

Mangrove dynamics in the southwestern Caribbean since the 'Little Ice Age': A history of human and natural disturbances

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Abstract

Relatively little is known about the long-term response of Caribbean mangroves to human and natural disturbances during the 'Little Ice Age' (LIA). We present new palynological information on the dynamics of the Bahía Honda mangrove from the eastern coast of San Andrés Island in the southwestern Caribbean for the late Holocene. Major changes in the Bahía Honda pollen record show the combined effects of natural events (strong storms and sea-level rise), and human disturbances. These changes are supported by ¹⁴C dates, sedimentological and palynological information. A storm (most probably a hurricane) was recorded around AD 1600, caused sediment reworking and the subsequent loss of about 2000 years of the vegetation record. The devastation of tree vegetation by this event allowed the expansion of heliophytic vegetation (e.g. grasses and vines). Mangroves and coastal vegetation started to recover at AD 1700, reaching their maximum extent within a few decades, when microforaminifera shells became abundant at the coring site, thus suggesting a relative sea-level rise because of the geomorphic reconfiguration of the coastal plain after the storm. Furthermore, the pollen evidence indicates more humid regional climates during the late LIA (AD 1700–1850). Mangrove and coastal vegetation declined sharply as a consequence of the establishment of coconut plantations around AD 1850. The recovery of the mangroves after AD 1960 is a result of the combined effect of relative sea-level rise and drastic changes in the local economy from coconut plantations to commerce.

Keywords

Colombian Caribbean, human impact, 'Little Ice Age' (LIA), mangroves, paleoenvironmental reconstruction, palynology, sea-level, tropical storms

Introduction

Mangroves are well known for their ecological importance and their strong link to the socio-economical development of tropical and subtropical coasts. They occupy the transitional zone between the continent and the ocean. In such ecotones complex interactions take place between vegetation and climatic, geomorphological, fluvial and oceanographic variables (e.g. Hogarth, 2007; von Prahll *et al.*, 1990). Mangroves are relatively simple ecosystems in terms of their floristic composition, where each species has its own, rather well-defined, set of ecological and environmental tolerances and responses to environmental changes. Spatially, mangrove species are frequently distributed in a banded pattern parallel to the shoreline (Duke *et al.*, 1998). These belts or zones may be either monospecific or strongly dominated by a few species, and are well correlated with ecological and environmental variables (e.g. Duke *et al.*, 1998; Sánchez-Páez *et al.*, 1997).

The ecological singularity of mangroves denotes their sensitivity to environmental changes in the coastal and inland realms (Blasco *et al.*, 1996), mainly controlled by regional climate, micro-topography, hydrologic conditions, and human disturbance. One of the most important factors determining the dynamics of mangroves is relative sea-level change, through the influence of tidal amplitude, frequency of storm surges, and the intrusion of seawater into surface waters (Hay and Mimura, 2005). All these environmental changes influence the habitat and physiology of mangrove

species and thus exert a strong impact on their composition and structural dynamics (McKee and Faulkner, 2000). In order to cope with rising sea level, rates of sedimentary vertical accretion and subsurface accumulation of organic materials (McKee *et al.*, 2007) should equal rates of sea-level rise; otherwise mangroves would experience erosion of their substrate, inundation stress, increased salinity, and eventually their disappearance (Ellison, 1993). Recent data compiled by the Intergovernmental Panel on Climate Change (Bindoff *et al.*, 2007) report that during the last century global sea level rose at a rate of about 1.7 mm/yr, with a notable increment of up to 3 mm/yr during the last decade (Bindoff *et al.*, 2007). Contrastingly, the evaluation of stratigraphic sequences and direct

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measurements on mangroves have shown a highly variable natural range of sedimentation rates, i.e. 0.8–6 mm/yr (Ellison, 1993, 1996; Woodroffe, 1999 and references therein), which depends on natural rates of sediment supply and erosion. Therefore, the assessment of natural recovery processes of individual mangrove types is crucial for the understanding of their survival ability under future scenarios, which project accelerated sea-level rise rates between 0.18 mm/yr (Bindoff *et al.*, 2007) and 13 mm/yr (Grinsted *et al.*, 2009) for the next century.

In addition to sea-level change, hurricanes are a frequent source of major disturbance and mortality in mangrove ecosystems and tropical coastline vegetation. Relatively little is known about the transition from severely damaged mangrove forests to regenerated forests. These long-term recovery patterns of mangrove forests after hurricane damage require decades to centuries, which are beyond the scale of most ecological studies, and thus these processes have been poorly understood (Chen and Twilley, 1998; Piou *et al.*, 2006). Therefore, before predicting the imminent loss of mangrove ecosystems under future climate change scenarios, it is necessary to consider the effects of various stress factors. Further knowledge on the availability of suitable coastal areas, the amount and seasonality of fresh water and sediment supply, the proximity of neighboring mangrove areas, and the disturbance history are required in order to understand the long-term dynamics of particular mangrove areas and to predict their ability to cope with climate change.

Insular Caribbean mangroves are among the coastal ecosystems most vulnerable to sea-level rise (Mimura *et al.*, 2007). Vertical sedimentary accretion in these environments occurs primarily through autochthonous processes, e.g. the 'carbonate factory' (James, 1984), since the great distances from mainland and the limited fluvial sediment yield restrict the supply of allochthonous material. Under these conditions, organic matter deposition from the mangrove community greatly contributes to vertical accretion. Furthermore, in carbonate settings where mineral sediment input is limited, such as San Andres Island, subsurface production of peat is the primary soil-building mechanism, which restricts the availability of suitable areas for inland migration of mangroves (Snedaker, 1995). Despite the growing interest on the effects of sea-level rise on shorelines and coastal ecosystems (e.g. Ellison, 1993; Field, 1994; Snedaker, 1995; Woodroffe, 1990, 1992), studies on long-term dynamics of Caribbean mangroves are still scarce (Ellison, 1993, 1996, 2008; Peros *et al.*, 2007; Vegas-Vilarrúbia and Rull, 2002; Wooller *et al.*, 2004).

San Andres Island belongs to the Archipelago of San Andres, Providencia and Santa Catalina, which hosts the Seaflower Biosphere Reserve, designated by UNESCO in 2000 (<http://www.unesco.org/mab/wnbrs.shtml>). Insular areas of this marine reserve are surrounded by coastal mangroves that are associated with one of the largest coral reefs in the Americas, recognized as a biodiversity 'hotspot' and a secondary endemic bird area. From our ecological reconstruction in this small Caribbean mangrove area, we provide insight into the delicate interplay between mangrove development, and natural and human influences which may be relevant to oceanic islands that depend mostly on biogenic sediments for their sedimentary accretion. The information obtained, therefore, may be of use as a frame of reference for managers and stakeholders to design adaptation strategies to climate change in small Caribbean islands.

Present environmental setting

Bahia Honda mangrove (12°33'50"N, 81°42'W; 1 m above sea level) lies on the eastern coast of San Andres Island. It belongs to the broadest area covered by mangroves on the island and it is the only patch that has direct contact with the sea (Figure 1). San Andres is the largest island (13 km × 3 km) of the Archipelago of San Andres, Providencia and Santa Catalina in the Colombian Caribbean (Figure 1). It is about 800 km from the Colombian continental coast and about 150 km off Nicaragua, and comprises an area of ~25 km² (Instituto Geográfico Agustín Codazzi (IGAC), 1986). This coralline island consists mainly of Oligocene–Miocene reef-limestones resting on a submerged volcanic cone, upon which a recent carbonate platform has developed (Geister, 1975).

