



Modern pollen rain in mangroves from San Andres Island, Colombian Caribbean

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ABSTRACT

The precise characterisation of present-day mangrove ecosystems from modern pollen rain facilitates the accurate use of fossil pollen data for late Quaternary sea level and environmental reconstructions. Here, we investigate whether the analysis of pollen rain data corroborates existing floristic and structural characterisation of different mangrove types at the Caribbean island of San Andrés, Colombia. At 82 plots along 20 transects of four distinct mangrove types, samples were obtained of (i) surface sediments for pollen analysis, and (ii) a range of environmental parameters (including inundation levels, salinity and pH). This information was compared to previously sampled mangrove composition and tree basal area. In surface sediment samples 82 pollen taxa were found, from which 19 were present in the vegetation plots. However, because pollen may be transported by wind and/or watercourses, the overall floristic composition of the different forest types may not necessarily be reflected by the pollen spectra. Local vegetation (i.e. mangroves and beach) represented >90% of the pollen spectra, while the regional one (i.e. hinterland forests) represented <5% of it. Unlike the four mangrove types that were previously described in the vegetation, the analysis of pollen samples suggested only three distinct types of forest.

The groups were characterised based on (i) the dominance of at least one of the true mangrove species from pollen data ordination and the presence of associated species, and (ii) their relationship with environmental parameters. *Rhizophora* was present in all plot samples, but did not contribute to forest type separation. In fact, just three true mangrove species proved reliable indicators of (i) high salinity and fringe mangroves (i.e. *Avicennia*), (ii) high pH levels and landward mangroves (i.e. *Conocarpus*), and (iii) natural or anthropogenic caused disturbance of forest stands (*Laguncularia* and associated *Acrostichum* fern). Hence our study confirms that mangrove pollen spectra can be accurately used to describe different mangrove environments for fossil based palaeoecological reconstructions.

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1. Introduction

Fossil pollen records of mangrove forests have been widely used to reconstruct past environmental changes of tropical and subtropical coastal zones at different time scales. For example, mangrove expansion during the marine transgression following the Last Glacial Maximum (Scourse et al., 2005; González et al., 2006; Hooghiemstra et al., 2006; Tossou et al., 2008) and during the late Holocene (Behling et al., 2001; Cohen et al., 2005; Ellison, 2005, 2008). Research indicates that the dieback of mangroves in the late Holocene period arose as a consequence of sea level rise, coastal erosion and submersion of coast of islands (Ellison, 1993). The combined effect of increased fluvial sedimentation and coastal dynamics (Parkinson et al., 1994; Grindrod et al., 1999) has facilitated the adaptation of mangroves to changing sea levels and consequently, expand or contract along coastal plains. Natural catastrophic events such as hurricanes and tsunamis or

human activities such as mangrove replacement by coconut plantations (Donders et al., 2008; González et al., 2010) have also affected mangroves. Nevertheless, a more precise characterisation of present-day mangrove ecosystems based on pollen rain is required to accurately interpret fossil pollen data.

A number of studies have explored the relationship between vegetation composition and pollen occurring in the surface sediments of mangroves. Prime examples include the western Pacific and the Malayan region (Ellison, 1989; Kamaludin, 1993), tropical Africa (Elanga et al., 2000; Van Campo and Bengo, 2004), and China (Sun et al., 1999; Mao et al., 2006; Li et al., 2008). However, there is a paucity of information for South America, limited to studies at the Orinoco Delta in Venezuela (Muller, 1959; Hofmann, 2002), north-east Pará, Brazil (Behling et al., 2001) and Cispatá Bay in the Caribbean region of Colombia (Urrego et al., 2009a).

At a landscape scale, existing literature indicates that high proportions of pollen ($\geq 60\%$), of the wind-pollinated species of *Rhizophora*, typically indicate the presence of mangrove forests in the vicinity of adjacent coastal zones (Muller, 1959; Grindrod and Rhodes, 1984; Chappell and Grindrod, 1985; Woodroffe et al., 1985;

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Hooghiemstra and Agwu, 1986; Grindrod, 1985, 1988; Elenga et al., 2000; Behling et al., 2001). On the other hand, low proportions of this taxon's pollen (<25%) may indicate the downstream transport of pollen grains, comprising either landward or disturbed mangrove stands (Hooghiemstra and Agwu, 1986; Lézine and Hooghiemstra, 1990; Van Campo and Bengo, 2004; Engelhart et al., 2007; Urrego et al., 2009a). Changes in the relative abundance of this taxon have been used to interpret sea level reconstructions at a range of tropical and subtropical coastal zones across the globe (e.g. north-west Africa, Hooghiemstra et al., 2006; Indonesia, Engelhart et al., 2007; and other locations, Ellison, 2008). Along the continental shelves, historical sea level rise and pro-gradation have been indicated by increased proportions of *Rhizophora*. In comparison, the diminution of pollen proportions of this taxon on carbonate mudflats of oceanic islands has been associated with coastal erosion and/or the submersion of mangroves as a result of sea level rise (Ellison 2008). The fact that mangroves are set in a heterogeneous environment, with a broad spectrum of associated vegetation between and within forest stands, has been given limited consideration. For example, the pollen rain signature of an individual species may not necessarily be representative of all mangrove forest types. Furthermore, the strong relationship between mangrove forest structure and composition with environmental parameters has been overlooked in palaeoclimatic studies. Such parameters include regional climate, geomorphology, hydrology (Thom, 1967; Woodroffe, 1992), local slope, drainage, tidal amplitude and sediment type (Méndez-Linares et al., 2007). A close relationship between vegetation type and pollen signature has been established for several coastal systems (e.g. Willard et al., 2001). However, aside from *Rhizophora*, the indicative potential of important mangrove taxa such as *Avicennia*, *Conocarpus* and *Laguncularia*, has received limited consideration due to their relatively low pollen rain contribution in comparison to that of *Rhizophora* (Behling et al., 2001; Hofmann, 2002; Li et al., 2008). Modern mangrove ecology indicates that the occurrence of these species is linked to clear ecological and environmental preferences (Hogarth, 2007; Tomlinson, 1986). For example, the high relative abundances of *Avicennia* are indicative of high salinity conditions, while *Conocarpus* indicates the proximity of mangroves to the hinterland and a reduced tidal influence. On the other hand, the dominance of *Laguncularia* indicates an open forest canopy as a result of natural or anthropogenic disturbance (Tomlinson, 1986; Benfield et al., 2005; Hogarth, 2007).

The accurate characterisation of the relationship between pollen rain, vegetation and environmental parameters may provide the ability to determine whether fluctuations in the relative abundance of mangrove pollen species have the potential to indicate climate change, sea level, the flooding of soils and geomorphology, as well as endogenous forest dynamics and/or anthropogenic disturbance. Small islands have been shown to provide ideal environments in which to evaluate such parameters in mangrove systems, due to their isolation from other landmasses and usually complete floristic descriptions (Lowy, 2000). Previous research at the Caribbean island of San Andrés, Colombia has indicated the differentiation of four types of mangrove forest (two riverine and two fringe) based on floristic and structural vegetation characteristics (for details see Urrego et al., 2009b). However, there are distinct differences in edaphic and hydrological characteristics of these forests, which may additionally influence their structure and composition.

Hence, in this study we set out to corroborate the findings of Urrego et al. (2009b) through the analysis of pollen rain spectra in surface sediments at the San Andrés mangroves. Our primary objective was to evaluate whether the pollen rain signature of surface samples for each forest stand serves as a reliable indicator for (i) the composition of the vegetation growing at the sampled sites, and (ii) the degree of environmental variability between coastal sites on the island. The identification of this relationship would provide a basis from which

mangrove palynological records could be used to infer past climatic and environmental changes on the island and the wider Caribbean region.

1.1. Study area

The Colombian island of San Andrés (Fig. 1, 25 km², 12° 29'–12° 36' N and 81° 41'–81° 43' W) is located in the south-west Caribbean, 800 km north-west off mainland Colombia and 150 km east off Nicaragua (Díaz et al., 1995; Baine et al., 2007). It is the largest island of the San Andrés, Old Providence and Santa Catalina Archipelago that comprise the Seaflower Biosphere Reserve (Baine et al., 2007).

