Understanding Grenada's Mangroves: Zonation, Plasticity, and the Potential for Restoration

by

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A Thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfilment of the requirements of the degree of

MASTER OF NATURAL RESOURCES MANAGEMENT

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Abstract

The white mangrove (*Laguncularia racemosa*) is widely distributed throughout both the Caribbean region and the mangrove ecosystems (mangals) it inhabits, despite being considered restricted to the landward fringes of the forest (i.e., the back mangal). In Grenada, it has been observed expressing various forms of phenotypic plasticity, including aerial root expression, prompting questions about the link between its plasticity and mangrove community zonation. I hypothesized that mangal zonation and white mangrove plasticity were influenced by both site-level (forest type) and plot-level factors (edaphology and hydrology), and that plasticity also contributed to the zonation observed through niche expansion. I conducted vegetation surveys at one basin forest and one fringe forest in Grenada in summer 2020–2021, collecting environmental (site characteristics and soil chemistry) and vegetation data (tree height and size, aerial root presence, leaf size and thickness). I also surveyed white mangroves at nine additional sites across three islands in the country to further document the extent of white mangrove plasticity. Overall, the species was more structurally important (i.e., had a higher relative density and dominance) than both red and black mangroves and was well-distributed in all zones except the fringe forest's seaward zone. White mangroves showed preference for higher-elevation habitat with a limited hydroperiod, including the seaward zone of the basin forest, revealing that their distribution is driven by elevation and not zone *per se*. White mangroves exhibited trait plasticity in tree height, diameter, leaf size, and root form in response to salinity and elevation. Plasticity in root form was most interesting, as white mangroves produced pneumatophores in shallow water and adventitious roots in deeper water, allowing the species to survive in varying water depths and defy expected zonation patterns. The link between these two concepts should be explored in other forest ecosystems to further understand the effects of intraspecific variation and plasticity on community structure and zonation. These findings can also help improve mangrove restoration planning in the Caribbean by highlighting the versatility of the white mangrove. Incorporating the species into a multi-species approach can improve the success rates, cost-effectiveness, and sustainability of restoration in the region.

Keywords: Caribbean, Grenada, *Laguncularia racemosa*, mangrove, phenotypic plasticity, white mangrove, zonation

Acknowledgments

My gratitude is immeasurable, as this work would not have been possible without the following people:

- My incredible team of field technicians—Kendon James, Amonie Holas, Shawn Allard, and Myles Romain—who endured mangrove mud and worse for this data;
- My colleagues at Gaea Conservation Network—Dr. Jody Daniel and Wayne Smart—who provided guidance, help with logistics, and much-needed pep talks throughout the last three years;
- My advisor Dr. Nicola Koper and my committee—Dr. Gordon Goldsborough, Dr. Gregg Moore, and Dr. John Markham—whose invaluable feedback improved the contents of this document and its contribution to the body of knowledge;
- And my family, without whose support I may have accomplished nothing at all.

I am also grateful for the following financial support. My degree was funded by the Government of Grenada through the Island Scholarship awarded in 2016, with additional support from the Faculty of Graduate Studies at the University of Manitoba. Funding and technical support for this research was provided by Gaea Conservation Network, through a grant from Environment and Climate Change Canada.

It has been one of the most fulfilling experiences of my life (albeit not without its challenges) to spend the last three years researching something I love somewhere I love, and to leave with a tangible contribution to science, mangrove management, and my home country. Thank you all.

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1 Introduction

1.1 Background and rationale

Mangroves fill a unique ecological niche by creating and supporting a complex ecosystem in the harsh intertidal zone. Mangals (the term for mangrove ecosystems, *sensu* Tomlinson 1986) house a variety of fauna, from resident species to temporary visitors such as juvenile fish and invertebrates (Mumby et al. 2004; Hogarth 2015). Other seasonal visitors include migratory birds, many of which rely on mangals as a stop-over site during migration (Layman et al. 2006; McNair 2008; Sánchez-Arias & Rodríguez 2010).

Like other wetlands, mangals provide a suite of ecological services, from provisioning services like fisheries to supporting services like nutrient cycling (Jennerjahn et al. 2017). The trees and soil are estimated to store up to five times as much carbon as other forest types, making them critical global carbon sinks (Twilley et al. 2017). The trees' complex root structures offer significant protection for coastal communities and can reduce loss of life from storms and tsunamis; *Rhizophora* mangroves were experimentally found to attenuate up to 80% of wave energy, reducing wave height regardless of the arrangement of the trees (Hashim & Catherine 2013). Mangals are also socioeconomically important, as they are heavily relied on by surrounding communities for their livelihoods, through charcoal production, fishing, and hunting (Hudson 1997; Biswas et al. 2009; Huxham et al. 2017).