San Andres Island comprises two contrasting landscapes: (1) a hilly system along the central part, and (2) a coastal plain of emerged marine terraces. The hills, that can reach 100 m high, are partially covered by eroded material. By contrast, coastal plains are composed of emerged coralline terraces, sandy beaches, and lacustrine deposits filled with organic rich sediments (Díaz *et al.*, 1995).

The Archipelago is floristically close to the Central American and northern South American floras, where a combination of tropical dry forest and tropical moist forest species occurs (Lowy, 2000). At present, the island has almost no remnants of the original vegetation (Urrego *et al.*, 2009). Crops, especially coconut palms (*Cocos nucifera*), occupy wide areas and are largely mixed with natural vegetation cover. Grasses, secondary forests, and bushes cover the hills. Marshes and coastal depressions are covered by halophytic vegetation, mainly mangrove forests, that are mostly composed of three true mangrove species, i.e. *Rhizophora mangrove*, *Avicennia germinans*, and *Laguncularia racemosa*, the mangrove associate *Conocarpus erectus* and the mangrove fern *Acrostichum aureum*. In less saline environments, and on coralline substrates, mangroves can coexist with other salt-tolerant and secondary forest elements such as *Randia armata*, *Capparis* cf. *indica*, *Dalbergia brownii*, *Bursera simaruba*, *Myrcia fallax*, *Coccoloba uvifera*, *Cordia sebestena*, *Cocos nucifera*, *Zanthoxylum fagara*, *Alibertia edulis*, *Morinda* sp. and *Polygonum punctatum* (Urrego *et al.*, 2009a). Sandy beaches are covered by herbaceous species such as *Sesuvium portulacastrum*, *Hymenocallis litoralis*, *Ruellia tuberosa*, *Batis maritima*, *Tournefortia gnaphalodes*, *Ipomoea pes-caprae*, and some arboreal elements such as *Hippomane mancinella*, *Chrysobalanus icaco*, *C. uvifera*, *Hibiscus tiliaceus*, *Stigmaphyllon* sp., and *C. nucifera*.

Currently, mean annual temperatures are about 27.4°C and the average total annual precipitation is ~1900 mm (Díaz *et al.*, 1995). Unimodal precipitation is mainly governed by the meridional displacement of the Intertropical Convergence Zone (ITCZ). The dry season extends from February to April and the rainy season from June to December. Since San Andres Island does not have any permanent freshwater source, it is strongly susceptible to prolonged droughts. Thus, fringe mangrove communities highly depend on seasonal runoff and are under stress during intense and long dry seasons. Particularly long droughts have been reported in San Andres for the AD 1928–1930 and AD 1958–1959 periods (Parsons, 1985), being responsible for plague attacks that strongly affected coconut plantations. However, the effect of droughts on mangroves in the island has not been documented.

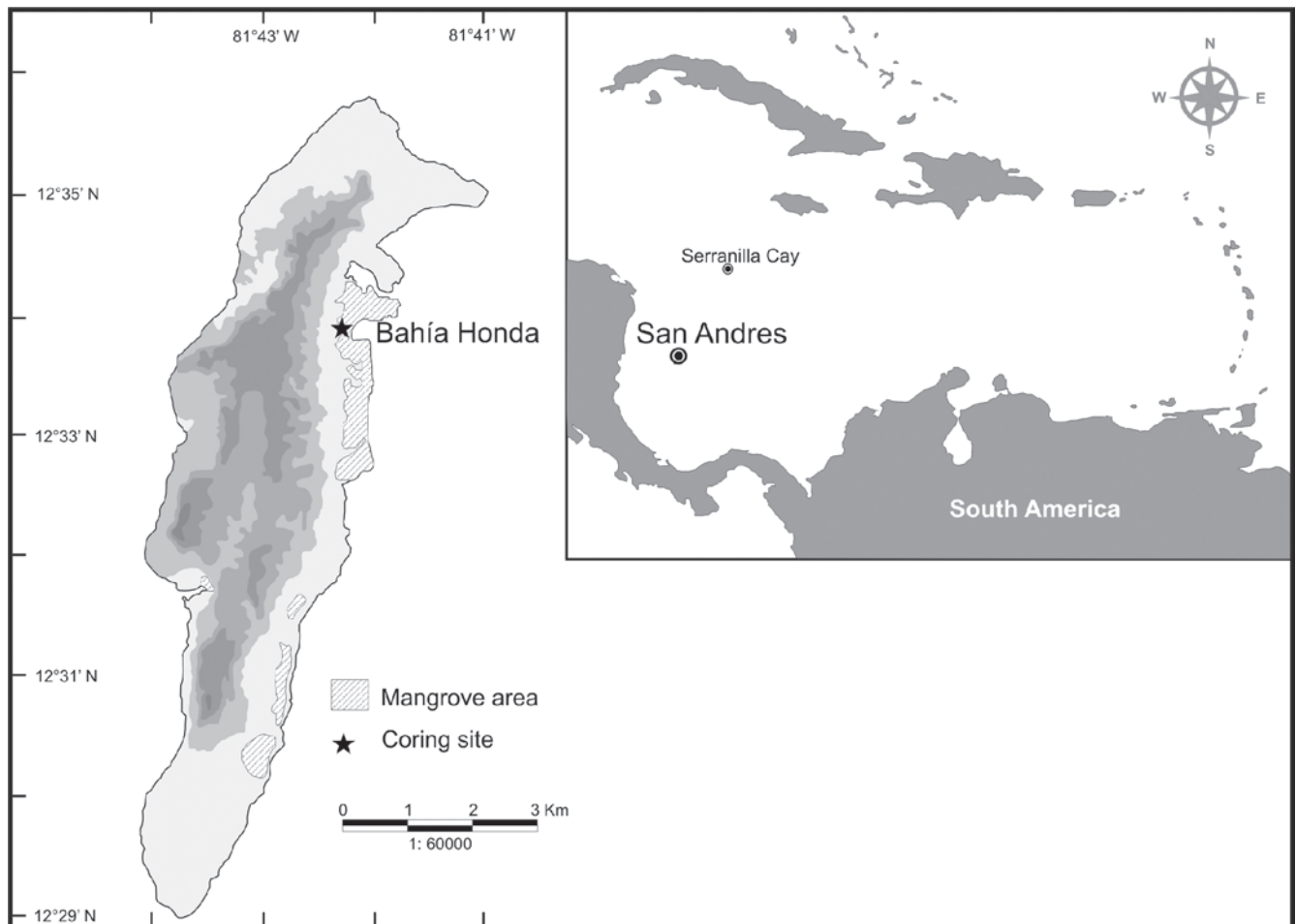


Figure 1. Location of San Andres Island, the Bahia Honda coring site, and the Serranilla Cay. Gray areas represent altitude contours every 25 m

Predominant west and northeast trade winds are especially intense between November and April, and June and July; and weakest during May and September–October (Díaz *et al.*, 1995). At interannual timescales the El Niño–Southern Oscillation (ENSO) phenomenon is the largest source of climate variability in the tropics, typically causing drier-than-average conditions in the southern Caribbean (Giannini *et al.*, 2000).

