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Research Article

Oceanic and climatic drivers of mangrove changes in the Gulf of Urabá, Colombian Caribbean

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ABSTRACT. The Gulf of Uraba is the largest estuary on the Caribbean coast of Colombia. The aim of this research was to analyse the oceanic, climatic and environmental variables that influence mangrove structure and composition in the gulf. Based on the availability of remote sensing, the study area was divided into western and eastern zones. The spatial pattern of environmental variables (water salinity, pH and percentage of organic matter, sand, silt and clay in the soils) and oceanic and climatic variables (winds, wave height and wave period) was analysed. The relationship of these variables with variables of vegetation structure (basal area, diameter at breast height, tree height, and abundance of seedlings of mangrove species in 1 m^2 subplots) was analysed in 27 plots of 500 m^2 containing fringe mangroves and 5 plots containing basin mangroves. Mangroves of the western zone showed a higher structural development and were dominated by *Rhizophora mangle (*red mangrove). This zone is supplied by fresh water and sediments, and the soils have a high content of organic matter and clay and a low degree of anthropogenic disturbance. The eastern zone was characterized by higher pore water salinity due to lower freshwater input from rivers. In this area there is a smaller impact of waves and winds, higher sedimentation rates, high anthropogenic disturbance and mangroves are dominated by *Avicennia germinans (*black mangrove). Although *Laguncularia racemosa* (white mangrove) did not show a particular spatial pattern, due to its tolerance to open canopy conditions it was commonly found in anthropogenically disturbed areas.

Keywords: coastal ecosystems, swell, winds, coastal erosion, sediment transport, river flow, Colombian Caribbean.

Controladores oceánicos y climáticos de cambios en los manglares en el Golfo de Urabá, Caribe colombiano

RESUMEN. El Golfo de Urabá es el mayor estuario en la costa caribe de Colombia. El objetivo de esta investigación fue analizar las variables oceánicas, climáticas y ambientales que influyen en la estructura y composición de los manglares en el golfo. Según la disponibilidad de información de sensores remotos, el área de estudio se dividió en una zona occidental y otra oriental. Se analizó el patrón espacial de las variables ambientales (salinidad del agua, pH y porcentaje de materia orgánica, arena, limo y arcilla en los suelos) y las variables oceánicas y climáticas (vientos, altura y período del oleaje). Se analizó la relación de estas variables con las variables estructurales de la vegetación (área basal, diámetro a la altura del pecho, altura de los árboles y abundancia de plántulas de especies de manglar en sub-parcelas de 1 m^2), en 27 parcelas de 500 m^2 que contienen manglares de borde y 5 parcelas que contienen manglares de cuenca. Los manglares de la zona occidental mostraron un desarrollo estructural superior y fueron dominados por *Rhizophora mangle* (mangle rojo). Esta zona recibe gran cantidad de agua dulce y sedimentos, y los suelos tienen alto contenido de materia orgánica y arcilla, y bajo grado de perturbación antrópica. La zona oriental se caracteriza por mayor salinidad del agua debido a una menor entrada de agua dulce de los ríos. En esta zona se presenta un menor impacto de oleaje y vientos, altas tasas de sedimentación, alta perturbación antrópica y los manglares están dominados por *Avicennia germinans* (mangle negro). Aunque *Laguncularia racemosa* (mangle blanco) no mostró un patrón

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espacial particular, debido a su tolerancia a las condiciones abiertas de dosel, se encuentra comúnmente en áreas con mayor intervención antrópica.

Palabras clave: ecosistemas costeros, mar de fondo, viento, erosión costera, transporte de sedimentos, caudal del río, Caribe colombiano.

INTRODUCTION

Mangroves are important ecosystems for human communities not only because of their economic benefit but also because they protect coasts from tsunamis, storm surges and erosion (Mazda *et al*., 1997; Alongi, 2008). In addition, they reduce coastal water eutrophization, contribute to sediment and human waste uptake and play an important role in organic matter exchange, carbon assimilation and faunal feeding and reproduction (Ewel *et al*., 1998; Alongi, 2008). Since they are restricted to the ocean-continent ecotone and catch high fluvial water and sediment loads, mangroves structure, floristic composition and natural regeneration of mangrove vegetation are determined by several biotic, abiotic and anthropogenic drivers, and are vulnerable to global and regional environmental and climatic changes. Regional climate change, especially that related to precipitation patterns, the flooding of rivers, rises in sea level and ocean circulation patterns (Duke *et al*., 1998; Gilman *et al*., 2008) may influence mangrove distribution and dynamics. Local drivers, such as the magnitude and direction of winds, geomorphology, pore water salinity, and soil conditions also play an important role in vegetation patterns (Krauss *et al.*, 2006).

Tidal range and amplitude, and sea level rise may affect the distribution of mangroves, depending of the rate of fluvial sediment supply. If the rate of sea level rise is higher than sediment input, coastal erosion occurs and the mangroves may disappear (Parkinson *et al*., 1994), but if the rate of sediment supply exceeds the increase in sea level rise, mangroves may colonize on prograding deltas and beaches (Gilman *et al*., 2008; Perillo *et al*., 2009; Shearman, 2010) or may even be replaced by upland forests.

Despite the low tides on the Colombian Caribbean coast (0.40 m), a decreasing west-eastern gradient in rainfall drives deterioration in the mangrove vegetation structure. In the Gulf of Urabá, located at the Colombian Caribbean coast, higher mean annual precipitation (2,500 mm), means that mangrove forests can reach 9 m average height and contain about 10 tree species (Urrego *et al*., 2014). In contrast, in La Guajira in the north-eastern extreme of the country, significantly drier conditions (mean annual precipitation 500-1000 mm) mean that trees reach only 5 m in average height and no more than three true mangrove species are found (Ulloa-Delgado *et al*., 1998). Along the coast of the Gulf of Urabá, where there are more than 4500 ha of mangroves, structural, floristic and environmental differences have also been identified (Urrego *et al*., 2014). In these forests, flooding, pore water salinity and sediment input are responsible for differences in physiographical mangrove types (García-Valencia, 2007; Hoyos *et al*., 2012; Molina *et al*., 2014; Urrego *et al*., 2014).

