Variation in Mangrove Forest Structure and Sediment Characteristics in Bocas del Toro, Panama

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ABSTRACT.—**Mangrove forest structure and sediment characteristics were examined in the extensive mangroves of Bocas del Toro, Republic of Panama. Forest structure was characterized to determine if spatial vegetation patterns were repeated over the Bocas del Toro landscape. Using a series of permanent plots and transects we found that the forests of Bocas del Toro were dominated by *Rhizophora mangle* with very few individuals of *Avicennia germinans* and *Laguncularia racemosa*. Despite this low species diversity, there was large variation in forest structure and in edaphic conditions (salinity, concentration of available phosphorus, Eh and sulphide concentration). Aboveground biomass varied 20-fold, from 6.8 Mg ha^{-1} in dwarf forests to 194.3 Mg ha^{-1} in the forests fringing the land. But variation in forest structure was predictable across the intertidal zone. There was a strong tree height gradient from seaward fringe (mean tree height 3.9 m), decreasing in stature in the interior dwarf forests (mean tree height 0.7 m), and increasing in stature in forests adjacent to the terrestrial forest (mean tree height 4.1 m). The predictable variation in forest structure emerges due to the complex interactions among edaphic and plant factors. Identifying predictable patterns in forest structure will aid in scaling up the ecosystem services provided by mangrove forests in coastal landscapes.**

KEYWORDS.—*Rhizophora mangle*, dwarf forests, biomass

INTRODUCTION

Mangrove forests of the Caribbean encompass some 9800 km^2 of the coastal zone (Spalding et al. 1997) and perform a wide range of ecological functions (Ewel et al. 1998). They protect the coast from erosion, buffer adjacent marine ecosystems (often coral reefs) from terrestrial inputs, and form the primary habitat for a high diversity of fish and invertebrates, some of which are commercially important (Rützler and Feller 1996; Mumby et al. 2004; Layman et al. 2004). Mangroves are threatened environments, as they are being cleared at a high rate for aquaculture and other human uses (Ellison and Farnsworth 1996; Valiela et al. 2001; Rivera-Monroy et al. 2004) in addition to being impacted by natural disturbances (e.g., Cahoon et al. 2003). Many mangrove forests in the Caribbean Region have very low stature, i.e., dwarf forests, and are consequently often targeted for conversion to other uses such as aquaculture (Primavera 1998; Murray et al. 2003). However, often these are old-growth forests often associated with carbon rich, peat substrates (Lugo 1997).

Better assessment of spatial variation in forest structure across the intertidal zone and over larger spatial scales is needed to quantify mangrove productivity (Saenger and Snedaker 1993) and carbon stocks (Twilley et al. 1992; Field et al. 1998; Jennerjahn and Ittekkot. 2002; Chmura et al. 2003), and to validate assessment of these parameters using remote sensing technology (e.g., Green and Clark 2000). In the Caribbean basin, forest structure and productivity is highly variable despite low tree species diversity (UNESCO 1998). Studies that have examined the links between forest structure and environmental conditions (e.g., Cintrón et al. 1978; McKee 1993; Fromard et al. 1998) suggest that the wide variation in tree height and productivity

are in response to temporal and spatial variation of environmental factors across the intertidal zone, such as soil salinity, soil waterlogging, and nutrient availability (McKee 1993; Koch 1997; Feller et al. 2002, 2003). Despite our detailed knowledge of the covariation in mangrove forest structure and environmental factors at some sites (e.g., Cintrón et al. 1978; McKee 1993; McKee et al 2002; Feller et al. 2002) our understanding of how repeatable these patterns are across broad spatial scales is limited, which in turn limits our capacity to scale data to the landscape level. Thus, accurate assessment of both above and below-ground carbon stocks in all types of mangrove forests is critical to understanding the impact of clearing of mangroves for aquaculture and other uses on local ecosystem functioning, on the regional and global carbon budget, and for understanding the effects of inputs of nutrient inputs and other pollutants on mangroves.

On the Caribbean coast of the Republic of Panama there is an extensive mangrove forest within Almirante Bay and the Chiriquí Lagoon. These two bays encompass a vast network of islands and mainland peninsulas fringed by mangroves, mangrove overwash islands, seagrass beds and patch coral reefs (Guzmán and Guevara 1998a,b). The mangrove forest is estimated to cover approximately 28 km^2 (D'Croz 1993), approximately half the mangrove area on the Caribbean coast of Panama, and is representative of the variable nature of Caribbean mangrove forests. The forests are largely intact and some forests are contained within Bastimentos National Park. We characterized the forest structure throughout Bocas del Toro, investigating whether patterns in forest structure were repeatable over the landscape. We used transects and a network of permanent plots established across the intertidal zone at four sites within the Bay to obtain a thorough description of forest structure.

