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Vegetation History and Estuarine Ecology of the Texas Gulf Coastal Plain in Relation to Climate and Sea-Level Changes According to Three Pollen Cores

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Abstract: The vegetation history of the Texas Gulf Coastal Plain in the Holocene is considered according to pollen evidence from three coring sites where both terrestrial and marine ecology are reconstructed. These pollen sites record oscillations in the limit of the Southeastern US Forest zone in relation to climate changes, with a major, southward migration of the forest limit and expansion of the range limit of *Betula nigra* being recorded in the 6th millennium BP and a northward migration in the 4th millennium BP. The appearance of *Rhizophora* pollen also indicates increased tropical influence in the Middle Holocene. Moreover, changes in the salinity profiles of estuaries are reconstructed in relation to broader coastal environmental changes, such as sea-level oscillations and the formation of barrier islands, with a major sea-level transgression phase being recorded in the 4th millennium BP and still-stand conditions after the 3rd millennium BP. These vegetation changes are finally compared to occupational evidence of prehistoric humans in the Central Texas Gulf Coastal Plain region in relation to ecological factors. Here, human occupation of the coastal zone is correlated with afforestation, the proliferation of pecan and the emergence of low-salinity estuaries.

Keywords: Texas Gulf Coastal Plain; palynology; archaeology; mangroves; estuaries



Citation: Albert, B.M. Vegetation History and Estuarine Ecology of the Texas Gulf Coastal Plain in Relation to Climate and Sea-Level Changes According to Three Pollen Cores. *Quaternary* **2023**, *6*, 19. <https://doi.org/10.3390/quat6010019>

Academic Editors: Elda Russo Ermolli, Henry Lamb and María Fernanda Sánchez Goñi

Received: 13 October 2022
Revised: 27 February 2023
Accepted: 1 March 2023
Published: 9 March 2023



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1. Introduction

1.1. Ecological Overview

In this study, pollen data are used to reconstruct vegetation in the Central and South Texas Gulf Coast Plain (hereafter, TGCP) with the aim of defining floral changes in relation to climate and sea-level changes. Importantly, the marsh and riparian verge flora in this region form a critical environment for a variety of fauna, including fish [1] and avifauna [2]. Moreover, the sustainability of these coastal freshwater (to slightly brackish) marshes is ultimately dependent on inputs of fresh water from rivers and the sheltering of marshlands from hyper-salinity and marine influence (e.g., with barrier island formation).

For human populations, the estuaries form a locus for concentrated food resources in addition to floodplains of entrant rivers. Within the latter, inland zone, the main biogeographic division encountered is the forest–prairie ecotone, whose position is determined by climate conditions, fire history [3] and, to a limited extent, human influences on the environment [4]. While prairies provide ecologies for grazing animals, the highest biomass and most abundant food resources for herbivores as well as humans are found in forest environments, with the highest concentrations of food resources being found in nut-mast trees, including different oak and hickory species, with maximum caloric production (of nut masts) being encountered in the case of pecan (*Carya illinoensis*) [5,6]. In this study, both coastal and inland vegetation are considered, with an assessment of environmental factors, focusing on (1) climate and (2) sea-level history during the Holocene. Vegetation impacts of humans, by fire setting and then fire suppression, are recoded during the last 500 years in the region, emerging from bison hunting and early farming practices [7].

1.2. Application of Palynology to Climate and Sea-Level Studies

In terms of biogeography, the Guadalupe River valley constitutes an important ecotone at the southern limit of the Southeastern United States oak–pine–hickory mixtures. This forest limit is controlled by precipitation differences across a significant (NE-to-SW) gradient, while temperature differences are minor within the TGCP. Pollen results of this study are used to reconstruct changes in this ecotone of the TGCP based upon tree pollen levels. Here, discussion is limited to two categories of analysis, including range data of trees that have critical climatic requirements, such as precipitation requirements, for example, the Betulaceae [8–12]. Secondly, absolute climatic requirements for tropical plant species remote to the Modern TGCP are used to establish parameters such as past temperature conditions. In this study, the presence of fully tropical, frost-intolerant species, such as red mangrove (*Rhizophora mangle*) [13], is important, and a use of analogs is made to establish the presence of mangroves. These analogs use modern land-surface samples proximal to living mangroves, and, notably, these insect-pollinated taxa are expected to produce minimal pollen unless communities are well-established under optimal temperature conditions [14,15].

Coastal pollen data are used to reconstruct effects of sea-level changes on the ecology of coastal marshes. Most important for pollen analysis is the distinction between halophytic plants (salt-marsh flora) promoted by sea-level transgressions, and, conversely, freshwater or slightly brackish plants that are promoted by still stands or recessions of sea level [16–19].

1.3. Study Site Overview

In this work, the sites chosen for study derived pollen from both alluvial and estuarine sources and provided pilot pollen data from submergent deposits of the coastal zone. These coring sites included the alluvial site of Core P1 at Buckeye Knoll (hereafter, BK) in the Lower Guadalupe River valley in Victoria County, the estuarine site of Core 2 at Swan Lake (hereafter, SL) in Aransas County and the marine site of Nueces Bay (hereafter, NB) in Nueces County (Figure 1). These sites differ, moreover, from many near-coastal studies in the Mississippi Delta region [20–22] in that pollen cores are situated in localities profoundly influenced by coastal processes (see, however, [23]). Long valley profiles of rivers in proximity to the examined pollen sites range in length from 25 km in the case of the Mission River near the SL site to 370 km in the case of the BK site in the Guadalupe River valley to 500 km in the case of the NB at the entrance of the Nueces River in Nueces Bay.

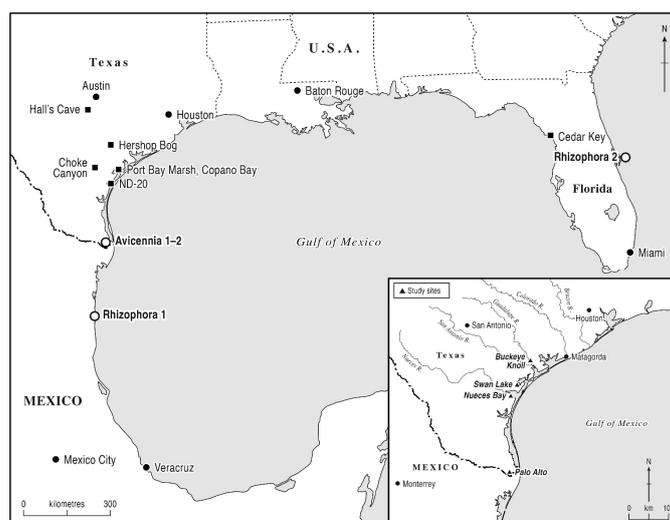


Figure 1. Map of pollen sites in the Texas Gulf Coastal Plain study region (inset, triangles), pollen analog sites (circles) and background sites (squares).

2. Study Region

2.1. Geography and Climate

The TGCP is the focal region of study (Figure 1 and Table 1), a plain situated along the Western Gulf of Mexico and intersected by multiple river valleys, including, most importantly (from north to south), the Brazos River, the Colorado River, the Guadalupe River, the Nueces River and the Rio Grande, with corresponding estuarine and deltaic deposits. Offshore or barrier islands are important in the regional geography and consist of sand deposited by wave action, providing protective barriers for estuarine marsh environments. The climate in the region is subhumid and subtropical in aspect, with mean annual temperatures approximating 22° to 23° C (in the Rio Grande valley) [12]. A significant precipitation gradient is encountered in the study region. For example, precipitation at the BK site is 97 cm per annum, while precipitation at SL is only 92 cm per annum.

Table 1. Summary climate history model and testing by palynology.

Climate Period	Approx. Dating	Hypothetical Pollen Response
Early Holocene mesic phase	9000–6000 BP	High AP
Middle Holocene (1) mesic phase	6000–4500 BP	AP rise with <i>Betula</i>
Middle Holocene (2) xeric phase	4500–3000 BP	AP decline
Late Holocene mesic phase	3000–1000 BP	AP rise with <i>Carya</i> rise

2.2. Flora and Fauna

Vegetation in the study region varies principally according to the precipitation variation in the Guadalupe River region. Thus, climax forests are limited to the Guadalupe River valley and the Colorado and Brazos River valleys, where *Quercus* spp. (oak, multiple species) and *Carya illinoensis* (pecan) are important taxa [24]. Southward of the Guadalupe River valley, *Quercus virginiana* (live oak) constitutes the main tree or shrub. Finally in the southern aspect of the study region, grasslands and prairies prevail, including, today, many invasive species, such as *Bothriochloa ischaemum* (King Ranch bluestem, from East Asia). Along the coast, an intermittent growth of *Avicennia germaniens* (black mangrove) mangle is also encountered in major estuaries of the Rio Grande and the San Antonio–Guadalupe delta. These mangroves occur at the margins of resource-rich estuarine marshes, or else inland, near coastal depressions with brackish water seeps. Their present distribution is limited by Modern land use. In coastal areas without rivers, near-shore conditions are more brackish, and here *Spartina* spp. (cordgrass) and *Salicornia bigelovii* (glasswort) are typical in coastal salt marshes, while *Typha* spp. (cattails) and Cyperaceae (sedges) are common in freshwater estuarine marshes. Such marshlands are most extensive in the deltas of rivers, such as the Guadalupe or Brazos Rivers [25].

Migratory bird species inhabiting coastal estuaries are numerous and include *Egretta thula* (snowy egret) and *Rynchops niger* (black skimmer). Alligator (*Alligator mississippiensis*) is also present in protected coastal marshes as well as inland river valleys, such as the Nueces River at Choke Canyon State Park. Important coastal fish species include *Sciaenops ocellatus* (red fish) and *Pogonias cromis* (black drum). Shellfish in TGCP estuaries include, most importantly, *Rangia cuneata* or Gulf wedge clam.

2.3. Quaternary Geology and Associated Vegetation Communities

The morphology of the TGCP is of low relief and geologically consists of Quaternary-age sediments with Holocene fills predominating in the river valleys. Important morphological features relating to Quaternary sea-level changes are notable and include the Deweyville Terrace (as old as Marine Isotope Stage 5). Near-surface deposits of Pleistocene-age Beaumont clay are the major units in coastal areas, overlain in places with Holocene sands derived from barrier islands, for example, the South Texas sand sheet situated behind Big Shell Beach in the middle of Padre Island. Notably, barrier islands formed in the

Holocene protect marshes that developed in the deltas of major rivers, for example, above prograding deltaic deposits of the Guadalupe River [19,26].

Relationships between vegetation and geology are also important to note in this regional and historical study. For example, important correlations are observable between the accumulation of sand along the TGCP coast and the growth of sub-xeric arboreal flora, such as *Quercus virginiana* (live oak). In this case, the extent of *Quercus virginiana* stands (with elements of bay laurel or *Laurus nobilis*) on dry and acidic substrates depends on the availability of sediment from sandy barrier islands; thus, the most extensive scrub woodlands of *Quercus virginiana* are found in the South Texas sand sheet (pers. observation, King Ranch, 2005). Where clay is exposed at the surface (Beaumont formation), scrub vegetation consists of *Prosopis* (mesquite) with an understory of various Asteraceae spp. in inland areas.

