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Research Article

Environmental Influences on the Distribution of Mangroves on Bahamas Island

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Abstract

Mangrove forests provide valuable ecosystem services but are declining in many tropical locations. The abundance of mangrove species in coastal fringe forests is related to biotic processes such as species succession or competition and abiotic factors, including nutrient availability, physiochemical water quality, soil composition, and tidal inundation. We examined the abundance of *Rhizophora mangle* and *Avicennia germinans* relative to environmental factors, including porewater chemistry, soil substrate, and distance from the ocean, on Bahamas Island. In this system, *R. mangle* were primarily found in litter-dominated soils and abundances were positively related to distance from the ocean, while *A. germinans* was only found in sandy soils closest to the ocean. Although phosphate, alkalinity, and salinity in porewater did not explain the distribution of species, free chloride varied significantly with distance from the ocean. These results suggest that soil conditions and tidal inundation may help determine the distribution of mangrove species on Caribbean islands.

Key words: *Avicennia germinans*, Bahamas, Hummingbird Cay, *Rhizophora mangle*, salinity, tidal inundation

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INTRODUCTION

Mangroves are salt-tolerant trees and shrubs that live in the intertidal zones of tropical coastal marshes, lagoons, riverines, and shores. Mangrove forests are an important source of social and ecological services for tropical coastal communities (Walters et al. 2008). Roots and stems of mangroves help build coastal soils, protecting shorelines and intertidal zones from erosion and reducing the impact of storms on terrestrial communities (Marchand et al. 2004). The habitats created by mangroves are highly productive (Komiyama et al. 2008), providing habitat for a variety of marine, bird, vertebrate, and invertebrate species (Mumby et al. 2004; Manson et al. 2005; Nagelkerken et al. 2008). However, mangrove forest ecosystems are threatened by a number of anthropogenic activities: forests are a source of wood for charcoal and construction, cleared and filled in for development, destroyed by offshore oil production and oil spills, and removed for mariculture—especially shrimp farming (Ellison and Farsworth 1997; Walters et al. 2008). As sea levels rise due to global climate change, important habitat for mangroves will disappear (Nicholls et al. 2007) and many scientists predict that mangroves will retreat landward (Gilman et al. 2008) with expected increases in tidal inundation further reducing the zone of habitable land for mangroves (Pernatta 1993; Hoppe-Speer et al. 2011).

Mangrove forests vary in composition and structure based on local physical conditions, with some forests consisting of one or more species demonstrating a distinguishable pattern of zonation (Snedaker 1982) due to distinct species responses to environmental parameters (Luzhen et al. 2005). In the Caribbean, mangrove forests are primarily composed of three species: red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), and white mangrove (*Laguncularia racemosa*). Many hypotheses have been proposed to explain these patterns in mangrove growth and abundance. Davies (1940) first attributed mangrove zonation in Florida and the Caribbean to successional growth based on the soil building properties of mangroves. However, evidence for the succession hypothesis is sparse (Lugo and Snedeker 1974) and the hypothesis is

inconsistent with geological data in some instances (Egler 1952). Lugo (1980) argues that the cyclical succession of mangroves applies to certain species under certain conditions and that in low-energy, tropical environments, mangroves represent a steady-state. Some species patterns have not changed for millennia, suggesting that the importance of the soil-building properties of mangroves may not be consistent between species (Thom 1967). Additionally, Ball (1980) concluded that succession in Southern Florida was occurring, but that interspecific competition for light was driving species distribution.

Another common hypothesis explaining mangrove abundance patterns is the tolerance of each species to flooding conditions (McKee 1993; Youssef and Saenger 1998). The mangrove environment varies greatly with tidal frequency, soil salinity, freshwater inputs, nutrients and climate—all shifting from a terrestrial to a marine system (Parida and Jha 2010). Intertidal soils, which are affected by topography, tidal height, and tidal frequency, are a heterogeneous, complex mixture of sand, mud, and organic material (Carlson et al. 1983), and some species of mangroves are co-located with distinct hydrology and soil biogeochemistry (Lee et al. 2008). Tidal inundation may also affect porewater phosphate concentrations (Silva and Sampaio 1998), root oxygen deprivation, and soil redox potential (McKee 1993). Cohen et al. (2004) demonstrated that the inverse relationship between tidal inundation and low-tide/high-tide pH ratios is relevant to the stability of phosphorous compounds in coastal soils.