The mean annual precipitation of 1800 mm is determined by the north-east trade winds, with 80% of rain falling between October and December (IGAC, 1986). The average annual temperature is 27 °C. There are no permanent surface freshwater sources on the island, however small watercourses form during the wet season. There is one semi-permanent gully which primarily flows westward to the Cove Inlet (Fig. 1), while other gullies flow eastward to the mangrove forests (IGAC, 1986). There are also underground water deposits which are supplied by percolation of 21% of the island's rainfall through the calcareous rocks (Díaz et al., 1995).

The San Andrés landscape is composed of (i) a hills system of up to 100 m elevation above sea level in the central part of the island, and (ii) a coastal plain composed of emerged coralline terraces located a few meters above sea level (Fig. 1; Cortés, 1982). The original vegetation type of the hills was described as a combination of dry and moist forest (Lowy, 2000). However, today the island lacks primary vegetation, and is dominated by secondary forests formations (Bolívar and Vélez, 2004). On the landward sandy substrates neighbouring the mangrove forests, important species include: *Cocos nucifera* L., *Terminalia catappa* L., *Guazuma ulmifolia* Lam., *Casearia aculeata* Jacq., *Annona glabra* L., *Spondias mombin* L., *Psidium guajava* L., *Dalbergia brownii* (Jacq.) Schinz., *Artocarpus altalis* (Parkinson) Fosberg, *Morinda citrifolia* L. and *Leucaena leucocephala* (Lam.) de Wit (Bolívar and Vélez, 2004). Beach vegetation and mangrove forests dominate the coastal plains (Díaz et al., 1995; Lowy, 2000). On sandy beaches herbaceous vegetation predominates, including *Sesuvium portulacastrum* (L.) L., *Hymenocallis littoralis* (Jacq.) Salisb., *Ruellia tuberosa* L., *Batis maritima* L., *Tournefortia gnaphalodes* R. Br. ex Roem. & Schult., *Ipomoea pes-caprae* (L.) R. Br., and tree species include *Hippomane mancinella* L., *Chrysobalanus icaco* L., *Hibiscus tiliaceus* L., and *C. nucifera* (Díaz et al., 1995; Lowy, 2000). In this landscape besides coconut plantations (*C. nucifera*) other crops, such as *Morinda citrifolia* (L.), *Manihot esculenta* Cranz and *Musa* spp., are commonly found (Bolívar and Vélez, 2004).

Most of the 96 ha of mangrove forests are located along the eastern coast of the island, but a small patch can be found on the western coast (Fig. 1). According to Urrego et al. (2009b), four mangrove types can be found in the island. Two of the forests on the east coast are classified as riverine mangroves (see Lugo and Snedaker, 1974) due to their isolation from direct tidal influence with only sporadic flooding from freshwater streams. The other two are classified as fringe mangroves, due to their being directly influenced by tides. The two types of mangrove forest differ in their edaphic and hydrological characteristics, forest structure and composition. The forests were primarily dominated by true mangrove species, including *Avicennia germinans* (L.) L., *Rhizophora mangle* L., *Laguncularia racemosa* (L.) C.F. Gaertn. and *Conocarpus erectus* L. and some non-mangrove species.

1.2. Riverine mangroves

There are two groups of riverine mangroves on the island. The first group is located along the lower half of the south-east facing part of the island. These mangroves are characterised by high mean fresh water inundation levels (57.4 ± 16.9 cm), low sediment salinity levels (1.4 ± 1.6‰). The dominant species are *Laguncularia racemosa* and

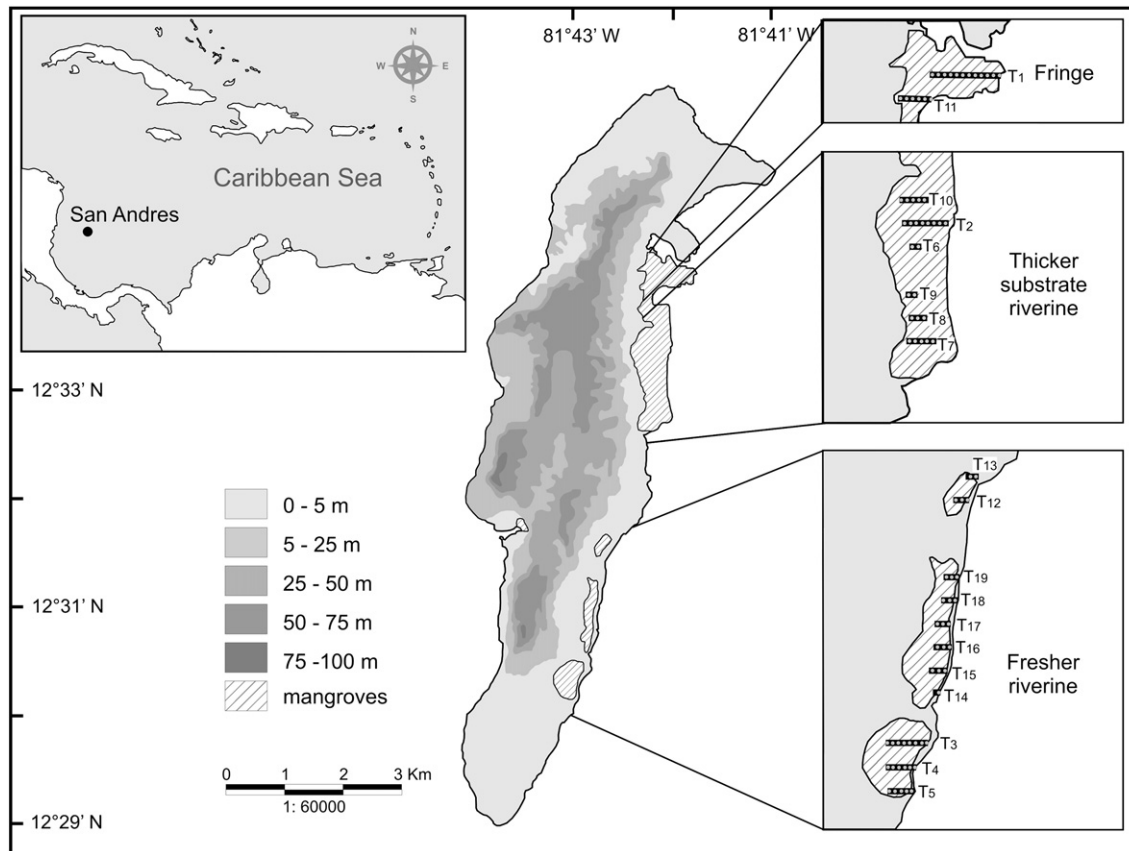


Fig. 1. Location map of San Andrés Island in the Caribbean Sea (top left). Sampling transects (black lines) over the mangrove forests (slanted gray lines) in San Andrés are shown (right). Fringe mangroves (upper right), riverine mangroves that grow on a thicker sandy substrate, located at the north (middle window) and riverine mangroves with high fresh water inundation levels (bottom), located at the south of the island, are indicated. Shaded gray scale corresponds with height (m) above sea level.

Rhizophora mangle, however other species can be found, such as *Annona glabra*, *Avicennia germinans*, *Phyllanthus acidus* (L.) S., *Terminalia catappa*, *Ficus trigonata* L., *Eugenia* sp. and the palm *Coccothrinax argentata* (Jacq.) L.H. Bailey. The second group is located along the upper half of the north-east facing part of the island. This group is characterised by a sandy ($74.2 \pm 17.3\%$) and thicker sediment substrate (156.7 ± 10.1 cm) that has accumulated over the calcareous rock. The dominant species are *Conocarpus erectus*, *R. mangle* and *L. racemosa*, while other species include *Cocos nucifera* L. is abundant, and *Randia armata* (SW.) DC. and *Neea* sp. (Fig. 1, Urrego et al., 2009b).

1.3. Fringe mangroves

There are also two different groups of fringe mangroves on the island. These are differentiated based on influence of freshwater and hence in salinity. The first group of fringe mangroves grows on saline sediment ($31.0 \pm 10.3\%$) that is less thick than that of the riverine (78 ± 60 cm). This is because they are adjacent to coralline outcrops along the upper part of the north-east coast. The dominant species include *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*, in addition to tropical dry forest species, such as *R. armata*, *Capparis* cf. *indica* (L.) Druce, *Bursera simaruba* (L.) Sarg., *Myrcia falax* (Rich.) DC., *Coccoloba uvifera* (L.) L., *Cordia sebestena* L., *Zanthoxylum fagara* (L.) Sarg and *Polygonum punctatum* (Elliot). The second group of fringe mangroves were present on the most saline sediment ($35.1 \pm 5.1\%$) with low freshwater inundation levels (15.4 ± 3.8 cm) and a thick sediment layer (160 cm). These groves were dominated exclusively by true mangrove species *Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa* and *Conocarpus erectus* (Urrego et al., 2009b).