However, the extent of mangals worldwide is decreasing due to unsustainable harvesting of mangrove wood for construction or charcoal, deforestation for development or aquaculture, pollution, and natural disasters (FAO 2007; United Nations 2016). The total extent is estimated at 15.2 million hectares (152,000 km^2) with an approximate loss of almost 1% per year (FAO 2007; Spalding et al. 2010). Climate change is also an increasingly important threat with its associated changes in sea level, air and sea surface temperatures, and weather conditions, which can encroach on available habitat, alter the hydrology of coastal sites, and result in environmental conditions exceeding mangrove tolerance ranges (Jennerjahn et al. 2017). Mangals worldwide are expected to decline in extent and complexity, even as temperature increases facilitate their poleward range expansion (Alongi 2015; Jennerjahn et al. 2017); however, as the biogeography and ecological requirements of many mangrove species are not fully understood, the extent and nature of the potential threats from climate change are yet unknown.

To combat mangal degradation and loss, mangrove restoration has been attempted in several countries with varying levels of success; Lewis (2001) provides a review of restoration projects before the turn of the century, and more recent reviews and case studies are available. Globally, a recognized limitation of success is the potential mismatch between the species planted and the environmental conditions, particularly the hydrology (water conditions) and edaphology (soil conditions) of the mangal (Van Loon et al. 2016; Kodikara et al. 2017); for instance, species may be planted at elevations too low or in soils too saline for their biological needs. In Grenada, my focal country, most restoration efforts have been led by the Grenada Fund for Conservation Inc., who exclusively plants red mangrove propagules because of their large size and ease of collection (Moore 2014). The exclusion of the other local mangrove species (white and black) from restoration efforts has resulted in vastly disparate success rates, as the red mangrove is not well suited to the soil and water conditions at every site; restoration in some sites has failed entirely, with no long-term establishment of mangroves (personal observation). Thus, to improve success rates and ensure the recovery of mangals in Grenada, the factors influencing natural zonation within the systems must be investigated.

This study was conceived to fill some of the knowledge gaps that exist around the occurrence and zonation of mangroves in Grenada to inform restoration efforts. This thesis forms part of a larger project by the Gaea Conservation Network funded by Environment and Climate Change Canada to protect and restore migratory bird habitat in Grenada through a baseline study and experimental mangrove restoration. The first phase of the project (which lasted ~1.5 years) collected baseline data on the natural soil and water conditions of several mangals, and the second phase (also 1.5 years, to conclude later in 2022) involves practical application of these data to design and test a new mangrove restoration protocol suited to the local conditions of each site. My thesis has focused on the white mangrove—a recognized pioneer species with a rapid growth rate—and attempted to fill the sizeable knowledge gap that exists on the autecology and distribution of this species. If the results support my preliminary observations that white mangroves are phenotypically plastic and can occupy a wider range of conditions than the other species of mangroves, this might contribute significantly to the success rates of mangrove restoration in the Caribbean.

The white mangrove (*Laguncularia racemosa* [L]. Gaertn. f.) is the one of the most widely distributed species in the Atlantic, Caribbean, and Eastern Pacific (ACEP) region, alongside the red and black mangroves (*Rhizophora mangle* and *Avicennia germinans,* respectively). White mangroves are typically classed as a “back mangal” species, existing on the landward fringes of any mangrove forest (Tomlinson 1980). However, in Grenada they have been observed expressing significant phenotypic plasticity and occupying various positions throughout the mangal (personal observation). Thus, many questions remain about the plasticity of the white mangrove and its ability to occupy other positions within the mangal.

The mangal is characterized by its anaerobic soils, tidal influence, and high and inconstant salinity (Hogarth 1999), and each species of mangrove has adapted unique ways to survive in these conditions. For white mangroves, these adaptations are facultative (Tomlinson 1986), being expressed only when needed in conditions of greater water depth and/or salinity. They include salt secretion from epidermal glands, leaf succulence, decreases in leaf size, increases in xylem frequency, and the development of aerial roots like pneumatophores (Tomlinson 1986; Sobrado 2004; Parida & Jha 2010; Hogarth 2015; Jantsch et al. 2018). Thus, a white mangrove living in well-aerated, non-saline soils in the back mangal may look significantly different than a white mangrove living in waterlogged, saline soils in another zone of the mangal (Fig. 1).

Figure 1: Two possible growth forms of the white mangrove: A) dense shrub in saline tidal conditions, and B) tall tree (comparable in height to a coconut tree) in non-saline conditions. C) shows the same shrub as A) through a gap in the surrounding vegetation, which are also white mangroves.

