF). With the prior assumption that samples are ordered chronologically, a Bayesian statistical function within the program reduces the PDFs of overlapping radiocarbon data (31). Subsequently, the reduced 1σ intervals were used for construction of the age-depth model (Table 1 and Fig. 2).

A semiquantitative technique is available for reconstructing paleohydrology by identifying the closest modern analogue from different vegetation units across hydrological and salinity gradients (18). To describe the main trend and interpret observed changes within the fossil samples, the data were compared with the surface samples by means of a correspondence analysis, thereby closely related samples could be identified (see supporting information, which is published as supporting information on the PNAS web site). A study on subfossil peat from the FSPSP showed that the technique accurately detects documented hydrology changes that occurred in the 20th century (21).

Chronology. The trend in organic matter content indicates several stages of peat decomposition and, consequently, some changes in apparent sedimentation rate are expected. The prior assumption of chronologically ordered samples in the OxCal calibration procedure significantly reduced several calibrated age ranges (Table 1). One sample was considered an outlier and was excluded from the set. Its position on the end of a core section might indicate contamination with younger material during coring.

The ^{14}C ages on both bulk peat and macro remains are effectively identical (Table 1), which indicates that the use of bulk peat for dating is justified. However, contamination with small rootlets cannot completely be excluded for the lowermost ^{14}C data (Fig. 2), but this conclusion has to be confirmed. Based on the radiocarbon data, an age-depth curve was constructed by plotting a different (simple) models through
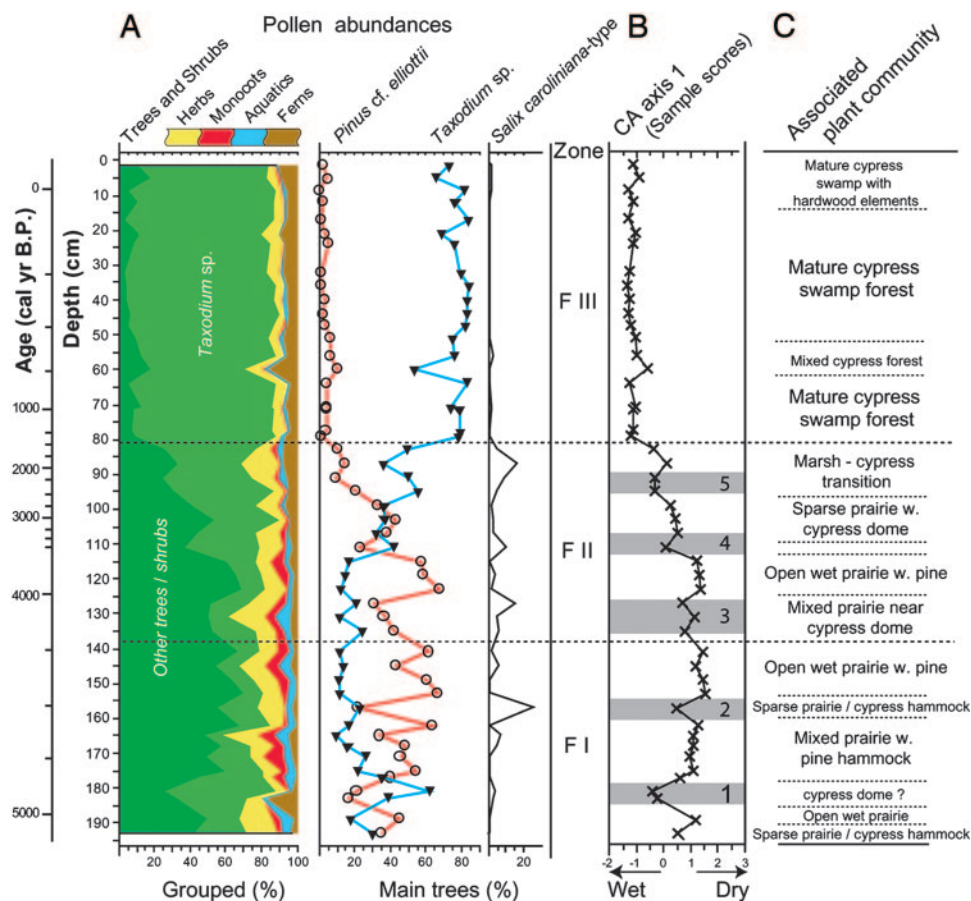
Fig. 3. Pollen percentage diagram and reconstructed past vegetation from the FSPSP wetland in Florida. Major pollen curves (*A*) and general trend between dry and wet assemblages (*B*) and the associated vegetation units (*C*). *Pinus* represents relatively dry conditions in contrast to wet *Taxodium* phases. Numbers 1–5 represent short wet pulses characterized by high *Salix* and increased *Taxodium* as referred to in the text.