3. Previous Environmental Research in the TGCP and Present Hypothesis Testing

3.1. Regional Climate History

The history of vegetation history research in the TGCP and adjacent regions begins with the palynological work of Larson at the Hershop Bog pollen site in South–Central Texas (Figure 1) [27]. Wetland conditions at the site are the result of seepage from sandstone reservoirs, and, importantly, the bog itself accumulates pollen mostly from the local bog sub-environment, according to its dimensions, after the aerodynamic model of Jacobsen and Bradshaw [28]. Within this site, containing only three radiocarbon dates, important finds of *Betula* pollen of Late Pleistocene age occur in bottom-set sediments. These finds suggest the use of changes in the range of *Betula* in the tracking of past Texas climate variability, given the present limit of *Betula* to high-rainfall regions of Texas today [8]. Also noted is testing work of the author at the pollen site at Palo Alto–Resaca in the Lower Rio Grande valley (Ref. [29], Figure 1), at the southern limits of the TGCP. Here, an assessment for the National Park Service of this site showed low arboreal pollen (tree and shrub pollen or “AP”) in the Middle and Late Holocene (please see the Palo Alto pollen diagram supplemental file). The appearance of *Carya* (cf. *illinoensis*) in a sample dating to the 6th millennium BP is significant at this latitude and indicates relatively mesic conditions at this interval. Conversely, a significant increase in xerophytic pollen is notable in the Late Holocene at Palo Alto, as indicated by a rise in Amaranthaceae pollen levels. Further vegetation history records for the TGCP and adjacent regions are also limited, but of note are data of grass phytoliths studied by Robinson for the Choke Canyon project directed by Tom Hester [30]. Data recovered at archaeological sites in Live Oak and McMullen Counties show two important trends. First is the composition of phytoliths recovered from “Middle Archaic” (4000–3000 BP) sites that contain phytoliths indicating xeric, short-grass flora. Subsequently, “Late Archaic” and “Transitional Archaic” (3000–1500 BP) sites at Choke Canyon contain a different phytolith assemblage that indicates mesic, long-grass flora.

Pan-Holocene studies of terrestrial fauna in the TGCP region are limited to coastal archaeological sites [19], to be discussed in the following section relating to sea-level changes. Regarding terrestrial fauna, the speleological site of Hall’s Cave in Central Texas, a Late Quaternary-age cave formed in Cretaceous limestone and containing Late Pleistocene- and Holocene-age sediments [31] is considered. The faunal studies at Hall’s Cave are unique for the state as a whole and are also considered pertinent to this work due to the near-continuous 13,000-year time depth of sediments in the sequence [32]. Within the strata of this cave examined by Toomey and others at the University of Texas at Austin, climate changes are assessed according to proxy data, and, specifically, climatic characteristics of rodents, including finds of the shrew taxa *Notiosorex* (desert shrew) and *Cryptotis* (small-eared shrew), each with desert versus forest distributions in Texas today. Trends noted by Toomey include a rise in *Cryptotis* in the Early Holocene, then circa 5000 BP, and, finally, from 2500 to 1000 BP, indicating afforestation and mesic conditions relative to today. Importantly, these trends are consistent with phytolith data from Choke Canyon with respect to a reconstruction of mesic conditions after 3000 BP. Combined regional proxy

climate data thus may be characterized as a succession of provisional xeric and mesic phases that can also be tested in relation to pollen data.

In this study, arboreal pollen (hereafter, AP, calculated as a percentage of total land pollen or TLP, excluding *Pinus*) is considered, with higher AP values indicating mesic conditions of higher precipitation and lower drought frequency, with lower AP indicating xeric conditions of greater moisture stress on plant communities. Relative climate changes assessed according to AP can also be employed to reconstruct past forest vegetation using pollen of modern samples from different vegetation zones. Such surface samples provide analogs for assessing afforestation levels at different localities within the TGCP region in the past. Further, special attention is paid to *Carya* in pollen diagrams, as this nut-mast tree is an important measure of woodland subsistence potential after 3000 BP (see Table 1). Notably, Texas archaeologists, including Brown [5] and Hall [6], link the development of cemeteries and increased settlement density post-3000 BP to increased exploitation of nut-mast trees, including a variety of oak, hickory and pecan species providing subsistence to human populations. Expected results (hypothesis testing) of stratigraphic pollen analyses are thus noted in column three in relation to four provisionally defined phases (“Climate model”) characterized as xeric versus mesic in aspect. The Early Holocene mesic phase is only provisionally defined according to faunal data (*Cryptotis* at Hall’s Cave). Subsequent climate phases are defined according to data from at least two sites.

3.2. Regional Sea-Level History

Past sea-level changes have also been a focus of study in the Western Gulf of Mexico region and include data of (1) sedimentary geology, (2) foraminiferal studies and (3) settlement archaeology. The geological work here includes sedimentation studies (based on offshore coring data) of Frazier from the continental shelf [33]. In work, sedimentary episodes on the continental shelf are interpreted in terms of still-stand conditions and increased discharge of fine sediments offshore, with a most significant phase of sedimentation post-dating 3000 BP. A second geological data point was identified by Mike Blum, in the morphological remains of a raised beach on Copano Bay, dated by foraminifera to circa 7700 BP [34]. This deposit, indicating a sea-level high stand in the earlier Holocene, is importantly proximal to the SL pollen site examined in this work. Sea-level changes at Copano Bare are also assessed according to foraminiferal studies at the Port Bay Marsh, in sediment cores examined by Harry Williams of the University of North Texas [35]. These studies reconstruct a sea-level still stand 3000 to 1000 BP, with resumption of sea-level rise after 1000 BP according to the benthic requirements of foraminifera encountered in the sediment core [35]. Notably, a single basal sample suggests a possible lowering of sea level around 5800 BP, but this is not considered conclusive by Williams [35]. Most recent geological work in the region includes the examination of multiple sediment cores in the Nueces River Delta by Rice and others for the National Science Foundation [36]. This major project defines multiple “retreats” of the Nueces River Delta, attributed to sea-level rise and lowered sedimentation. The most significant “retreats” of the delta date to (1) 6600 and (2) 3800 BP (Table 2).

Table 2. Summary sea-level history model and testing by palynology.

Sea-Level Period/Oscillation	Approx. Dating	Hypothetical Pollen Response
Earlier Holocene high stand	Circa 7700 BP	Salt-marsh pollen flora rise
Middle Holocene (1) still stand	6000–4500 BP	Freshwater estuarine pollen flora rise
Middle Holocene (2) high stand	4500–3000 BP	Salt-marsh pollen flora rise
Late Holocene still stand	3000–1000 BP	Freshwater estuarine pollen flora rise

Finally, archaeological settlement patterns between NB and BK in the TGCP region (Figure 1) studied by Robert Ricklis of the University of Texas at Austin for the National

Science Foundation [19] are considered. Within the region, large shell middens and other human occupation sites have been linked to freshwater estuarine conditions according to salinity indicative values of shell eco-facts and dated to two periods. An initial, low-density settlement period has been dated by Ricklis to the earlier part of the Middle (6000–4500 BP, Port Bay marsh base). Following a hiatus of coastal occupation (4500–3000 BP, retreat of Nueces River Delta defined by Rice [35]), a post-3000 BP settlement phase consisting of a large number of intensively occupied sites was then identified [37,38] (Port Bay marsh still stand defined by Williams [35]). Significantly, after 2000 BP, fish otoliths (*Sciaenops ocellatus* and *Pogonias cromis*) become numerous at shell midden sites in the TGCP [19], a trend linked by Ricklis to the development of barrier islands and thus sheltered breeding grounds for these aquatic faunas. These archaeological remains are ascribed to the activities of small bands of hunters and fishers, but during 3000 to 2000 BP, mortuary sites, possibly with greater human population densities, become common in the northern parts of the Lower Guadalupe and Brazos River valleys [38,39]. Conversely, a relative poverty of human settlement remains in the coastal zone is pronounced during certain periods, particularly 4500 to 3000 BP, which is associated with a hiatus in sedimentation on the continental shelf due to sea-level rise [33]. Combined proxy sea-level data thus may be characterized as a succession of sea-level rises and still stands hypothetically defined in four phases as follows (Table 2):

This four-phase model (“Sea-level model”) is tested through stratigraphic pollen data, with expected pollen responses noted in column three at sites (BK, SL and NB) also proximal to embayments, as described below (Section 4).

4. Materials: Pollen Site Sediment Cores

Pollen sites reported on here are influenced by coastal marsh flora in terms of their local settings and, moreover, crosscut the present forest limit of the oak–pine–hickory/pecan mixtures on the TGCP, this ecotone being determined by climate conditions. As such, pollen sites are suitable for testing both climate and sea-level models for the TGCP (Tables 1 and 2). These sites are geo-located, with environmental contexts described as follows:

- Buckeye Knoll (BK), Lower Guadalupe River valley, Central Texas Coast slack-water paleo-channel deposit, 28°39′16.4″ N, 96°57′40.0″ W (7 m a above msl); sediments were retrieved in a 4.8 m core via the Geo-probe 54 LT operated by Glenn Doran. The site is situated in a within the pre-Modern floodplain of the main river channel below the Holocene terrace of the Guadalupe River, approximately 500 m distant from Green Lake, an earlier Holocene embayment [39]. Modern lobes of the Guadalupe River are situated east of Green Lake. Earliest sediment core strata are thus in close proximity to the coast at the time of sedimentation. Present vegetation consists of mixed oak–pecan woodland. The sediment core is named after the adjacent Buckeye Knoll archaeological site (itself containing two further terrestrial sediment cores, “P2” and “P3”), designated during archaeological site mitigation for the US Army COE Galveston District.
- Swan Lake (SL), Copano Bay, Central Texas Coast estuarine deposit in incised Pleistocene valley, 28°3′10.2″ N, 97°9′49.9″ W (0 m above msl); sediments were retrieved in a 5.45 m core via the Geo-probe 54 LT. The site is accessed using a corduroy track built for the purpose. Sandy sediments below 5.45 m are poorly consolidated and have not been retrieved for detailed study. The sediment core is situated in an estuarine marsh consisting of *Typha domingensis* (cattail) and *Spartina spartinae* (cordgrass) approximately 2 km southeast of the entrance of the Mission River. The position of Copano Bay was stable in the Holocene [26]. The marsh sediment core is named after the adjacent Swan Lake archaeological site (itself containing one terrestrial sediment core, “S1”), designated by site records on file at the Texas Archeological Research Lab, University of Texas at Austin.

- Nueces Bay (NB), near Nueces River delta, Central Texas Coast pro-grading deltaic deposit, 27°50'19.3" N, 97°29'11.5" W (2 m below msl); sediments were retrieved in an 8.0 m vibracore. The site was accessed by a boat operated by Mike Blum and Robert Ricklis. This near-shore site is below sea level (ca. -2 m) but in close proximity (~50 m) to heavily disturbed shoreline vegetation consisting of *Salicornia* spp., Asteraceae and Poaceae. The position of Nueces Bay was stable in the Holocene [40], although changes in the position of the Nueces River Delta have been reconstructed according to sea-level and mean discharge factors during the Holocene [36]. The site is named after its project designation by Mike Blum and Robert Ricklis (for NSF grant no. SBR-942-3650).

Pollen site deposits described here (Tables 3–5) consist of reduced, largely mineragenic sediments in sub-aqueous settings, where pollen is preserved by virtue of a reducing environment and concentrated in low-energy settings [40]. The sediments are described according to Troels-Smith [41] and discussed in this section. First, at BK, sediments are based in Beaumont (Pleistocene) clay which is deeply weathered. Unconformably above the Beaumont, sandy strata occur with calcium carbonate nodules of possible marine biota origin suggestive of a near-coastal context prior to the progradation of the Guadalupe River beyond the Green Lake (earlier Holocene) embayment. The main (sandy silt) layer of the core whence most pollen samples originate is completely reduced, and an intermittent presence of *Rangia* fragments suggest a freshwater or marginally brackish floodplain environment. An increased terrestrial influence in the sedimentation regime of the core site is then suggested by oxidation evident in top-set aspects (90–130 cm, not sampled) and archaeological artifacts at the edge of a Late Archaic occupation of the Buckeye Knoll site. The latter include burned clay from hearths.