Based on climatology, northernmost South America has a 1–5% chance of a direct hurricane strike (Pielke *et al.*, 2003). According to documentary sources, a total of 38 tropical cyclones have affected the South American continent since AD 1588 (García Herrera *et al.*, 2005), and San Andres Island has only been directly hit by four hurricanes during this period. Hurricanes are associated with high-energy winds, high tides and heavy rainfall. In October 1961 hurricane *Hattie* passed west of San Andres Island, destroying most of the coconut plantations (García-Barriga *et al.*, 1969) and affecting remnants of native vegetation. In 1971, before becoming hurricane *Irene*, a tropical storm brushed the Island with no major damages (Simpson and Hope, 1971), and more recently in 1988 hurricane *Joan* caused large waves and had serious consequences on public infrastructure, even when it did not hit the island directly (Díaz *et al.*, 1995).

Around AD 1621 San Andrés was firstly occupied by English puritans. The island remained sparsely inhabited until AD 1780 when it became prosperous, because of the widespread establishment of cotton and sugar cane plantations. During this period

much wood was extracted to supply the naval manufacture (Díaz, 1978). During AD 1853–1953, the island became an exclusively coconut-cultivated island owing to the increase in US demand for the fruit (Parsons, 1985). The most productive period for this activity was at the beginning of the twentieth century. The free port designation given to San Andrés Island in AD 1953 shifted drastically the economic base of their inhabitants. Currently San Andrés is the most densely populated oceanic island of the Americas, where tourism and a very active informal economy are the main sustenance for locals, exerting a very strong pressure on its natural resources (Martínez, 1992).

Materials and methods

The Bahia Honda sediment core, 175 cm long and 5 cm in diameter, was drilled in the central part of the mangrove, 10 m from the coast with the aid of a Dachnovsky corer. Subsections of 25 cm long were sampled and stored in a refrigerator at 4°C. For pollen analysis, 1 cm³ samples were taken every 5 cm along the core. One tablet of exotic *Lycopodium* spores was added to each sample to calculate pollen concentrations and pollen fluxes. All samples were treated with standard preparation techniques including acetolysis (Erdtman, 1960), KOH (10%), sodium pyrophosphate (10%), HF (1%) and HCl (10%). As with most organic-rich mangrove sediments, no sieving was required. Residues were mounted in glycerine jelly and analyzed with a light microscope. A total of 200–250 pollen grains

were counted including trees, shrubs, herbs, vines, and climbers. Fern spores, fungal spores, musci, algae, foraminifera, and other palynomorphs were also counted, but not included in the pollen sum. Identification of pollen grains and spores was aided by modern pollen samples taken in San Andrés, pollen atlases and other published morphological descriptions (Blasco *et al.*, 1980; Herrera and Urrego, 1996; Palacios-Chávez *et al.*, 1991; Roubik and Moreno, 1991), and the reference collection held at the Ecology Laboratory, Forestry Science Department of the National University of Colombia in Medellín. According to modern vegetation distribution (González *et al.*, 1995; Lowy, 2000; Urrego *et al.*, 2009a; W³ Tropicos database, <http://www.tropicos.org>), pollen taxa were classified into seven ecological groups: (1) mangroves, (2) sandy beaches, (3) backswamps, (4) herbs and open vegetation, (5) tropical dry forests, (6) crops, and (7) offshore transported elements. Additionally, pteridophytes, fungi and bryophytes, and aquatic microfossils were grouped and their relative abundances were calculated in relation to the pollen sum. The identified taxa are listed in Table 1. For calculation of pollen sum, cluster analysis and diagram plotting Tilia, CONISS and Tiliagraph software (Grimm, 1993) were used.

Organic fragments (plant debris) were selected for AMS ¹⁴C dating at 105, 140 and 155 cm (see Table 3). Calibration of the dates was performed using the Oxcal software (Bronk-Ramsey, 2003), and the age model was defined by linear interpolation between dated samples.

Results

Bahía Honda core mainly consists of mud and clay sediments. The detailed sedimentological description is shown in Table 2 and a graphical summary accompanies the pollen diagrams (Figures 2 and 3).

According to the established age model, the Bahía Honda core comprises the period between *c.* AD 1600 and the present day, although the 2457 ± 36 ¹⁴C yr BP date at 155 cm core depth could imply older sediments below 140 cm. The absence of dates below 155 cm and the possible presence of a layer of reworked sediments make it difficult to interpret this latter date. For the better age-constrained interval (younger than AD 1600), estimated sedimentation rates were in the order of 0.29–0.41 cm/yr. These values are in the lowest range of vertical accretion reported for mangroves (Woodroffe, 1999 and references therein), typically corresponding to carbonate settings in small islands with low allochthonous input (Ellison, 1993).

Pollen record

In total 220 different pollen taxa were found. Based on cluster analysis and down-core changes in pollen assemblages, three biostratigraphic zones were recognized. Relative abundances of most frequent taxa are summarized in the pollen percentage diagram (Figure 2). Abundances and pollen concentration of the ecological groups, pollen sum, cluster analysis and main stratigraphic features are shown in the individual taxa and summary diagrams (Figures 2 and 3). Pollen zones, from bottom to top, consist of the following.

Pollen zone BHON-I (175–128 cm; 10 samples). This zone is characterized by the dominance of beach vegetation (20–70%) and low mangrove percentages. The zone is divided in two subzones

(BHON-Ia and BHON-Ib) with its boundary at 150 cm. The interval between 154 and 148 cm is barren of palynomorphs. Subzone BHON-Ia (175–155 cm) has low pollen concentrations and is dominated by sandy beach vegetation, mostly *Stigmaphyllon* (42%) and *Hippomane* (>60% at the end of the subzone). Open vegetation is also well represented (45%) especially by Poaceae, Asteraceae, Piperaceae, *Borreria* and *Solanum*. Simultaneous peaks of mangroves (25%), dry forest (20%), and back swamp vegetation (10%) occur at the bottom of the subzone, with a subsequent drop to less than 10% in all the cases. Fungi and Pteridophyta spores also show high abundances in this subzone. Subzone BHON-Ib (145–128 cm) is characterized by higher pollen concentrations. The first sample, overlying the sterile fraction (at 145 cm), is dominated almost exclusively by *Ceiba pentandra* (>90%), which is otherwise nearly absent (we excluded this sample from the later discussion and statistical analysis). *Stigmaphyllon* reappears with high percentages (60%), accompanied by open vegetation elements (25%), especially *Solanum* and *Borreria*. Mangrove, back swamp and aquatic elements reach their lowest values throughout this subzone. Fungi and Bryophyta recover after a drop at around 158 cm.