In some regions, soil conditions, including salinity (Ball and Pidsley 1995; López-Hoffman et al. 2007), soil redox potential (Matthijs et al. 1999), or porewater sulfide concentration (Nickerson and Thibodeau 1985; McKee 1993) have also been correlated with the abundance of mangrove species. A variety of studies have shown that nutrient availability and salinity affect mangrove productivity, growth, and mortality (Boto and Wellington 1983; Naidoo 2006; Sabrado and Ewe 2006). In many mangrove forests, the physiological tolerance to flooding or salinity may drive species distributions (Walsh 1974) and rhizosphere oxidation or nutrient cycling processes may alter local soil conditions, further complicating things (Gleasen et al. 2003; Whigham et al. 2009). Soils underlying mangrove forests are generally considered nutrient deficient despite the abundance of decomposing litter due to the consistent turnover of stems, roots, and leaves (Alongi 1996). Additionally, Koch (1997) demonstrated that phosphorous is the limiting factor affecting seedling development and Koch and Snedeker (1997) provided evidence that growth of *R. mangle* and anoxia due to soil structure can influence root development.

In the Bahamas, previous studies have demonstrated the importance of reducing conditions and sulfide concentrations in mangrove porewater for determining the distribution of mangrove species (Nickerson and Thibodeau 1985). Although the Bahamas are well known for having calcium-carbonate rich sediments that are generally phosphorous poor (Morse et al. 1985), there are few studies that have tested whether this affects the distribution of mangroves. We set out to test the hypothesis that mangrove species distribution is related to tidal inundation (measured by distance from the ocean), porewater chemistry (phosphorous, chloride, alkalinity, salinity), and soil substrate on Bahamas Island.

MATERIAL AND METHODS

Study Site

Data were collected during the dry season in March 2010 at the Hummingbird Cay (HBC) Field Station, Jewfish Island, Bahamas, 23°32'N 75°50'W. HBC is located west of Georgetown in the Great Exuma portion of the Central Bahamas Island Chain (Figure 1). Mangroves grow in two locations on the island: along the exposed northern end of the low-energy western shore, and in a tidal marsh on the northeasterly coast. Along the western shore there is a lagoon where most of the mangroves are found. Soil substrate varied from primarily calcium carbonate oolite sand to mostly decomposing litter with overlying oolitic silt. In the marsh, oolite contributed less to the soil substrate. Soils farther inland within the lagoon were more litter-dominated.

Field Measurements

Sites were determined by locating 80-meter transects starting with the farthest extent of upland mangrove growth and citing points 20 meters apart towards the ocean following Ukpong (2000). Four transects were placed on the western shore between 20 and 30 meters apart, and a fifth transect was placed in the marsh based on McKee et al. (2007). The abundances of *R. mangle* and *A. germinans* were measured within a 1.83-meter (six-foot) radius circle (10.52 m²) centered at each site and the number of adult plants, defined by four or more prop roots, was also quantified for each species. Only individuals larger than 2 cm in diameter at the high water mark were counted as adults with smaller trees counted as seedlings and pneumatophores ignored. The soil type (sandy or leaf-litter dominated) was determined visually using a soil core.

Porewater chemistry was measured at low tide by driving a 7.62-centimeter (3-inch) diameter piece of polyvinyl chloride (PVC) pipe into the substrate approximately 15 centimeters, sealing it from the surface water, as described in Nickerson and Thibodeau (1985). Using a 5.08-centimeter (2-inch) diameter piece of PVC pipe, a 30-centimeter core of

substrate was then removed within the large PVC pipe. Following core removal, porewater would fill the space from the subsurface. Measurements of water chemistry were made from this porewater. Salinity was measured directly using a YSI 85 multipurpose meter (Yellow Springs Inc., Yellow Springs, Ohio, USA), and water samples were taken using 250 ml HDPE bottles. In the laboratory, orthophosphate (PO_4^{3-}) was measured using the ascorbic acid method, free chloride (Cl) using the DPD method, and total alkalinity using a titration of 0.16 N H_2SO_4 with bromocresol green-methyl red indicator (APHA 1995).