This plasticity also affects the zonation of the mangrove community. Zonation is a complex phenomenon influenced by species-specific characteristics, interspecific interactions, and abiotic gradients (Tomlinson 1986; Ye & Cao 2008). The key environmental factors include hydrology, elevation, substrate type, nutrient availability, and salinity

(Tomlinson 1986). Disturbances, such as hurricanes and pollution, have also been known to disrupt community zonation, sometimes favouring pioneer species such as the white mangrove (Hogarth 1999; Piou et al. 2006; Fickert & Grüninger 2010). Because of these interacting factors, the community often exists as a “mosaic” with no distinct bands or transitions from one species to the next (Tomlinson 1986 p. 16) and white mangroves are often mixed in among the other two species, exhibiting their facultative features in these zones. This ability to survive and thrive in multiple zones of the mangal may have positive implications for the use of white mangroves for mangrove restoration.

1.2 Purpose and objectives

The purpose of this study was to elucidate the key factors influencing the occurrence and zonation of white mangroves within mangals in Grenada, with the aim of improving restoration success rates through more appropriate species selection.

Objectives:

1. To identify any differences in white mangrove occurrence and the overall community composition and structure of two mangals in Grenada, one fringe forest and one basin forest
2. To document the plasticity of white mangroves (growth form, leaf size, salt secretion, and the expression of facultative aerial roots) in as many mangals as possible
3. To relate the above observations of plasticity and aerial root expression with environmental conditions like elevation, salinity, soil nutrient content, and porewater pH and redox potential
4. To seek ways to apply these findings on the autecology of white mangroves to improve restoration efforts in Grenada and the wider Caribbean

2 Literature Review

2.1 Mangroves in the Caribbean

There exist between 70 and 75 species of true mangroves worldwide, depending on the definition of a “true mangrove” and the treatment of subspecies and hybrids (FAO 2007; Spalding et al. 2010). Of these, twelve species are found in the ACEP region, within the main families Avicenniaceae, Combretaceae, Pellicieraceae, and Rhizophoraceae (Spalding et al. 2010). The family Combretaceae contains only a handful of true mangroves and associates in the ACEP region, including the white mangrove. True mangroves are defined here as those meeting most or all of the conditions outlined by Tomlinson (1986), i.e., fidelity to the mangal, structural significance in the community, and taxonomic isolation from terrestrial relatives. By this distinction, *Laguncularia* is the only genus of true mangrove within Combretaceae found in the region, with *Conocarpus* being a mangrove associate (because it lacks fidelity to the mangal and can be found in upland habitats). However, there is still some confusion regarding the number of species within *Laguncularia*, with most sources identifying one (Tomlinson 1980, 1986; FAO 2007; Spalding et al. 2010) while Exell & Stace (1972) and Harris (2004) claim there to be two; the latter sources provide no species names (beyond brief mention of *L. racemosa*) or distinguishing features, and thus are likely outdated overestimates of diversity. I will proceed with the assertion that *Laguncularia* is a monotypic genus comprising only my focal species, the white mangrove.

2.2 Mangroves in Grenada

Grenada is a small island nation (of approximately 350 km^2) in the southern Caribbean comprising three inhabited and several uninhabited islands (the Grenadines). The country has at least three species of true mangroves and two species of mangrove associates: buttonwood (*Conocarpus erectus*) and the mangrove fern (*Acrostichum aureum*). White, red, and black mangroves are all well-documented in the country. However, some accounts identify a fourth species of mangrove that may occur in Grenada: *Avicennia schaueriana*, a closely related species of the black mangrove (FAO 2005, 2007; Spalding et al. 2010). The discrepancy between accounts may be due to this species’ absence, its misidentification in the field as *A. germinans*, or its frequent hybridization with the latter (Tomlinson 1986; Mori et al. 2015). Thus, pending further investigation in the field, I will refer to the three confirmed species of true mangroves: white, red, and black.

The extent of mangal habitat in the country is similarly uncertain. Figures reported by the FAO (2005) range from 190 to 535 ha due to differing sampling methods and scales; methods ranged from aerial photograph to map analysis. Only two studies documented mangal extent on both the main island of Grenada and all its Grenadines: an FAO (2007) estimate from 1992 of 255 ha, and a more recent estimate of 298 ha by Moore et al. (2015), obtained via both remote mapping and extensive ground-truthing. Of these 298 ha, 181 ha are located on the largest island of Grenada across approximately 30 sites.