2. Methods

Twenty 10 m-wide transects were established in all mangrove forests following an east–west direction (Fig. 1), where 82 rectangular plots (500 m² each) were delimited for modern vegetation analysis. The transect lengths was determined on the size of particular forest stands. Surface sediments (5 × 5 cm surface, and 2 cm depth) were collected for pollen analysis in the centre of each vegetation plot. Within each 500 m² plot, the normal diameter (*D*) of trees with *D* > 2.5 cm was measured 1.3 m above the ground, or 30 cm above the highest aerial root (for details see Urrego et al., 2009b). The thickness of the sediment above the carbonate rock was measured. This variable provided information on nutrient availability, plant root development and pollen preservation. Other environmental variables such as freshwater inundation level, soil texture, distance from coastline, interstitial salinity and pH, were also measured at each plot.

Surface sediment samples of 1 cm³ were prepared for pollen analysis using standard laboratory methods. This included pre-treatment with KOH (10%) followed by Erdtman's (1960) acetolysis technique. Spore and pollen grain identification was based on the pollen reference collection held at the Ecology Laboratory of Forestry Science Department of the National University of Colombia, and published pollen atlases (Roubik and Moreno, 1991; Herrera and Urrego, 1996; Colinvaux et al., 1999; Willard et al., 2001; Bush and Weng, 2007). For each sample, a minimum of 300 palynomorphs were counted when possible, including trees, herbs and the fern *A. aureum* (i.e. pollen sum). The proportion of each taxon was calculated as a percentage per sample based on this pollen sum. Fern spores other than *A. aureum*, were grouped together and expressed as a percentage of the pollen sum.

Diagrams showing the percentage of pollen were drawn using C2 software (Juggins, 2003). Simple regression analysis (STATGRAPHICS

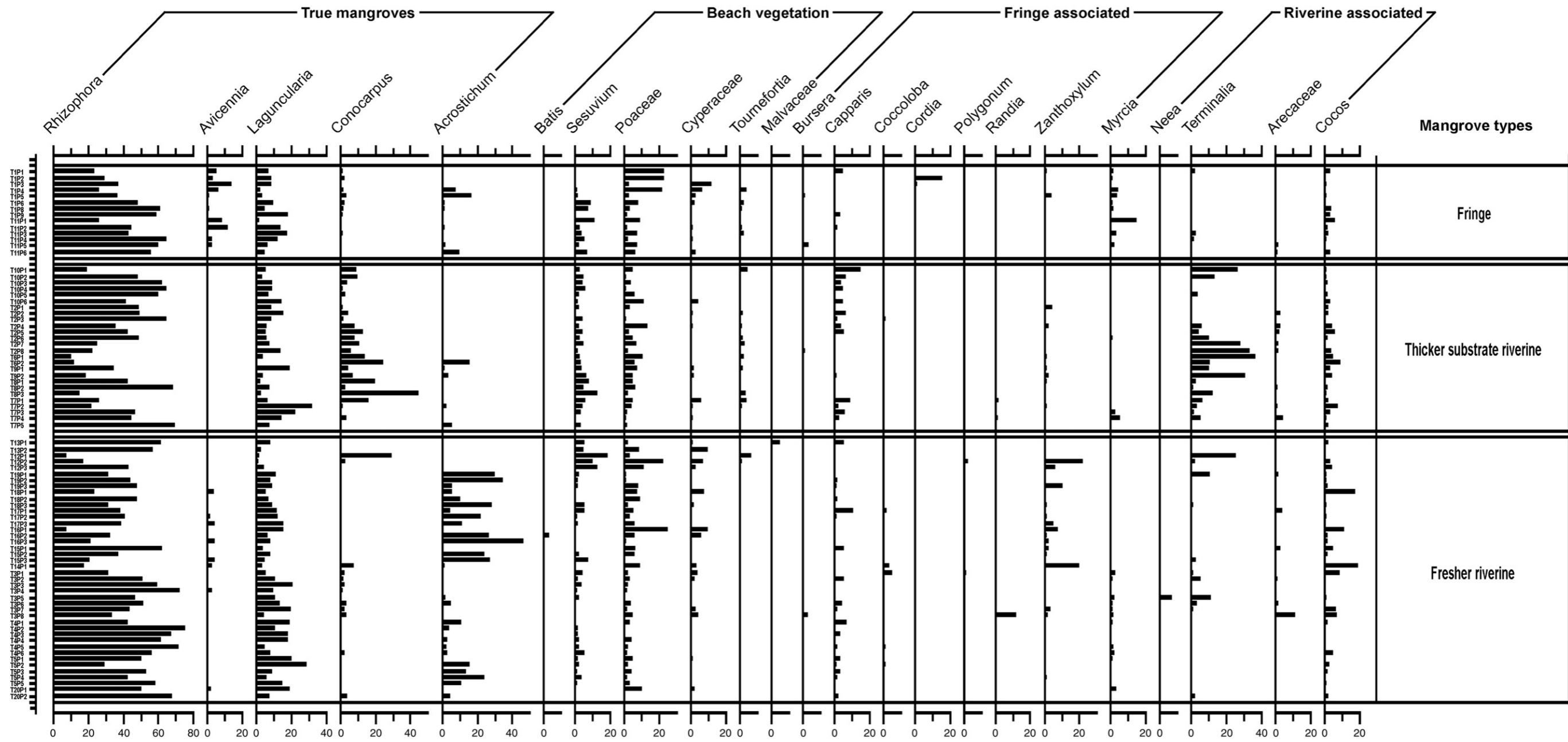


Fig. 2. Diagram of pollen percentages of taxa found in surface sediments of mangroves of San Andrés Island. At the left, samples are ordered from top to bottom following the sequence of transects from north to south of the island and separated by mangrove types identified in the Island. At the top, main pollen taxa ordered by their presence in the mangrove types recorded in the island.

Centurion XV, Version15.1.02) was used to evaluate the relationship between the pollen percentages of surface samples (e.g. pollen signature) with respect to the basal area of tree species of the sampled vegetation (e.g. actual vegetation). This relationship was also tested by calculating the association (A), under-representation (U) and over-representation (O) indices proposed by Davis (1984):

$$A = B_0 / P_0 + P_1 + B_0 \quad U = P_1 / P_1 + B_0 \quad O = P_0 / P_0 + B_0$$

where B_0 equals the number of samples in which a species is present as a pollen type in the surface sample and as a plant in the vegetation plot; P_0 equals the number of samples in which the pollen type is present in the surface sample but absent in the vegetation plot; and P_1 equals number of samples in which the pollen type is absent in the surface sample while the plant is present in the vegetation plot. Ordination of the pollen percentages of the main taxa was determined using detrended correspondence analysis (DCA). The relationship between the ordination of taxa with respect to environmental variables was determined using canonical correspondence analysis (CCA). The analyses were calculated using CANOCO 4.5 software (Ter Braak and Smilauer, 1997–2003). Multiple regression analysis (STAT-GRAPHICS Centurion XV, Version15.1.02) was used to evaluate the relationship between individual taxa of mangroves with respect to environmental variables. The spatial distributions of the pollen percentages with respect to environmental variables were drawn using SURFER version 8.02 (Golden software, INC., 2002) and the kriging interpolation method.

3. Results

3.1. Pollen rain

In total, 82 pollen taxa were found in the surface sediment samples from the four San Andrés mangrove forests. Of these, five taxa were true mangrove species, 16 taxa were associated species that co-exist with true mangrove species, and 15 taxa corresponded to the vegetation of neighbouring sandy beach species. For the purposes of this study, true, associated and neighbouring species have been termed 'local vegetation'. Only three pollen taxa were transported from the continent (*Alnus*, *Hedyosmum* and *Pinus*) but their relative abundance (<1.6%) and frequency (<5 samples) were too low to have significance for further analysis. The remaining 43 pollen taxa were transported by wind or watercourses from adjacent secondary forests in the hills down to the mangrove floor, and for the purposes of this manuscript have been termed 'regional vegetation'. Fig. 2 shows the pollen percentages of taxa that exceeded proportions of 2% in the surface sediment samples. The samples were ordered according to their location along the vegetation transects. The transect lines were sorted from north to south along the east coast of the island, and grouped according to differences in their pollen assemblages based on multivariate ordination. A clear distinction between three different mangrove forest types was obtained; one fringe, one riverine on a thick sandy sediment layer and one riverine that was subject to high levels of inundation.