Table 3. Troels-Smith’s description of Buckeye Knoll (BK) sediments [41].

Depth Range	Granulometry	Munsell Hue	Other Notes
0–45 cm	Silt 3, sand 1, humus +	10 yr3/1 very dark gray	Humus 0–10 cm
45–60 cm	Clay 3, silt 1	10 yr4/1 dark gray	
60–90 cm	Clay 3, silt 1	10 yr3/1 very dark gray	
90–110 cm	Clay 3, silt 1	10 yr5/2 grayish brown	Redox (red-colored) features
110–120 cm	Clay 2, silt 1, sand 1	10 yr2/1 black	Redox (red-colored) features, burned clay nodules
120–130 cm	Silt 2, sand 2	10 yr3/1 very dark gray	
130–145 cm	Clay 3, silt 1	10 yr5/2 grayish brown	
145–450 cm	Clay+, silt 3, sand 1	10 yr3/2 grading to 3/1	<i>Rangia</i> shell fragments
450–460 cm	Silt 1, sand 3	10 yr4/1 dark gray	CaCO ₃
460–490 cm	Clay 1, sand 3	10 yr5/1–6/2 gray grading to light brownish gray	
490–550 cm	Clay 4	10 yr7/4 very pale brown	Deep weathering

Table 4. Troels-Smith’s description of Swan Lake (SL) sediments [41].

Depth Range	Granulometry	Munsell Hue	Other Notes
0–12 cm	Clay 3, silt 1	10 yr3/1 very dark gray	Illuviation of clay
12–53 cm	Sand 4	10 yr5/1 gray	Lower limit limus 4 (sharp boundary)
53–81 cm	Clay 3, silt 1	10 yr3/1 very dark gray	Illuviation of clay
81–285 cm	Clay 3, silt 1	10 yr5/1 gray	Redox (red-colored) features
285–305 cm	Sand 4	10 yr5/1 gray	Lower limit limus 4 (sharp boundary)
305–460 cm	Clay 3, silt 1	10 yr5/1 gray	
460–480 cm	Sand 4	10 yr5/1 gray	Lower limit limus 4 (sharp boundary)
480–525 cm	Clay 3, silt 1	10 yr5/1 gray	
525–548 cm	Sand 4	10 yr5/1 gray	Slumping 548–600 cm

Table 5. Troels-Smith's description of Nueces Bay (NB) sediments [41].

Depth Range	Granulometry	Munsell Hue	Other Notes
0–60 cm	Clay 3, sand 1	10 yr6/1 gray	
60–140 cm	Clay 2, sand 2	10 yr6/1 gray	
140–240 cm	Clay 3, sand 1	10 yr6/1 gray	
240–300 cm	Clay 2, sand 2	10 yr6/1 gray	<i>Rangia cuneata</i> layer
300–400 cm	Clay 3, silt 1	10 yr6/1 gray	
400–440 cm	Clay 3, silt 1	10 yr6/1 gray	<i>Rangia flexuosa</i> layer
440–790 cm	Clay 3, silt 1	10 yr6/1 gray	

Swan Lake sediments are represented by intervals of sand and fine sedimentation. A massive basal sand deposit, only partly retrieved by the Geoprobe 54 LT, extends to a minimum depth of six meters (or a minimum thickness of 75 cm). This basal deposit might be interpreted as an earlier Holocene beach remnant. Three subsequent sand strata (20–41 cm thick) then exhibit sharply defined lower boundaries (limus score: 4/4 [41]) and might be interpreted as storm splays with a shoreward and longshore reworking of barrier island sands. Important for the question of pollen preservation/degradation, redox features have, furthermore, been noted between 285 and 81 cm (oxidation). Moreover, a possible paleosol is evident (82–53 cm, with clay illuviation), representing a period of reduced marine influence. It is possible that increased terrestrial influence led to diagenetic oxidation in underlying sediments to a depth of 285 cm. Finally, a relatively uniform sequence, dominated by light-gray reduced fines with variable sandy inputs, was observed at NB. This final sequence contains two dense layers of clam, each constituted of a different species: *Rangia flexuosa* in the lower layer and *R. cuneata* in the upper aspect, which have been interpreted as shellfish beds [42].

5. Methods

5.1. Pollen Sampling of Sediment Cores

Work at the alluvial pollen sites reported here was guided by practical experience at multiple sites of this type in the Old and New World, beginning with work on sediments of interdigitated organic and mineragenic aspect in the chernozem lowlands [43]. These sites provided a basis for further site selection and site analysis in major projects, for example, among sites in North Mexico (Refs. [44–46], University of Texas Laguna Project) and East Texas (Refs. [47,48], Texas Department of Transport, Environmental Affairs Division mitigation projects). This research has shown the potential of slack-water alluvial sites with fine sedimentation for pollen analysis. In this work, pollen sampling avoided coarse sands (pollen concentration potential low) at NB and oxidized deposits (pollen preservation potential low) at SL and BK. Further, at NB, aspects of the core were not sampled due to the presence of dense *Rangia* shell strata that provide insufficient sediment for laboratory work.

5.2. Analog Methods in the Reconstruction of Tropical Conditions

The potential growth of mangrove trees (mangle) at the examined pollen sites was established through the use of pollen analogs, with the ultimate aim of reconstructing relative tropical influence at examined pollen sites. These mangrove tree analogs included two sites where stands of *Avicennia* (cf. *germinans*) native to Texas were found and two sites consisting of stands of *Rhizophora* (cf. *mangle*) native to tropical Mexico and Florida. Importantly, *Rhizophora mangle* is excluded from the TGCP today due to climatic requirements, including the poor frost-resistance of this species. The actual presence of these taxa, found in sediment cores in the past vegetation of the study region, was ascertained by sediment surface samples collected from present stands. From the perspective of climate reconstruction, a presence of *Rhizophora* indicates a more tropical regime and, inferably, a major shift in the boundary of the Intertropical Convergence Zone in the past, with the

exclusion of freezing conditions in winter weather (patterns driven by jet-stream drag of Arctic fronts [49]), with a high sensitivity to temperature conditions in terms of its pollen response [14]. Surface analogs from four mangrove sites in South Texas, North Mexico and Central Florida were sampled using ten pinch samples of 1 cc volume separated by a minimum distance of 1 m. Mangrove pollen analog sites from widely separated areas were chosen according to the northern distribution limits of the main two genera (*Rhizophora* and *Avicennia*):

- *Rhizophora* Site 1, La Pesca, Tamaulipas State, Mexico, Gulf of Mexico Coast, 23°46'4.3" N 97°44'21.3" W (0 m amsl). The site consists of a one-hectare red mangrove mangle in coastal shallows north of La Pesca accessed during a special-purpose trip.
- *Rhizophora* Site 2, Orchid Island, Atlantic Coast, Florida, 27°51'30.2" N 80°27'33.9" W (0 m amsl). The site consists of a multi-hectare (10 + hectare) red mangrove mangle in the Indian River estuary south of Orchid Island. The center of this red mangrove stand was sampled in a one-hectare area accessed during a special-purpose trip.
- *Avicennia* Site 1, Laguna Atascosa Wildlife Refuge, Texas, Gulf of Mexico Coast, 26°12'13.9" N 97°24'44.7" W (2 m amsl). The site consists of a ten-hectare black mangrove mangle in a coastal depression in the Laguna Atascosa Wildlife Refuge. The outer edge of this black mangrove stand was sampled.
- *Avicennia* Site 2, Laguna Atascosa Wildlife Refuge, Texas, 26°12'17.6" N 97°24'48.8" W (2 m amsl). The site consists of a ten-hectare black mangrove mangle in a coastal depression in the Laguna Atascosa Wildlife Refuge. The center of this black mangrove stand was sampled.

5.3. Reconstructing Tree-Limit Oscillations and Precipitation Changes

Towards the testing of the climate conceptual model (Table 1), relative (mesic vs. xeric) climate conditions were assessed according to multiple lines of evidence, including changes in the southern limit of the Southeast US Forests (oak–pine–hickory/pecan mixtures) in the TGCP. Pollen data from three sites presented in detail here, as well as supplemental data (please see the Palo Alto pollen diagram supplemental file) from the southern limit of the TGCP, provided initial pollen data for reconstructing levels of afforestation along a 400 km coastal transect over the last 8000 years. Analogs comparing actual afforestation levels to AP used (Modern) near-surface or top-set samples in sediment cores with the aim of defining prairies and forests in pre-Modern pollen spectra. Modern, top-set spectra were thus used as analogs for past vegetation reconstruction and established a statistical baseline for defining the forest–prairie ecotone based upon ideal vegetation types. The types considered included “prairie” (consisting of interfluves dominated by grasses and forbs and alluvial woodlands mostly restricted to riparian verges) and forest (with partially wooded interfluves near the ecotone and extensive alluvial woodlands on the floodplains of major rivers). Here, the minimal arboreal threshold for “forest” vegetation was defined palynologically by the lower boundary of the AP percentage 95% confidence interval at the forest vegetation type site at BK (AP%_s above this threshold thus indicate forest), while the maximal arboreal threshold for “prairie” vegetation was defined by the upper boundary of the AP percentage 95% confidence interval at the forest vegetation type sites close to the present ecotone (NB and SL; see Sections 6.2.1–6.2.3). The ecotone, which is a transition as opposed to a sharp biogeographic boundary, itself lies between the BK and SL sites, and AP% values in between the limits described above were considered indeterminate, with the default assumption being made that Modern-type vegetation was present. Past vegetation changes were reconstructed according to vegetation at three reported pollen sites (and the Palo Alto pollen site in the supplemental data). This forest-limit reconstruction defined as “mesic” any southward advance of the forest limit beyond the Guadalupe River valley. A northward forest migration beyond the Guadalupe River valley (i.e., prairie environment reconstructed at all sites) defined a “xeric” interval. In the calculation of AP percentages, long-distance transport types, particularly *Pinus*, were excluded from the AP sub-total.

The reconstruction of precipitation changes in relation to forest-limit changes focused on climatically sensitive taxa, such as *Betula*. In this work, the pollen percentage values of *B. nigra* [9], in particular, were considered—*B. nigra* being a tree whose precipitation requirements are of value in climate reconstruction in the regional context, thriving in East Texas today on relatively shaded and wet floodplains [10–12]. Analyses of *Betula nigra* pollen recorded in examined pollen sites [9] focused on establishing a range presence in the TGCP according to sustained (2+ consecutive samples) and significant (2+% TLP) values. This standard was intended to exclude statistical outliers, including occasional long-distance transport of pollen grains and short-term, localized growth of this tree beyond its main range. As noted above (Section 3), *Betula* exhibited a major extension of its range in the Late Pleistocene and Early Holocene in South–Central Texas, while Modern precipitation variability in the TGCP itself is significant, with a steep gradient extending into Eastern Texas (see Section 2, above). In this study, a key reference point for climate reconstruction was provided by precipitation levels observed at the western range limit of *B. nigra* in Eastern Texas (~116 cm *per annum* [8,12]). Beyond this limit, seasonal moisture stress in river-valley floodplains prevents its growth, and it is presently excluded from the Colorado and Guadalupe River valleys.