In addition, large temporal changes in mangrove forest expanses and composition recorded in the Caribbean have been related to coastal erosion and accretion processes (Torres *et al*., 2008; Rangel *et al*., 2012), as have extreme events like hurricanes (Ortiz-Royero, 2012) and storm surges as well as anthropogenic disturbances (Urrego *et al*., 2014). In fact, between 2004 and 2011, 16% of the Colombian Caribbean mangroves were lost due to both causes (Rangel *et al*., 2012). Despite the current sea level rise (Torres *et al*., 2008) in the Colombian Caribbean, mangrove colonization has taken place along river deltas and beaches that receive high fluvial sediment input (Parkinson *et al*., 1994; Urrego *et al*., 2014). Nevertheless, it is not clear how important drivers such as winds, marine currents and sediment dynamics are associated to both coastal geomorphology and mangrove distribution and dynamics (Posada, 2011).

However, neither the sedimentation-erosion processes that are closely linked to wave dynamics in the gulf (Molina *et al*., 2014), nor sea level changes and sediment transport and dispersion have as yet been related to mangrove vegetation (García-Valencia, 2007). As a first approach, we propose the hypothesis that besides continental processes related to geomorphology, the force of winds and waves and their influence on sediment composition and dynamics (sedimentation and erosion) play an important role in the structure, composition and dynamics of mangroves in the Gulf of Urabá. This is in spite of the gulf's pocket shape that could homogenize marine conditions and their influence on vegetation.

MATERIALS AND METHODS

Study area

The Gulf of Urabá is located in the northwestern corner of the Colombian Caribbean (Fig. 1). The study area covers 10,461 ha, of which 2,874 ha were covered with

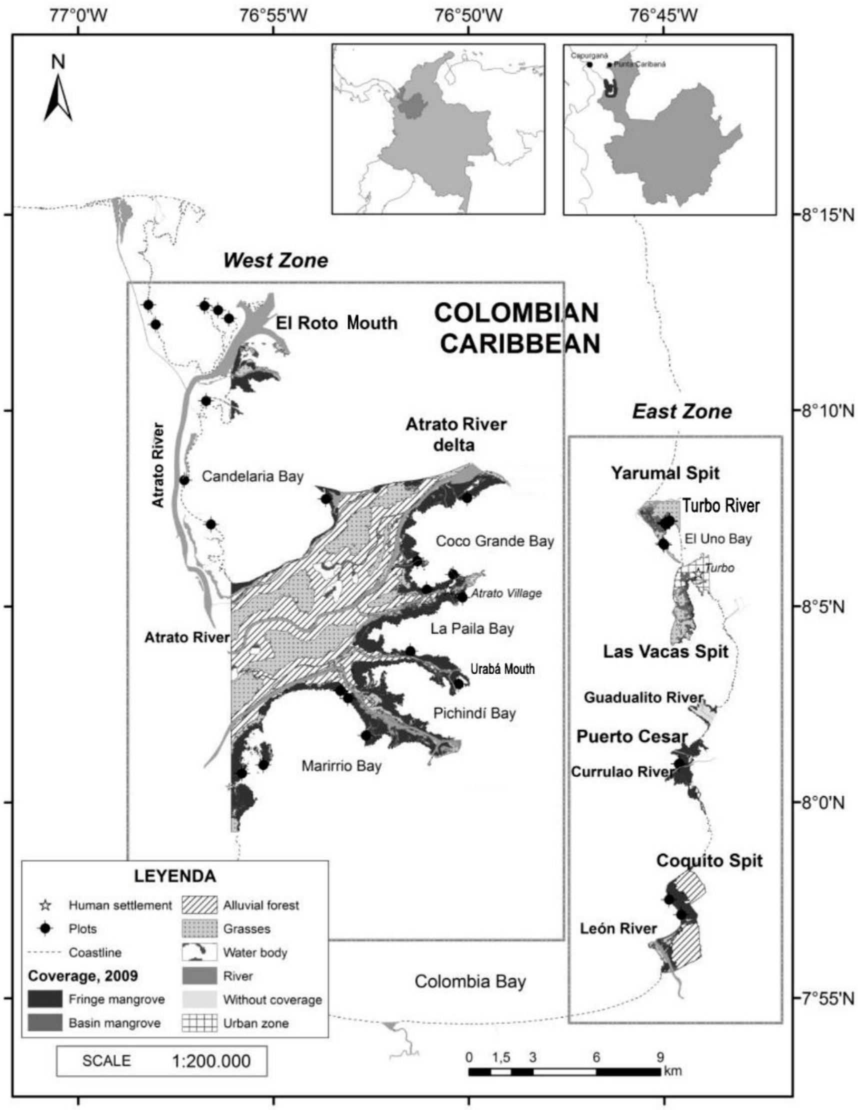

Figure 1. Location of the study area showing the two zones, the sampling sites and the main vegetation types found in the Gulf of Urabá.

mangrove forests in 2009. Other vegetation types present are tropical rain forests and open vegetation (grasslands). Water bodies and urban constructions are also present in the area. Based on the availability and dates of remote sensing (satellite images and aerial photographs), the study area was divided into two zones: the western zone that includes the Atrato River delta, and the eastern zone that includes the mouths of the Turbo and Currulao rivers (Fig. 1).

In the gulf, the mean annual precipitation is 2,500 mm. The mean monthly precipitation is 250 mm during the rainy season (from May to November) and 100 mm during the dry season (From December to April). The mean annual temperature is 27°C (CIOH, 2010) and the greatest variation (26-28ºC) occurs during the day time (Francois *et al.*, 2007). According to the Holdridge classification system it is a typical tropical rainforest climate (Espinal, 1990).

The Intertropical Convergence Zone (ITCZ) modulates the annual rain fall distribution in the gulf. During the dry season, when the ITCZ is farthest from the gulf, winds come from a north-easterly direction. The circulation currents present in these winds are persistently high speed and are characterized by dry atmospheric stability, low levels of cloud and precipitation, and low atmospheric humidity (Francois *et al.*, 2007).

The Gulf of Urabá is a pocket shaped water body located near the Caribbean border between Panamá and Colombia. While the northern part of the gulf is wider and west-east oriented, the southern part is semi-closed and north-south oriented. The length of the gulf from north to south is approximately 80 km, and the average width is 25 km. The microtidal regime is mixed semi-diurnal with an average maximum height between 0.30 and 0.92 m. While the deepest waters (80 m) are found towards the northern part of the gulf the shallowest ones (30 m) are concentrated towards the southern area (Bernal *et al*., 2005a; Montoya & Toro, 2006; Francois *et al*., 2007).

The winds enter the gulf seasonally from several directions and at different speeds. While during the wet season the south-west winds had a speed between 1.5 and 2.7 m s^{-1}, during the dry season the north to north-easterly winds reached speeds of 3-4 m s^{-1} with maximum of 10 m s^{-1} (Francois *et al*., 2007).