The first group contained pollen assemblages of fringe mangroves (Fig. 2, Transects T1 and T11). A total of 63 pollen taxa was recorded, of which 31 taxa belonged to the local vegetation category with 13 taxa corresponding to mangrove vegetation and 18 taxa corresponding to beach vegetation. The remaining 32 taxa corresponded to the regional vegetation category. The proportion of *Rhizophora* pollen increased along transects in a seaward direction (from 22% to >60%). *Laguncularia* proportions were in the range of 2–18%. A maximum of 12% for *Avicennia* and 17% for the fern *Acrostichum aureum* were reached in some samples. Additional taxa of interest corresponded to beach vegetation (i.e. Poaceae, *Sesuvium* and Cyperaceae). Dominant trees in the sampled vegetation, such as *Bursera*, *Capparis*, *Cocos*,

Cordia, *Myrcia* and *Zanthoxylum*, reached rather high percentages in the pollen record, but *Coccoloba*, *Polygonum* and *Randia* had percentages lower than 1%.

In the second group the pollen record percentages represented riverine mangroves that grow on a thick sandy sediment layer (Fig. 2, Transects T10, T2, T6, T9, T8 and T7). A total of 60 pollen taxa were recorded, of which 32 taxa belonged to the local vegetation. Just seven taxa found in the pollen record were present in the sampled vegetation. The remaining 28 taxa belonged to that of regional vegetation. The highest pollen taxa percentages for *Conocarpus* (45%), *Laguncularia* (32%) and *Cocos* (9%) were recorded in this group, and represented the sampled vegetation. In contrast to the fringe mangroves, the percentages of *Rhizophora* pollen were highest in a landward direction (range: 10–70%). *Avicennia* was almost absent in both the pollen record and the sampled vegetation. While *Neea* and *Randia* were present in the sampled vegetation but had low pollen record percentages. On the other hand, the highest pollen record percentage was recorded for *Terminalia* in this group, yet it was scarce in the sampled vegetation. Taxa from beach vegetation had lower percentages than in the fringe group.

In the third group, the pollen record percentages represented riverine mangroves that grow on highly inundated low salinity sediments (Fig. 2, Transects T13, T12, T19, T18, T17, T16, T15, T14, T3, T4, T5 and T20). A total of 72 pollen taxa were recorded, of which 35 taxa corresponded to that of local vegetation. Just 12 of the taxa found in the pollen record were present in the sampled vegetation. The remaining 37 pollen taxa corresponded to that of regional vegetation. Both *Laguncularia* and *Rhizophora* were dominant, reaching values of 28% and 72%, respectively. *Conocarpus* and *Avicennia* reached values of 30% and 5%, respectively. Other tree taxa, found both in the sampled vegetation and pollen record, included *Terminalia*, *Cocos*, *Randia*, *Arecaceae* and *Myrcia*. On the other hand, important taxa such as *Annona*, *Ficus* and *Phyllanthus* were scarce in the pollen record. The relative abundance of *Acrostichum* was as much as 46% in some samples. Beach vegetation taxa, such as Poaceae, *Sesuvium* and Cyperaceae, were also abundant in the pollen record of this group.

3.2. Pollen–vegetation relationships

Simple regression analysis indicated that the basal area of tree species in sampled vegetation was significantly correlated with pollen percentages in surface sediment samples for just three of the true mangrove taxa: *Avicennia* ($R = 0.70$, $F_{1,15} = 14.42$, $P < 0.00$), *Rhizophora* ($R = 0.59$, $F_{1,62} = 32.48$, $P < 0.00$) and *Conocarpus* ($R = 0.63$, $F_{1,20} = 13.17$, $P < 0.00$). The results of the analyses for all species of sampled vegetation are presented in the supplementary material. Non significant correlations were attributed either to very low pollen percentages or to their absence in most of the pollen samples.

The calculated A, U and O indices are presented in Table 1. A high association index ($A \geq 0.5$) was only obtained for true mangrove species (*Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*). *Conocarpus erectus* had an intermediate value ($A = 0.35$), indicating a close association between plant presence and pollen occurrence. The value of this index was low for all other taxa ($n = 14$, $A < 0.2$), which indicated that the presence of pollen in the sediment samples may not necessarily be related to the presence of plants in the sampled vegetation. High values of the under-representation index ($U \geq 0.5$) were obtained for eight non-mangrove taxa (i.e. *Annona*, *Capparis*, *Coccoloba*, *Ficus*, *Neea*, *Phyllanthus*, *Randia* and *Zanthoxylum*). True mangrove taxa, in addition to *Arecaceae*, *Bursera*, *Cocos*, *Cordia*, *Myrcia*, *Terminalia*, had low values of this index ($U < 0.35$). With the exception of the three true mangrove species (*R. mangle*, *A. germinans*, *L. racemosa*), all other taxa expressed high values of the overrepresentation index ($O \geq 0.5$). According to Davis (1984), high values of both U and O indices indicate species with low pollen production but good dispersal properties. In contrast, low values of U

Table 1

Values of representation association (A), under-representation (U) and overrepresentation indexes (Davis, 1984) for species present in the standing vegetation and in pollen samples in mangroves of San Andrés island. $A = B_0/P_0 + P_1 + B_0$, $U = P_1/P_1 + B_0$, and $O = P_0/P_0 + B_0$, B_0 equals the number of samples in which the species is present as a pollen type in the surface sample and as a plant in the vegetation plot; P_0 equals the number of samples in which the pollen type is present in the surface sample but absent in the vegetation plot; and P_1 equals number of samples in which the pollen type is absent in the surface sample while the plant is present in the vegetation plot.

Species	Bo	Po	P1	(A)	(U)	(O)
<i>Annona glabra</i>	7.00	10.00	12.00	0.24	0.63	0.59
<i>Coccothrinax argentata</i>	2.00	39.00	1.00	0.05	0.33	0.95
<i>Avicennia germinans</i>	18.00	11.00	4.00	0.55	0.18	0.38
<i>Bursera simaruba</i>	2.00	14.00	0.00	0.13	0.00	0.88
<i>Capparis cf. indica</i>	1.00	45.00	1.00	0.02	0.50	0.98
<i>Coccoloba uvifera</i>	0.00	24.00	1.00	0.00	1.00	1.00
<i>Cocos nucifera</i>	13.00	61.00	0.00	0.18	0.00	0.82
<i>Conocarpus erecta</i>	21.00	37.00	2.00	0.35	0.09	0.64
<i>Cordia sebestena</i>	1.00	6.00	0.00	0.14	0.00	0.86
<i>Ficus trigonata</i>	0.00	15.00	8.00	0.00	1.00	1.00
<i>Laguncularia racemosa</i>	60.00	21.00	0.00	0.74	0.00	0.26
<i>Myrcia falax</i>	5.00	35.00	0.00	0.13	0.00	0.88
<i>Neea</i> sp.	1.00	3.00	1.00	0.20	0.50	0.75
<i>Phyllanthus acidus</i>	1.00	6.00	1.00	0.13	0.50	0.86
<i>Randia armata</i>	2.00	15.00	3.00	0.10	0.60	0.88
<i>Rhizophora mangle</i>	64.00	18.00	0.00	0.78	0.00	0.22
<i>Zanthoxylum fagara</i>	1.00	49.00	1.00	0.02	0.50	0.98
<i>Terminalia catapa</i>	5.00	43.00	1.00	0.10	0.17	0.90

index and high values of O indicate taxa with poor pollen production and/or dispersal. This may explain the absence of correlation for the tree basal area of non-mangrove species with respect to their pollen percentages.

3.3. Pollen distribution along environmental gradients

The pattern of ordination for pollen data, tested with a DCA, is shown in Fig. 3A and B. The first two ordination axes, with eigenvalues of 0.35 and 0.14 respectively, explained 35% of variance in the datasets. A discrete separation among mangrove types (see Urrego et al., 2009b) was not shown in the ordination of the surface sediment samples (Fig. 3A). However, an indirect edaphic-salinity gradient was indicated. For example, pollen samples from riverine mangrove subject to high levels of inundation were found in the upper part of the figure plot, while samples from riverine mangroves growing on sandy and thinner sediment layer were found near the bottom of the figure plot. On the other hand, fringe mangroves were clustered in the right section of the figure plot, with some samples overlapping with the previous two groups.