5.4. Relative Sea-Level Changes

The examined sites in the present study region (see Section 2) are situated in proximity to estuarine environments that are potentially affected by sea-level changes. These are classified as salt marshes and freshwater marshes, the biota being determined by the salinity gradients of their constituent water bodies. In this study, a low biomass salt-marsh flora was defined, including most importantly Amaranthaceae and Bataceae, plant families tolerant of salty soils and saline wet areas. Sea-level transgressions promote the formation of these salt-marsh taxa. Conversely, stable sea level (still stands) allows delta sedimentation to attain equilibrium with base sea level, promoting also the formation of shallows in prograding deltaic regions and embayments. These shallows are prerequisites for the development of a high-biomass freshwater marsh flora. This freshwater marsh biota includes plant taxa represented by pollen types including *Nymphaea*, *Potamogeton*, *Polygonum hydropiper* and *Typha* spp. Importantly, these taxa include aquatic and insect-pollinated species that are poorly dispersed and thus under-represented in pollen diagrams.

5.5. Pollen Lab Techniques

Ten-cubic-centimeter sample volumes were employed with reduction to pollen facilitated by a multi-stage process. Following deflocculation via 5% sodium hexa-metaphosphate filtering and filtration through 177-micron and 8-micron (Nitex) screens, respectively, samples were treated with HCL and KOH and 49% hot HF. At the HCL stage, a *Lycopodium* tablet was also added for the calculation of pollen concentration. Acetolysis was limited to less than 60 s (with acetic acid). Samples were dyed in saffranine and tetra-butanol and placed in 2000-viscosity silicone oil for purposes of light microscopic work [50].

5.6. Methods of Interpretation

Pollen diagrams were drawn using the TILIA program. Zonation was performed using a stratigraphically constrained incremental sum of squares cluster analysis according to percentage data, facilitated by the CONISS program of Eric Grimm [51]. This measures the dissimilarity of sample clusters in terms of Edwards and Cavalli-Sforza's chord distance. A uniform chord distance is chosen in each diagram for grouping of pollen spectra into stratigraphic zones. Pollen taxa are grouped according to the divisions of trees and shrubs on the one hand and herbaceous pollen on the other.

In terms of inferring land areas represented by the analyzed pollen data, the examined sites were divided into inland and coastal groups that may vary in aspect through time according to river sedimentation and delta progradation, influencing the representative flora in different geographic zones. Differential taphonomic characteristics may also be

inferred according to geographic context itself. For example, a prevalence of air vs. water transport of pollen grains might be determined by the position of the sediment core relative to river entrants or position within a floodplain, where an alluvial situation, in particular, favors water transport. In estuaries at a remove from river entrants, air transport of pollen generally prevails, and at SL a significant component of sea transport of floating saccate grains, such as *Pinus* grains, into tidally influenced deposits might also be expected (Table 6). NB, a fully submergent site, is less subject to major influxes of floating saccate pollen grains.

Table 6. Inferred taphonomic characteristics of pollen sites (BK, SL and NB).

	Pollen Taphonomy	Coastal Floral Component	Inland Floral Component
BK	Fluvial hydrological pre-2000 BP, air and gravity deposition post-2000 BP	Significant pre-7000 BP, minimal post-7000 BP	Dominant (regional pre-2000 BP, local post-2000 BP)
SL	Air and gravity, sea transport (<i>Pinus</i>)	Dominant, local	No significant representation
NB	Fluvial hydrological from inland areas, air transport from coastal areas	Significant, local	Significant, regional

5.7. Dating Methods

For chronological control, nine samples (~10 cc) of bulk sediments were dated via AMS 238 (and one by standard radiocarbon in the case of Beta 164200). The humic acids derived from such bulk sediments originate principally from shallow A-horizons of regional soils. Bulk sediments used in dating were screened for rhizomous, indeterminate wood and indeterminate molluscan or gastropod remains in a 177-micron brass screen from cleaned, one-meter-long sleeved sediment core segments. Rhizomous and indeterminate wood were removed with a view to potentially erroneous dating caused by penetrated tree or herb roots. Indeterminate molluscan or gastropod remains were not considered for dating, as their biotic origins, potentially affecting the dating methodology, were unknown. Such pre-processed sediments were mailed to the Beta Analytic Radiocarbon Laboratory in Miami, Florida, with instructions to assay the humic fraction of each bulk sediment sample. Radiocarbon and AMS dating performed by Beta Analytic employed the CALIB program [52]. Linear age estimates for the dating of sediments used a median calibrated age. Bayesian methods that presume uniformitarian sedimentary conditions were self-evidently not applicable. Expressions of age were made in terms of (calibrated) years before present (BP) significant to century-level timescales.

6. Results

6.1. Dating

All AMS and standard radiometric dates at the examined pollen sites were sequential with respect to depth (Table 7). Inferably, low-energy sites chosen here reduced the potential for the re-working of dated material. The median ages of calibrated ranges of delta-Carbon 13-corrected dates were used for linear age estimates of pollen zones (Sections 6.2.1–6.2.3). These estimates at BK and SL are indicated within a two-Sigma error band (Figures 2 and 3). The age of BK 1 (Section 6.2.1 below) was estimated to be 9300 to 8300 BP after the sedimentation rates established by the lowest two AMS dates here. The dating of this zone was thus extrapolated.

Table 7. Pollen site dating by radiocarbon, geology and biostratigraphy. Materials for dating BK and SL derived from bulk sediments in sediment cores. The dating of the NB site relied on relative biostratigraphic indications of *Rangia* spp. according to finds in regional archaeological sites and geological dating according to the emergence of base-level conditions at the coring site (delta formation at site sedimentation itself prior to 8000 BP can thus be excluded).

Pollen Site	Depth (cm)	Material Dated	Lab Number	¹⁴ C Age	Calibrated Age BP	Relative Age BP
BK	420–440	Humic fraction	Beta 164222	6820 ± 40	7700–7660	N/A
BK	370–390	Humic fraction	Beta 16421	5260 ± 40	6010–5940	N/A
BK	240–260	Humic fraction	Beta 164220	4420 ± 40	5050–4950	N/A
BK	190–210	Humic fraction	Beta 164200	3920 ± 40	4420–4290	N/A
BK	150–170	Humic fraction	Beta 164218	2780 ± 110	3210–2740	N/A
BK	70–90	Humic fraction	Beta 164217	1840 ± 40	1830–1720	N/A
SL	490–510	Humic fraction	Beta 194902	6130 ± 40	7130–6940	N/A
SL	425–450	Humic fraction	Beta 194901	5150 ± 40	5940–5790	N/A
SL	250–280	Humic fraction	Beta 194899	3920 ± 40	4410–4290	N/A
SL	80–102	Humic fraction	Beta 194900	130 ± 50	250–0	N/A
NB	790–800	Core base level	N/A	N/A	N/A	Geological 8000 max.
NB	400–450	<i>Rangia flexuosa</i>	N/A	N/A	N/A	Biostrat. 6000–4500
NB	250–300	<i>Rangia cuneata</i>	N/A	N/A	N/A	Biostrat. post-3000

Important for the relative dating of NB, Central Texas Coast shell middens, including those situated around Nueces Bay itself, exhibited an absolute shift of composition of clam species between 6000 and 4500 (*Rangia flexuosa*) and post-3000 BP (*R. cuneata*). The absolute chronological separation of *Rangia* species derived from a corpus of archaeological work on the TGCP [32], expressed by an absence of shell midden sites altogether in the interval from 4000 to 3000 BP, according to radiocarbon dating of shell midden sites. The relative dating of NB pollen core shell layers at 400 to 450 cm (with *R. flexuosa*) and 250 to 300 (with *R. cuneata*) cm follows this biostratigraphic pattern for relative dating. Further limits on the absolute age of the NB core follow from base-level conditions necessary for sedimentation of a reduced and prograding deposit, as low sea level until 8000 BP would preclude such sedimentation [36]. From this, as a relative geological dating, the 7.9 m base of NB may be no older than 8000 BP [15].

6.2. Palynology

Laboratory techniques allow for the achievement of pollen counts ranging from 150 to 600 grains per sample in large samples. It is noted that a maximal differentiation of pollen taxa was achieved in conjunction with University of Texas at Austin Herbarium (Main Building) materials. A differentiation of *Carya* was not absolutely achieved, but a tendency of the examined pollen grains from BK and NB to exhibit relatively heavy exine thickening around pores was noted which corresponded to *Carya illinoensis* (this was less evident in hickory species of *Carya*). An absolute separation of all individual specimens was not possible. It was further noted that the *Betula* pollen grains encountered exhibited poor vestibulum development (thin endexines) and very likely belonged to the species *B. nigra* or river birch, according to comparative morphology [9]. Preservation was pristine for the examined samples. All dating estimates below are presented as calibrated ages in years BP.

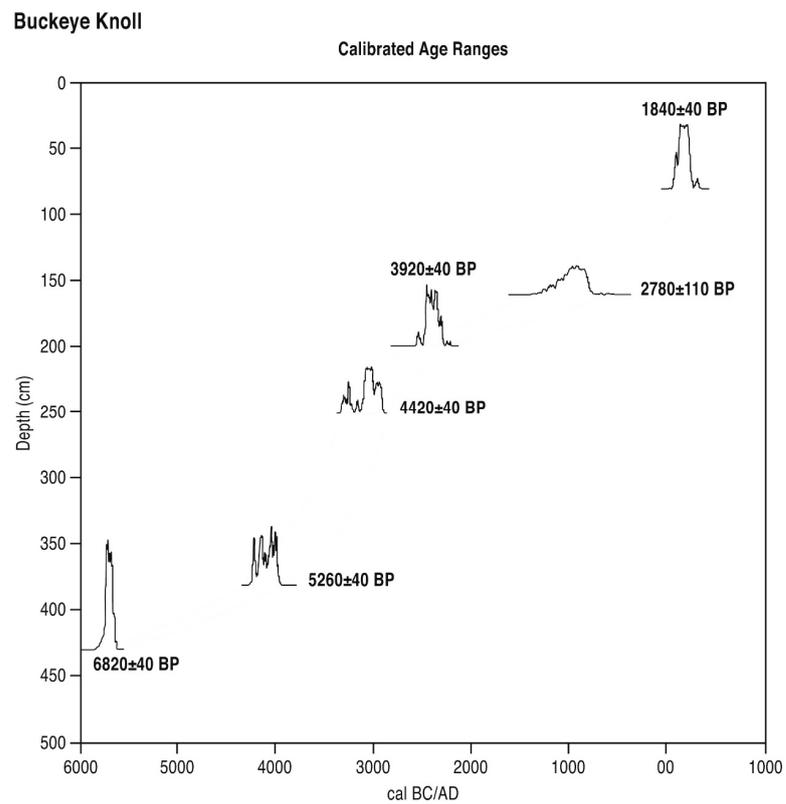


Figure 2. Age–depth graph of probability distributions of individual AMS and standard radiocarbon dates at Buckeye Knoll (BK) pollen site. Linear age estimates for dating of sediments used median calibrated ages.