MATERIALS AND METHODS

Site description

The Bocas del Toro archipelago (9° 21'N, 82° 15'W) in Eastern Panama encompasses two large bays: Almirante Bay and the Chiriquí Lagoon. The extensive mangrove forests fringing the islands and continental peninsulas of the archipelago are growing on peat that is approximately 2-3 m in depth (K. L. McKee unpublished data) resting on top of ancient coral reef (Coates et al. 2003). The mangrove forests are directly adjacent to high diversity tropical rainforest. The rainfall is high (3-5 m of rainfall annually) with little seasonality. Hurricanes are rare in the area as Bocas de Toro lies outside the hurricane belt, although high rainfall and flooding associated with hurricanes passing to the north is common. Earthquakes are episodic (Phillips et al. 1994; Phillips and Bustin 1996) and are likely to be the major non-anthropogenic disturbance influencing the forests.

Characterizing forest structure

Four sites were chosen within Almirante Bay: 1) Mangrove point on the Peninsula close to the laboratory of the Smithsonian Tropical Research Institutes Marine Field Station on Isla Colón (close to site 40 in Guzmán and Guevera 1998a), 2) Isla San Cristóbal (close to site 24 in Guzmán and Guevara 1999), 3) Cayo Solarte (close to site 35 in Guzmán and Guevera 1998b), and 4) Isla Popa (close to site 47 in Guzmán and Guevara 1999). At each site, 10 × 10 m permanent plots were established at 4 locations across the intertidal zone. At each site, one plot was located in each of four zones: 1) fringing the lagoon, 2) to landward of the fringe (seaward transition), 3) in the dwarf stand, 4) fringing the land (landward transition), for a total of 16 plots over the lagoon. In each plot all trees were tagged and both tree height and diameter at breast height (dbh) were measured (Cintrón and Schaffer-Novelli 1984).

Rhizophora mangle, the most abundant species, has prop-roots and multiple stems, requiring dbh to be measured above the highest prop-root where the root no longer influences the diameter of the stem. Biomass was estimated using a number of different allometric equations. Due to the large range in tree sizes at the site biomass

of *R. mangle* was calculated using the equations of Cintrón and Schaffer-Novelli (1984). Equations of Fromard et al. (1998) were used to estimate biomass of *Avicennia germinans* and *Laguncularia racemosa*. Leaf area index (LAI) for each plot was assessed by analyzing three hemispherical photographs per plot (Nikon Coolpix 995 with fisheye lens, Nikon, Tokyo, Japan) using the Hemiview software package (Version 2.1, Delta T Devices, Cambridge, UK). At each of the sites we also characterized forest structure by establishing transects across the intertidal zone, using the point-center-quarter method (Cintrón and Schaffer-Novelli 1984).

At each permanent plot, pore water salinity was measured at 30 cm depth at 5 random positions per plot using the methods of McKee et al. (1988). A detailed study of sediment physical and chemical characteristics was made along the point-center-quarter transect established on Isla San Cristóbal. On Isla San Cristóbal two replicate measurements of sediment and pore water chemistry were conducted at ten points over the intertidal zone from the seaward edge to the landward rainforest. Soil samples were collected with a piston-type corer for determination of bulk density, percent organic matter (loss on ignition), and extractable and total phosphorus according to standard techniques (EPA 1983). Soil redox potentials at 1, 15, and 30 cm depths were measured with bright platinum electrodes equilibrated *in situ* for 30 min (McKee et al. 1988). Each electrode was checked before use with quinhydrone in pH 4 and 7 buffers (mV reading for quinhydrone is 218 and 40.8, respectively, at 25°C). The potential of a calomel reference electrode (+244 mV) was added to each value to calculate Eh. Interstitial water was collected from a depth of 15-20 cm as described in McKee et al. (1988). An aliquot of each water sample was added to an equal volume of an antioxidant buffer and was analyzed for sulfide with a sulfide microelectrode (McKee et al. 1988). Additional aliquots were used to measure pH and salinity.