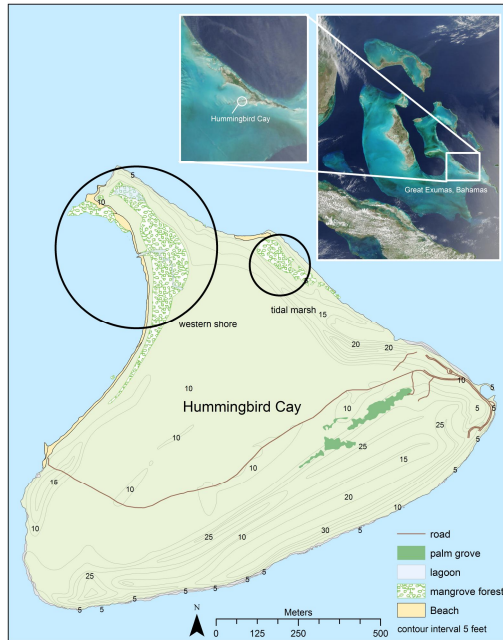


Figure 1 Map of Hummingbird Cay within Great Exuma, Bahamas.

Data Analysis

Mean and standard error of the abundance of adults for each species were determined in the western shore and marsh. Significant differences in mangrove abundance at each location were determined using an unequal variance student's *t*-test. Since no *A. germinans* were found in the marsh and the sample size was so small, these data were left out of all subsequent analyses. Bivariate plots of the abundance of each species with the distance from the ocean were graphed and linear regression analysis used to determine significant relationships using JMP statistical software (version 5.0.1.2, SAS Institute Inc.). To assess the relative abundance of *R. mangle* and *A. germinans*, the ratio of *R. mangle* to *A. germinans* was also determined at each site and analyzed using linear regression based on distance from the ocean. Sites were also grouped by soil substrate (sandy vs. leaf-litter) and significant differences determined using unequal variance student's *t*-test. Mean and standard deviation of porewater parameters were calculated for each soil substrate and relationships between porewater chemistry and distance from the ocean examined by linear regression. The coefficients of determination adjusted for sample size are provided.

RESULTS AND DISCUSSION

Distribution of Species

The most common species in both regions of the island was *R. mangle*, while *A. germinans* was absent in the marsh (Figure 2). *R. mangle* was significantly more abundant than *A. germinans* on the western shore ($t = 5.38$, $df = 18$, $p < 0.0001$). The abundance of *R. mangle* increased significantly ($R^2 = 0.44$, $n = 19$, $F = 13.1$, $p = 0.002$) with distance from the ocean (Figure 3a). *A. germinans* tended to be more abundant near the ocean, although this was not significant ($R^2 = 0.13$, $n = 19$, $F = 2.42$, $p = 0.14$; Figure 3b), the ratio of *R. mangle* to *A. germinans* increased with increasing distance from the ocean. In terms of soil substrate, *R. mangle* were significantly more abundant in the litter-dominated soils than in sandy soils ($t = 2.51$, $df = 17$, $p = 0.023$), while *A. germinans* were significantly more abundant in sandy soils ($t = 4.29$, $df = 17$, $p = 0.0005$; Table 1). Our

results suggest that *A. germinans* prefer sandy soils closest to the ocean, while *R. mangle* prefer litter-dominated soils farther from the ocean. Similar patterns in distribution have been found in other regions, as previous studies demonstrate the intolerance of *Rhizophora* species to water-saturated, saline environments (MacNae and Kalk 1962; Naidoo 1985; Lin and Sternbers 1993).

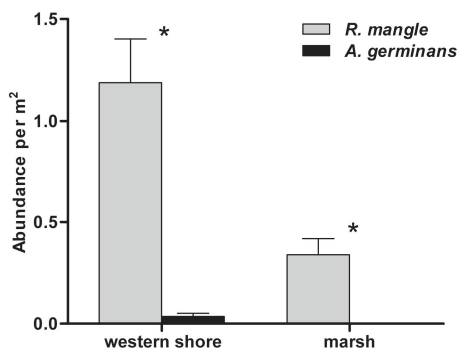


Figure 2 Mean (\pm SE) abundance of adult red mangrove (*R. mangle*) and black mangrove (*A. germinans*) in two locations on Hummingbird Cay, Bahamas. Asterisk represents a significant difference based on unequal variance *t*-test.