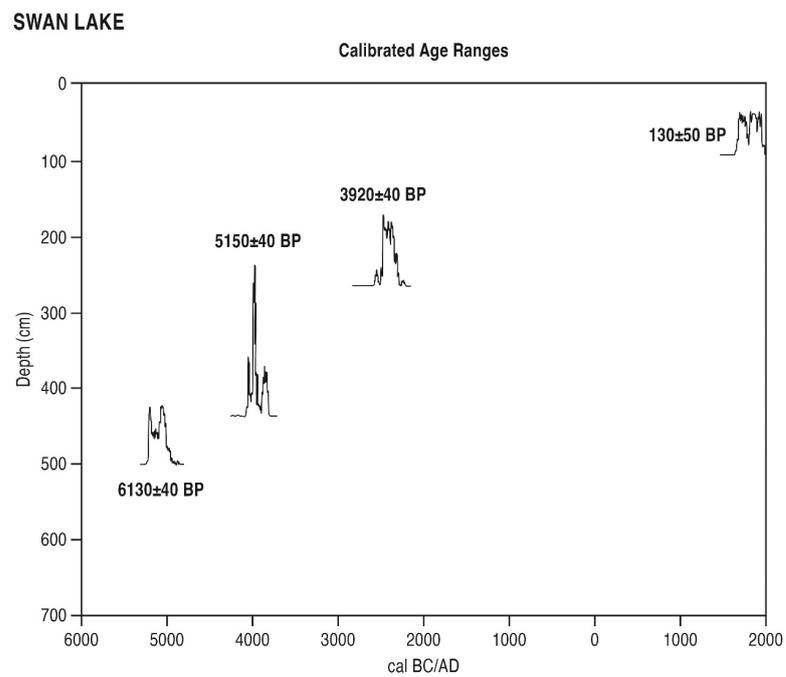


Figure 3. Age–depth graph of probability distributions of individual AMS and standard radiocarbon dates at Swan Lake (SL) pollen site. Linear age estimates for dating of sediments used median calibrated ages.

6.2.1. Buckeye Knoll (BK, Figures 4 and 5)

BK Zone 1 (450–480 cm, est. 9300–8300 BP) *Quercus* (29.2% max.), *Carya* (8.8% max.), *Betula* (5.4% max.) and riparian *Salix* are important trees and shrubs in this pollen zone. Isolates of *Alnus* and *Acacia* are noted here. Poaceae (30.7% max.), Asteraceae and other composites are important herbs. *Artemisia* is present, while values of the xerophyte Amaranthaceae rise (4.2–22.4%). An *Opuntia* isolate is noted. Freshwater isolates include Cyperaceae.

BK Zone 2 (420–440 cm, 8000–7300 BP). Amaranthaceae values (26.7% max.) remain elevated in this zone, while values of tree pollen (esp. *Carya* and *Betula*) decline; however, those of shrubs of the riparian verge as represented by *Salix* remain unchanged (ca. 5–6%). Isolates of *Acacia* and *Palmae* are noted. Herbs include most importantly Poaceae and Asteraceae. Isolates of Cyperaceae are noted.

BK Zone 3 (350–410 cm, 7000–5750 BP). Amaranthaceae pollen levels decline (20.9% min.) in this zone, while tree pollen, particularly *Quercus* (39.0% max.), rises. *Carya* establishes a significant presence (ca. 4–6%). Herbs include most importantly Poaceae and Asteraceae. Isolates of Cyperaceae are also noted.

BK Zone 4 (327 cm, 5600 BP). A secondary maximum of Amaranthaceae pollen (48.7%) is noted here as *Quercus* pollen declines to an absolute minimum (3.7%) as other trees decline. Forbs, as represented by general Asteraceae, exceed grasses, as represented by Poaceae pollen for the first time. Cyperaceae rises here.

BK Zone 5 (237–307 cm, 5400–4800 BP). Tree and shrub pollen led by *Pinus* (15.6% max.), *Quercus* (40.8% max.), *Carya* (19.6% max.), *Betula* (11.7% max.), and *Salix* (7.7% max.) increases very significantly in this zone as Amaranthaceae pollen declines markedly (to 0.5% min.). Isolates of *Juglans*, *Alnus*, and *Myrica* are noted. Poaceae rises (to 18.9% max.), also, as Asteraceae declines (to 4.4% min.). *Typha* grains are further noted.

BK Zone 6 (217 cm, 4600 BP). *Quercus* (44.3%) dominates tree pollen here, while lower levels of *Carya*, an absence of *Betula*, and isolates of *Fraxinus* and *Myrica* are noted. Herbaceous pollen is represented by lower values of Poaceae (10.8%) and Asteraceae (6.7%).

BK Zone 7 (167–207 cm, 4400–3200 BP). Lower *Quercus*, oscillating values of *Carya*, and rising *Salix* characterize the tree and shrub pollen of this zone. Herbaceous pollen, particularly Asteraceae (absolute max. 52.5%), rises as Amaranthaceae also increases somewhat (10.5% max.). An isolate of *Typha* is noted.

BK Zone 8 (137–157 cm, 2900–2600 BP). A further rise of *Carya* (18.1% max.) is noted along with *Quercus* pollen as *Salix* declines in this zone. Herbaceous pollen is constituted principally of Poaceae as Asteraceae declines (to 4.9% min). A maximum of Cyperaceae (10.3%) is noted.

BK Zone 9 (37–80 cm, 1800–400 BP). Tree and shrub pollen consists largely of (declining) *Quercus*, (oscillating) *Carya* and *Salix* in this zone. Isolates of *Fraxinus*, *Myrica* and *Acacia* are noted. Herbaceous pollen consists largely of Poaceae and Asteraceae, while an absolute maximum of Amaranthaceae pollen (58.6%) is noted.

6.2.2. Swan Lake (SL, Figure 6)

SL Zone 1 (481–525 cm, 7100–6650 BP). Relatively low levels of *Quercus* pollen are observed here, along with isolated *Ulmus*, *Betula*, and *Salix*. A rational representation of *Avicennia* is observed. Herbaceous pollen consists largely of Amaranthaceae with a significant admixture of Poaceae, Asteraceae, and Bataceae pollen. Freshwater types are represented by isolates only of *Typha* and Cyperaceae.

Buckeye Knoll Core P1, Texas, palaeo-channel deposit (7 m above msl, 28°39'16.4"N 96°57'40.0"W), relative pollen diagram

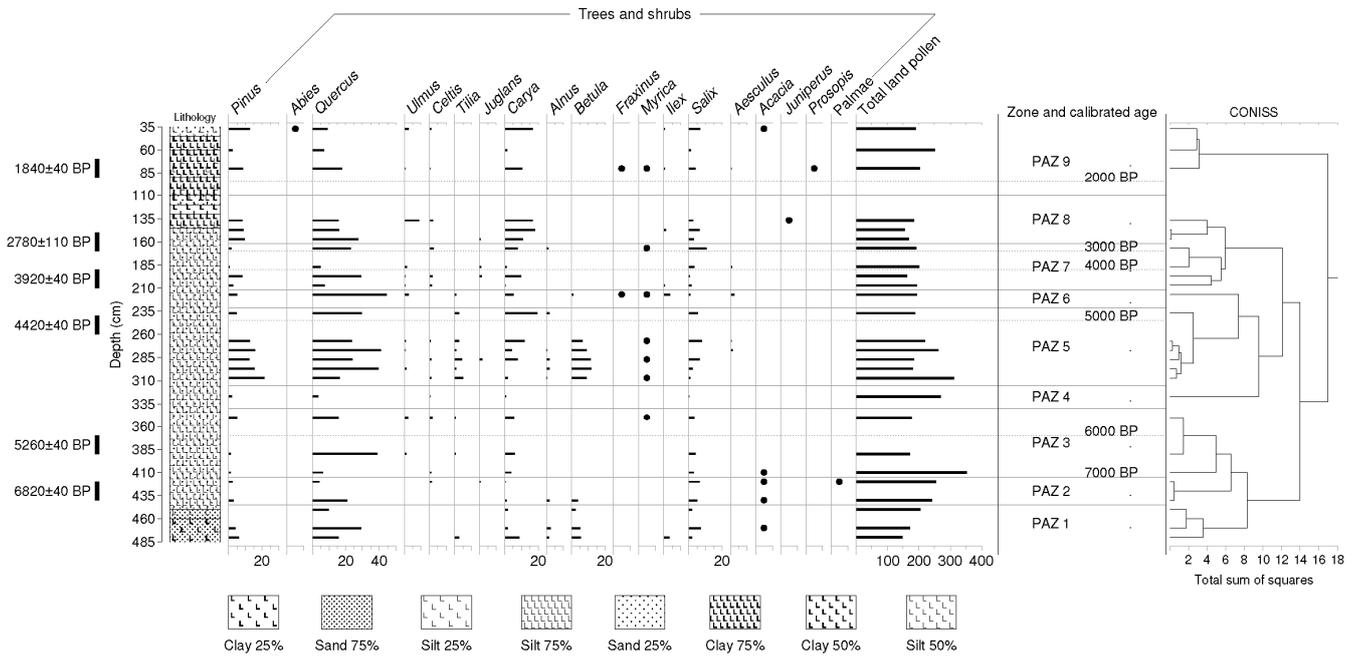


Figure 4. Buckeye Knoll (BK) relative pollen diagram (arboreal pollen as percentage of TLP) and Troels-Smith lithology. Note redox (red coloration) features.

Buckeye Knoll Core P1, Texas, palaeo-channel deposit (7 m above msl, 28°39'16.4"N 96°57'40.0"W), relative pollen diagram

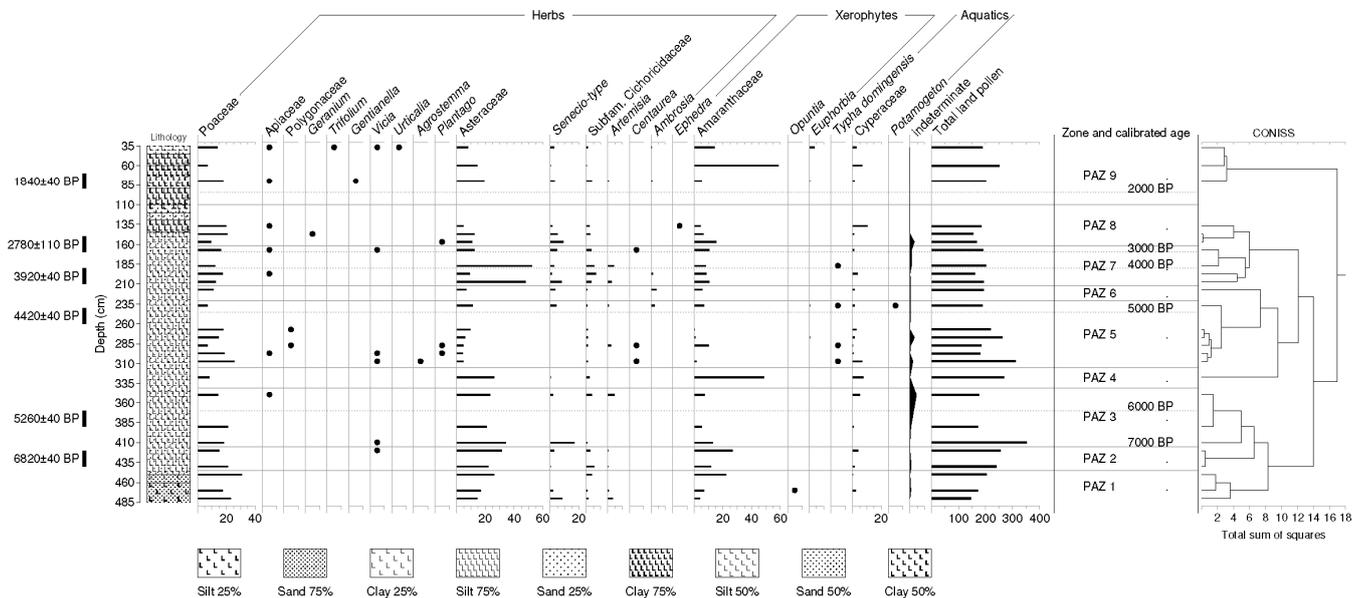


Figure 5. Buckeye Knoll (BK) relative pollen diagram (non-arboreal pollen as percentage of TLP) and Troels-Smith lithology. Note redox (red coloration) features.