three data subsets (Fig. 2). The lower two sections are described well by a linear model. A second-order model is used for the uppermost part, because gradual decomposition clearly influenced the compaction rate, which is in accordance with earlier radiocarbon data from the site (27). The basal age of the profile is ≈5.2 ka B.P., which is the base of the peat. The second (II) model clearly shows a reduced accumulation rate between 1.2 and 3.8 ka B.P., roughly equivalent to pollen zone FII (Fig. 3, see below). Models I and III have a broadly comparable high accumulation rate, which is promising for further high-resolution studies on selected time windows during the mid-Holocene.

Vegetation Development. Both the major pollen groups and associated vegetation units indicate significant change over the past 5 ka (Fig. 3). The pollen assemblages were divided into three zones based on the output of optimal sum-of-squares partitioning (32). The prime feature of the pollen diagram is the turnover between *Pinus cf. elliottii* (slash pine, presently the only naturally occurring *Pinus* in southeast Florida, ref. 33) and *Taxodium* sp. (bald cypress). *Pinus cf. elliottii* prevails in zone FI but is gradually replaced during zone FII by *Taxodium* sp., which eventually dominates in zone FIII. Second, significant change of dynamics between zones characterizes the succession. The *Pinus* phase is characterized by large fluctuations from low (20%) to high (70%) values in alternation with *Salix caroliniana*-type (Carolina willow), whereas the *Taxodium* sp. high phase is far more stable.

These changes are the most pronounced features of compo-

sition shifts in entire plant communities. In zone FI, *Pinus-Salix* phases occur with low, but significant, abundances of wet prairie vegetation elements, notably Asteraceae and Amaranthaceae-type, *Ambrosia* sp., *Sagittaria* sp., and Poaceae and Cyperaceae (grass and sedge) pollen (see supporting information). In zones FII and FIII, the wet prairie elements gradually decrease in favor of hardwood trees associated with *Taxodium* swamps (*Fraxinus caroliniana*-type, *Acer rubrum*, *Quercus* spp.) and fern understory elements. Additionally, abundant "Type 182" spores in zone FIII are indicative of wet conditions (34).

The apparent *Taxodium* sp. peak at 181 cm is not considered representative because the sample counting sum is very low, resulting in underestimation of large pollen types like *Pinus* (35). The lowermost samples appear to be slightly different, with above-background levels of oak (*Quercus* spp.) and nearly 20% Asteraceae followed by short peaks of fern abundance. Clearly, short fluctuations are present but there is no long-term change within zone FI.

The assemblage change within zone FII is not unidirectional but exhibits stepwise increases interrupted by stable and regressive phases. The peaks of wet-tolerant *Salix* of up to 20% are mostly short, and no further succession occurs. Only at the FII/FIII zone boundary ≈1.3 ka B.P., *Salix* is followed by relatively high abundance of *F. caroliniana*-type (>5%) after which *Taxodium* sp. pollen fully dominates the assemblage.

The vegetation dynamics are well captured by the trend curve displayed in Fig. 3, which represents the shifts between drier prairie and wet swamp forest vegetation inferred from the correspondence analysis. Based on the identification of similar

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surface samples, each phase in the pollen record is coupled to a vegetation unit, which confirms a stepwise development from wet prairie to swamp forest. Spread of taxa along the correspondence analysis axes allows interpretation of the trend curve, even for samples with no clear modern analogue, and, therefore, it is a good index of hydrological conditions. The main variability occurs in zones FI and FII. However, in zone FIII a short decrease in *Taxodium* sp. is evident ≈750 yr B.P., and values are clearly reduced in the 20th century, which is in accordance with recent drainage activities (21).

Interpretation of Shifts and Mechanisms. The pollen assemblages and derived vegetation units are reconstructions of the local environment and do not represent average regional vegetation cover. However, the local environment depends on a precipitation-driven surface sheet flow across South Florida (10, 11). And because the reconstructed vegetation changes are primarily shifts between vegetation types adapted to different hydroperiods, they are a measure for the intensity of surface sheet flow across South Florida (21).

The onset of peat formation is the first key feature of the record. The basal age of ≈5.2 ka B.P. needs to be confirmed by additional dating, preferably on macrofossil remains, but seems evident from the extrapolation of the age-depth model below 180 cm (Fig. 2). Second, the main transition phase between 3.5 and 2 ka B.P. from wet prairie to swamp forest environments is important. Both events are clear increases in water availability, the first indicates the onset of conditions moist enough for peat accumulation, whereas the second prolonged the annual inundation period from ≈3 to 9 months (18, 21).