The ordination of pollen taxa (Fig. 3B) did not indicate the presence of distinct groups. This may have been due *Laguncularia* and *Rhizophora* taxa being present in most samples. A large proportion of the associated taxa did not contribute to data ordination along gradients due to their very low pollen percentages. The ordination of some taxa was related to the distribution of mangrove types along edaphic-salinity gradients: taxa characterising high salinity fringe mangroves (i.e. *Avicennia* and *Cordia*) were located to the right of the figure plot, while taxa characterising riverine mangroves (i.e. *Terminalia* and *Conocarpus*) were located to the left of the figure plot. On the other hand, *Zanthoxylum* (which represented fringe mangroves) was located at the top of the figure plot while *Neea* (which represented riverine mangroves) was located at the bottom of the figure plot. This indicated the link of these taxa to specific forest stands and their restricted distribution along the environmental gradients.

The results of the distribution of mangrove pollen taxa along environmental gradients, tested using a canonical correspondence analysis (CCA), are presented in Table 2 and Fig. 4A and B. The eigenvalues of the first and second ordination axes were low (0.105 and 0.054 respectively), however the percentage of cumulative

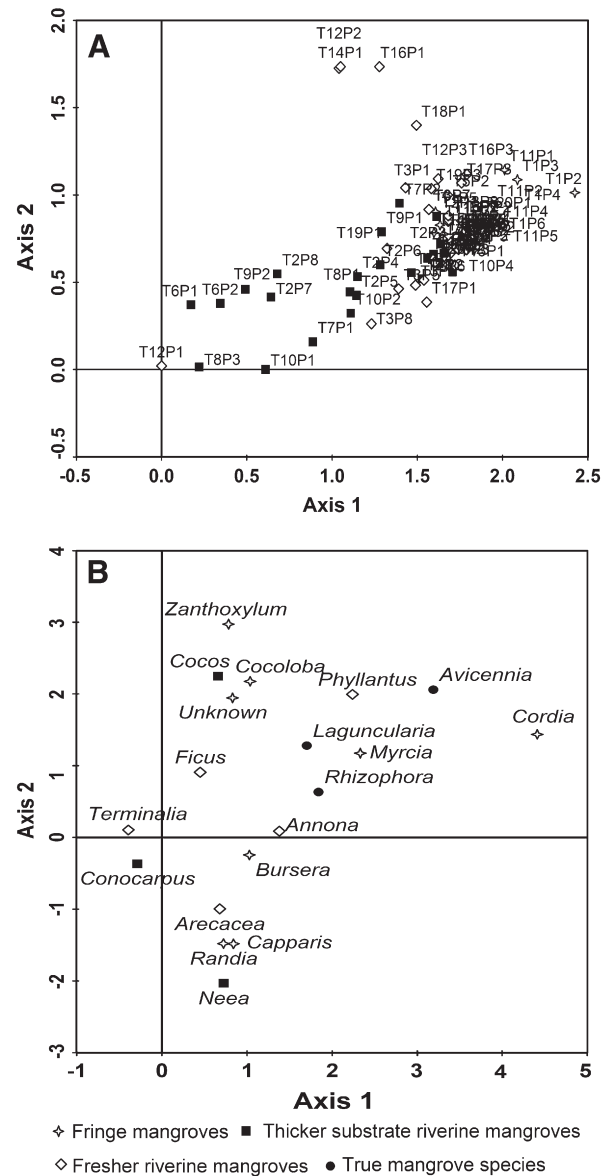


Fig. 3. Detrended correspondence analysis biplots in surface pollen samples of San Andrés mangroves. A. Samples of each mangrove type are identified by a symbol. B. Taxa grouping by mangrove type.

variance (explained by the eigenvalues) was high (66%). This reflected the way in which the mangroves were distributed along the environmental gradients, which was also indicated in the sampled vegetation datasets (Fig. 4A). Two main gradients were identified: (i) that of soil salinity and pH, which had the highest correlation and

Table 2

Inter-set canonic and correlation coefficient values for surface pollen samples in mangroves of San Andres Island, obtained from Canonical Correspondence Analyses.

Variable	Canonic coefficients		Correlation coefficients	
	Axis 1	Axis 2	Axis 1	Axis 2
Salinity ^a (‰)	0.15	0.27	0.47	0.12
pH ^a	-0.69	-0.29	-0.53	-0.01
Inundation level (cm)	-0.04	-0.17	-0.06	-0.18
Soil depth (cm)	-0.05	0.59	-0.08	0.32
Sand (%)	-0.26	0.96	-0.18	0.36
Silt (%)	0.24	-0.51	0.004	0.15
Distance to sea (m)	0.34	-0.19	0.36	0.13

^a Measured in interstitial water.

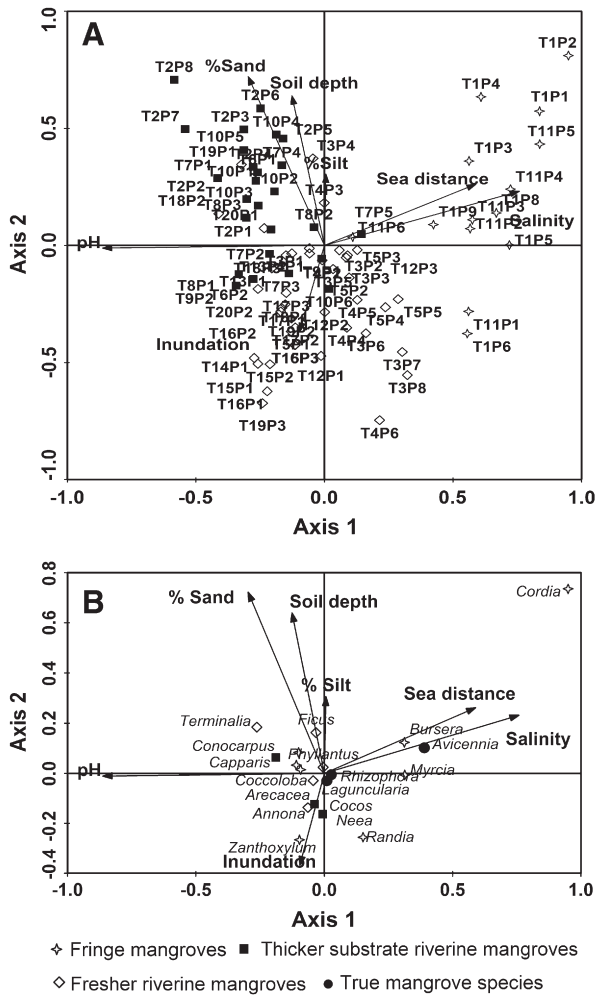


Fig. 4. Canonical correspondence analysis biplots in surface pollen samples of San Andrés Island mangroves. A. Samples grouped by mangrove type and environmental variables. B. Species grouping and environmental variables.

canonical coefficients, and (ii) that of sediment layer thickness and proportion of sand. As a result, the different mangrove types were separated into distinct groups. For example, fringe mangrove vegetation was clustered to the right of the figure plot, particularly taxa of *Bursera*, *Avicennia*, *Myrcia* and *Randia*. On the other hand, riverine mangrove vegetation, growing on thick sandy sediment layers, was clustered to the upper left of the figure plot. Finally, riverine mangroves that are subject to high levels of inundation were grouped to the centre and bottom left of the figure plot. Examples of riverine taxa that were located to the left of the figure plot include *Terminalia*, *Conocarpus*, *Neea* and *Zanthoxylum*. The two types of riverine mangrove taxa were less conspicuous when using pollen record samples, rather than vegetation samples.