Data were analysed by one way ANOVA testing for the significance of main effect Zone over replicate sites using Data Desk 6.1 (Data Descriptions, NY, USA). Pairwise tests of individual means were done using least significant differences (P < 0.05). Inspecting residual plots assessed suitability of ANOVA models.

RESULTS

The mangrove forests of Almirante Bay and the Chiriquí Lagoon are dominated by *Rhizophora mangle*, with other mangrove species being uncommon (in 2470 trees sampled within the 16 permanent plots established, only 10 individuals of *Laguncularia racemosa* and 9 of *Avicennia germinans* were found). Although the forests were essentially monocultures of *R. mangle*, at each site forest structure varied enormously over the intertidal zone (Fig. 1, Table 1). Tree height declined from 3-5 m at the seaward fringe to less than 1 m in the interior of the stand, increasing again when nearing the landward edge of the mangrove. Tree height was correlated with dbh, LAI, basal area and biomass over all tree sizes (Table 1). However, at all four sites, the structure of the forest varied predictably across the intertidal gradient despite differences in the extent of the interior dwarf stands (Fig. 1).

Soil physico-chemical properties, measured on Isla San Cristóbal also varied across the tree height gradient (Fig. 2). Extractable phosphorus declined from the seaward fringe to the dwarf stands, increasing slightly close to the landward edge of the mangrove. Soils were more reducing (lower Eh) with higher pore water sulfide concentrations in the dwarf stands compared to the seaward and landward fringes. Salinity of the pore water remained near sea-strength for most of the height gradient, but decreased close to the landward margin. Greater height and dbh of trees on the landward margin were associated, at least partially, with lower levels of soil salinity (Fig. 3, Table 1). There was evidence of significant fresh water inputs (i.e., lower pore water salinity) in the dwarf zone at Cayo Solarte and in the seaward transition zone on Isla San Cristóbal (Fig. 3).
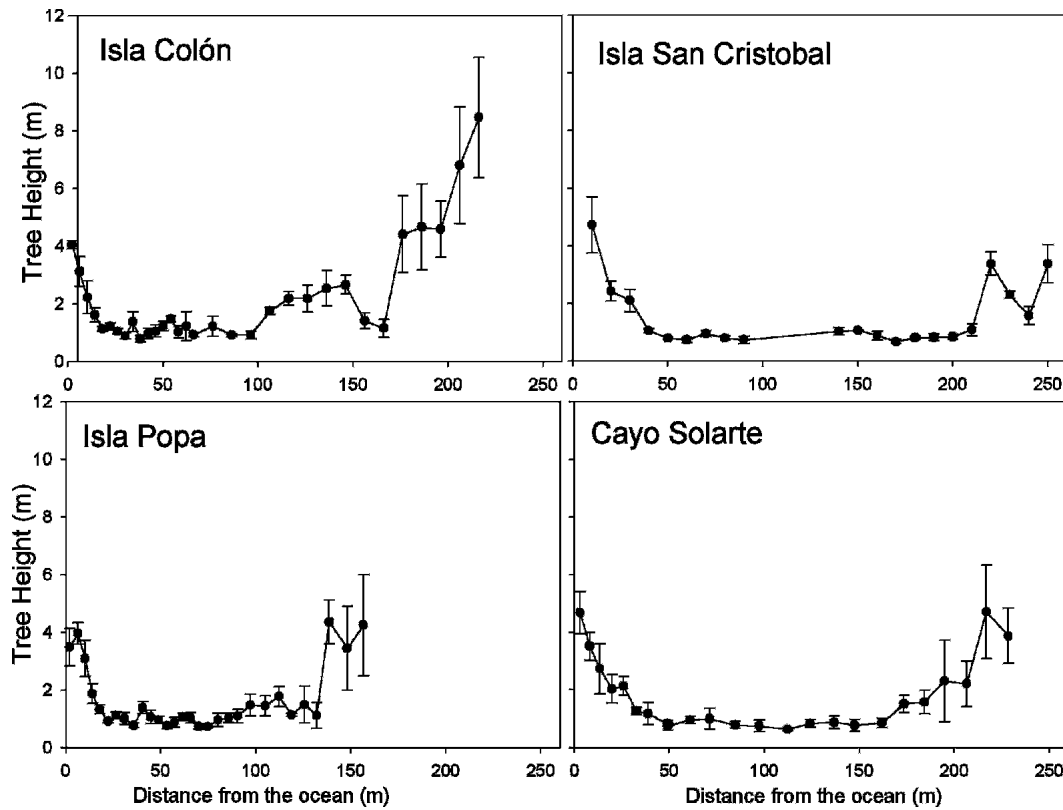
FIG. 1. Variation in mangrove tree height over transects from the seaward edge (0 m) to the landward edge of the mangroves at four sites within the Chiriquí Lagoon, Bocas del Toro, Republic of Panama. Each point is the mean (± standard error) of four trees, one from each directional quadrant closest to the transect point.