The start of the peat record confirms earlier dates for the main expansion phase of the Everglades (12) and is in marked concurrence with the transition to modern ENSO periodicities reported in refs. 1, 2, and 36. Furthermore, ENSO intensification after ≈3.5 to ≈3.1 ka B.P. shown from records centered around the Indo-Pacific Warm Pool (1, 36–38) are coincident with the initial transition to long hydroperiod vegetation during zone FII in our record. A more indirect runoff record from ODP site 1002 in the Cariaco Basin offshore Venezuela confirms ENSO intensification starting ≈3.8 ka B.P (39). Although these records do not agree on the exact timing, the evidence for the two-stepped ENSO intensification is clear and, as shown here, not limited to the Indo-Pacific Warm Pool.

An alternative explanation for the increase in moisture involves the contribution of relative sea level (RSL) rise to wetland conditions in Florida. Although no agreement exists about the exact RSL development in the Gulf of Mexico (see supporting information), recent studies suggest that no stepwise increases occurred (40). Alternative views even point to a mid-Holocene highstand (41), followed by a RSL drop, which would cause drier conditions onshore. However, an increase in wetness is actually recorded ≈3 ka B.P. A recent regional western Atlantic RSL record shows a very gradual rise during the Holocene (42). A slowly declining gradient between the Florida aquifer and the coast during the late-Holocene would most likely be balanced by the rate of peat accumulation (≈2 m since 5 ka B.P.), because peat accumulation ultimately develops into drier hammock formation filling up the slough (11). However, a significant change to wetter, long hydroperiod systems is actually observed, whereas a stepwise increase in RSL ≈3 ka B.P. is not obvious from the sea-level reconstructions. Possibly the start of the peat record is a combination of factors, because the main rise in Holocene RSL occurred before 5 ka B.P., and the rate of change in the FSPSP record before that period is not known. A primary RSL cause for all of the observed changes in our record is considered unlikely. Additionally, a climatic cause is supported by mois-

ture increase recorded in "upland" Florida records (14, 17), although much reduced because of a lesser dependence on winter precipitation in these ecosystems.

During zones FI and FII, superimposed centennial shifts between short and moderate hydroperiod vegetation units indicate subtle shifts resulting from water availability fluctuations. These phases of *Salix* abundance and increased *Taxodium* sp. indicate wetter periods, relative to the prairie. They are likely caused by short periods of increased ENSO intensity as described from beach ridge deposits (43). However, comparing timing and duration of these events with other records is, given the limitations on the available chronologies, difficult and a likely source of confusion. A better approach would be to establish and compare event frequencies for available records and, thus, create an integrated paleo-ENSO record through time. In our record, five clear wet pulses occur between 5 and 2 ka B.P., which points to an existent, but fairly limited, ENSO activity or weakened teleconnections. Short wetter phases after 2 ka B.P. are probably not reflected because the *Taxodium* swamp is the region's ecosystem most adapted to wet conditions and can survive, but not reproduce, in permanent flooding (44).

Although earlier records from Florida show increased wet conditions in the mid-Holocene (14, 19), the two-stepped increase is not very clear. Changes are concurrent, especially for the Lake Annie pollen record (19), but much suppressed, and a clear link with the ENSO system was therefore not perceived. However, the great dependence of the FSPSP vegetation on ENSO-tied winter precipitation implies an enhanced response and, thus, a clear record of paleo-ENSO conditions outside the Indo-Pacific Warm Pool.

Clearly, the FSPSP pollen record displays significant shifts in hydrology during the mid- to late-Holocene, in agreement with an existent ENSO between 5.2 and 3.5 ka B.P., which intensified to resemble modern conditions after 3.5 ka B.P. A definite answer to the exact contribution of ENSO dynamics to the hydrological change in Florida, especially in relation to past sea level change, might come from highly detailed analysis of selected time windows in peat records. Recent high resolution palynological studies indicate that pollen productivity responds to annual climatic variability (21, 45), and can therefore potentially reflect 2- to 7-year ENSO dynamics. Periods indicative of reduced ENSO activity can thus be tested in terrestrial ecosystems, analogous to coral studies in marine systems.

Holocene hydrological conditions have shown significant, nonlinear response to gradually changing insolation, amplified by large climate systems like ENSO (6, 46). This study shows that ENSO-related changes are not confined to the tropics but are pronounced in the subtropics as well. Understanding and documenting these patterns of change better is a prime task for further research, because future climate warming will likely impact the global hydrological cycle to a large degree through nonlinear responses like ENSO.

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