2.3 White mangroves

The white mangrove is characterized by its small green ribbed fruit, rounded leaves, and white flowers (Fig. 2A–B). The trees vary in form (from dwarf plants < 3 m [Piou et al. 2006; Reef et al. 2010] to trees up to 30 m tall; Fig. 1), and the bark is often fissured and scaly with a grey or orange tint (Tomlinson 1980, 1986; Nelson et al. 2014). Where present, the pneumatophores are “blunt-tipped” and rarely longer than 20 cm (Tomlinson 1986); they are easily distinguished from the pneumatophores of black mangroves as they are shorter, thicker, and often a lighter orange colour that resembles the tree trunk (personal observation; Fig. 2C–D).

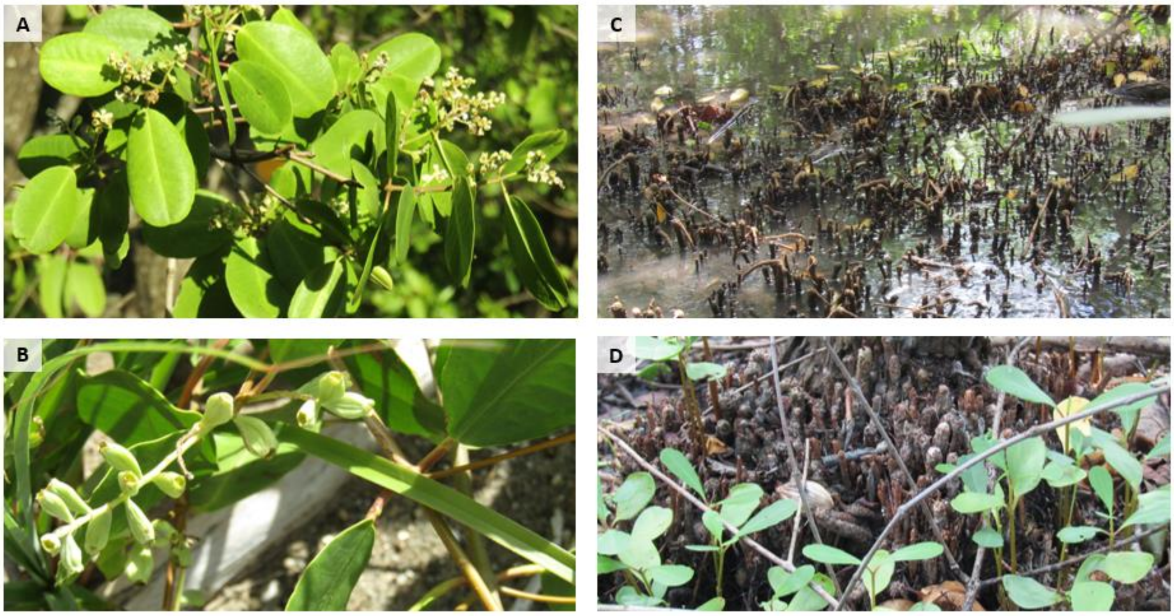

Figure 2: Characteristic features of white mangroves: A) bright green rounded leaves and very small white flowers; B) small, flat, ribbed fruits; and C–D) short, stubby pneumatophores.

Genetic analyses have shown that the physical differences among white mangrove individuals are not necessarily due to true genetic variation within the population. Lira-Medeiros et al. (2010) found that significant differences in tree height and diameter observed in two Brazilian mangals were due instead to epigenetic modifications. Individual trees from both mangals were genetically similar, but their patterns of epigenetic methylation varied greatly, facilitating the expression of different phenotypic characteristics in response to their environment. This is phenotypic plasticity—environmentally induced variability in physical traits (Arrivabene et al. 2014). Epigenetic modification is a recognized mechanism of phenotypic plasticity, and the link between the two is an emergent field of study in several taxa (e.g., insects [Duncan et al. 2022] and fish [Budd et al. 2022]). Epigenetic changes are non-permanent but heritable (Lira-Medeiros et al. 2010) and allow a species to express plasticity and acclimate to site-specific conditions without altering or compromising the population's genome, allowing the population to remain adaptable and resilient to an ever-changing environment. Thus, even within a single, closely related population, white mangroves can individually acclimate to their environment through epigenetic modifications, and this ability is likely responsible for their widespread distribution both within the mangal and throughout the ACEP region.

The white mangrove has also been found to be genetically similar throughout its range in the Caribbean Sea. Grenadian white mangroves are in the same genetic clade (98–100% bootstrap confidence) as those in Antigua, Aruba, and Puerto Rico, showing unexpected connectivity in the population through seed dispersal (Hodel et al. 2018). Thus, understanding the complex relationships between this species and its environment within Grenadian mangals will inform conservation and management of the species throughout the region.

2.4 The mangal environment and white mangrove adaptations

The mangal environment has unique physicochemical characteristics that shape the species living within. These hydrological and edaphic conditions differ from terrestrial systems, and white mangroves are specially adapted to live in this environment. Morphological adaptations include mechanisms for processing excess salt and aerial root systems for oxygenation.