From a hydrodynamic perspective, wave modelling data that included both average and extreme conditions validated with wave sensors identified two areas dominated by different types of waves in the gulf (Osorio *et al*., 2010). The first area is located to the north of the boundary between the Atrato and Turbo rivers deltas and the offshore limit of the gulf. The second is located towards the south between the aforementioned deltas and the end of the gulf in the Bahia Colombia. While the first area was strongly dominated by swell waves (waves coming from deep water), the second area was strongly dominated by sea waves (waves generated by local winds). Deep surge energy is dissipated while propagating landwards into the gulf and especially near the mouth of the Atrato River (Molina *et al*., 2014). Our main study area is located in the south (see the eastern and south-western zone in Fig. 1).

The Atrato River is the main source of freshwater and sediments to the gulf. The river flow distribution is synchronous with that of precipitation. The multi-annual mean runoff flow of the river is 2372 m^3 s^{-1} (Francois *et al*., 2007; Posada, 2011). The coastal erosion- sedimentation pattern is spatially variable along the gulf's shores. Strong erosion processes have been recorded in the eastern zone as a result of the Turbo River being artificially diverted in 1954. On the other hand, the western zone is dominated by the highly dynamic Atrato River delta. In this area both erosion processes and the deposition and accumulation of sediments take place (Bernal *et al*., 2005b; Francois *et al*., 2007).

Six percent of Colombian Caribbean mangroves are found along the coasts of the Gulf of Uraba (INVEMAR, 2012). In the tidal flooded zones and swamps, two physiographic mangrove types are present: fringe mangroves dominated by *R. mangle* and basin mangroves dominated by *A. germinans.* In alluvial flooded zones that are not heavily influenced by the tide, other mangrove species such as *Conocarpus erectus* (button mangrove) and *Pelliciera rhizophorae* (tea mangrove), and transitional tropical rain forest species such as *Montrichardia arborescens* (yautia madera), *Raphia taedigera* (yolillo palm), *Pterocarpus officinalis* (corkwood) and *Margaritaria nobilis* (bastard hogberry) are commonly found (Sánchez *et al*., 1997; Urrego *et al*., 2014).

Space-time analysis of mangroves

Oceanic and climate variables such as wave height (Hs) and peak period (Tp) of the mean regime, modelled by Molina *et al*. (2014), were included in our analysis. For the analysis of oceanic and climatic variables, only data values obtained during the rainy season were available. The sediment dynamics in each plot were included as nominal variables in accordance with the classification of Bernal *et al.* (2005b) (erosion: 1, sedimentation: 100 and stability: 50).

The analysis of forest structure and floristic composition was based on field data from 32 plots each of 500 m^2, mostly located 100 m landwards along the coasts at both sides of the gulf. At each plot, the diameter at breast height (DBH), mean tree height and basal area of all trees with DBH >2.5 cm were measured. Values of pH and the percentages of sand, silt, clay and organic matter in surface soil samples, as well as the salinity and pH of pore water, were also measured during the rainy season and included in the analysis as environmental variables of each plot.

Temporal mangrove extension changes in the gulf were based on analysis of aerial photographs and were used for correlations with oceanic and climatic features. While changes in vegetation cover in the western zone were analysed between 1975 and 2009, in the eastern zone they were assessed between 1980 and 2009. Gains and losses in expanses of fringe, riverine and disturbed mangroves were analysed. Net gain occurred when non-mangrove coastal vegetation such as tropical rain forest and herbaceous vegetation, or bare soil zones, water bodies (sea, rivers, lakes and lagoons) and urbanized areas, were converted into mangroves. Net losses occurred when mangroves shifted into any one of the aforementioned areas. The anthropogenic influence on vegetation structure was assessed by measuring the distance between each plot to the closest human settlement (the city of Turbo in the eastern zone and the Bocas de Atrato Village on the western side), since such a distance influences the feasibility of humane displacement to mangroves for harvesting.

Mangrove sedimentation rates were obtained from two sediment cores of 50 and 60 cm deep, retrieved using a Mackauley corer (Traverse, 1988). The first in

El Uno Bay (eastern zone) and the second in The Candelaria Bay (western zone). In order to estimate the chronology, isotopic analysis with ^{210}Pb was achieved at My Core Scientific Inc., Laboratory (Dunrobin, Ontario, Canada)

Based on environmental variables recorded at each plot, the spatial variation of the percentages of sand and organic matter in the soil, the magnitude of the winds and coastal sediment dynamics (sedimentation or erosion) in the study area were assessed using trend analysis with Arcgis 9.3 software (ESRI. Inc., 9.3).

After performing the Kolmogorov-Smirnov normality test using Statgraphics Centurion XV software (Statpoint, 2005), vegetation, hydrodynamics and climatic variables were normalized by means of the function log(x) + 6, where x is equal to a variable value and 6 was added to eliminate the negative values. In order to establish the relationship between vegetation and environmental, climatic and oceanic variables, and to look for spatial differences in mangrove vegetation patterns, Principal Component Analysis (PCA) and Redundancy Analysis (RAD) were performed using Canoco 4.5 (Ter Braak & Smilauer, 2002). The relative weight of each of the oceanic, environmental and anthropogenic variables was established through multiple regression analysis.

RESULTS

Spatial analysis of hydrodynamic and vegetation variables

Mangrove extension changes based on analysis of aerial photographs, were correlated with oceanic and climatic features and show the impact of oceanic and environmental variables on the spatial distribution of the mangrove species. Winds from south-western with mean speed between 1.5 and 2.7 m s^{-1} were included in the analysis. The areas sheltered from winds were located mainly inside the bays of the western gulf. However, the effects of waves (Hs and Tp) on vegetation structure were spatially heterogeneous. Even though some areas were sheltered, they were highly influenced by waves (Hs of 0.17 and 0.22 m and Tp between 2.4 and 2.8 s). Along most of the coasts, especially in the bays, the magnitude of waves was lower (Hs of 0.1 m and Tp between 1.5 and 2 s) in both seasons and its effect on vegetation structure was also softer since it was protected from the direct action of waves (Fig. 2).