Pollen zone BHON-II (128–68 cm; 12 samples). This zone is divided into two subzones. Subzone BHON-IIa (128–112 cm) is an organic-rich interval where *Stigmaphyllon* diminishes abruptly, and *Hippomane* reaches its maximum relative abundance (50%). Mangrove pollen abundances start rising, especially *Rhizophora* (12–47%) that is accompanied by *Laguncularia* (8%) and *Avicennia* (2%). Herbaceous taxa representing open vegetation decrease, whereas backswamp and dry forest pollen relative abundances remain low. Subzone BHON-IIb (112–68 cm) is characterized by high relative abundances of mangrove elements (30–55%) mainly *Rhizophora* and *Laguncularia*. *Hippomane* values are also high, with a peak (50%) at the end of the subzone. Microforaminifera show their highest values in the core at around 110 cm. Grasses and other open vegetation elements reach their minimum values in the core. Ferns start rising but are still low. Organic matter contents decrease in the upper part of the subzone.

Pollen zone BHON-III (68–0 cm; 14 samples). This zone is characterized by low pollen concentrations and the expansion of *C. nucifera* and backswamps. Ferns, especially *Polypodium* reach their maximum relative abundances, as beach elements diminish. Three subzones can be differentiated with boundaries at 48 cm and 16 cm. Subzone BHON-IIIa (68–48 cm) shows a drastic drop in the relative abundance of sandy beach elements (<20%) and the simultaneous increase of *C. nucifera* (12%), grasses (10%), and backswamp elements (30%) mainly Cyperaceae, *Randia*, *Psychotria* and *Typha*. The highest percentages of Pteridophyta (45%) in the core are reached in this subzone. Subzone BHON-IIIb (48–16 cm) differs from the former subzone because it contains the lowest mangrove values (10%) of the core. Beach vegetation (*Batis*, *Sesuvium* and *Hippomane*) also reaches its minimum percentage values, which persist throughout the zone. Cultivated plants (*C. nucifera* and *Zea mays*) are even more abundant than in the previous subzone. Fern relative abundances are still very high. Subzone BHON-IIIc (16–0 cm) is characterized by an increase in pollen concentrations and mangrove relative abundances. *Rhizophora mangle* (18%), *C. erecta* (14%), *A. germinans* (8%), and *L. racemosa* (9%) are present. Backswamp elements and fern relative abundances diminish.

Table I. Main pollen types found in the Bahia Honda core, San Andres Island, Colombian Caribbean

	Mangrove	Sandy beach	Backswamp	Herbs & open vegetation	Tropical dry forest	Crops	Offshore transported
Mangrove							
<i>Avicennia germinans</i>	***	**					
<i>Conocarpus erecta</i>	***	**	**				
<i>Laguncularia racemosa</i>	***	**	**				
<i>Rhizophora mangle</i>	***						
<i>Acrostichum aureum</i>	***		**				
Sandy beach							
<i>Batis maritima</i>		**					
<i>Caesalpinia bonduc</i>		**		*			
<i>Coccoloba</i>		**					
Convolvulaceae		**		**			
<i>Crotalaria</i>		**					
<i>Hippomane mancinella</i>	**	**			**		
<i>Sesuvium portulacastrum</i>	**	**					
<i>Stigmaphyllon</i>	**	**	**				
<i>Tournefortia gnaphalodes</i>		**			*		
Brackish backswamp							
Araceae			***				
<i>Calophyllum</i>			**	**	*		
Commelinaceae			***	**			
Cyperaceae			***	**			
<i>Dalbergia</i>			***				
<i>Eugenia</i>			***	*			
<i>Ficus trigonata</i>	*		**				
Polypodiaceae	**		***				
<i>Randia</i>	*	**	***				
<i>Ruellia</i>		*	**	*			
<i>Grias</i>							
<i>Tabebuia</i>		**	**		**		
<i>Terminalia catappa</i>		**	***		*		
<i>Thelypteris</i>	**		***				
<i>Typha dominguensis</i>			**				
Herbs and open vegetation							
Apocynaceae		**		**	*	*	
<i>Aeschynomene</i>				***			
Asteraceae		*		***	*		
Bignoniaceae				***	*	*	
<i>Borreria</i>				***	*		
<i>Celtis</i>				***	**		
<i>Cestrum</i>				**			
<i>Desmodium</i>				**			
MoraceaeUrticaceae				**	**		
Piperaceae				**	*		
Poaceae			*	**			
Scrophulariaceae			**	**			
<i>Sida</i>				**	**		
<i>Solanum</i>				**			
<i>Trema</i>				**	**		
Well drained dry forest							
Anacardiaceae					***	**	
Arecaceae				*	***		
Bromeliaceae			*	**	***		
<i>Bursera simaruba</i>					***		
Cactaceae					***		
<i>Casearia</i>			*		***		
<i>Ceiba pentandra</i>					***		
<i>Drypetes</i>		*	*		***		
<i>Guazuma ulmifolia</i>			*		***		
<i>Guettarda</i>			*	*	***		
Menispermaceae			*		***		
<i>Ochroma</i>			*		***		
<i>Paullinia</i>					***		
<i>Protium</i>					***		
<i>Psychotria</i>					***		
<i>Sapium</i>			**		***		
<i>Senna</i>					***		
<i>Spondias</i>					***	**	
<i>Trichilia</i>			*		***		
<i>Zanthoxylum</i>				*	***		

(Continued)

Table 1. (Continued)

	Mangrove	Sandy beach	Backswamp	Herbs & open vegetation	Tropical dry forest	Crops	Offshore transported
Crops							
<i>Cocos nucifera</i>	*	***	*		*	***	
<i>Zea mays</i>						***	
Transported							
<i>Pinus</i>							***

Columns represent six different ecological groups, and asterisks denote the degree of affinity of species with the respective ecological groups according to local and regional distribution of modern vegetation : *** representative species of the group; ** can occur in the group; * rare species in the group.

Table 2. Sedimentological description of Bahia Honda core

Depth (cm)	Description
0–20	Dark gray-brownish (2.5Y 3/2) silty clay, with some oxidation spots and organic particles.
20–75	Dark gray-brownish (2.5Y 3/2) silty clay, with oxidation spots.
75–115	Light olive-brownish (2.5Y 5/3) silty clay, with oxidation spots.
115–140	Gray (5Y 5/1) clayed clay.
140–145	Gray clay, very rich in organic matter and organic debris, with abundant coarse (2–4 mm) calcareous and terrigenous particles.
145–155	Gray (5Y 5/1) clayed clay, with some calcareous and terrigenous particles.
155–157	Gray clay, rich in organic matter.
157–168	Light gray clayed clay, with abundant coarse (2–5 mm) carbonate particles.
168–175	Light gray (5Y 6/1) clay, oxidized, with abundant coarse (2–5 mm) carbonate particles.