Multiple regression analysis indicated a significant correlation for the three dominant mangrove species with respect to environmental variables, when using the pollen records. Analysis indicated that *Rhizophora* was correlated to inundation levels and distance to the sea ($R=0.31$, $F_{1,80}=39.93$, $P<0.001$). On the other hand, *Avicennia* was correlated to sediment salinity ($R=0.56$, $F_{2,79}=4.38$, $P<0.02$). Finally, *Conocarpus* was correlated to sediment pH ($R=0.29$, $F_{1,80}=4.31$, $P<0.01$). Other local vegetation, such as the fern *Acrostichum* sp., also showed significant correlations with inundation level, distance to sea and proportion of sand in the sediment. A correlation with environmental variables was also found for local herbaceous taxa that were indicative of these conditions. For example, *Poaceae* was correlated to salinity ($R=0.26$, $F_{1,80}=5.98$, $P<0.02$), while *Tournefortia* ($R=0.31$,

$F_{1,80}=8.49$, $P<0.01$) and *Sesuvium* ($R=0.30$, $F_{1,80}=7.96$, $P<0.01$) were correlated to the proportion of clay in the sediment.

4. Discussion

The surface sediment samples indicated that the pollen of local vegetation (i.e. mangroves) was more dominant than the pollen of regional vegetation (i.e. secondary forest) in the San Andrés mangroves. Furthermore, local pollen was strongly related to the proximity of source vegetation. Similar findings have been observed in other mangroves (e.g. *Elenga et al. 2000*; *Behling et al., 2001*) and neotropical forests (e.g. *Bush and Rivera, 1998*). The percentage of pollen from true mangrove species was above 60% when obtained from surface sediment samples at pure mangrove stands, supporting existing literature (*Hooghiemstra and Agwu, 1986*; *Lézine and Hooghiemstra, 1990*; *Van Campo and Bengo, 2004*; *Engelhart et al., 2007*). The percentage of pollen of local vegetation exceeded 90% of the pollen sum when beach vegetation was included within this category. A lower proportion of pollen from true mangrove taxa (i.e. 34–55%) was generally found in sediment samples obtained from areas at the transition from mangrove forests to hinterland. Here, the highest proportion of pollen taxa from regional vegetation was recorded, indicating the complexity of regional vegetation plant diversity, as found in previous research (*Weng et al., 2006*).

Pollen transport from long distances may be indicated by taxa where pollen was found in low proportions but across a large number of sediment samples, for example non-mangrove species (*Elenga et al., 2000*). Non-mangrove vegetation originates from the island's hinterland forest, which suggests that the catchment area of the pollen is larger than the sampling area within the mangrove forests, which supports the published literature (*Sugita, 1993*; *Elenga et al., 2000*; *Court-Picon et al., 2005*; *Mao et al., 2006*). On the other hand, the copious presence of high pollen producing taxa, e.g., most anemophilous plants (see *Bush, 1995*) in the pollen spectra of surface samples of mangrove forests indicate that watercourses and wind may have a significant effect on the transport and redistribution of pollen grains, affecting the pollen record composition. On San Andrés Island, the prevailing Caribbean trade winds, from November to April and June to July, are east–west and north–east in direction. However, during May and September to October the trade winds are weaker (*Díaz et al., 1995*), and may have a limited influence on the pollen transport from the upland forests to the lowland mangroves, which are primarily located along the island's east coast. However the combination of north-easterly trade winds and the wet season in May to November may facilitate the transportation of pollen from regional hill sources to the mangroves by running surface water. Of additional consideration, the Intertropical Convergence Zone forms a cyclonic belt in August, resulting in a prevailing westerly wind (*Andrade, 1993*), that reinforces the pollen transport. Overall, the pollen recorded in this study was primarily limited to the local and regional vegetation of San Andrés Island. This is to be expected because this small island is separated by 90 km from Providencia, its closest neighbouring island, and 150 km from the Central American continent. Hence the transport of pollen grains from these adjacent areas is rare, as evidenced by the sparse presence of strictly continental taxa such as *Alnus*, *Hedyosmum* and *Pinus* in the pollen record of this study. In this way, the pollen spectra recorded in San Andrés Island mostly reflect the local and regional vegetation derived from the island with an almost neglectable input from further distances.

4.1. Outline of mangrove types

Previous research on San Andrés Island delineated four distinct mangrove types (two fringe and two riverine) based on the analysis of modern mangrove vegetation (*Urrego et al., 2009b*). However, in the current study multivariate ordination of the pollen data resulted in

the definition of only three distinct mangrove forest types (one fringe and two riverine). In both vegetation and pollen sampling three mangrove species (*Rhizophora mangle*, *Conocarpus erectus* and *Avicennia germinans*) dominated these three categories with differences in their relative proportions contributing to the separation of the forest types. The correlation between the proportion of pollen from mangrove species with the forest types was also supported by the high values of the A index and the low values of the U index, according to Davis (1984).

Differentiation between mangrove forest vegetation types was primarily influenced by associated taxa. However, the ordination of the pollen data of these associated taxa was not necessarily correlated with the sampled plant composition. The CCA results indicated that fringe mangrove taxa (i.e. *Bursera*, *Cordia*, *Myrcia*, *Randia* and *Zanthoxylum*) and riverine mangrove taxa (i.e. *Cocos*, *Neea* and *Terminalia*) were highly correlated to the forests where they grow. However, some of these taxa expressed low values of the U index but high values of the O index (i.e. *Bursera*, *Cordia*, *Myrcia*, *Cocos* and *Terminalia*). It is possible that insect pollination (see Bush, 1995; Hofmann, 2002) or poor pollen production (Davis, 1984) may explain the low correlation obtained between the tree basal area and pollen data of these taxa, while low levels of dispersal may explain their high correspondence with the forest type (Davis, 1984). On the other hand, some important taxa identified from sampled vegetation (i.e. *Annona*, *Arecaceae*, *Capparis*, *Coccoloba*, *Ficus* and *Phyllanthus*) expressed high values of both the U and O indices, suggesting that they are poor pollen producers, but with good dispersal properties (Davis, 1984). This was supported by the poor pollen data records for these taxa (<2%), their weak correlation with the tree basal area and poor contribution to forest differentiation.

Apart from the three true mangrove species tree basal area and pollen percentage were not significantly correlated as in many tropical forest species (Bush and Rivera, 1998; Elenga et al., 2000). The absence of correlation in all other species may be attributed to the high degree of variability of each pollen assemblage, differences in pollen production and/or dispersal among species (Elenga et al., 2000; Watrin et al., 2007). In addition, features of the catchment area, distance from the source and/or degree of representation of the source vegetation (Roe and Van de Plassche, 2005) may also play a role.

4.2. True mangrove species as environmental indicators along environmental gradients

The three dominant mangrove taxa (i.e. *Rhizophora*, *Avicennia* and *Conocarpus*), all of which expressed significant correlations with the tree basal area of the sampled vegetation. This indicates a short dispersal distance and strong species representation for these taxa, which is consistent with findings from other mangrove ecosystems worldwide (e.g. Muller, 1959; Behling et al., 2001 and Hofmann, 2002 in South America; Hooghiemstra and Agwu, 1986; Elenga et al., 2000, Van Campo and Bengo, 2004 and Hooghiemstra et al., 2006 in Africa; Moss et al., 2005 in Australia; Sun et al., 1999, Mao et al., 2006 and Li et al., 2008 in China).

The local distribution of mangrove pollen explains the CCA derived correlation between the forest types found in both the sampled vegetation and the pollen spectra. In addition, significant correlations between pollen samples and certain environmental variables contributed towards (i) the delineation of the forest types and (ii) determining the relative distribution of mangrove species along environmental gradients. The separation of mangrove types was strongly related to the distribution of forest stands along a salinity and edaphic gradient. The former is closely related to the distance to the sea for fringe mangroves. The latter is related to pH and the percentage of sand in sediment for both types of riverine mangroves. As found for mangrove forests in Indonesia (Engelhart et al., 2007), the DCA and CCA indicated that just a few associated taxa from fringe

mangroves (i.e. *Bursera*, *Cordia*, *Myrcia*, *Randia* and *Zanthoxylum*) and riverine mangroves (i.e. *Cocos*, *Neea* and *Terminalia*) significantly contributed to the differentiation of the forest types. Furthermore, similar to observations made in China (Li et al., 2008), the correlation of the pollen representation with physical variables indicates that the local mangrove environment strongly contribute to the separation of forest types at San Andrés.