Porewater Chemistry

Porewater chemistry varied little between soil types or with distance from the ocean (Table 1). Sandy soils tended to have greater PO_4^{-3} and less alkalinity than litter-dominated soils, but this was not statistically significant. The only porewater parameter that differed between soil substrates was salinity, which was significantly greater in litter-dominated soils ($t = 3.52$, $df = 17$, $p = 0.003$). Not surprisingly, litter-dominated soils were found farthest from the ocean. In previous studies of tropical carbonate systems, phosphorous availability limited primary production (Short et al. 1985; Short et al. 1990; Powell et al. 1989), which may not be the case here. Connor (1969) demonstrated that nutrients such as potassium and calcium suppress mangrove growth, but the addition of other nutrients, such as sodium and iron, may enhance mangrove growth (Sato et al. 2005). Nutrients (PO_4^{-3} , alkalinity) did not relate to the abundance of either mangrove species, suggesting that at least on HBC, phosphorous and calcium are not limiting. However, small sample sizes may have prevented us from detecting a trend. Porewater PO_4^{-3} concentrations measured here were consistent with those measured near *A. germinans* by Vazquez et al. (2000). Ukpogon (1994) demonstrated that distance from the ocean and tidal inundation influence the variation of soil nutrients in mangrove forests, and in Nigeria, *R. mangle* were positively correlated with calcium and negatively correlated with phosphorous (Ukpogon 2000). Although we detected few differences in porewater chemistry between substrates, we did not monitor porewater nitrogen, which may affect the microbial community in mangrove soils (Wigham et al. 2009). Mangrove soils are also known to be large sinks for cations, which may have influenced these results (Naidoo 1980). Gleason et al. (2003) concluded that soluble reactive phosphorous was negatively related to soil redox potential, but only for negative potentials. Further study is needed to understand rhizosphere redox potentials in relation to species abundance, soil-substrate, and nutrient availability.

Environmental Influences on Species Distribution

There was no difference in the abundance of adult *R. mangle* between soils substrates, while adult *A. germinans* were only found in sandy soils (Table 1). Since total *R. mangle* abundance was more common in litter-dominated soils farther away from the ocean, we looked at the influence of tidal inundation (distance) on porewater chemistry. Overall, there were no significant relationships between distance and porewater PO_4^{-3} , alkalinity, or salinity, while porewater Cl increased significantly with greater distance from the ocean ($R^2 = 0.53$, $F = 14.46$, $df = 14$, $p = 0.002$; Figure 4). Further, soil in sites farthest from the ocean spent the most time exposed to the atmosphere at low tides. Evapotranspiration can increase local salinity levels above that of ocean water (Lee et al. 2008), generating a longitudinal salinity gradient (Wolanski et al. 1980). By contrast, in East Africa, *Rhizophora mucronata* was found closest to the ocean and *Avicennia marina* was found in the upslope region (Matthijs et al. 1999). Some mangroves exclude salt in the uptake of water, also contributing to the local salinity of soils (Lugo 1980; Passioura et al. 1992). As salt accumulates in the environment, growth rates and transpiration may limit water

uptake until a steady-state is achieved (Passioura et al. 1992). Both *Avicennia* and *Rhizophora* species are known to exclude, accumulate, and secrete salt in different tissues (Griffiths et al. 2006; Parida and Jha 2010).

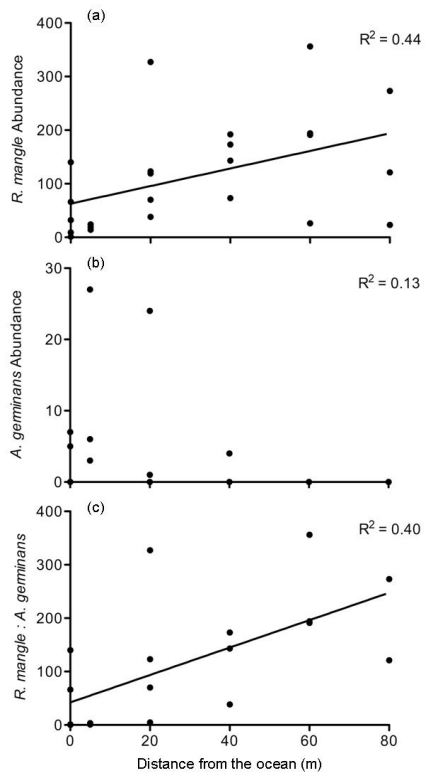


Figure 3 Abundance of (a) *R. mangle* and (b) *A. germinans* as a function of distance (meters) from the ocean and (c) the relationship between the ratio of *R. mangle*: *A. germinans* and distance with significant ($p < 0.05$) linear regression lines and the coefficients of determination given.