Interpretation and discussion

Mangrove recovery after a hurricane

The base of the Bahia Honda core shows stratigraphic evidence of a strong disturbance around AD 1600 probably related to a storm event. Particularly, the loss of more than 2000 years of record coincides with the barren interval (154–148 cm), which was followed by deposition of a layer of organic matter mixed with gravels. This suggests the occurrence of simultaneous erosive and depositional processes. Typical hurricane deposits are characterized by a specific size-sorted sedimentary fingerprint (Morton and Sallenger, 2003), which do not correspond to what is observed in the Bahia Honda sedimentary succession. However, storm surges associated with strong winds and cyclones might produce analogous mixed depositional layers, especially in locations away from the direct path of hurricanes (Goodbred and Hine, 1995; Switzer and Jones, 2008). During strong storms, both erosive and high sedimentation processes take place, the former being related to the high energy action of the waves, and the latter to the transport and the deposition of sedimentary and organic material (Michener *et al.*, 1997). Indeed, the Bahia Honda record shows both processes simultaneously, the erosion and corresponding loss of *c.* 2300 yr of the record, and the later deposition of coarse grained sediments followed by the accumulation of a layer of organic sediments. According to historical documentary records, the last decades of the sixteenth century were characterized by a high frequency of tropical storms and hurricanes in the Caribbean Sea (García-Herrera *et al.*, 2005). More specifically, in November AD 1605 a strong hurricane was reported in the Serranilla Cay area, very close to San Andrés Island (Figure 1). This hurricane caused *c.* 1300 deaths, and the sinking of four galleons and two other boats

Table 3. List of AMS radiocarbon dates for the Bahia Honda core from San Andres Island, Colombian Caribbean

Sample	Depth (cm)	Material	¹⁴ C yr BP	Calibrated calendar age
BHON109 ^a	105	Plant debris	150 ± 50	AD 1670–1700, AD 1720–1780
BHON144 ^a	140	Plant debris	230 ± 60	AD 1490–1710, AD 1720–1860
BHON-159 ^b	155	Seed	2457 ± 36	BC 780–680, BC 550–480

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(García-Herrera *et al.*, 2007). It is very likely that the Bahia Honda core provides new, direct evidence on the effects of this AD 1605 hurricane, one of the strongest striking San Andrés Island during the last five centuries.

Changes in the pollen record are concordant with abrupt changes in the structure and composition of vegetation as the result of a strong disturbance in the coastal environment. The dominance of sandy beach and open vegetation elements (*Hippomane* and *Stigmaphyllon*) in the lowest part of the pollen diagram (zone BHON-Ia) suggest that before 2457 ± 36 yr BP mangrove forest already existed, being in agreement with previous findings that place the origin of island mangroves in the Caribbean around the middle Holocene (Ellison, 1996). A broader carbonate platform existed between the coring site and the tidal zone, thus favoring the broad development of coastal vegetation (Geister, 1975). Low percentages of microforaminifera support the interpretation of a weak influence of tides on the coring site.

After the AD 1605 storm *Hippomane* disappeared abruptly as well as all the other arboreal elements, i.e. *Rhizophora*, *Laguncularia*, *Avicennia* and *Conocarpus*. The prevailing vegetation suddenly changed into a heliophytic-dominated community (pollen zone BHON-Ib) composed mostly by climbers (e.g. *Stigmaphyllon*, *Dioclea*, *Celtis*, and Apocynaceae) and herbs (e.g. Asteraceae, *Borreria*, *Solanum*), which have been reported as first colonizers after hurricane disturbances (e.g. Hogarth, 2007; Smith *et al.*, 1994; Vegas-Villarrubia and Rull, 2002). *Stigmaphyllon*, in particular, has been described as an heliophytic climber indicative of disturbed beaches and mangroves (Anderson, 1997). It seems that storms affect more strongly tall trees than small plants (e.g. Loope *et al.*, 1994; Michener *et al.*, 1997; Woodroffe and Grime, 1999), causing canopy opening that triggers plant succession processes and favors the expansion of herbs and heliophytic elements (Piou *et al.*, 2006).

Some 50 to 70 years after the hurricane disturbance, at ~AD 1710 arboreal species started to return: *Hippomane* appeared first followed by mangrove species, i.e. *Rhizophora*, then *Avicennia*,

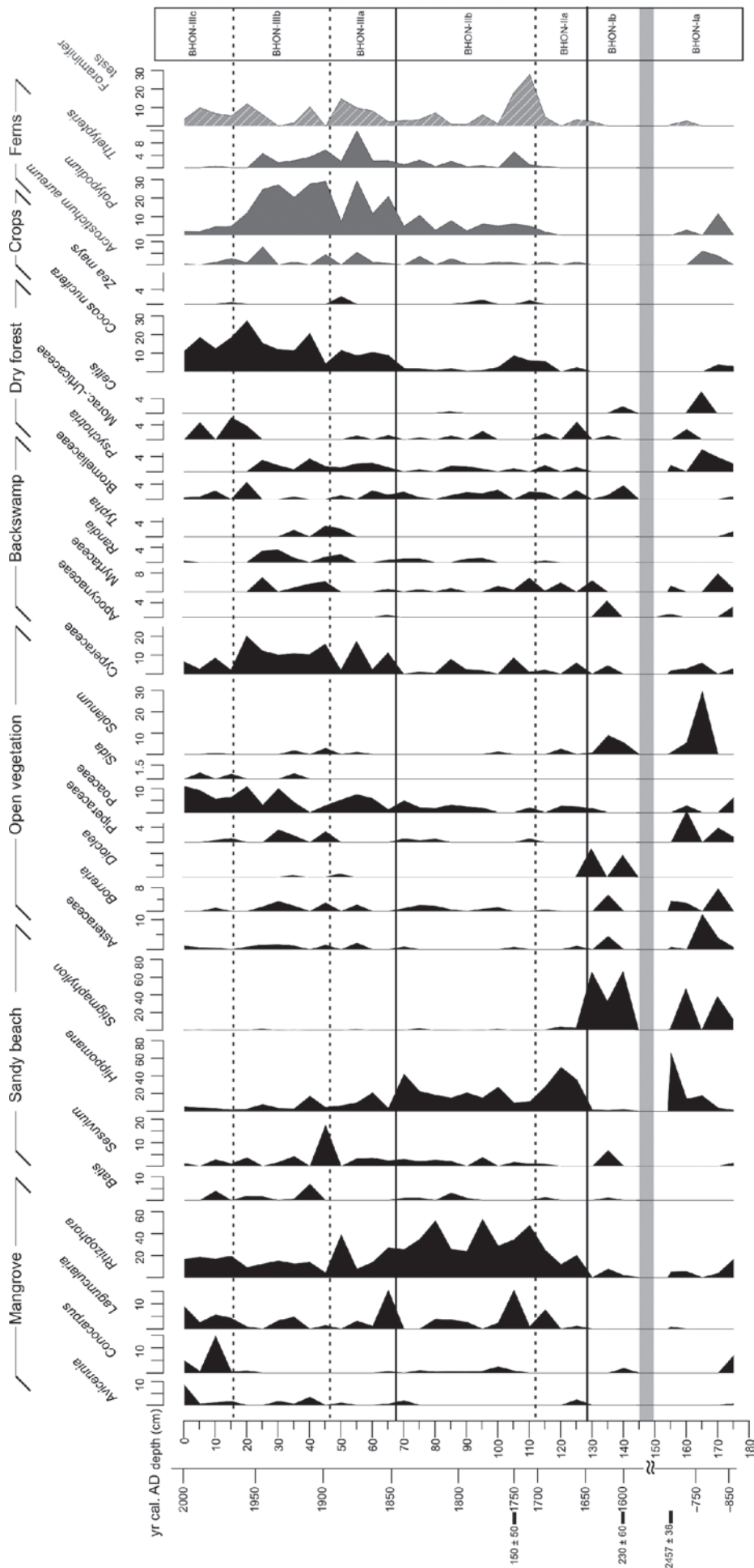


Figure 2. Percentage pollen diagram of selected taxa of the Bahia Honda core, San Andres Island, Colombian Caribbean, against depth (cm). A timescale, supported by three AMS ¹⁴C dates is added to the left