4.3. *Rhizophora*

The high pollen percentages, high A index values and a significant correlation with tree basal area of *Rhizophora* demonstrated its dominance in local stands, which supports studies in mangroves worldwide (e.g. Behling et al., 2001; Hofmann, 2002; Li et al., 2008). However, *Rhizophora* did not contribute to the differentiation of forest types, despite its widespread dominance in all mangrove stands of the island. In fact, *Rhizophora* pollen was prevalent, even in stands dominated by *Avicennia*. It is possible that the low contribution of *Rhizophora* to forest differentiation may arise as a result of its high pollen production (Muller, 1959; Tomlinson, 1986; Hogarth, 2007), the mobility of pollen grains and the reworking of sediments by watercourses. For example, existing literature indicates that the volume of watercourses (i.e. streams, rivers, estuarine inlets and marine currents) plays an important role in the mixing and dispersal processes of pollen and spores in mangrove and offshore sediments (Van der Kaars, 2001; Hofmann, 2002; Van Campo and Bengo, 2004; Moss et al., 2005; Engelhart et al., 2007; Urrego et al., 2009a). Furthermore, a significant positive correlation was found for the pollen percentages of *Rhizophora* with respect to inundation levels and distance to the sea, suggesting that this species may be a reliable indicator for these two environmental variables. However, on San Andrés the highest levels of inundation are recorded at riverine mangroves characterised by highly seasonal freshwater influges absent of direct tidal influence (see Fig. 5A–C). The pollen percentages of *Rhizophora* at riverine mangroves were relatively high, which suggests that this taxon may not exclusively indicate sea level as has been previously proposed at other sites worldwide (e.g., Scourse et al., 2005, Engelhart et al., 2007, Ellison, 2008). Evidence from our study supports that in certain circumstances *Rhizophora* may serve as an indicator of high freshwater availability and/or high fluvial input, as has been shown for Late Quaternary records from tropical Africa and South America (Behling et al., 2001; Scourse et al., 2005; González et al., 2006; Ellison, 2008; González and Dupont, 2009). Hence, the interpretation of *Rhizophora* pollen percentages should be made with caution, ensuring that changes in fluvial inundation regimes of mangrove swamps are taken into consideration (Scourse et al., 2005).

4.4. *Avicennia*

Varying pollen percentages, high A index values and a significant correlation with the tree basal area indicated that *Avicennia* is dominant in some mangrove forests, resulting in it being important for forest differentiation, supporting existing research (Li et al., 2008). *Avicennia* pollen has been considered to be under-represented in a large number of mangroves (Behling et al., 2001; Van Campo and Bengo, 2004). For example, while *Avicennia* pollen was found close to tree sources in our study, its values were always below 12% (typically 7–9%), which contrasted to *Rhizophora* which had values in excess of 70% with a wide distribution. However, the analysis of data in this study (e.g. correlations and low U index values) showed these values provided a reliable indication of the presence of *Avicennia* in the vegetation stands, despite the low pollen percentages. These findings for the San Andrés Caribbean mangroves support that found for mangroves in New Zealand and China (Deng et al., 2006; Mao et al., 2006). In addition, a significant correlation was found between

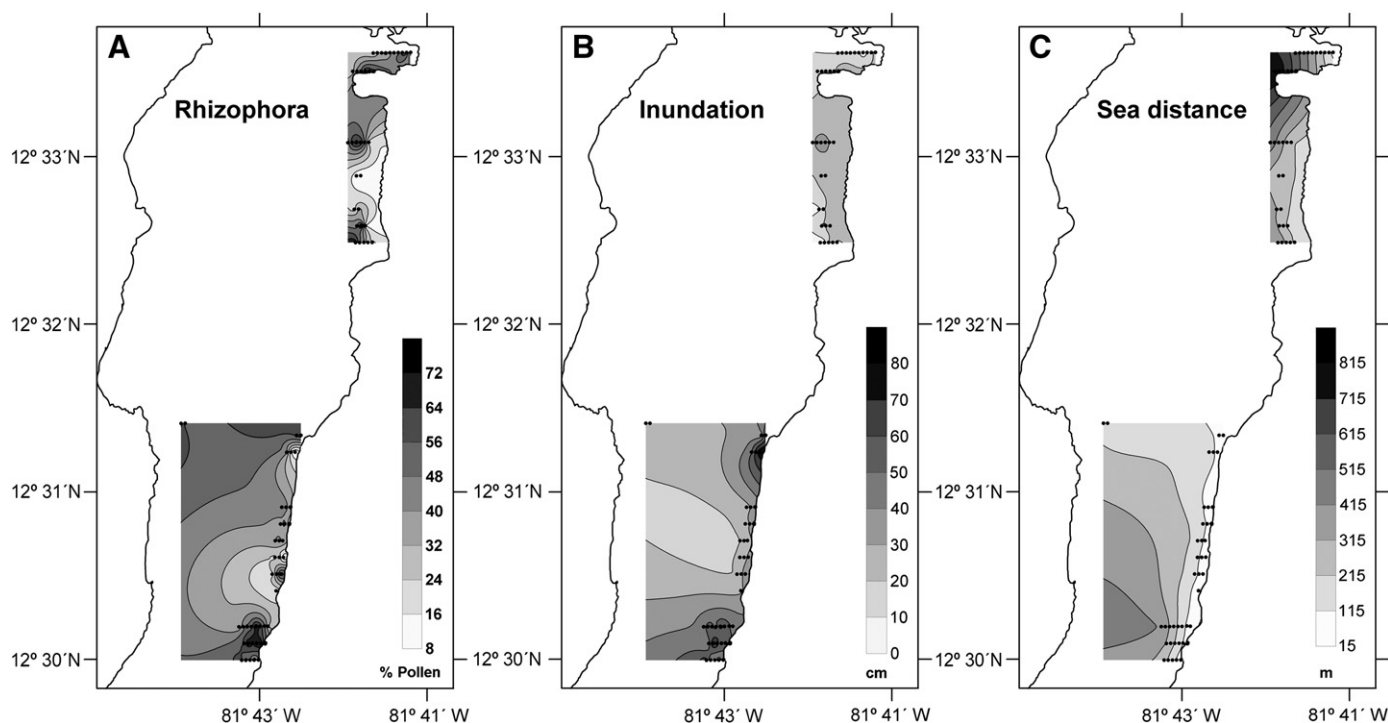


Fig. 5. A. Spatial distribution of *Rhizophora* pollen. Shading scale corresponds to pollen percentages in surface sediment samples and; B. the correspondence with distribution of fresh water inundation levels (cm) and C. sea distance values (m).

Avicennia pollen percentages and salinity, matching the environmental conditions of the forest where this taxon was found. In fringe mangroves that were dominated by *Avicennia*, salinity ranged from 24 to 45 ppm, while riverine mangroves where *Avicennia* reached proportions around 3% exhibited salinities (e.g. 2–5 ppm) due to scarce freshwater inputs (Fig. 6A and B). The latter differed from the other riverines where *Avicennia* was absent and salinities ranged from 0 to 2 ppm. Even low percentages of *Avicennia* may be representative of mangroves with higher than average salinity. We propose that low percentages of *Avicennia* may indicate the dominance of fringe conditions (i.e. intertidal mudflats) and direct tidal influence, confirming that some under-represented taxa might serve as more reliable indicators of environmental conditions than more abundant taxa (Watrin et al., 2007; Moscol-Olivera et al., 2009).

4.5. *Conocarpus*

Despite the low pollen percentages, the high A index values and a significant correlation with the tree basal area, pollen of *Conocarpus* matched the dominance recorded in the sampled vegetation for this species. This species is commonly found landwards on sediment with low inundation levels (Cintrón and Schaeffer-Novelli, 1983; Tomlinson, 1986), which was supported by our study indicating a significant correlation between pollen percentages and sediment pH values, with a concurrent spatial distribution (Fig. 7A and B). *Conocarpus* pollen had a strong correlation with the tree basal area of the sampled vegetation, and a strong correlation with high sediment pH values, making this taxon a reliable indicator of supra-tidal conditions with low inundation levels. In fact, it is possible to infer the significant distance of *Conocarpus* from the shoreline based on the low pollen percentages of this taxon.