SL Zone 2 (452 cm, 5800 BP). Pollen types of trees and shrubs, including, most importantly, *Quercus*, *Pinus*, *Carya*, and *Betula*, rise in this zone. Isolated *Alnus* and *Myrica* also appear here. Herbaceous pollen types include rising *Poaceae* and *Asteraceae*. Notable are finds of *Opuntia* and *Artemisia* pollen. A rise in *Typha* and *Cyperaceae* pollen is observed.

SL Zone 3 (284–425 cm, 5700–4250 BP). Pollen types of trees and shrubs, including, most importantly, *Quercus* and *Carya*, decline in this zone. Isolated *Ulmus*, *Celtis*, *Alnus*, *Myrica*, *Salix*, *Prosopis* and *Avicennia* also appear here. Herbaceous pollen types include

rising Poaceae and Asteraceae, along with declining Amaranthaceae. Initial *Potamogeton*, *Polygonum hydropiper* and declining Cyperaceae pollen are further observed here.

SL Zone 4 (247 cm, 3650 BP). Pollen types of trees and shrubs, including *Quercus* and *Celtis*, rise in this zone. Isolated *Fraxinus* also appears here. Herbaceous pollen types include rising Poaceae and Asteraceae, along with declining Amaranthaceae. *Typha* pollen is also observed.

SL Zone 5 (230 cm, 3450 BP). Pollen of trees and shrubs, including, most importantly, *Quercus*, decline in this zone. Isolated *Avicennia* also appears. Herbaceous pollen types include Poaceae and Asteraceae, along with rising Amaranthaceae and a Bataceae grain.

SL Zone 6 (213 cm, 3050 BP). Pollen of trees and shrubs, including, most importantly, *Pinus* and *Quercus*, rise in this zone. Isolated *Celtis* and *Alnus* also appear. Herbaceous pollen types include declining Poaceae and Asteraceae, along with rising Amaranthaceae. Low levels of *Typha* and an isolated *Potamogeton* grain are noted.

SL Zone 7 (10–114 cm, 700 BP to recent). Pollen of trees and shrubs declines progressively in this zone. Isolated *Alnus* and *Myrica* also appear. Herbaceous pollen types include rising Poaceae and Asteraceae, along with moderate levels of Amaranthaceae and rising terminal values of *Typha* and Cyperaceae. An isolate of (freshwater) *Nymphaea* is further noted. Finally, low levels of both *Opuntia* and *Ambrosia* are observed here.

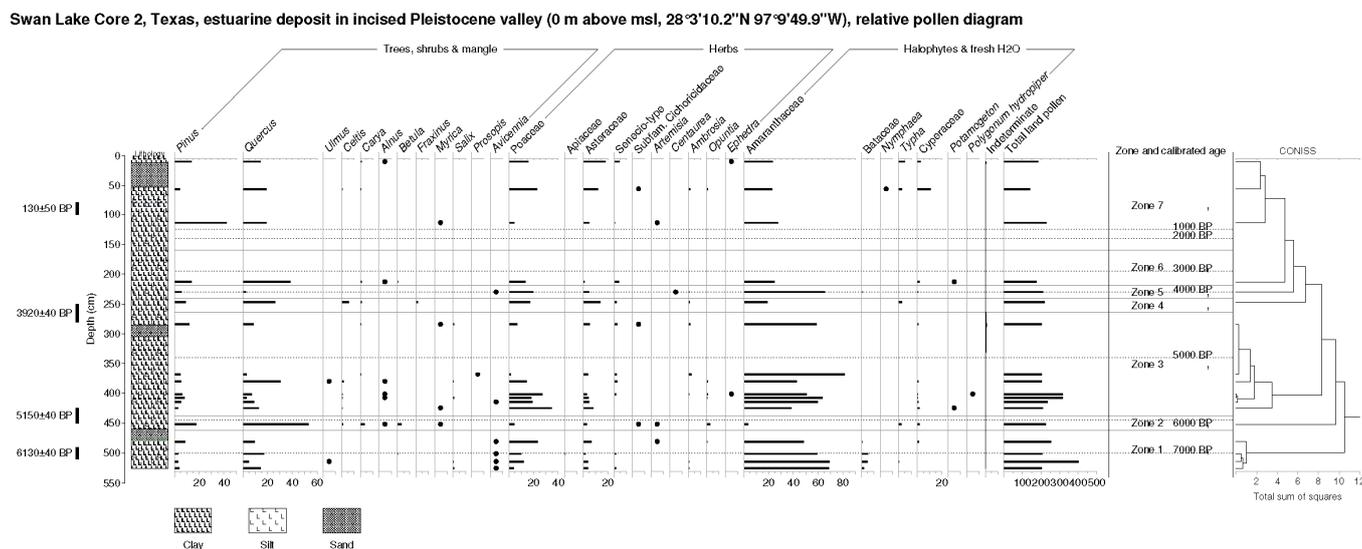


Figure 6. Swan Lake (SL) relative pollen diagram (percentage of TLP) and Troels-Smith lithology. Note redox features and pollen hiatus 130–280 cm and absence of pollen samples in sand layers.

6.2.3. Nueces Bay (NB, Figure 7)

NB Zone 1 (549–793 cm, ~8000–6000 BP). Arboreal pollen (esp. *Quercus*, *Celtis*, *Ulmus* and *Salix*) rises in this zone. Isolates include *Juglans*, *Alnus*, *Betula*, *Myrica*, *Rhamnus*, *Rhus*, *Acacia*, *Prunus*, *Prosopis*, *Ericaceae* (cf. *Arbutus*) and *Avicennia* (terminally). Herbaceous pollen types include Poaceae and Asteraceae, along with declining Amaranthaceae (site max., at base of sequence) and rising terminal values of *Typha* and Cyperaceae.

NB Zone 2 (366–519 cm, ~6000–4500 BP). Levels of AP, including *Quercus*, *Celtis* and *Salix*, are stable. In addition to moderate levels of *Pinus*, isolates of *Alnus*, *Betula*, *Acacia*, *Prunus*, and *Prosopis* occur. A near-rational representation of isolates of *Avicennia* as well as *Rhizophora* is achieved. Among herbaceous pollen types, Poaceae values decline somewhat, while those of Asteraceae and Amaranthaceae remain stable. Pollen grains of *Vicia* and *Apiaceae* are further noted. Freshwater plant pollen now includes *Typha*, Cyperaceae, *Polygonum amphibium* and *Mentha*.

NB Zone 3 (31–336 cm, post-4000 BP). With the exception of *Pinus*, AP declines, led by *Quercus*, *Celtis* and *Salix*. Isolates of *Ulmus*, *Carya*, *Juglans*, *Alnus*, *Fraxinus*, *Acacia*,

Mimosa, *Prunus* and *Avicennia* occur. Non-arboreal pollen, led by Poaceae, Asteraceae and Amaranthaceae, are oscillatory. Maxima of *Typha* and Cyperaceae are noted in the middle part of this zone (~3000 BP).

Nueces Bay, Texas, prograding deltaic deposit (~2 m below msl, 27°50'19.3"N 97°29'11.5"W), relative pollen diagram

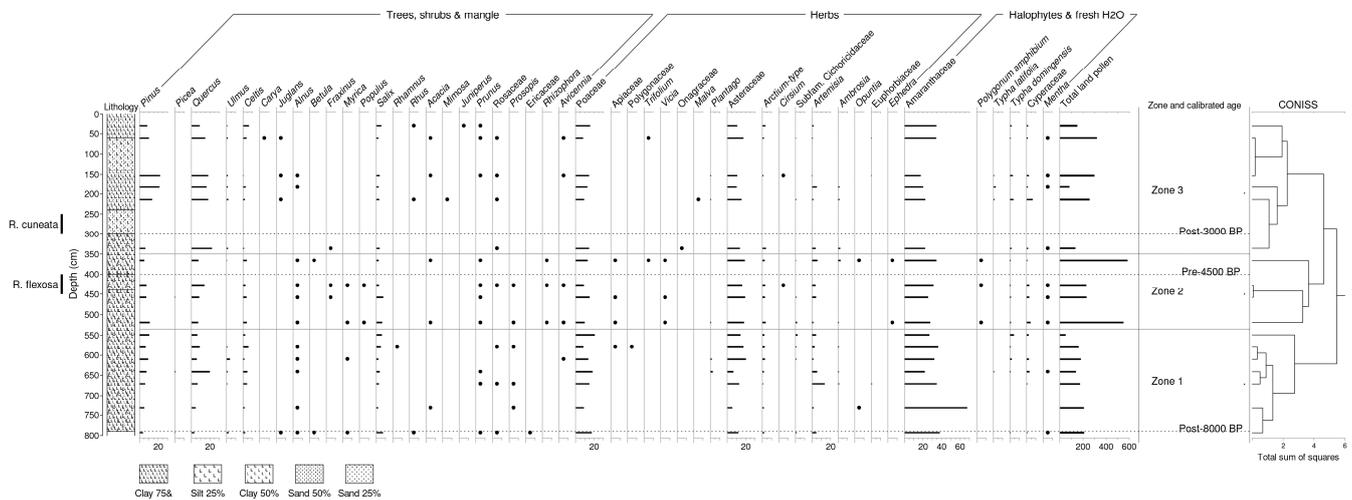


Figure 7. Nueces Bay (NB) relative pollen diagram (percentage of TLP) and Troels-Smith lithology. Note that the shellfish stratum with *Rangia cuneata* is unsampled due to the density of this shellfish bed.

6.2.4. Definition of the Forest–Prairie Ecotone

In the reconstruction of the past, the forest–prairie vegetation changes in the TGCP; a definition of the regional forest–prairie ecotone according to pollen statistics is necessary. In this section, the most recent, top-set samples of the examined pollen sites and the supplemental site of Palo Alto at the southern limit of the TGCP are employed (as analogs) to define the forest–prairie ecotone in terms of AP percentage levels. The sum of AP is calculated as all tree and shrub pollen minus (long-distance) *Pinus* pollen. These samples were used to statistically define ideal vegetation types, with error bands of the AP level defined by upper confidence limits of AP (%) at prairie sites and the lower confidence limit of AP (%) at the forest site (BK). According to pollen analyses (Sections 6.2.1–6.2.3, please see the Palo Alto pollen diagram supplemental file), the top-set samples at BK, SL, NB and Palo Alto produced AP values ranging from 36.5% at BK in the north to 3.5% at Palo Alto in the south. Notably, top-set AP levels at SL and NB, within 13 min latitude of each other, produced near-equivalent AP levels, with a uniform trend towards higher AP at higher latitudes being evident (small sample number, low statistical noise; Table 8). The sample at SL was chosen to establish expected AP levels in the prairie environment near the ecotone because of its higher pollen count (smaller confidence interval) and biogeography (prairie sample in closest proximity to forested zone). The confidence interval upper boundary here was 22.4% AP, while the lower boundary of BK (sole forest zone site) was 30.0% (**bold**). According to these data, it was inferred that an AP above 30.0% indicates a forest vegetation type in paleo-pollen spectra. Below 22.4% AP, a prairie vegetation type is indicated, while intermediate AP levels (22.4–30.0%) are deemed transitional or indeterminate as to vegetation type and contain the theoretical ecotone. The application of these results is discussed below (Section 7.1) in an assessment of Holocene climate changes according to earlier sediment core pollen data and comparative (Section 3) data.