In the study area, sea waves predominated (Hs decreased to about 0.1-0.4 m) due to the dissipation of swell energy, especially when they approached the Atrato River delta. However, the north-westerly waves were influenced by swell waves, where the waves reached up to 1.2 m in the dry season and affect the fringe mangroves. In contrast, the lowest Hs were recorded along the internal bays of the Atrato River delta in the west (Hs of 0.1 m and wave periods of 1.5 to 2 s), which were sheltered from the direct impact of winds and waves, and where both fringe and basin mangroves were found. At the eastern, along the prograding zone of the spits of the rivers, where the waves reached up to 0.5 m in some areas, mangroves were influenced the least by the waves.

Regarding environmental variables (Fig. 3), mangroves in the western zone of the gulf were characterized by low values of water salinity (nearly 0) and pH (average 3.8), but high percentages of organic matter (30-50%) and clays (20-65%) in the soils. The high flow of the Atrato and León rivers diminished the pore water salinity and the impact of wave energy on fringe mangroves and tropical rain forests that were highly influenced by the sediment loads of these rivers. In contrast, the mangrove stands of the eastern zone showed higher values of pH (7.1-7.5), higher percentages (100% in basin mangroves and 0-18% in fringes) of sand in the soils, and greater pore water salinity (13.8-20.8).

The relationship between oceanic, environmental and anthropogenic variables and the structure and composition of mangrove vegetation was evaluated by multiple regression analysis and is shown in Table 1. A strong relationship was found regarding the structure of the three main mangrove species. While the averaged DBH and basal area of *R. mangle* and *A. germinans* adult trees increased with distance to human settlements, the abundance of seedlings and saplings declined in the first species but increased in the second. On the other hand, the averaged DBH and basal area of saplings and small trees of *L. racemosa* showed an inverse relationship with distance to human settlements. Therefore, distance from mangroves to human settlements better explained the variability in the structure of *L. racemosa* than other variables (Hs, pore water salinity and river flow).

The averaged DBH (of trees with DBH >10 cm) of *A. germinans* showed a stronger relationship with distance from human settlements than with the soil pH and percentage of clay. The seedling abundance was also more strongly related to this distance than pore water salinity and river flow. However, when the averaged DBH of saplings and small trees (DBH <10 cm) were the dependent variables, the negative relationship was stronger than previously important variables such as the percentage of sand in the soil, wind speed and Hs.

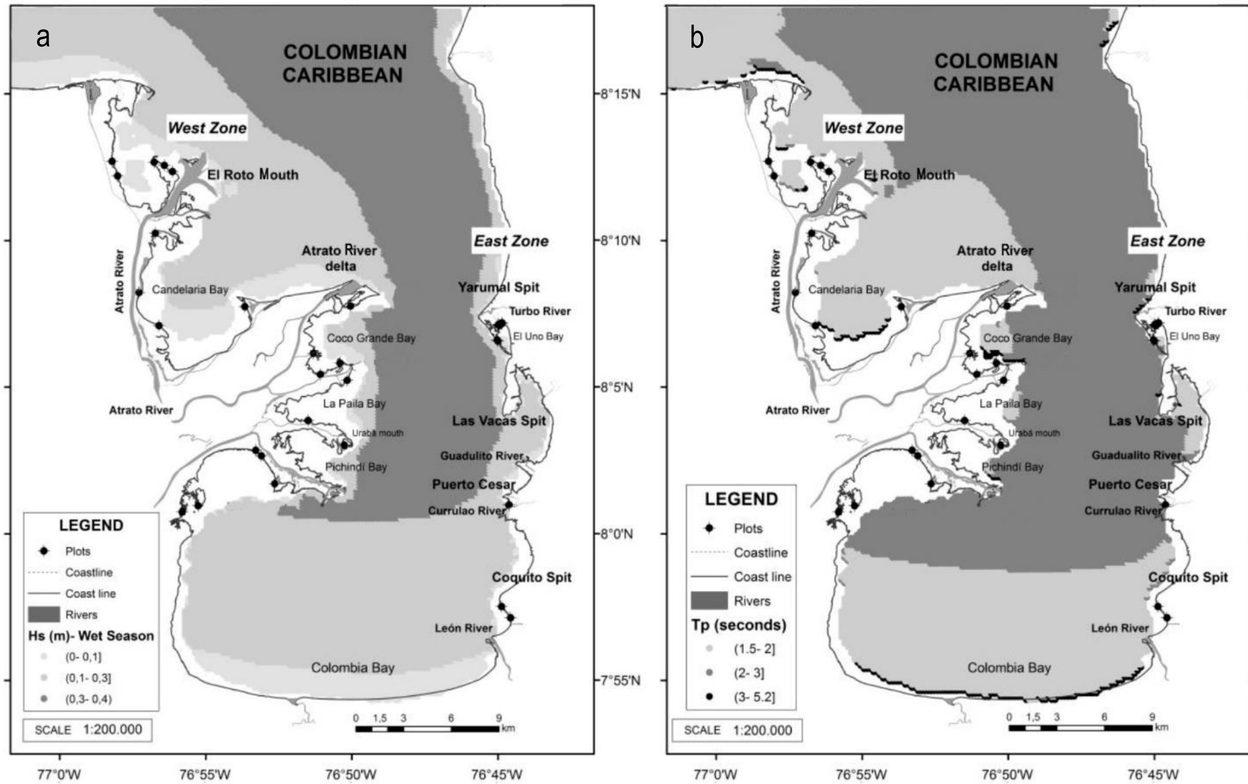

Figure 2. a) Wave height (Hs), b) peak period (Tp) in the mean wave regime for the most likely magnitudes of winds and swell during the wet season.

Three groups of mangrove stand related to the environmental variables analysed were identified by the RDA (Fig. 4, Table 2). The first group corresponds to the *A. germinans* dominated mangrove stands of the eastern zone that had the highest values of pore water pH and the greatest percentages of sand in the soil, but lower wave periods (Tp) and wind speed. This group recorded the highest basal area of *A. germinans* (10 m^2 ha^{-1}) and not only had the greatest density of small trees (2.5 < DBH <10 cm) but also the lowest mean basal area (3.59 m^2 ha^{-1} of *R. mangle* and 1.31 m^2 ha^{-1} de *L. racemosa) R. mangle* had the highest seedling abundance. All these parameters were also related to lower percentages of clay and organic matter in the soils when compared to the other groups.

The second group includes the mangrove stands located to the north of the western zone and is characterized by the high relative abundance of *L. racemosa* adult trees, as well as *L. racemosa* and *R. Mangle* seedlings. These vegetation features were positively related to sediment deposition and pore water pH, but negatively related to the wave period (Tp).