TABLE 1. Characteristics of mangrove forests in permanent plots across the intertidal zone within the Chiriquí Lagoon, Bocas del Toro, Republic of Panama. Values are means and standard errors for 3-4 sites per intertidal position. Means with differing letters are significantly different at P < 0.05.

	Fringe	Seaward transition	Dwarf	Landward
Height (m)	3.94 ± 0.10 a	1.54 ± 0.25 b	0.74 ± 0.06 c	4.14 ± 0.89 a
Dbh (cm)	5.27 ± 0.64 a	2.69 ± 0.51 b	1.45 ± 0.12 b	6.64 ± 1.54 a
Density (stems per 100 m^2)	85.0 ± 31.6 a	178.0 ± 45.5 b	335.7 ± 26.7 c	47.3 ± 14.7 a
Basal area (m^2 ha^{-1})	15.8 ± 1.8 a	11.2 ± 1.6 ab	6.8 ± 1.2 bc	30.1 ± 14.8 a
Biomass (Mg ha^{-1})	59.5 ± 7.0 a	22.2 ± 4.4 b	8.3 ± 0.4 c	194.3 ± 127.3 a
Leaf area index	1.77 ± 0.05 a	1.08 ± 0.07 b	0.65 ± 0.08 c	1.83 ± 0.06 a
Salinity	34.4 ± 0.6 a	32.8 ± 1.5 a	33.3 ± 1.9 a	19.6 ± 3.6 b

Note: Biomass allometries are from Cintrón and Novelli (1983) for *R. mangle* and for *A. germinans* and *L. racemosa* from Fromard et al. (1998).

Percent organic matter and bulk density of soils were slightly lower in the dwarf zone compared to landward and seaward fringe zones, but indicated peat formation throughout the tree height gradient (organic matter content > 40%; Fig. 2D). Pore water pH and ammonium concentrations did not vary significantly across the tree height gradient and averaged 6.66 ± 0.05 and 4.45 ± 1.04 μM, respectively.
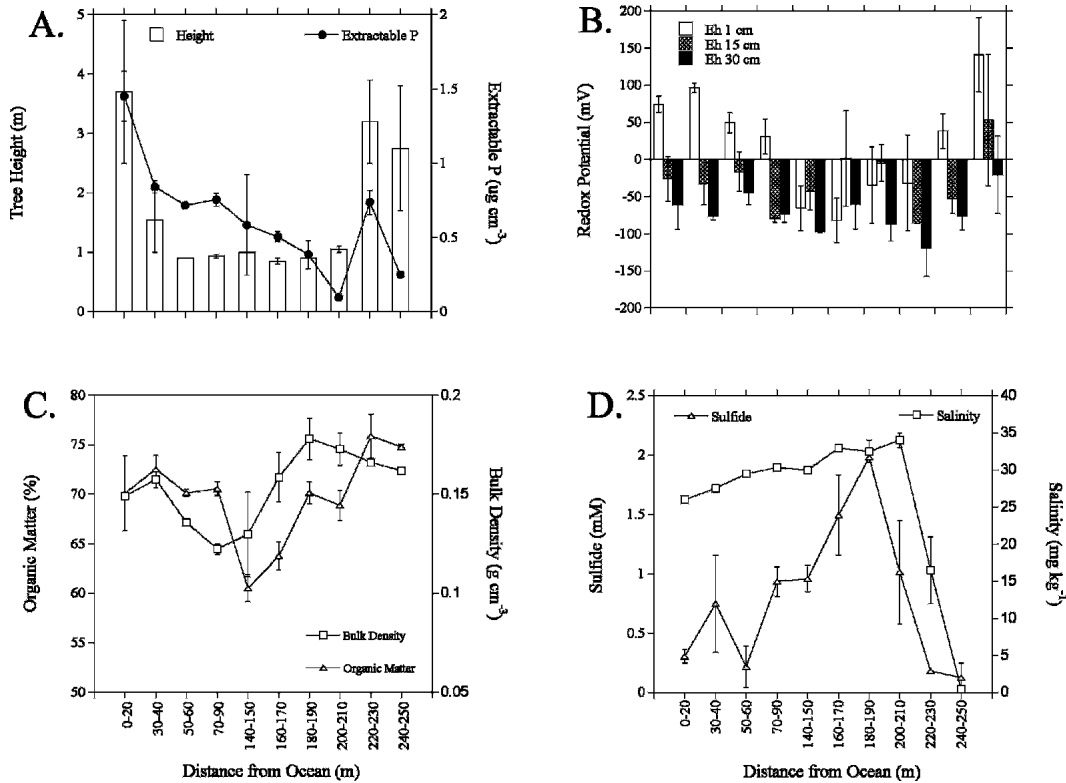
FIG. 2. Variation in sediment physico-chemical characteristics across the intertidal zone at Isla San Cristóbal. A) Tree height and extractable phosphorus, B) Redox potential, C) % organic matter and bulk density, D) Sulphide and pore water salinity.