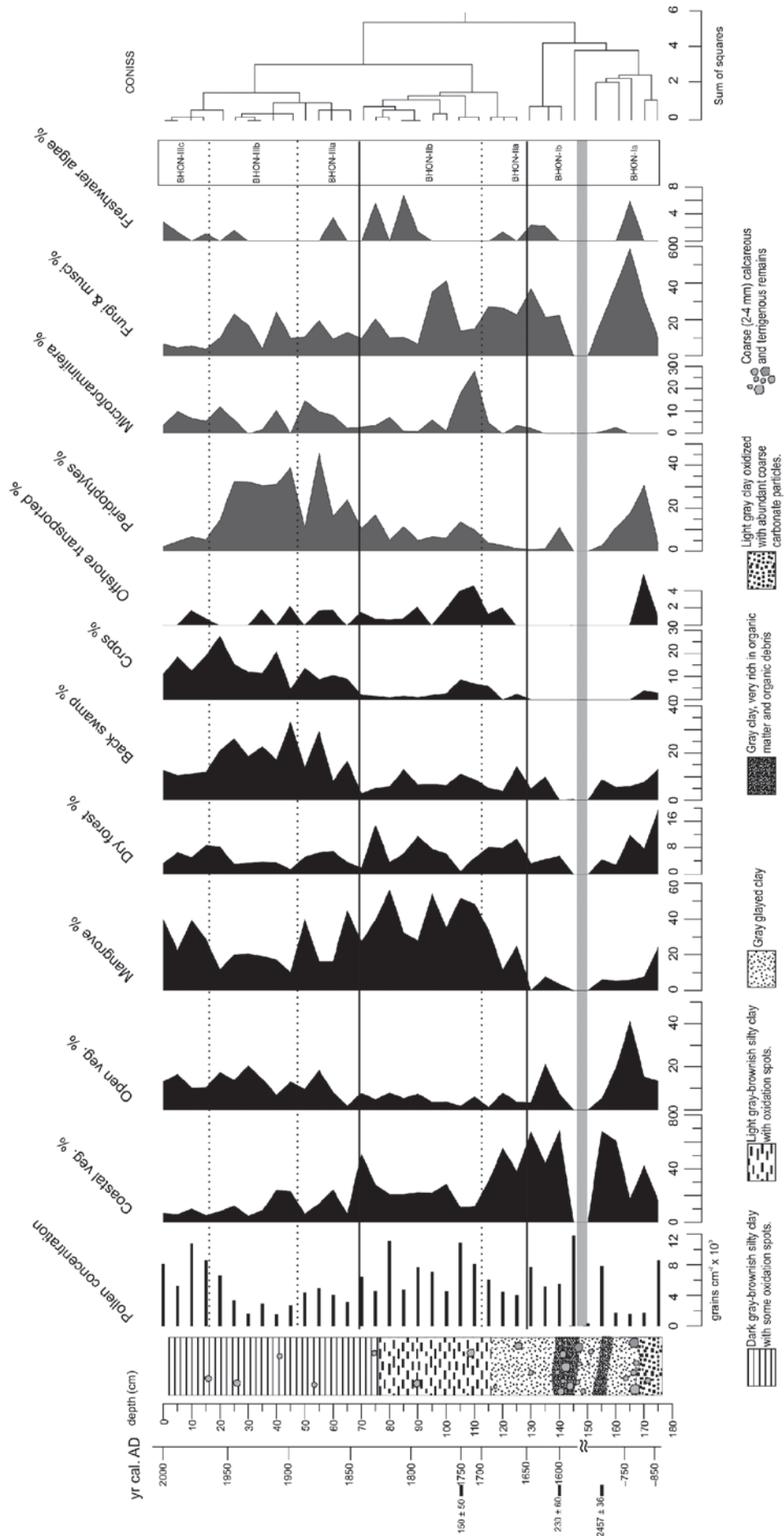


Figure 3. Summary pollen diagram of the Bahia Honda core, San Andres Island, Colombian Caribbean, against depth (cm). Relative abundances of ecological groups, pollen concentration, stratigraphy, cluster analysis dendrogram, and pollen dates. A timescale, supported by three AMS ¹⁴C dates is added to the left. Note the different horizontal scales

Laguncularia and *Conocarpus*, displacing the previous herbaceous vegetation. The ability of mangroves to regenerate following hurricane events has been previously noted, but long-term successional processes following disturbance by hurricane winds and storm tides have been poorly studied. The initial post-hurricane stage dominated by herbaceous taxa (e.g. Poaceae, Cyperaceae, Asteraceae, *Acrostichum*) recorded in the Bahia Honda sedimentary sequence has been already reported in previous studies, whereas the duration of this early stage varies from years to centuries, depending on the extent of the damage caused by the winds and storm surges, and by the original vegetation that stays alive (e.g. Baldwin *et al.*, 2001; Sherman *et al.*, 2001; Urquhart, 2009). According to the Laguna Negra pollen record in the Nicaraguan Caribbean, post-hurricane regeneration processes took between 200 and 300 years to reach a mature state similar to that of the original forests, since fires truncated the natural succession pathway (Urquhart, 2009). By contrast, from more recent hurricane records there is evidence that mangroves can have faster recovery times, as is the case of mangroves from Isla del Venado in Nicaragua (Roth, 1992), where mostly the larger trees were selectively affected by winds during hurricane *Joan* in 1988, thus favoring a fast recovery of the forests. Similarly, mangroves that were severely damaged by hurricanes *Donna* (1960) and *Betsy* (1965) recovered almost completely after three decades (Baldwin *et al.*, 1995, 2001). In the Everglades (Florida), hurricane *Andrew* affected mangrove differentially, and after less than a decade there was already evidence for mangrove tree species development overtaking herbaceous taxa (Urquhart, 2009).

Some factors might have been responsible for the relatively long duration of the recovery phase and the relatively late reappearance of mangrove trees in the Bahia Honda pollen record. First, individuals need at least five years to reach their reproductive maturity and produce flowers abundantly (Asaeda and Kalibbala, 2009), meaning that mangrove species are only recorded in the pollen signal after that point. On the other hand, the low sediment yield and the almost complete dependence on autochthonous material to build up new substrates have a profound impact on the ability of mangroves to recover after strong erosive events and sea level rise (Mckee *et al.*, 2007). In addition to these ecophysiological and geomorphological features, the history of previous disturbances might have weakened the recovery capacity of Caribbean mangroves. According to García-Herrera *et al.* (2005), the last decades of the sixteenth century were characterized by very frequent storms, and the accumulative effect of these successive disturbances might have affected the resilience of coastal ecosystems, thus reducing their ability to recover after an exceptionally strong disturbance event.