The third group includes the forests located towards the south of the western zone and is characterized by the high dominance of *R. mangle* in all size categories and the low relative abundance of *Pelliciera rhizophorae* and non-mangrove species. In this area there were higher percentages of clay and organic matter in the soils and high wind speeds. The third group is clearly related to the maximum values of Hs (0.15 m) and Tp (4.5 s). The strong relationship between Tp and *R. mangle* seedling density (Fig. 4b, Table 2) might be the result of wider propagule dispersion due to the increase in Tp.

In summary, the vegetation structure was highly correlated not only to physical environmental variables such as the percentage of organic matter in the soils and pore water salinity and pH, but also to hydrodynamic variables like the maximum Tp, wind speed and river flow (Fig. 4, Table 2).

Temporal vegetation analysis and sediment dynamics

According to the remote sensing and the ^{210}Pb analysis, the highest sediment deposition rate was recorded at

Table 1. Multiple regression analysis between dependent variables (vegetation variables) and environmental, oceanic, climatic and anthropogenic variables (independent variables). DBH: diameter at breast height (cm), Hs: significant wave height, Tp: peak period of waves, coastal processes, 100: sedimentation, 50: stability, 1: erosion, river flow ($m^3 s^{-1}$), wind speed measured during the wet season, distance Hs: distance to humane settlements (m).

Variable	*P*-values	R2 (%)	slope	Environmental variables												
				Hs	Tp	Sedimentation erosion processes	River flow	Clay (%)	Silt (%)	Sand (%)	Pore water pH	Pore water salinity	Soil pH	OM (%)	Wind speed (m s^{-1})	Distance H.S
DBH *R. mangle* >10 cm	0.047	57.309	108.67	0.52	3.72	-	-0.05	5.35	-	-	-7.99	-	-12.86	-6.63	0.81	1.51
DBH *R. mangle* <10 cm	0.048	57.173	-42.18	0.32	2.18	1.28	-0.10	-3.35	-0.07	-	-	0.83	-	1.18	-	3.78
Seedling abundance m^{-2} *R. Mangle*	0.043	53.819	184.78	-1.57	-	-1.00		-4.82		-0.38	-	0.73	-19.22		-0.56	-0.05
Averaged height (m) *R. mangle*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Basal area ($m^2 ha^{-1}$) *R. mangle*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DBH *L. racemosa* 10 cm	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DBH *L. racemosa* <10 cm	0.027	75.248	459.09	-0.82	-22.07	0.38	-0.17	2.76	-9.80	10.79	-42.85	-0.62	0.47	-4.31	0.18	-1.37
Seedling abundance m^{-2} *L. racemosa*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Averaged height (m) *L. racemosa*	0.043	69.360	597.79	-0.65	-23.48	0.64	-0.04	0.40	-6.75	7.50	-49.65	-	-8.79	-3.56	0.30	-3.08
Basal area ($m^2 ha^{-1}$) *L. racemosa*	0.029	68.068	662.08	-0.80	-24.54	0.55	-	-1.31	-6.69	7.41	-52.69	-	-12.41	-3.44	0.40	-3.04
DBH *A. germinans* >10 cm	0.010	79.710	82.33	0.01	-7.75	-0.44	0.16	2.26	0.40	-0.02	-26.75	-0.87	21.36	-1.53	-0.40	1.39
DBH *A. germinans* <10 cm	0.028	60.536	-74.02	-0.08	-5.10	-	-	-	2.39	-2.36	-	0.07	14.21	5.15	-0.47	-2.44
Seedling abundance m^{-2} *A. germinans*	0.002	84.603	2.80	-0.40	-6.02	-0.50	0.11	-2.69	-0.07	0.28	-9.25	0.17	17.25	1.43	-0.50	0.24
Averaged height (m) *A. germinans*	0.021	76.451	54.26	-0.09	-7.85	-0.15	0.18	-3.67	-0.25	0.39	-15.11	-0.67	16.63	3.70	-0.56	-0.04
Basal area ($m^2 ha^{-1}$) *A. germinans*	0.015	77.979	53.87	-0.19	-8.29	-0.27	0.20	-3.50	-0.33	0.51	-15.94	-0.73	17.96	3.38	-0.42	0.16

sites flooded by rivers, mainly in deltas and on river banks where either the river flow or the wind speed was rather low (Fig. 3). However, both zones showed contrasting sediment dynamics. The sedimentation rates measured along sediment cores showed changes between 1939 and 2009, from 0.41 to 1.37 cm yr^{-1} (mean= 0.96 cm yr^{-1}) in Candelaria Bay (western zone), 0.34 to 1.50 cm yr^{-1} in El Uno Bay (eastern zone) (mean= 1.16 cm yr^{-1}). While new accreted zones increased 0.4% in the western zone between 1975 and 2009, in the eastern zone they grow 14.9% between 1980 and 2009.

The multi-temporal analysis based on aerial photographs, revealed that 26.6% of the study area was occupied by fringe mangroves. Of these, 83.7% were located along the western zone of the gulf and 16.3% are along the eastern zone. Along the western zone, the expanse of fringe mangroves, dominated by *R. mangle*, on newly deposited substrates offshore increased by 22% between 1975 and 2009 (Table 3). These new areas were formed by accretion processes along the banks of the Atrato River in wind and surge protected bays.

While mangrove areas increased in accreted places previously occupied by water bodies (rivers, lakes or sea), mangroves losses occurred in eroded zones formerly covered by mangroves but appeared occupied by these water bodies at the end of analysed period.

The eastern zone had a higher input of sediments and was less affected by strong winds than the western zone. The higher percentages of sand found in the soils (Fig. 3) were associated to littoral drift, higher significant wave height and sedimentation along the river beds. It caused increased of bare area by about 500% between 1980 and 2009. During this time span, 78 ha of fringe mangroves were lost due to coastal erosion and onshore coastline displacement (Fig. 3). In addition, the urbanized area increased by 20% (1.13 ha yr^{-1}) at the expense of basin and fringe mangroves. Fringe mangroves were dominated by *R. mangle* close to the shoreline, but where daily tidal influence diminished onshore, the dominance of *A. germinans* and *L. racemosa* increased.

In the western zone, between 1975 and 2009 the mangroves grew on 80.4 ha of newly deposited substrates along the Atrato River banks. Besides these new areas, 62.2 ha were colonized by grasses and salt marshes and the bare areas diminished. The highest rates of erosion and the greatest mangrove losses were recorded (195 ha) at both the north and south extremes of the Atrato River delta. These processes were associated to the highest recorded wave energy, with Hs values of 0.2 m in the wet season and 0.5 m in the dry season, respectively.