2.4.1 Hydrological conditions

One of the defining characteristics of a mangal is its tidal influence. Mangroves must cope not only with inundation (resulting in waterlogged soils, [expanded in section 2.4.2]) but also fluctuating water levels and salinity levels. The tides rise and fall about every twelve hours, influencing the water depth conditions in which mangroves must grow (Hogarth 1999; Friess 2017). Some species of mangroves are better adapted to living in deeper water, such as red mangroves whose prop roots offer additional structural support in standing water; white mangroves are expected further inland where there is shallow or no standing water (Hogarth 2015).

Tidal fluxes also influence the salinity of the system, measured in practical salinity units (psu, equivalent to parts per thousand [ppt]; UNESCO 1981). Typical salinity ranges between that of freshwater (0 psu) and seawater (35 psu), and can vary as a result of freshwater input from rain or streams, evaporation due to high temperatures, or physical barriers that can impede free water flow between the mangal and the sea (Hogarth 1999, 2015). Thus, mangroves must deal both with higher salinities than terrestrial plants and regular fluctuations in salinity.

In some cases, mangroves may limit their energy expended in processing saline water by accessing alternative water sources, such as groundwater or rainfall (Hogarth 2015). Mangrove trees are able to access and use both saltwater and freshwater (Sternberg & Swart 1987), and thus, mangrove species may employ different strategies to deal with and/or circumvent the saline conditions in which they grow. The water sources used by individual trees can be investigated using stable isotope analysis (Sternberg & Swart 1987), which have been conducted in Grenada (Gaea Conservation Network, unpublished data) but were outside the scope of this study.

The ability to tolerate salt is a necessity that facilitates life in the mangal. All species of true mangrove have developed some form of salt tolerance mechanism—whether exclusion, accumulation, and/or secretion—and white mangroves are classified as ‘salt secreters’ (Tomlinson 1986; Parida & Jha 2010; Hogarth 2015).

Salt tolerance mechanisms

A “secreter” is one that allows the uptake of salt at the roots and then accumulates and excretes it at the leaves (Tomlinson 1986; Hogarth 1999, 2015; Parida & Jha 2010). White mangroves have prominent petiolar glands, analogous in structure to salt glands, but there is no direct evidence of this function. Tomlinson (1986) posited that these petiolar glands are nectaries, secreting a sugary rather than salty solution, while others have found these glands are vestigial structures and secrete nothing at all (Kemis & Lersten 1984; Parida & Jha 2010). However, it is possible that salt is secreted from epidermal cells on the leaf itself, from microscopic pits or depressions in the surface (Tomlinson 1986; Nelson et al. 2014), and studies have found salt secretion in white mangroves to be facultative and increase as the environmental salinity increases (Sobrado 2004).

Leaf structure

In saline conditions, white mangroves may also demonstrate some degree of leaf succulence, measured as the mass of water per unit leaf area. This translates into variable leaf thickness depending on salinity, where higher salinity conditions result in thicker leaves. Several studies have found significant differences in leaf water content between trees grown under differing salinities, both in mensurative and experimental designs (Sobrado 2004, 2005, 2007; Arrivabene et al. 2014). Thus, leaf thickness can be directly correlated with environmental salinity.

Other leaf characteristics have also been observed to change with salinity. Leaves were significantly smaller in more saline conditions, and also had fewer and less dense stomata on both leaf surfaces (Sobrado 2007; Lira-Medeiros et al. 2010). Notable increases in the density of salt glands on the leaf surface were also observed, supporting earlier findings that salt secretion in white mangroves is facultative (Sobrado 2007). The correlations between environmental salinity and leaf structure is so strong that Arrivabene et al. (2014) have suggested white mangroves as a suitable bioindicator species of environmental conditions.

2.4.2 Edaphic conditions

Periodic inundation causes mangal soils to differ from terrestrial forest soils in several ways. Mangal soils are saline and waterlogged, with chemical properties tending to be reductive due to the lack of oxygen in the soil. This typically results in a distinctive sulphide odour (from the reduction of sulphates to sulphide) and a black or dark grey hue (Hogarth 1999, 2015; Hossain & Nuruddin 2016). The reductive conditions also affect important biochemical processes like the nitrogen cycle, and by extension, the availability of other nutrients, like iron and phosphorous, in the sediment (Reef et al. 2010; Hossain & Nuruddin 2016). The topsoil may remain aerated, resulting in a transition zone between the well-aerated topsoil and anaerobic subsoil called the Redox Potential Discontinuity layer; the depth of this transition will vary based on inundation and oxygenation of the sediment (Gerwing et al. 2015).