DISCUSSION

Rhizophora mangle was overwhelmingly dominant within Almirante Bay. This could be associated with subsidence of the region due to tectonic activity (Phillips et al. 1994; Phillips and Bustin 1996), which may favor the success of *R. mangle* recruits because of its enhanced ability to survive inundation compared to *A. germinans* (McKee 1996), and/or its ability to colonize inundated substrates (McKee 1995). Despite the dominance of one species, forest structure was highly variable at any one site, but the pattern of variation across the intertidal zone was similar and predictable over all sites.

Globally, biomass estimates in mangrove forests range from 7-440 Mg ha^{-1} (Saenger and Snedaker 1993). Our estimates for forests in Bocas del Toro fell within the lower end of this range, but varied over 20-fold (8-194 Mg ha^{-1}). Estimation of biomass is highly dependent on the allometric equations used (Clark and Clark 2000), and thus our estimates of biomass could be improved with the development of site-specific allometries (*cf.* Ross et al. 2001).

Wide variation in forest structure has been correlated with variation in soil physico-chemical characteristics and particularly with variation in salinity, e.g., hypersaline conditions prevailed in interior scrub forest stands (e.g., in Puerto Rico, Cintrón et al. 1978). In Bocas del Toro pore water salinity was generally lower in the taller landward forests, possibly indicating that salinity may partially limit forest stature. However, pore water salinity in seaward and dwarf forests was similar and close to that of seawater, suggesting other environmental parameters are important in controlling variation in forest structure.

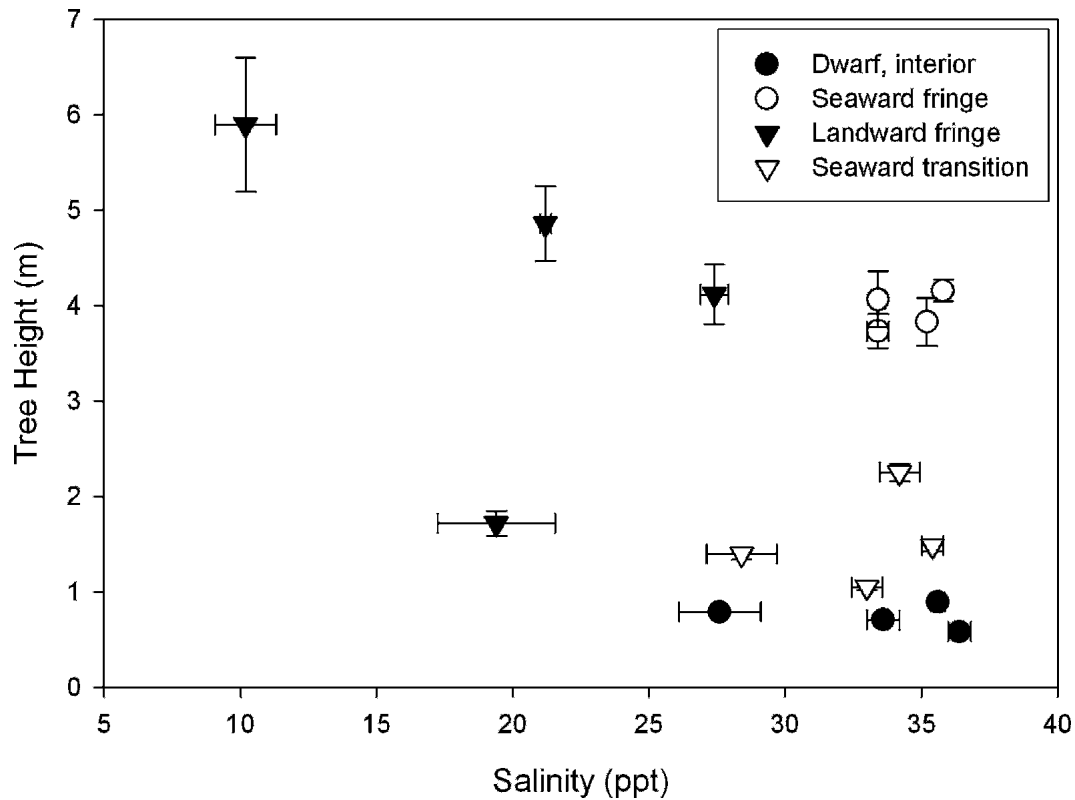A fertilization experiment of dwarf trees in Bocas del Toro found that tree growth