The accumulation of low-molecular-mass compounds counters high environmental osmolarity in some mangroves, although such mechanisms have yet to be identified in either *R. mangle* or *A. germinans* species. However, there may be little biological significance since mangroves can tolerate large fluctuations in salinity (Parida and Jha 2010). In this study, sites closest to the ocean were more often inundated with tidal water than sites farther away confirming *Rhizophora*'s intolerance to highly saline waters. The combination of gradients created by salinity and tidal inundation may drive species zonation.

Table 1 Mean (SD) of site characteristics by soil substrate, including total number of red mangrove (*R. mangle*) and black mangrove (*A. germinans*) plants (seedlings and adults), adult red and black mangroves, and porewater chemistry in the lagoon and exposed shore on Hummingbird Cay, Bahamas. Unequal variance student's t-test between substrates is provided. n = number of sites, distance = distance from ocean or ocean inlet, Alk = total alkalinity

	leaf-litter soil	sandy soil	t-test
n	11	8	
<i>R. Mangle</i> total	180 (105)	71 (71)	$t = 2.71, df = 16, p = 0.015$
<i>A. germinans</i> total	0.3 (0.9)	9.1 (10.5)	$t = 2.39, df = 7, p = 0.048$
<i>R. Mangle</i> adult	3.3 (3.0)	2.8 (2.4)	$t = 0.42, df = 16, p = 0.68$
<i>A. germinans</i> adult	0 (0.0)	1.5 (1.6)	$t = 2.65, df = 7, p = 0.033$
distance (m)	44.1 (25.8)	8.8 (14.3)	$t = 3.81, df = 16, p = 0.0015$
PO ₄ ³⁻ (mg L ⁻¹)	0.32 (0.25)	0.57 (0.40)	$t = 1.54, df = 10, p = 0.15$
Cl (mg L ⁻¹)	0.57 (0.67)	0.54 (0.44)	$t = 0.12, df = 16, p = 0.91$
Alk (mg L ⁻¹)	2384 (2064)	1461 (2003)	$t = 0.98, df = 15, p = 0.34$
Salinity (ppt)	41.3 (1.4)	37.6 (3.03)	$t = 3.21, df = 9, p = 0.0105$

Differences in total mangrove abundance between soil substrates suggest that substrate conditions might be influencing mangrove colonization (Rabinowicz 1976). Salt marsh soil substrates, including texture and organic content, can influence a soil's salinity, pH, and ability to store nutrients (Callaway 2001). Hesse (1961) examined fibrous mud from a *Rhizophora* swamp and non-fibrous mud from an *Avicennia* swamp and concluded that mud around *Rhizophora* roots contained more moisture due to increased litter content, which increased sulfur oxidation and local acidity. Marchand et al. (2004) concluded that differences in species abundances were due to strongly reducing conditions associated with anaerobic, decomposing litter-dominated soils. Previous results demonstrating that mangrove zonation can be related to sulfide (Nickerson and Thibodeau 1985) or soil redox potential (Matthijs et al. 1999) are also consistent with these results.