Living in these low-oxygen and highly reductive conditions, mangrove trees face the challenge of absorbing oxygen from soils where oxygen is scarce or absent. Most true mangrove species have developed some form of aerial root—with lenticels and aerenchyma for oxygenation—though these roots may not always be expressed (Tomlinson 1986; Hogarth 2015).

Root structure

Aerial roots for oxygenation are developed in addition to absorptive roots for nutrient and water uptake (Tomlinson 1986; Hogarth 2015). The two main types of aerial roots are pneumatophores, negatively geotropic vertical roots that emerge from shallow cable roots and are most common in mudflat-occupying *Avicennia* mangroves (Hogarth 2015), and adventitious roots, structural and aerating prop roots that radiate from the stem and are most associated with *Rhizophora* mangroves (Steffens & Rasmussen 2016). Even in species characterized by their aerial roots, such as the black mangrove, the presence of these roots depends on environmental conditions and the trade-off between the increased capacity for oxygen absorption and the cost of growing and maintaining the pneumatophores (Hogarth 2015). For white mangroves, these root structures are entirely facultative, often absent in the field, and thus excluded from many field guides (such as Nelson et al. 2014). The very development of pneumatophores is a morphological adaptation to the environment, though the triggers are yet unknown (Tomlinson 1986). The presence of white mangrove pneumatophores in mangals in Grenada (Fig. 2C–D) is the most visible expression of the species' phenotypic plasticity and was one of the first observations that prompted this study.

White mangrove roots may also vary when exposed to differing levels of pollution; in Brazil, highly polluted areas were correlated with larger air gaps within absorptive roots and a thicker outer layer on pneumatophores (da Souza et al. 2014). Thus, white mangroves are a suitable bioindicator species for both natural and anthropogenic environmental conditions.

Other morphoanatomical adaptations

The xylem and wood of white mangroves may also differ based on the conditions in which a particular tree is growing. As xylem are directly responsible for water transport in any plant, their frequency and size are expected to change as the challenges of water uptake increase with salinity. Plants grown in more saline conditions have much more abundant xylem vessels but differing xylem widths, as the relationship between salinity and vessel size is a trade-off between efficient conductivity and protection against rupture (Sobrado 2007; Jantsch et al. 2018). These variations are also reflected in the overall size and stature of the plant. White mangroves grown in low salinity conditions like a riverside can be several times taller than those grown in saline conditions like a salt marsh, and have significantly larger trunks as well (Lira-Medeiros et al. 2010).

For white mangroves, the structure of the leaves, roots, and stems are all plastic and can vary significantly with the hydrological and edaphic conditions. These features are thus all suitable as measures of environmental variation, making the species a useful bioindicator (Arrivabene et al. 2014; da Souza et al. 2014).

2.5 Zonation and its determinants

A species' location within its environment influences the degree to which its biological needs are met. Within communities, where several species coexist, niche specialization and relative tolerance ranges may interact to determine which species are found in which zones (DiMichele et al. 2017). During restoration efforts, this natural zonation should then inform which species are planted in which areas, to maximize their survival and most appropriately restore the structure and function of the ecosystem.

Zonation may be defined as a predictable pattern of species organization at a location, often parallel to the shore from the seaward edge inland (Ellison et al. 2000). It can be divided into species zonation, which refers to bands composed of a single species or a few associated species, and structural zonation, which refers to bands of trees differing in height, thickness, or density. Thus, even within a monospecific forest, there may be structural zonation where the trees along the seaward fringe are dwarves and increase in height and diameter with distance from the shore (Piou et al. 2006).

Like most forests, mangal communities may exhibit clear zonation. In the Caribbean, a common representation shows monospecific bands of red mangroves along the seaward fringe, black mangroves in back intertidal zone, and white mangroves furthest inland where it is mostly dry (Piou et al. 2006; Hogarth 2015; Friess 2017). However, reality often deviates from this simple zonation, resulting in a "mosaic" of multiple species at different positions within the mangal (Tomlinson 1986 p. 16).

The factors influencing zonation within a mangal may be separated into biotic and abiotic factors (Tomlinson 1986) or inherent and environmental factors (Ye & Cao 2008), respectively.

2.5.1 Inherent factors

Species-specific factors such as propagule dispersal and growth requirements may be initial determinants of zonation. Rabinowitz's Tidal Sorting Hypothesis (1978) suggests that zonation is due to the dispersal ability of mangrove propagules relative to their size: smaller propagules will be carried further inland by the tides and establish higher in the mangal, while larger propagules will be deposited and become established closer to the shore (Sousa et al. 2007). However, indiscriminate tidal deposition of propagules along the shore suggests that post-settlement factors may be more important in determining which propagules persist where they are stranded (Sousa et al. 2007). Once settled, seedlings of the different species may survive at different rates. White mangroves are shade-intolerant, but have a much faster growth rate than the other two mangrove species, so once established in well-lit areas, they can quickly outgrow the other species (Fickert & Grüninger 2010).