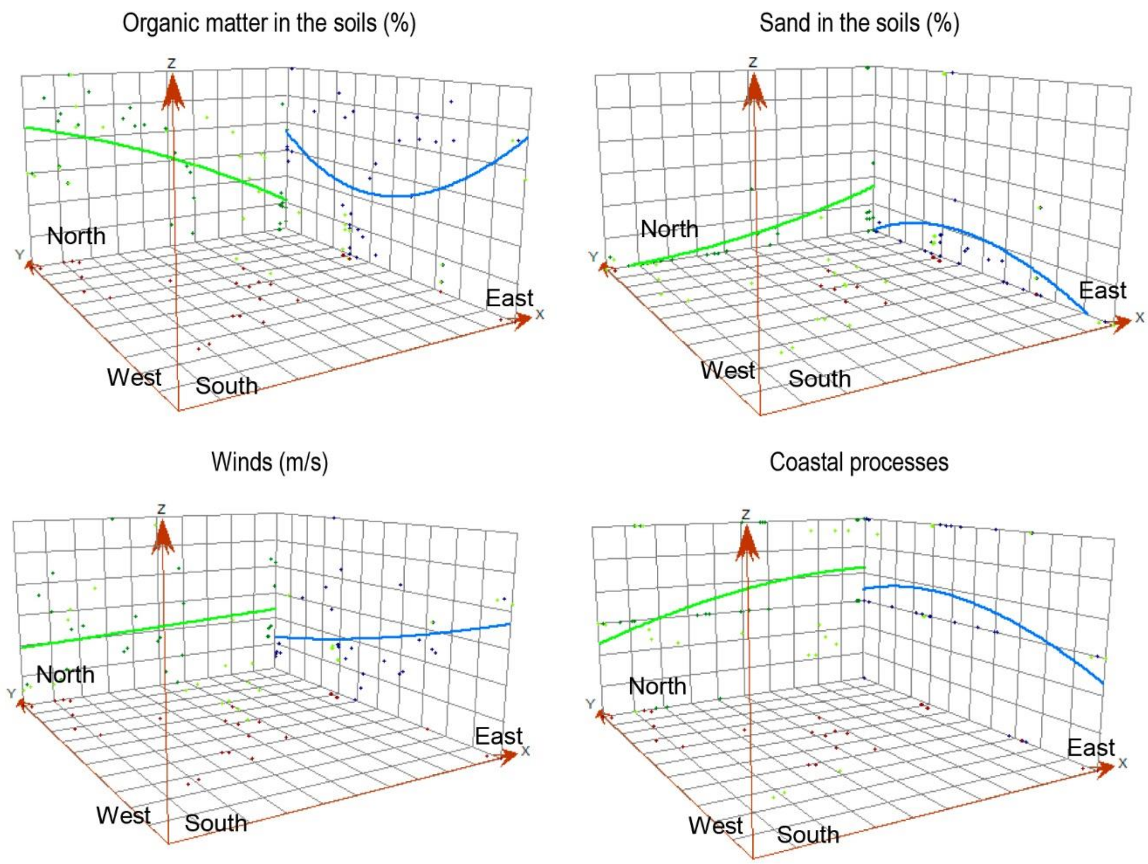

Figure 3. Environmental variables trend analysis. Green lines show the projection of the spatial variability of each variable from west to east (X axis). Blue lines show south-north variability (Y axis).

While in the western zone, 14.2 ha of early successional mangrove stands were lost due to coastal erosion, onshore tidal flooding and conversion into grasslands, in the eastern zone, 29.29 ha of these mangrove stands were lost in the studied periods. These mangroves were displaced by tropical rain forests, which grow on recent deposited due to the increase in alluvial sediment input, especially sands, as well as an improvement in drainage conditions and soil stabilization, and a decrease in pore water salinity. This impeded young mangrove tree species from competing with non-mangrove species. The remaining young mangrove stands (13.81 ha) of the eastern zone were lost due to coastal erosion in sites affected by strong winds (1.6 m s^{-1}), and waves (20 cm).

DISCUSION

Relationship between hydrodynamics and vegetation structure

The extended natural regeneration of mangroves in the gulf is related to physical and anthropogenic processes that have occurred in the region during last 30 years. In particular, changes in sedimentation processes have led to high relative abundances of *A. germinans* and *L. racemosa*. The influence of waves and littoral drift on the eastern gulf clearly shows that the accumulation of sediments along the river spits gave place to formation of new lands that plays an important role in the colonization of mangroves. The natural regeneration of *A. germinans* in the gulf is related to the high pore-water salinity and the percentage of sand in the soils. The survival of seedlings and saplings of this species is associated not only to higher salinity and sedimentation processes, but also to the increased availability of light caused by anthropogenic disturbance of the forest (Clarke & Allaway, 1993; Mckee, 1995). While the establishment of *Rhizophora* implies high soil humidity and organic matter accumulation (Lacerda *et al*., 1995), sites colonized by *Avicennia* are continuously losing organic matter due to the aforementioned factors (Rajkaran & Adams, 2012).

In the western zone, *R. mangle*-dominated mangroves recorded 19.2 cm and 12.8 m of average tree