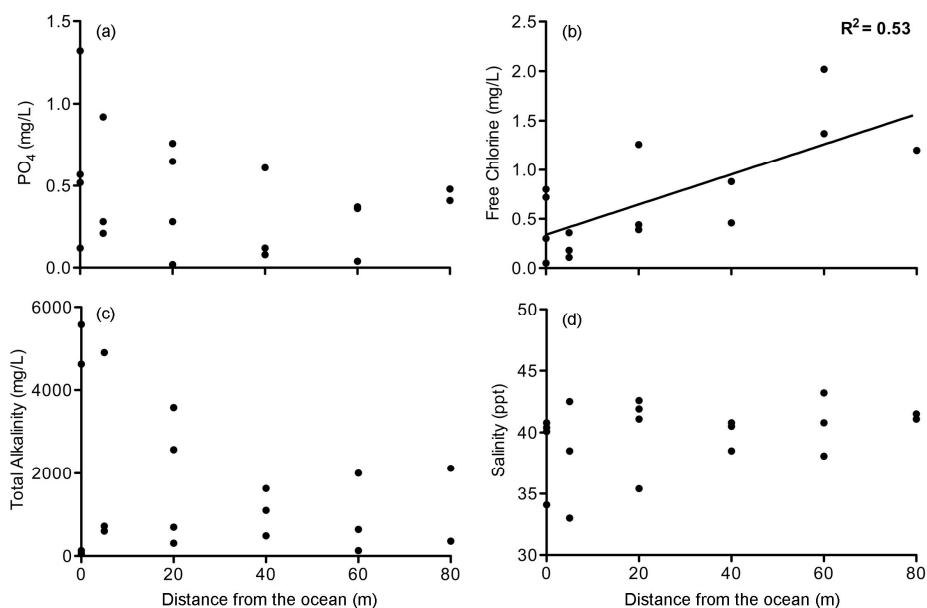


Figure 4 Bivariate plots of porewater (a) orthophosphate, (b) free chlorine, (c) total alkalinity, and (d) salinity, relative to distance from the ocean in a lagoon on Hummingbird Cay, Bahamas. The line represents a significant ($p < 0.05$) relationship based on linear regression analysis and the coefficient of determination is given.

Nickerson and Thibodeau (1985) found *R. mangle* abundance was greatest in regions with high sulfide concentrations generated from anaerobic respiration of mangrove litter and McKee (1993) postulated that reduced soil conditions and high sulfide concentrations inhibit *A. germinans* seedling growth. We also observed the absence of *A. germinans* seedlings in litter-dominated soils, which are presumably strongly reducing given the characteristic sulfur odor (pers. obs.), although McKee et al. (1988) demonstrated that both *R. mangle* and *A. germinans* are equally capable of exploiting reduced sediments. The mangrove rhizosphere may be altered by different oxidation rates due to distinct differences in above-ground root structures as *R. mangle* have been shown to alter their environment to improve growth (McKee 1993). Previous descriptions of Caribbean mangrove forests have identified the distribution of species using a gradient from the ocean (or channel) to the upland with *R. mangle* dominating the oceanfront and *A. germinans* dominating the upland (Davis 1940; Lugo and Snedaker 1974), suggesting that these patterns don't always hold. However, mangroves on HBC do not generally grow in bands parallel to the shore typical of other fringe forest systems in the Caribbean (Nickerson and Thibodeau 1985), and there are examples of overlapping distributions of mangrove species in other tropical systems (Bunt 1999). Alternatively, *R. mangle* is self-pollinating while *A. germinans* requires pollination for seed germination, suggesting that HBC may also be deficient in *A. germinans* pollinators limiting colonization (Lowenfeld and Klekowski 1992).

CONCLUSION AND RECOMMENDATIONS

The distribution of mangrove species is the result of complex interactions between physical, chemical, and biological characteristics with the chemical and biological composition of soils playing an important role influencing the structure and function of mangrove communities. Mangroves can also influence local soil conditions through litter deposition and salt excretion. Morphological differences between mangrove species may provide some clues to their differential growth or survival in oolitic soils in the Bahamas. For example, differences in the abundance of lenticels or aerenchyma tissue may influence gas exchange and affect the plant's access to oxygen in both anoxic substrates and under tidal water (Scholander et al. 1955). Even with closely related mangroves species, interspecific differences in growth characteristics can lead to unique tolerances to environmental conditions and differential distributions. Our results demonstrate that upland, litter-dominated soils are more favorable to *R. mangle* than sandy soils on Hummingbird Cay. The actual distribution of mangroves on Caribbean Islands is likely to be a complex relationship between a variety of environmental factors (nutrient availability, salinity gradients, silt deposition, climate, soil substrate) as well as biological factors (seedling survival, root foraging success, rhizosphere conditions) with each species exhibiting a unique response to each set of conditions. These results suggest that the interactions that govern mangrove abundance may produce different zonation patterns depending on the underlying environmental conditions. We suggest that the conservation of mangrove forest habitats not focus on a single environmental "type" and instead protect a range of conditions that are suitable for a variety of mangrove species.

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