After AD 1700 the pollen data suggest an increased marine influence over the coring site, evidenced by the maximum values of mangrove pollen and foraminifera tests. It seems likely that the storm surge derived from the hurricane event induced a retreat of the shoreline, exposing the Bahia Honda site to a more direct influence of tides. The subsequent expansion of low intertidal mangrove species, i.e. *Rhizophora* and *Avicennia*, coincided with the inland displacement of the shoreline. We hereby provide new evidence that in the long term tropical storms and cyclones have a strong influence on mangrove succession and zonation patterns by altering the spatial distribution of local resources (cf. Piou *et al.*, 2006). However, some notable changes occurred in the vegetation community during the interval of maximum mangrove expansion,

as evidenced by the alternation of true mangrove species. Although *Rhizophora* appears as the dominant taxon through the AD 1670–1840 period, it is important to recognize the ecological roles that other mangrove taxa might have played in the dynamics of the community. *Rhizophora* appears to be over-represented in the sediments, since as a wind-pollinated species it produces abundant pollen (Müller, 1959; van der Hammen, 1963). By contrast, *Laguncularia*, *Avicennia* and *Conocarpus* are insect-pollinated and produce low pollen amounts (Blasco, 1984; Müller, 1959; van der Hammen, 1963). Additionally, *Laguncularia* has been reported as one of the pioneer colonizer species after clearing and gap openings (Benfield *et al.*, 2005; Hogarth, 2007; Pinto-Nolla, 1999), whereas *Avicennia* has been shown to outcompete other species under high salinity conditions and to rapidly recover after strong winds due to its capacity of vegetative regeneration after massive defoliation (Smith *et al.*, 1994). Therefore, the expansions of *Laguncularia* and *Avicennia* in the Bahia Honda record may be used as indicators of early successional stages after disturbances. Two large peaks of *Laguncularia* mark both the onset and the end of maximum mangrove expansion. The first peak, at ~AD 1750, is most likely associated to the early recolonization stage of mangroves following the hurricane event, when light and nutrients were highly available. The second peak at ~AD 1850 seems to reflect the first human clearing activities during the early establishment of coconut plantations. Similarly, *Avicennia* shows increments at AD 1630 and during the first decades of the twentieth century, that despite the very low pollen relative abundances (<4%), are significant due to the marked under-representation of this species in the sediments. According to modern pollen rain results from the Island, very low pollen percentages of *Avicennia* represent mangrove stands completely dominated by this species. This proportion holds true for pollen percentages as low as 3%, which represent forests with c. 35% of *Avicennia* basal area (Urrego *et al.*, 2009b, 2010). Generally, *Avicennia* has been reported as a species that tolerates high salinities (e.g. Chen and Twilley, 1998). In San Andres Island *Avicennia* dominates fringe mangroves growing in the saltiest environments, while it is nearly absent under fresher conditions (Urrego *et al.*, 2009a). Thus, the marked affinity of *Avicennia* for salty environments, together with its synchronous occurrence with low pollen concentration in the Bahia Honda record, suggests that soils were highly saline during these two intervals as a consequence of reduced rainfall.

Regional climate change during the LIA

Besides the local vegetation dynamics mostly promoted by the natural succession process, the Bahia Honda palynological record offers evidence of regional climate change for the period between AD 1600 and 1850 which is the interval starting after the hurricane strike at AD 1605 and the strong human pressure that started at AD 1850.

Hydrological changes. A general trend from low pollen concentrations, sedimentation rates and mangrove abundances before AD 1700, towards higher concentration values and mangrove abundances between AD 1700 and 1850 suggests a change in the prevailing hydrology from dry to humid conditions (Figures 3 and 4). Low sedimentation rates imply either slow accretion velocities of autochthonous sediment, or reduced input of allochthonous sediment, which in any case, might have been the result of reduced rainfall. The presence of *Avicennia*, which typically tolerates high

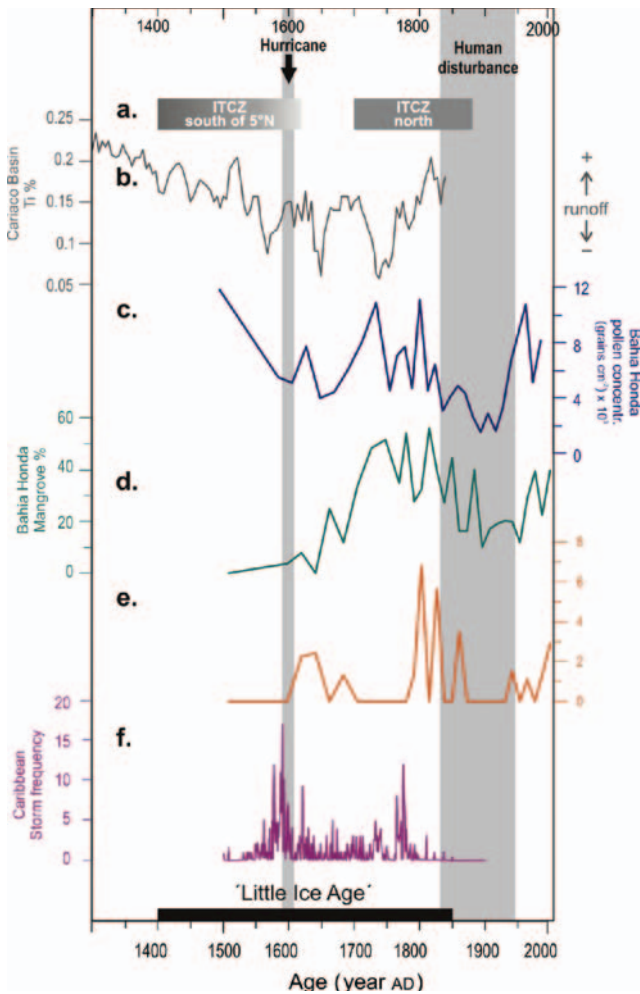


Figure 4. Regional comparison of climate records for the 'Little Ice Age' time interval. (a) Position of the Pacific Intertropical Convergence Zone between AD 1400 and 1850 (Sachs *et al.*, 2009); (b) bulk titanium concentration of Cariaco Basin sediments from ODP Site 1002 (Haug *et al.*, 2001); (c) pollen concentration (grains/cm²) from the Bahia Honda record (this study); (d) mangrove pollen relative abundance from the Bahia Honda record; (e) freshwater algae relative abundance from the Bahia Honda record; (f) annual frequency of storms in the Caribbean obtained from the Archivo General de Indias (García Herrera *et al.*, 2005). Shadings indicate the timing of the hurricane occurrence at *c.* AD 1605 and the interval of maximum human disturbance between AD 1850 and 1950

soil salinities, confirms the prevalence of water stressed and hypersaline environments, most probably caused by reduced rainfall (or excessive evaporation) during this first part of the LIA. In contrast, during the later part of the LIA, between AD 1700 and 1850, high mangrove abundances, higher pollen concentrations and the presence of freshwater algae are related to more alleviated soil conditions, due to the increased freshwater availability

The hydrological conditions in the Caribbean during the LIA, *c.* AD 1300–1850, are still not completely understood. It has been suggested that this interval was generally characterized by a 2–3°C cooling and the prevalence of drier climates over the Caribbean region (e.g. Haug *et al.*, 2001; Nyberg *et al.*, 2001; Winter *et al.*, 2000). Evidence from different locations and proxies agrees on a generally dry Caribbean region between AD 1500 and 1650. Laminated sediments from the Cariaco Basin off Venezuela record a general decrease in titanium, a proxy for precipitation in northern