4.6. *Laguncularia*

The pollen percentages of *Laguncularia* showed neither correlation with tree basal area nor any environmental variable in the island's mangroves. While *Laguncularia* pollen had a widespread distribution

in our study, it also had a high A index value, which contradicts its under-representation in the pollen spectra of Brazilian mangroves (Behling et al., 2001). The absence of correlation with tree basal area indicated it had a wide distribution, possibly due to the pollen grains being transported by watercourses. *Laguncularia* has the capacity to grow in open canopy forests, as well as the shores of streams and rivers of intermediate salinity (Medina et al., 1990). For this reason, this species may serve as an indicator of a stage of mangrove disturbance (natural or anthropogenic), as has already been recorded at other mangroves in the Caribbean (Tomlinson, 1986; Benfield et al., 2005). The presence of an open canopy, as a result of disturbance, may influence the species richness of the pollen rain (Elenga et al., 2000; Court-Picon et al., 2005). Disturbance may also explain the high proportion of *Acrostichum* fern spores recorded in several mangrove samples of San Andrés, also as found in other Caribbean mangroves (Ellison, 1989). Medina et al. (1990) have suggested that *Acrostichum* and *Laguncularia* colonise disturbed mangroves under similar salinity conditions. However, as the *Laguncularia* treelets become taller, they shade the forest floor impeding the growth of *Acrostichum*. The antagonism between *Laguncularia* and *Acrostichum* in the pollen diagram of this study (Fig. 2) supports this theory. This observation is significant because fern spores are generally transported long distances by watercourses and are abundant in marine records (Van der Kaars, 2001; Van Campo and Bengo, 2004; Moss et al., 2005).

4.7. Herbaceous taxa

A range of non-arboreal taxa (i.e. Poaceae, *Tournefortia*, *Sesuvium* and Cyperaceae) contributed substantially to the pollen record, even though they were not sampled in the vegetation plots. These taxa have been recorded on the sandy beaches and marshes that surround Caribbean mangroves (Hofmann, 2002; Willard et al., 2001). These species are also often found in the understories of mangroves, where the open canopies allows the arrival of wind-dispersed pollen (e.g., grasses and sedges; Sugita, 1993; Elenga et al., 2000; Court-Picon et al., 2005). As for *Acrostichum*, these species indicate the first stages of colonisation of disturbed forests. A

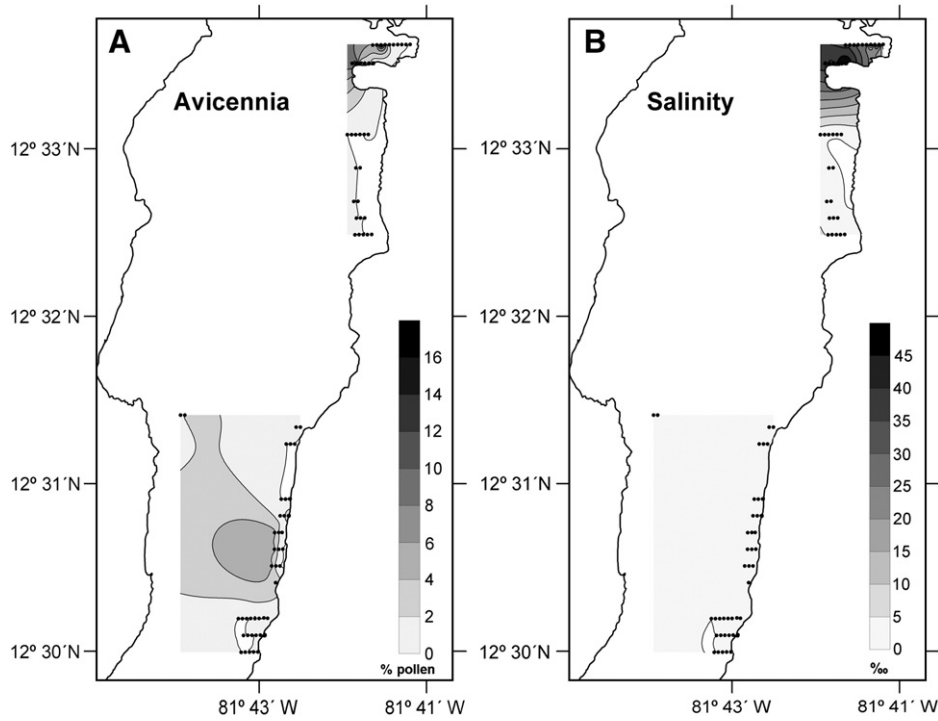


Fig. 6. A. Spatial distribution of *Avicennia* pollen. Shading scale corresponds to pollen percentages in surface sediment samples and; B. the correspondence with distribution of soil salinity (‰).

significant correlation was obtained for Poaceae with respect to salinity, possibly indicating that this is a beach-specialised species, rather than an indication for long distance pollen transportation, as has been suggested (Bush, 2002). On the other hand, *Tournefortia* and *Sesuvium* were related to clay type soils such as salt marshes and mangrove borders.

5. Conclusions

Our research provides one of the first comparisons between that of standing vegetation composition and surface sediment pollen representation in mangroves of small isolated Caribbean islands. Our results indicate that the surface sediments of mangrove stands

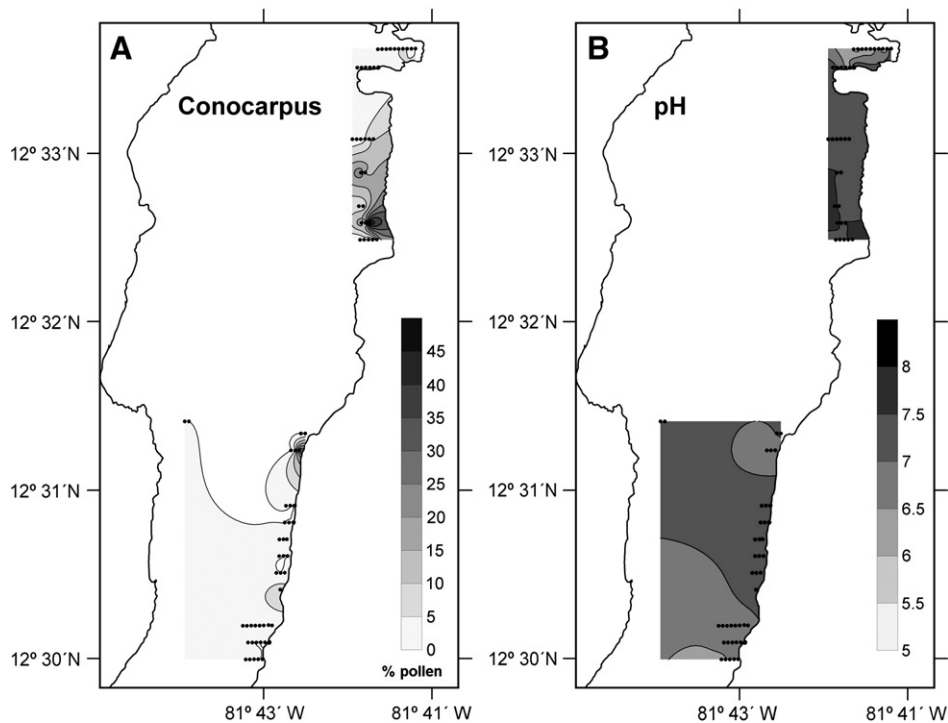


Fig. 7. A. Spatial distribution of *Conocarpus* pollen. Shading scale corresponds to pollen percentages in surface sediment samples and; B. the correspondence with distribution of soil pH values.

acquire the majority of pollen from local (i.e. coastal and mangrove vegetation) and regional sources (i.e. upland forests on the island), with negligible input from offshore and continental areas. Hence, this study confirms that the pollen rain can be used with confidence to reconstruct the composition of regional vegetation, as in other tropical ecosystems (e.g. Bush and Rivera, 1998; Mao et al., 2006). In the case of San Andrés Island, the pollen spectra of the local mangroves were characterised mainly by true mangrove species, since relative differences in dominance demonstrated the existence of different mangrove types on the island. *Rhizophora* was correlated with inundation level and distance to sea, *Avicennia* with salinity and *Conocarpus* with sediment pH of supra-tidal waters. This study clarified that because pollen may be transported by wind and/or watercourses, the overall floristic composition of the different forest types may not necessarily be reflected by the pollen spectra. However, we also established that even low pollen percentages of under-represented mangrove taxa, such as *Avicennia* and *Conocarpus*, may serve to indicate their dominance in the standing vegetation. We confirmed that the pollen percentages of certain mangrove, fern and herbaceous taxa, may serve as indicators of human disturbance to these forests. Finally, correlations between the pollen percentages of true mangrove species with certain environmental variables, suggests that these taxa could be used as indicators of different mangrove environments along the intertidal gradient for palaeoecological reconstructions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.revpalbo.2010.06.006.

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