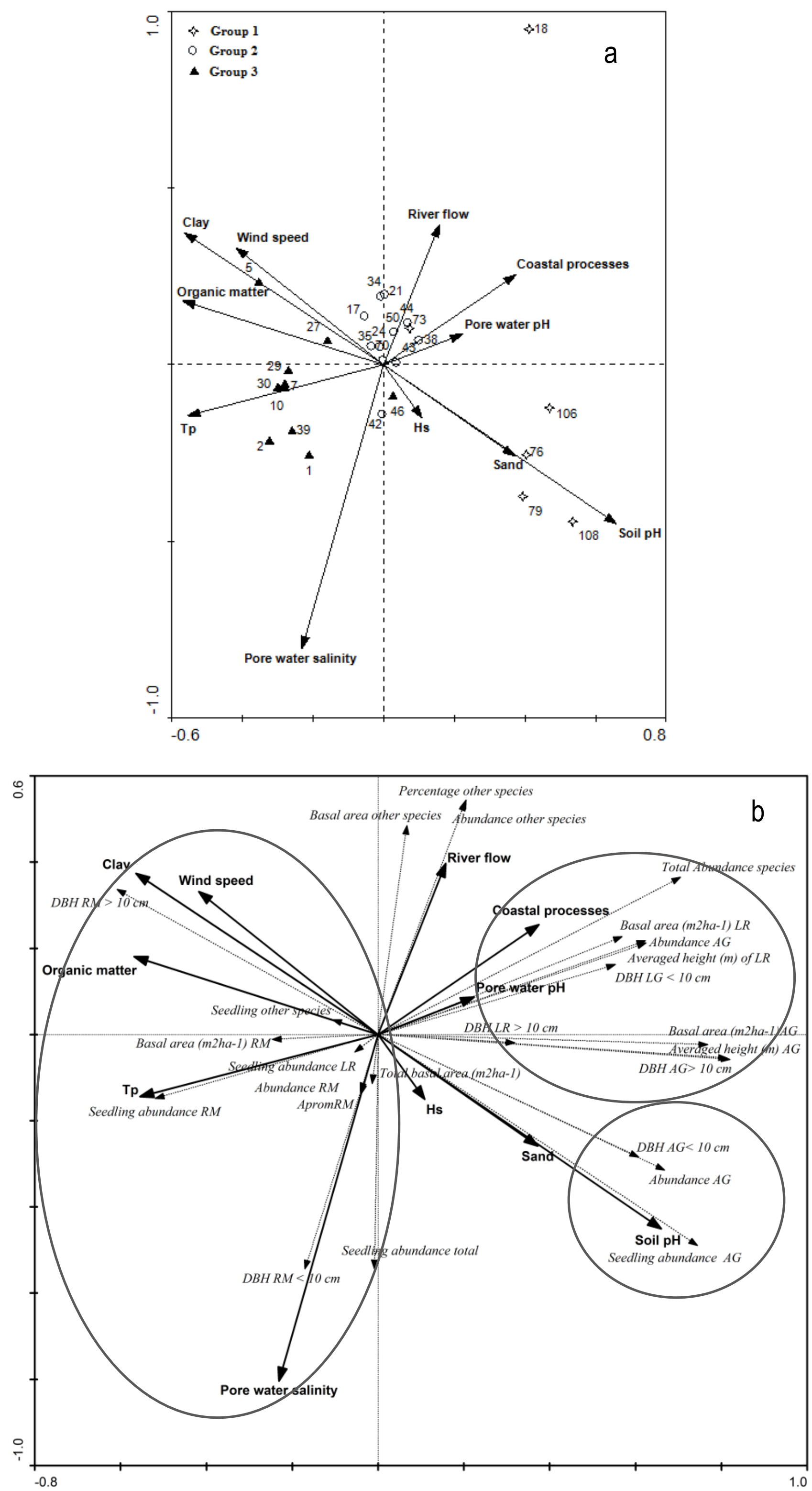

Figure 4. Relation among variables from the redundancy analysis. a) Biplot of vegetation plots (circles) and oceanic and climatic variables (arrows), b) biplot of vegetation variables (dotted arrows and solid arrows). AG: *Avicennia germinans*, RM: *Rhizophora mangle*, LR: *Laguncularia racemosa*.

Table 2. Results of the redundancy analysis, canonical coefficients and intra set correlations of environmental variables for the first two axes of RDA. Redundancy analysis of correlation matrix.

Axis	1	2	3	4	Total variance
Eigenvalues	0.28	0.09	0.08	0.03	1
Plot-variable correlations	0.89	0.76	0.64	0.67	
Cumulative percentage variance of plot data	28.1	37.4	45.5	48.7	
of the plot-environment relationship	51.1	68.1	82.8	88.8	

Variable	Coefficients		Correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Wave height	-0.25	0.009	0.1	-0.11
Peak period	**-0.78**	-0.28	-0.50	-0.11
Coastal processes	-0.03	0.15	0.33	0.19
River flow	0.24	0.13	0.14	0.30
Clay	-0.003	**1.31**	**-0.51**	0.29
Sand	0.39	0.48	0.33	-0.20
Salinity	-0.23	-0.58	-0.21	**-0.62**
Pore water pH	-0.35	-0.25	0.20	0.07
Soil pH	**0.51**	-0.22	**0.59**	**-0.35**
Organic matter	-0.11	**-0.98**	**-0.51**	0.14
Wind speed	-0.12	0.39	-0.37	0.25

Table 3. Expanses of the types of vegetation cover (m^2 ha^{-1}) in the western and eastern zones of the Gulf of Urabá. Losses and gains are indicated by negative and positive sign, respectively.

Coverage	Western zone			Eastern zone			Total		
	1975	2009	%	1980	2009	%	1975-80	2009	%
Fringe mangroves	1906.6	2325.3	+22	238.4	451.6	+89.4	2145	2777	+29.5
Basin mangroves				137.3	97.3	-29.1	137.3	97.3	-29.1
Early successional mangroves	286.8		-100	89.2		-100.0	376	0	-100
Alluvial forests	3291.2	3307.6	+0.5	321.4	381.2	+18.6	3612.5	3688.8	+2.1
Grasslands	2304.1	2494.8	+8.3	411.4	349.6	-15	2715.5	2844.4	+4.7
Without coverage	223.7	38	-83	11.6	71.8	+519	235.7	109.9	-53.4
Urban zone				158.2	191.1	+20.8	158.2	191.1	+20.8

DBH and height, respectively, and basal areas 17.39 m^2 ha^{-1}. These values are higher than those recorded in mangroves of La Guajira at the north-eastern Colombian Caribbean (Molina, 2009), where the *R. mangle*-dominated mangroves showed values of 8.8 cm and 6.6 m of average tree DBH and height, respectively, and mean basal areas of 12.9 m^2 ha^{-1}. And they are also higher than those exhibited by fringe mangroves in the Island of San Andrés (also in the Caribbean) with average values of 6.25 of DBH, 9 m of height, 16 m^2 ha^{-1} of basal area (Urrego *et al.*, 2009). These larger heights and basal areas recorded in mangrove trees in the gulf when compared with other Colombian Caribbean mangroves are a result of high rainfall, freshwater, nutrient and sediment input from rivers. This causes salinity diminutions and an improvement in mangrove productivity, as has been widely recorded for other mangroves (Menezes *et al*., 2003; Krauss *et al*., 2006a, 2006b; Rajkaran & Adams, 2012).