2.5.2 Environmental factors

Competition is an important factor in determining adult zonation in habitats where all species could potentially grow. In addition to interspecific competition among true mangrove species (Ball 1980), mangrove associates like the mangrove fern may also compete for space in well-lit areas and limit the growth of mangrove seedlings (Hogarth 1999).

Another biotic factor affecting establishment is herbivory on mangrove seedlings. Within the mangal community, only a handful of animals feed on mangrove leaves, foremost amongst which are crabs. In the Caribbean, the mangrove root crab *Goniopsis cruentata* may significantly affect the composition and zonation within a mangal through its herbivory on seedlings (Hogarth 1999; University of the West Indies 2013), and can deter mangrove restoration attempts by burying planted red mangrove propagules to access the leaves at the top (personal observation).

The physicochemical parameters of the environment—i.e., hydrological and edaphic factors like inundation, salinity, and nutrients—are suspected to be the greatest determinants of mangal zonation. Species have been shown to exist along several environmental gradients, which may be confounded by local factors. Salinity is perhaps the most important gradient, but the direction of the gradient depends on whether there is freshwater input to the system. Where there is a source of freshwater flowing into the mangal, the salinity will increase from inland (~0 psu) and be highest at the shore (~35 psu), but where there is no input, salinity may be highest inland due to evaporation (hypersaline conditions >35 psu) and decrease towards the shore (~35 psu) (Hogarth 2015). Thus, the most ‘salt-tolerant’ species may be found at either the seaward or landward zone (or both) of the ecosystem depending on its hydrology. However, salt tolerance is relative, and experimental studies have found that most species thrive at low salinities and differ only in their tolerance ranges (Hogarth 1999, 2015). These relative tolerance ranges for high salinity and fluctuations thereof will influence which species are found in which zones (Hossain & Nuruddin 2016).

Salinity is also related to hydroperiod, though the two may not always covary. Hydroperiod refers to the duration and frequency of inundation by tides, and different mangrove species are adapted, via their aerial root systems, to different levels of tidal inundation (separated into inundation classes per Watson 1928; Friess 2017). Red mangroves, which possess taller sturdier prop roots, are likely to be found at deeper inundation classes while white and black mangroves, which have shorter pneumatophores, may be better suited to zones with shallower and shorter tides (Hogarth 1999, 2015; Tomlinson 1986).

The physical features of the land such as topography may create zones that differ in elevation, soil stability, and runoff (Ellison et al. 2000). Elevation may also affect the hydroperiod as steeper inclines would limit the tidal range and perhaps result in more distinct bands of vegetation, whereas gentler inclines would result in greater tidal ranges and similar water depths over a larger area.

Other edaphic factors include the substrate type, particle size, and availability of nutrients (Hossain & Nuruddin 2016); higher density sandy soils tend to be better aerated than low-density clayey soils, and the latter tend to be richer in organic matter (Brown & Wherrett 2021). The reductive conditions in mangal soil also change the availability of key nutrients like nitrogen and phosphorous (Reef et al. 2010; Hossain & Nuruddin 2016), differentially affecting species with different nutrient requirements. Lastly, the depth of the Redox Potential Discontinuity (RPD; the depth at which there is a change from the aerobic topsoil to the anaerobic subsoil) will limit the growth of certain species, especially those unable to produce aerial roots (Tomlinson 1986), thus influencing species composition and zonation.

2.5.3 Disturbance and community composition

Zonation is further complicated by local disturbances. Many studies have shown that chronic disturbances like pollution can cause long-term degradation of mangal ecosystems. Oil spills, for instance, have immediate effects such as aerial root damage, but chemical persistence in the soils can reduce seedling survival and establishment for years to follow (Hogarth 1999); in extreme cases, pollution can result in an ecological regime shift where the mangal is converted to a completely different ecosystem, like mudflats or herbaceous coastal vegetation (De Lacerda et al. 1982; Tomlinson 1986; Osland et al. 2020). However, the effects of such disturbances will differ by species. da Souza et al. (2014) found that white mangroves can not only survive in but acclimate to high concentrations of pollutants like cadmium, mercury, and lead, and the physiological response of this species to pollution is an emergent field within toxicology (e.g., Sodré et al. 2013; Guedes et al. 2018). Thus, white mangroves may persist where other species have been damaged or removed by pollution—for instance, by altering their root morphology (da Souza et al. 2014)—and disrupt the expected species composition and zonation of the mangal.