Table 8. Present vegetation types and Modern AP levels defining the forest–prairie ecotone; 95% confidence interval boundaries used to establish forest–prairie ecotone (AP% band) are in **bold**.

Pollen Site	Palo Alto [29]	Nueces Bay	Swan Lake	Buckeye Knoll
Latitude and longitude	26°0′50.0″ N, 97°28′33.0″ W	27°50′19.3″ N, 97°29′11.5″ W	28°3′10.2″ N, 97°9′49.9″ W	28°39′16.4″ N, 96°57′40.0″ W
Vegetation type	Prairie	Prairie	Prairie	Forest
Top-set AP% and pollen count (#)	3.5% (189)	16.1% (149)	16.4% (186)	36.8% (190)
95% conf. inter. upper bound	7.5%	23.0%	22.4%	44.1%
95% conf. inter. lower bound	1.5%	10.6%	11.4%	30.0%

6.2.5. Results of Mangrove Pollen Analog Studies

Analogs for mangrove pollen of *Avicennia* and *Rhizophora* species from the Gulf of Mexico and the Central Florida Atlantic coast demonstrate that low levels of mangrove pollen can indicate a local presence (Table 9), conformably with the poor dispersion of most insect pollinated species. In general, pollen from the analog sites was dominated by the local herbaceous halophytic taxa (esp. Bataceae and Amaranthaceae) or (in the case of Orchid Island, Florida) other arboreal taxa of the floodplain. In the case of the Orchid Island sample (*Rhizophora* 2), a major pollen taphonomic influence of the Indian River (regional hydrological transport) was inferred according to the high pollen percentages of the mixed oak–pine forest (absent from the local sampling site). From La Pesca data at the northern climatic limit of *Rhizophora* in Mexico (*Rhizophora* 1), *Rhizophora mangle* pollen was found to be absent (comparatively, the pollen response of *Rhizophora* increased markedly in lower-latitude coastal regions of Mexico [53]). In the case of sampled *Avicennia* sites from the Laguna Atascosa Wildlife Refuge in the Rio Grande valley, *Avicennia* pollen percentages approached 2% TLP in both samples, although the sample from the central part of the mangrove stand (*Avicennia* 2) contained greater quantities of Bataceae, inferably due to greater local, non-anemophilous pollen influence with lower wind velocities. According to these analogs, isolated mangrove pollen grains at the SL and NB sites may thus be interpreted as small mangles representing vegetation patches in the order of one to ten hectares. An absence of mangrove pollen, however, was expected where local mangles were small, in the order of one hectare or less.

Table 9. Summary pollen percentages at mangrove analog sites.

	Rhizophora 1	Rhizophora 2	Avicennia 1	Avicennia 2
Extent of mangle	<1 hectares	>10 hectares	~10 hectares	~10 hectares
Sample aspect	Center	Center	Edge	Center
<i>Rhizophora</i>	0.0	1.0	0.0	0.0
<i>Avicennia</i>	0.0	0.0	2.7	1.7
<i>Pinus</i>	6.5	46.0	11.4	1.3
Deciduous trees	10.4	27.5	22.2	1.3
Amaranthaceae	33.8	5.0	30.6	6.4
Bataceae	1.2	0.5	5.4	89.0
Other herbs	35.1	17.0	27.8	0.4
Tropicals (varia)	13.0	3.0	0.0	0.0

In the case of NB (Zone 2), a presence of isolated grains of *Rhizophora* pollen indicated the local presence of this fully tropical mangrove and thus a boreal extension of its climatic limit. This inference further indicates a tropical Middle Holocene climate in the central TGCP circa 6000 to 4500 BP, according to biostratigraphic dating of proximal *Rangia flexuosa* fortuitously encountered in the NB pollen core. Importantly, *R. flexuosa* itself enjoys a tropical distribution today in the Gulf Coast of Mexico, supporting the interpretation of the analog data by virtue of an analogous climatic range change (see Section 7.1).

7. Discussion

7.1. Climate Model: Forest-Limit Oscillations and Range Changes of *Betula*

According to the climate model (Table 1), shifts in the forest–prairie ecotone (among other parameters) are used to define mesic and xeric climate phases, with the ecotone itself being defined according to an AP band between ideal vegetation type sites (here, SL and BK) in near-Modern samples. According to the latter analyses (Section 6.2.5) and age–depth estimates (Section 6.1) of sediment cores, mesic versus xeric periods are now definable according to the total sediment core (Sections 6.2.1–6.2.3) AP data.

Firstly, mesic periods of increased growing-season precipitation and lower drought frequency were reconstructed according to increased AP in the Guadalupe River valley (BK) and Copano Bay (SL). Arboreal pollen values exceeding 30.0% at SL were recorded during two periods, 5500 to 5000 and 3000 to 1000 BP. During these periods, a southward migration of the forest boundary was reconstructed, and thus relatively mesic climate conditions ([10,54]; Figure 8, dashed line). Importantly, grass phytolith data from Choke Canyon State Park in the Nueces River valley also conform to this reconstructed pattern, with an increase in mesic, C3 grasses noted at “Late Archaic” and subsequent archaeological sites (dating to post-3000 BP, according to the projectile point chronology of Tom Hester [30]). Notably, periods of high *Carya* pollen (19.6% max.) at BK are also evident at intervals within these periods (esp. ~5000 BP and 2900–2600 BP).



Figure 8. Oscillations of the Southeastern United States Forest Limit (oak–pine–hickory mixtures) during the Holocene, as reconstructed by multi-site pollen data. Estimates as to the position of the forest–prairie ecotone were made according to 20% AP levels not including *Pinus* at examined pollen sites. See supplemental data for the Palo Alto pollen diagram for the Lower Rio Grande valley (please see the Palo Alto pollen diagram supplemental file).

Near-Modern conditions, with a position of the forest limit within the Guadalupe valley, were reconstructed for a long period dated from 8000 to 6000 BP, according to near-Modern AP levels at all sites (Figure 8, stippled line). Within this time period, *Carya* was first established as a major tree at BK. Finally, xeric periods, with a northward migration of forest beyond the Guadalupe River valley, were defined by AP values below 22.4% at all examined sites during two periods (Figure 8, solid line), circa 5700 BP and between 4000 and 3000 BP. Increased drought frequency, reduced growing season precipitation and/or increased evaporation, promoting high moisture stress in mesophytic woodlands, were inferred. Importantly, the circa 5700 BP period is correlated with major deflation and erosion of the knoll top of the Buckeye Knoll archaeological site (adjacent to the BK pollen site), interpreted as a xeric phenomenon, according to geomorphological criteria of Robert Ricklis [39]. Significantly, the later xeric period (4000–3000 BP) is correlated also with Hall's Cave faunal data indicating deceased forest cover in Central Texas [27], as well as a predominance of shortgrass phytoliths (typical of dry prairies) at Choke Canyon archaeological sites of the "Middle Archaic" period as defined by Tom Hester. Notably, *Carya* pollen values at BK itself were consistently less than 10% (and episodically less than 2%) during both xeric periods.

Past range changes of *Betula* were also an important parameter for the reconstruction of climate changes, and, in relation to the present distribution of *B. nigra* in Eastern Texas (sole species of the genus [8]), annual precipitation levels of circa 116 cm are required for its growth under Modern temperature conditions [14]. This level is considerably higher than precipitation levels enjoyed today at BK (97 cm *per annum*). In this study, an enhanced range of this tree in the TGCP (5.3) was reconstructed in two periods. First, Early Holocene evidence for a southward migration of *Betula* occurs in initial spectra at BK (*Betula* max. 5.4%, est. age ~9000 BP). This phase might be correlated with final (declining) *Betula* at Hershop Bog [27], although dating controls are inadequate here for precision correlation (note three radiocarbon dates only). A subsequent, Middle Holocene (1) migration of *Betula* was then reconstructed at BK in Zone 5 (5400–4800 BP). This period consists of five consecutive spectra with *Betula* values well exceeding 2%, attaining an absolute maximum of 11.7%, suggestive of a presence in wet micro-environments in the Lower Guadalupe River valley. The high precipitation levels indicated correlate well with a southward migration of the forest limit in the TGCP (Figure 8, dashed line), with a relative increase in rainfall being modulated according to temperature conditions.

Although Early Holocene proxy temperature data are lacking in the present study, carbon isotope data in Central Texas are suggestive of a (relatively) warm climate [55,56]). Middle Holocene data in the TGCP region are more determinate and indicate higher mean temperatures according to range changes of tropical *Rhizophora mangle* (Section 6.2.5) and associated *Rangia flexuosa*. Importantly, the latter clam species enjoys a present distribution more tropical than Nueces Bay, where *R. cuneata* is presently exclusive [43,57], and *Rhizophora* pollen grains at NB were found in close proximity to *R. flexuosa*. These higher temperatures and evaporation potentials suggest that precipitation differentials circa 9000 BP (first *Betula* migration) and 5500 to 5000 BP (second *Betula* migration) significantly exceeded 19 cm per annum or an increase in regional rainfall exceeding 10% over secular (century-level time scale) periods.

The results of the pollen analyses thus conform to the Holocene Climate Model (Table 1), while adding further data to the model reconstruction. The Early Holocene (here, 9000 to 6000 BP) climate was reconstructed as mesic (initially, ca. 9000 BP) to near-Modern (8000–6000 BP), with initial increased precipitation in the region (+19 cm *per annum*) circa ~9000 BP and the establishment of the forest limit in the Guadalupe River valley subsequently. Middle Holocene (1) (6000 to 4500 BP) was reconstructed as mesic, with a migration of the forest limit to the Mission River–Copano Bay region in tandem with a range expansion of *Betula* 5500 to 5000 BP. The latter further indicate exceptionally wet conditions in the Guadalupe River valley. A fully established *Carya* presence in the Guadalupe River valley is noted at 5000 BP. Coeval temperature conditions were warmer,

moreover, according to NB data, with a presence of *Rhizophora* indicating fully tropical conditions in the central TGCP. The Later Middle Holocene (2) climate (4500–3000 BP) was reconstructed as xeric, with a retreat of the forest limit north of the Guadalupe River valley. Finally, a Late Holocene mesic phase was defined after 3000 BP, with a return of dense forest in the Guadalupe River valley and an extension to Copano Bay. Moreover, sustained high *Carya* values (in excess of 10%) obtained during the 3000 to 1000 BP period.