The best mangrove structure (*R. mangle*), represented by higher basal areas (22 m^2 ha^{-1}) and taller (7 m) trees, was recorded far away from urbanized areas like the city of Turbo (in the eastern zone) or the Bocas de Atrato Village (in the western zone). However, mangroves closer to them showed smaller tree diameters (8.3 cm) and basal areas (7.1 m^2 ha^{-1}) (Estrada, 2014). This is the reason for the dominance of small sized (<5 cm) *R. mangle* trees and a lack of trees with a DBH greater than 20 cm in the surroundings of urban areas. The same situation is found in other anthropogenically disturbed mangrove swamps (López-Hoffman *et al*., 2006). In mangrove swamps in the Gulf of Urabá, the selective logging of *R. mangle* of both large diameter mangroves for construction and small diameter mangroves to make fishing poles is quickly reducing their populations. The greatest number of juvenile trees, the smallest basal areas, and most light are commonly found in these anthropogenically disturbed forests (Walters, 2005b).

However, the distance to urban populations also explains the high relative abundance of *A. germinans*, since the increase in open canopies in disturbed areas favors its establishment and growth. In addition, close to towns selective logging removes juvenile and adult *R. mangle* and *L. racemosa* trees, allowing *A. germinans* trees to reach a higher DAP and establish extended stands in heavily managed patches, giving a higher density of trees of this species Human pressure on mangroves can lead to changes in the dynamics of the natural regeneration and structure of mangrove forests (Benfield *et al.*, 2005; Walters, 2005a), depending on the physiology and environmental requirements of each of the species.

Multi-temporal analysis of vegetation cover

The expansion of fringe mangroves along the Gulf of Urabá is mainly related to the formation of new available lands fed by the increase in fluvial sediment input. Major expansions have taken place in river mouths and deltas where the wave energy is dissipated by river currents and the sedimentation of coarse sediments is more feasible, as has been recorded in other areas of the Colombian Caribbean (Molina, 2009; Urrego *et al.*, 2014) and French Guyana (Proisy *et al.*, 2009). Mangrove expansion is favoured by two forces that counteract each other simultaneously: firstly, the increase in sediment accumulation (40 m yr^{-1} between 1940 and 1999 in the eastern zone in the mouth of the Turbo River) (Correa & Vernette, 2004) and secondly the sea level rise from 1993 to the present (Average global sea level rise of 3.1 mm yr^{-1}) (IPCC, 2007). An increase in the mangrove extensions was favoured by the sediment input from the Turbo River diversion in the 50´s which caused an increase of 32% (from 305.38 to 403.29 ton yr^{-1} km^{-2}) in sediment transport along the river bed between 1946 and 2004 (Posada, 2011) that created new deposited substrates to be colonized by vegetation.

Both processes have contributed to substrate stabilization and the creation of new sites for mangrove colonization (Parkinson *et al.*, 1994; Gilman *et al.*, 2008). However, mangroves may expand onshore as a response to sea level rise, when an extensive flat coastal plain is available. There, mangroves can establish themselves at the expense of other vegetation types or anthropogenic land uses. Such intertidal land reclamation by mangroves has been also recorded in other Caribbean regions (Benfield *et al.*, 2005) and has caused the replacement of some vegetation types by water bodies. The highest mangrove expansion recorded in the eastern zone is related to the small size of basins on the new lands created by the high sediment loads brought in by rivers (Restrepo & Kjerfve, 2000; Arroyave *et al.*, 2012). High sedimentation rates have been associated with the increase in river bank deforestation during the second half of the XX century which favoured the export of sediments (Arroyave *et al.*, 2012; Blanco-Libreros *et al.*, 2013). In fact, annual deforestation rates around the Turbo River headwaters from 1960-2007 are among the highest in the world (1.36%; Blanco-Libreros *et al.*, 2013). In addition, important vectors of regional development such as agricultural and urbanized lands (Taborda & Blanco, 2012) have expanded during recent decades at the expense of the natural vegetation covers. Increases in mangrove cover along the shorelines of the gulf are related to the increment in sediment input from the Atrato River, especially to the artificial Turbo River bed diversion created in 1954 (Posada, 2011). At these sites, the colonization of vegetation has followed the typical pattern recorded in other places, *e.g.*, the growth of *R. mangle* on recent river bank deposits and *A. germinans* on the boundary between the filling area and the dikes (Thom, 1967).

In addition, the direction of the littoral drift prevents deltaic sediments of the Atrato River from being distributed along the coasts of the gulf. Therefore, sand spits are also fed by biogenic contributions from cliffs in the western zone and small rivers in the eastern zone (Francois *et al.*, 2007). With regards to wave direction and geomorphological features, the prevailing drift has a southerly direction on both coasts, although seasonal variations occur (Molina *et al.*, 1992; Chevillot *et al.*, 1993; Bernal *et al.*, 2005a; Montoya & Toro, 2006). Despite the predominance of the high flow of the Atrato River in the western zone of the gulf, sedimentation and mangrove colonization rates are higher in the eastern zone. This is not only due to littoral drift and high river sediment loads, but more importantly due to low wave energy. According to Molina *et al.* (2014) the patterns of littoral drift along the Eastern Gulf are clearly dominated by the oblique incidence of the NW and NNW wave direction. This is the main mechanism of longshore currents along the eastern coast and therefore the main driver of littoral drift. For example, the magnitude of potential sediment transport (based on the influence of wave direction) in Punta Yarumal (the mouth of the Turbo River) is about 23,523 m^3 yr^{-1} during the dry season, when the littoral drift increases, and around 6,326 m^3 yr^{-1} during the wet season

(Posada, 2011). This pattern may explain the sedimentation of the spits and the mangrove colonization rates in the eastern gulf.

CONCLUSIONS

According to our results, the distribution, structure and composition of mangroves in the Gulf of Urabá are closely influenced by oceanic, climatic and anthropogenic drivers. There is a strong relationship between sediment acumulation and the increse in mangrove expanses in the gulf in sites sheltered from waves, winds and littoral drift where there is also a high fluvial sediment input. In contrast, the highest mangrove loss was recorded in sites highly impacted by waves (high values of Hs and Tp) and coastal erosion processes.

Although it is clear that the establishment and distribution of mangrove stands are strongly related to the influence of Tp and Hs, our results cannot be generalized since it is necessary to gather more field data about the relationship between wave speed (related to Tp) and the colonization process, as well as the drag force and mangrove hydraulic properties during extreme events.

Despite the relationship between mangrove distribution and physical factors, there is a clear anthropogenic impact on mangrove structure and composition. While the density of *A. germinans* increases with distance to human settlements, the relative abundance of *R. mangle* and *L. racemosa* decreases. However, it is necessary to carry out more detailed studies on the impact of human activities, like waste disposal, deforestation and chemical spills, on mangrove ecosystems.

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