South America, between ~AD 1550 and 1800 (Figure 4), reflecting reduced rainfall during this period, which was attributed to the southward migration of the ITCZ (Haug *et al.*, 2001). Similarly, an increase in the $\delta^{18}\text{O}$ values of X'caamal, a sediment core in the northwest Yucatan Peninsula, suggests drier climate conditions during the same period (Hodell *et al.*, 2005). Further evidence of a southward migration of the ITCZ towards a near-Equator position during the AD 1400–1640 period is provided by the comparison between δD records from Washington Lake in the central Pacific and the El Junco Lake in the Galapagos Islands (Sachs *et al.*, 2009). However, the hydrological conditions during the latest part of the LIA, *i.e.* AD 1700–1850, are less clearly resolved. The Cariaco Basin titanium evidence indicates the prevalence of dry conditions until AD 1800, thus suggesting a southward position of the ITCZ during the entire LIA. However, according to the El Junco Lake record, the ITCZ might have returned to its modern position 150 years before the return to warmer conditions at *c.* AD 1700 when the Galapagos Islands became substantially drier, and northernmost South America and the Caribbean turned wetter (Sachs *et al.*, 2009). The Bahia Honda pollen record, being independent from continental influences, gives insight into the debate, by providing new evidence of more humid conditions during the latest part of the LIA, supporting the idea of an earlier northward displacement of the ITCZ around AD 1700.

Hurricane and storm frequency. The overall trend from drier towards more humid climate conditions during LIA seems to be related to regional hydrological changes. However, by comparing the Bahia Honda pollen record with the documentary record of storm incidence in the Caribbean between AD 1500 and 1900, it becomes apparent that two phases (~AD 1580–1600 and ~AD 1770–1800) of great variability in the mangrove pollen concentrations and percentages coincide closely with two phases of great hurricane and storm frequencies in the Caribbean (Figure 4). Additionally, these two phases coincide with the increment of early successional species (e.g. herbs, *Laguncularia*, *Avicennia*) and freshwater algae confirming stronger rates of vegetation disturbance and precipitation that might have accompanied increased storm frequencies. Given the sampling resolution of the Bahia Honda core, it is not feasible to establish a direct cause–effect relationship between the frequency of storms and the observed variability of the pollen signal. However, our results confirm the compiled documentary information, suggesting that there might be a causal response between both variables, and if it is the case, storms are to some extent responsible for shaping the overall structure and diversity of mangrove forests in the Caribbean.

Effects of coconut-crop expansion on mangroves

After AD 1850 the Bahia Honda pollen record represents one of the most disturbed plant communities mostly related to anthropogenic activity. Historical data reveal that in AD 1853 San Andrés Island became an almost exclusive coconut producer, and this profitable activity favored the increase of the human population in the island (Parsons, 1985). This explains the abrupt reduction in the arboreal vegetation cover, giving way to new coconut plantations. It is reasonable that *Hippomane* disappeared before other taxa, because it naturally occupies the most suitable habitats for the establishment of coconut plantations. All the heliophytic vegetation (herbs, grasses, sedges, and vines) expand as a response to the improved light

availability in the understory of the plantations. The mangrove ferns *Acrostichum*, *Polypodium* and *Thelypteris* have also been reported as elements of disturbed mangroves and swamps (Caudales et al., 2000; Medina et al., 1990), thus their simultaneous expansion with the crops is the result of disturbance and clearance of swamp areas. The peak of *Laguncularia* is also an additional evidence of mangrove disturbance at this time (Benfield et al., 2005).

In AD 1900–1950, after the displacement of coastal vegetation, the crops continue to expand and took over the mangroves almost completely, which coincided with the most prosperous period of the coconut trade. The decline of the crops signal in the uppermost pollen zone coincided with a severe drought that occurred between AD 1928 and 1930 which triggered a plague affecting 30% of the coconut palms (Parsons, 1985).

The recent re-expansion of the mangrove forest, and the noteworthy appearance of early successional species such as *Laguncularia* and *Avicennia*, suggest that the pressure on the forests has diminished and recolonization process has resumed. Once more, the socio-economic factors in the island seem to have been driving the main changes in the plant communities. In AD 1953 San Andrés Island was declared a duty free port, and the new development policy of the island was not concerned with the coconut plantations.

The present plant composition of Bahía Honda mangroves is mainly dominated by *Avicennia* treelets. This suggests that global climate change could also be influencing actively the plant community, since *Avicennia* has been reported as the species that better tolerates the predicted effects of global climate change in the tropical coastal areas (higher frequencies of hurricanes, increased salinity, more intense droughts, and more extreme temperatures (e.g. Field, 1995). Some other palynological reconstructions in mangrove forests have also shown *Avicennia* expansions for the last century (Behling et al., 2001).

Sea-level rise may be the most important factor influencing the future distribution and structure of mangroves but its effect will vary significantly depending on the local rate of sea-level rise and the availability of sediments to support mangrove re-establishment. Mangroves keep pace with rising sea level through the process of vertical accretion (i.e. the build-up of organic material and sediments; e.g. Blasco et al., 1996). However, if mangroves do not accrete vertically at a rate equal to the rate of sea-level rise, they will be stressed and ultimately disappear (e.g. Parkinson et al., 1994; Woodroffe, 1990, 1999). Mangroves on small islands and on carbonate settings, where the geomorphological and functional dynamics are primarily dominated by tides, and where freshwater discharge and fluvial sediment yield are low, are less likely to survive the projected sea-level rise for the next century (Ellison, 1993) unless they can expand landwards (Parkinson et al., 1994; Woodroffe, 1990, 1999). But landward migration depends on the availability of suitable areas for mangrove colonization, in which case the immediate hinterland topography might be a limiting factor (Bacon, 1994), as would be the case of San Andrés Island (Figure 1).

Conclusions

Palynological results from Bahía Honda core provide insight into the response of mangrove ecosystems of the Colombian Caribbean to climate change during the latest Holocene. We found that the main driving factors on vegetation changes were storms, human disturbances and sea-level rise. The palynological reconstruction of Bahía Honda core starts before 2475 yr BP, when a sandy beach environment was

present in the coring site. At ~AD 1600 a strong erosive event, most likely associated to the occurrence of the nearby AD 1605 hurricane caused the loss of c. 2000 years of sedimentary record and the destruction of all the arboreal vegetation at the coast. After 50–70 years the mangrove started to recover as a response to local sea-level rise reaching its maximum development between AD 1750 and 1850. The establishment of large coconut (*C. nucifera*) plantations resulted in a strong pressure on the vegetation of the Island, especially on the coastal vegetation and mangroves. Since AD 1960, a recent expansion of the mangrove is recorded, coinciding with the duty-free port declaration of San Andrés Island and the recuperation of areas that were previously designated for coconut plantations.

Mangrove forests may be disrupted on shorter timescales by natural disturbances, such as catastrophic storms. Even though these seem to be devastating, given time, the forests may eventually recover. According to the Food and Agriculture Organization (FAO)'s Forestry Department, about 20% of mangroves have been lost since 1980 due to human activities (FAO, 2007). In this sense, human influences can be even more destructive, forcing these ecosystems beyond their natural resilience. Such anthropogenic disturbances may represent the ultimate disturbance to many large areas of mangrove forests that, linked to global climate change effects, could lead to the definitive loss of these valuable ecosystems.

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