7.2. Sea-Level Model: History of Estuarine Marsh Development

According to the sea-level model (Table 2), shifts in the level of freshwater estuarine, salt-marsh pollen flora in the sediment core data were used to assess the effects of sea-level changes on coastal environments, where geological and archaeological data define sea-level change itself. The results of pollen analysis of sediment cores (Sections 6.2.1–6.2.3) and chronometry (Section 6.1) can now be compared to hypothetical pollen responses modelled according to background data (Section 3). Most data pertaining to the sea-level model derive from the SL, where pollen responses were predominantly influenced by coastal environments and dating controls are adequate as to purpose (Table 6). The pollen responses at the study sites are described periodically as follows:

1. Early Holocene high stand 8000 to 6000 BP. NB Zone 1 site maximum of Amaranthaceae (cf. *Salicornia* spp.); interpretation: Nueces Bay salt-marsh flora. BK Zone 2 site maximum of Amaranthaceae, Palmae presence; interpretation: Green Lake (Early Holocene embayment) salt-marsh flora with presence of palm on sand deposits. SL Zone 1 high Amaranthaceae and trace values of *Typha* and Cyperaceae, Amaranthaceae and *Avicennia*; interpretation: salt marsh with freshwater marsh elements, including telematics, near the Mission River with scattered mangrove stands.
2. Middle Holocene (1) still stand 6000 to 4500 BP. NB Zone 2 declining Amaranthaceae with *Avicennia* and *Rhizophora*, establishment of mangroves communities and contracting salt marsh. SL Zone 2 rise of *Quercus*, *Typha* and Cyperaceae; interpretation: increased freshwater marsh elements in Copano Bay, establishment of oak mottes with increase in sand sedimentation (barrier island development). SL Zone 3 declining Amaranthaceae, *Potamogeton*, *Polygonum hydropiper* and Cyperaceae present; interpretation: continued slow contraction of salt marsh and appearance of perennial aquatic (freshwater) species as well as telematics.
3. Middle Holocene (2) high stand 4500 to 3000 BP. SL Zone 4 rising *Quercus*, declining Amaranthaceae and *Typha* presence; interpretation: contraction of salt marsh, establishment of oak mottes with sand sedimentation. SL Zones 5–6 rising Amaranthaceae, *Avicennia* presence, *Quercus* variable; interpretation: salt marsh with freshwater marsh elements near the Mission River with rare mangrove stands and intermittent oak motte formation.
4. Late Holocene still stand 3000 to 1000 BP NB Zone 3 low Amaranthaceae with *Avicennia*; interpretation: establishment of mangroves communities and contracting salt marsh (most recent spectra indicate final expansion of salt marsh). SL Zone 7 rising *Typha* and Cyperaceae, presence of *Nymphaea*; interpretation: slow contraction of salt marsh and appearance of deep freshwater species (incl. water lily) as well as telematics.

Comparison of pollen data (Sections 6.2.1–6.2.3) with the sea-level model thus confirms the model with respect to the Early and Late Holocene periods, while failing to confirm the model for the Middle Holocene (1–2). High halophyte influence at all study sites in the Early Holocene was interpreted as a low-diversity coastal environment, correlated with rapid sea-level rise in the Gulf of Mexico as a whole [58]. Contrary to the sea-level model (Table 1, rows 2–3), environmental variability in the Middle Holocene periods (1–2) may be greater than that resolved by geological data. Unfortunately, this variability is defined by single-spectrum zones and requires further investigation for validation. However, a tentative correlation might be proposed between a circa 5800 BP freshwater estuarine phase defined at SL on Copano Bay and the benthic indicative value of a foraminiferal

spectrum at the base of the Port Bay core, also on Copano Bay [35] (Figure 7). In the latter basal spectrum, the (limited) benthic data significantly indicate a possible fall in sea level. Finally, Late Holocene pollen data uniformly indicate still-stand conditions with a contraction of salt marsh (3000–1000 BP), with a close alignment of SL and Port Bay Marsh core environmental indicative values.

These initial pollen data thus indicate a significant level of variability in coastal marshland ecology during the Holocene, although the palynological assessment may be limited by the poor pollen productivity of deep, freshwater aquatics of strong indicative value (esp. low-salinity indicators, such as *Nymphaea* and *Potamogeton*), the isolated presence of which may be important for interpretations, though the absence is not significant. Relative Amaranthaceae provided the strongest indications (of relative salinity) in statistical terms, although a Modern rise in halophytes at NB was not emphatic, according to incremental sum of squares analysis [51]. Finally, freshwater estuarine development circa 5800 and after 3000 BP, which provides a highly productive biota [32], was also correlated with human occupation sites on the TGCP, according to Robert Ricklis (Figure 9), and geologically defined sea-level still stands. The palynological data presented here thus suggest a potential link between the high biotic productivity of estuarine marshes and sea-level still-stand phases in the TGCP during the last 8000 years.

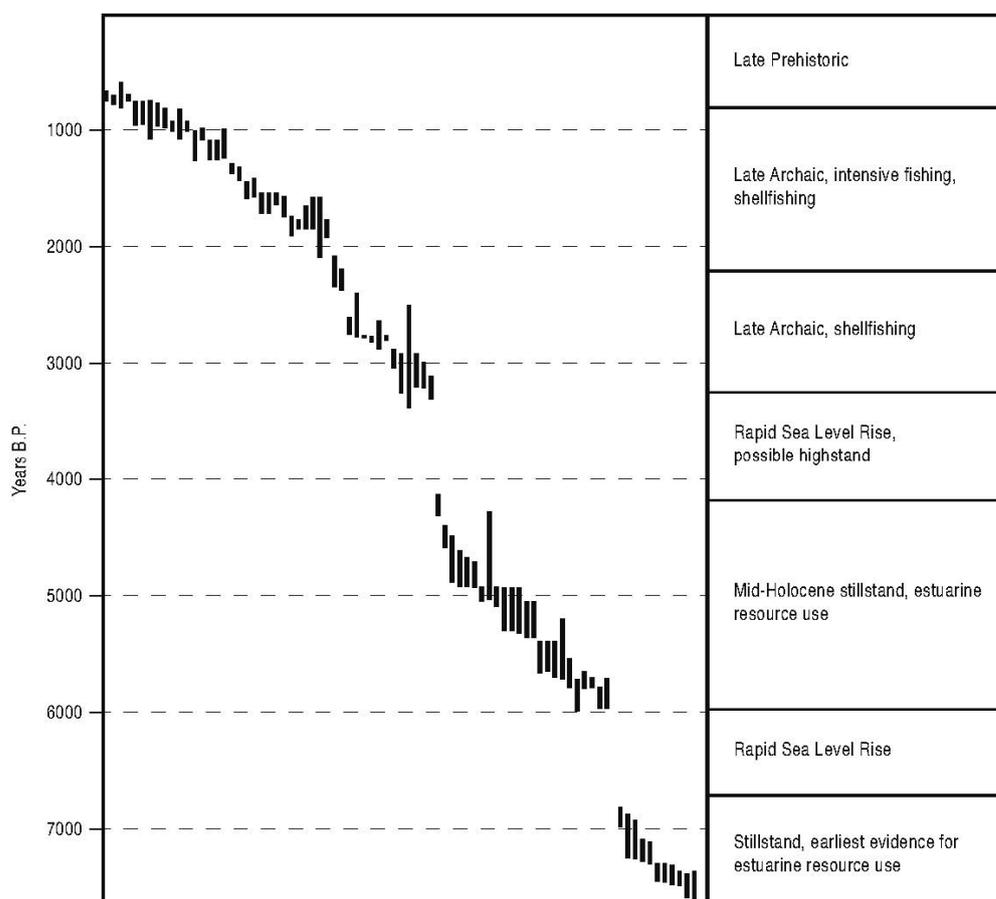


Figure 9. Radiocarbon date distribution of Central Texas Coast shell midden sites (source: [18]). Among clam species found at regional shell middens, *Rangia flexuosa* is limited to pre-4500 BP contexts, while *R. cuneata* appears first after 3000 BP (modified from [2,12]). Breaks in human occupation of the TGCP are inferred according to both a hiatus in dated remains as well as the absence of coeval diagnostic lithic artefacts for the periods 6700 to 6000 BP and 4000 to 3000 BP.

8. Conclusions

Pollen studies conducted in the TGCP show the potential for low-energy reduced alluvial deposits for regional paleo-ecological work in sub-humid zones for use in reconstructing past vegetation patterns, while submerged bay deposits at NB further illustrate the possibilities of pollen preservation in sub-aqueous coastal situations. In terms of pollen taphonomy, the study sites at BK and SL are similar to shallow lacustrine sites with inlet (and outlet) streams, and sorting of pollen according to factors such as size is not supported [40]; indeed, the results of pollen analysis show a strong relation between afforestation potential according to baseline climate conditions and levels of arboreal pollen in basin catchments [59]. In relation to sea-level history research, the highest potential floral sensitivity to salinity changes was noted at estuarine sites associated with small fluvial systems. For example, the SL site, associated with a 25 km-long valley profile (Mission River), exhibited great statistical variation in salt-marsh flora, with order-of-magnitude changes in halophytic pollen response, while only moderate variation was exhibited at the NB site, associated with a 500 km-long valley profile (Nueces River). Inferably, this was due to higher continuous freshwater inputs at NB, with a Modern sea-level rise [35] producing only moderate rises of (+30%) halophytes in samples near the surface.

Pollen data from three sites on the TGCP suggest, moreover, a significant correlation between high levels of afforestation and nut-mast tree growth (Section 7.1), freshwater estuarine development (Section 7.2) and archaeological indices for higher human settlement densities during the last 9000 years, with enhanced occupation evident in the earlier Middle Holocene (6000–4500 BP) and the Late Holocene (3000–1000 BP). Particularly notable here is the pollen response of *Carya*, a tree whose nut masts form a concentrated, reliable and storable food source for human populations. Maximum *Carya* values (19.6%) occur circa 5000 BP at BK and at high values (10+ %) from 3000 to 1000 BP. In contemporary coastal areas, the expansion of productive (high *K*-capacity) marshlands, moreover, produces a rich fishing niche for hunter-fishers (Early Historic Karankawa [60]). Conversely, periods of rapid sea-level rise (up to +2 m), particularly in the Early Holocene and later Middle Holocene (4500–3000 BP), are associated with high levels of halophytes and, inferably, minimal barrier island development, coeval with a retreat of forest vegetation (and associated nut masts) in inland areas (Figure 8). A combined use of both coastal and inland (river-valley) foods by the same human populations as part of a seasonal cycle, as defined by Ricklis [60], would increase the amplitude of human population fluctuation through time to a significant degree. This amplitude enhancement is due to a positive correlation between periodic changes in inland- and coastal-zone *K*-capacities (Figure 9). Importantly, a sensitivity of biotic productivity levels of estuarine marshes to sea-level changes is indicated.

The amplitude of regional climate change during the Holocene was also great according to this pilot study, with secular variation in precipitation increasing by a differential of 19 cm *per annum* during aspects of the 6th millennium BP (a relative increase in precipitation of 20% relative to Modern conditions on the TGCP). Finally, *Rhizophora mangle* and associated *Rangia flexuosa* range changes to include Nueces Bay, Texas, are strongly suggestive of a 200+ km northward shift of the Intertropical Convergence Zone boundary during the Middle Holocene according to the climatic requirements of these fully tropical mangroves.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/quat6010019/s1>, the Palo Alto pollen diagram supplemental file.

Author Contributions: B.M.A. is responsible for the fieldwork at Buckeye Knoll and Swan Lake, as well as all pollen laboratory work, pollen analyses, statistical analyses and writing. All authors have read and agreed to the published version of the manuscript.

Funding: National Science Foundation (US) grant no. SBR-942-3650; US Army Corps of Engineers, Galveston District: 41VT98 (Smithsonian trinomial) mitigation project; National Park Service (US), Palo Alto Battlefield Park testing project.

Data Availability Statement: Not applicable.

Acknowledgments: Robert Ricklis, Principal Investigator of Coastal Environments, Inc., Corpus Christi, Texas, US, is acknowledged for the formulation of research designs and the reported studies at Nueces Bay, Swan Lake and Buckeye Knoll and in the organization of the Nueces Bay marine fieldwork. Rolondo Garza's (Palo Alto Battlefield Park, Cultural Resources) kind assistance at Palo Alto (see supplemental data) is acknowledged. Also acknowledged is the assistance of Jim Innes and Christ Orton (Cartographic Unit) in the drawing of figures by the Department of Geography, Durham University, DH1 3LE, UK. Finally, the kind assistance of the late Glen Doran (Florida State University, Tallahassee) in the operation of the Geoprobe 54 LT at Buckeye Knoll (41VT98) is gratefully acknowledged.

Conflicts of Interest: The author declares no conflict of interest.

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