FIG. 3. Variation in average tree height with soil salinity in replicate 10 x 10 m plots in either the seaward fringing forest (open circles), seaward transition (open triangles), dwarf interior stand (closed circles) or landward fringe (closed triangles) over 4 sites within the Chiriquí Lagoon, Bocas del Toro, Republic of Panama. Each point is the mean height (± standard error) for all trees within each plot. Salinity values are the mean (± standard error) of 5 measures per plot.

was strongly enhanced with phosphorus and nitrogen fertilization (Lovelock et al. 2004). Across variation in tree height we found that phosphate availability varied widely (Fig. 3). Compared to other sites, external P availability in the dwarf forests of Bocas del Toro was moderately low (Carlson et al. 1983; Boto and Wellington 1984; Sherman et al. 1998; McKee 2001), but P availability was similar in taller landward forests as it was in parts of the dwarf forest, suggesting that nutrient deficiencies alone cannot explain variation in tree height. Reduced tidal flushing, reduced sediments and sulphide accumulation can also affect nutrient uptake and plant growth (McKee et al. 2002). Over variation in tree height, sediment Eh and sulphide concentrations were also highly variable. While sediment Eh tended to correlate with tree height,

which could reflect size and efficiency of oxygen transport by aerial roots, sulphide concentrations did not. Collectively, these data demonstrate that forest structure and sediment characteristics can vary widely in forests containing essentially one species of mangrove. Moreover, the predictable variation in tree height across the intertidal zone cannot be linked to one single factor, and patterns in the development of forest structure emerge from complex interactions among abiotic and biotic factors.

The predictability in variation in forest structure across the intertidal zone allows us to scale-up to estimate biomass for the lagoon complex. Diminutive (less than 1.5 m in height), interior dwarf stands account for half of the mangrove forest area, occupying 53% of the linear spread along the study transects. Extensive dwarf stands of

R. mangle have also been documented in Belize (Murray et al. 2003). Seaward and landward fringing forests account for approximately 47% of the linear distance along the transects (seaward 14%, and landward 33% respectively). Using the linear distances occupied by each forest type and their average characteristics measured within the plots, we calculated the contribution of each forest type (with the exception of the seaward transition) to total forest basal area and biomass. Despite the large area of the dwarf stands they account for only 22% of the total basal area and 5.7% of the total estimated aboveground biomass of the forest. The seaward fringe, which is the most conspicuous, accounts for only 15% of basal area and 10.8% of biomass. The landward stands account for 63% of the total basal area and 83.5% of the total estimated biomass of the forests.

The mangrove forests of Bocas del Toro are dominated by *R. mangle.* Despite the low diversity there was wide variation in both forest structure and sediment characteristics. However, the variation in forest structure is predictable, following a pattern of a taller fringing forest giving way to extensive dwarf stands to landward, and then returning to a taller forest on the terrestrial edge. Linking predictability in forest structure with that of function will permit scaling of ecosystem processes to the whole landscape scale. Facilitating scaling up to the landscape level is vital to fully understand the role of mangroves in carbon sequestration, nutrient cycling and the influence of mangrove forests on the biogeochemistry of lagoon waters, the provision of habitat for a diverse assemblage of organisms, and in predicting the vulnerability of mangroves to global climate change and other natural and anthropogenic disturbances.

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