Episodic disturbances like hurricanes also have a significant effect on community composition, as mangroves are geographically limited to the storm-prone tropics. While ecological regime shifts may occur following particularly destructive storms (e.g., Osland et al. 2020), mangrove forests often persist, albeit with different species and structural composition than before. The effect of storms is two-fold: species are selectively destroyed due to different resistance levels, and are unequally repropagated due to different colonization abilities (Hogarth 1999). The literature on mangrove resistance to hurricanes is varied and somewhat contradictory, but several factors suggest that red mangroves (especially dwarf trees low to the ground with dense root systems) may be most resistant to storm damage (Smith 1992; Hogarth 1999; Piou et al. 2006). Post-hurricane, white mangroves tend to recolonize most quickly, both due to seedling dispersal and vegetative regeneration; mangrove species generally have limited regenerative capacity but white mangroves may "coppice" and re-sprout from reserve meristems following damage within a certain threshold (Tomlinson 1986; Piou et al. 2006). White mangrove seedlings are also very efficient at filling in the gaps created by selective removal of trees, as they are fast-growing but shade-intolerant (Hogarth 1999); this is why Tomlinson (1986) classes the white mangrove as a pioneer species. Thus, red mangroves are most likely to survive a hurricane and white mangroves are most likely to recolonize after one, possibly resulting in shifts in the community composition.

Hurricanes have an effect not only on species zonation, but structural zonation as well. Where there has been widespread destruction, new trees grow in with fairly uniform structure, as they are equally aged (Fickert & Grüninger 2010). Furthermore, dwarf trees are more likely to survive a disturbance as they are closer to the ground and less susceptible to wind than taller trees. Hurricanes effectively "select for" smaller trees, and hurricane-prone areas have a shorter, more uniform mangrove forests than elsewhere (Hogarth 1999; Piou et al. 2006). Thus, structural homogeneity may be both a result of and a safeguard against disturbances like hurricanes.

In 2004 and 2005, Hurricanes Ivan and Emily respectively caused extensive damage to mangals across Grenada. Several sites experienced damage to vegetation, hydrological disruption, and/or deposition of anthropogenic debris (hurricane-mediated deposition could not be differentiated from prior intentional dumping; Layman et. al 2006; personal observation); Layman et al. (2006) provide a rapid post-hurricane assessment of 25 major mangrove sites throughout the country. Natural recovery rates varied among sites, and the Grenada Fund for Conservation Inc. began its formative work as an attempt to aid the recovery of the most severely damaged sites. Moore et al. (2015) note that mangrove extent and distribution may have been significantly altered by the abovementioned and previous hurricanes, and as historical records for the country are lacking, it is near impossible to know the historical community composition and zonation or how these may have changed in response to the disturbances.

2.6 Seedling growth

While adult zonation is relatively easy to observe, it provides only a partial picture of the myriad factors that influence a tree throughout its lifetime (Hogarth 2015). Despite indiscriminate propagule deposition along the shore, species still exhibit zonation as adults, suggesting that processes like competitive exclusion and niche specialization are at play (DiMichele et al. 2017). In the absence of these processes, it is possible that white mangroves could thrive within any zone of the mangal, as their phenotypic plasticity allows them to acclimate to a range of hydrological and edaphic conditions.

Several growth experiments have found evidence that white mangroves can grow outside of their expected back mangal zone. White mangrove seedlings were found to be as, if not more, tolerant of periodic flooding as red and black mangrove seedlings, even exhibiting faster growth and pneumatophore development under longer flood periods (Krauss et al. 2006). This is in contrast to expected results based on the white mangrove’s classification as a back mangal species affected only by a few extreme tides per month (Tomlinson 1980; Hogarth 2015; Friess 2017); the white mangrove may be more capable of growing in deep-water zones than most literature suggests. Another study found that white mangrove seedlings were able to acclimate over time to high salinity conditions, and did so more effectively when the salinity was increased slowly (Bompy et al. 2014); thus, the species is capable of growing and thriving in the more saline mangal zones, provided that the seedlings have sufficient time to adjust to their environment. It appears, therefore, that the general limitation of the white mangrove to the back mangal is due not to a physiological inability to grow in the other zones, but to other factors such as competition.

The less competitive white mangrove is likely excluded by the other species. As a pioneer species, white mangroves are outcompeted over time and replaced by the more competitive red mangroves (Ball 1980). Thus, the presence of white mangroves at any position within the mangal may be limited by interspecific competition, and in early successional forests this species may be found growing outside of its expected zone.

2.7 Implications for restoration

Restoration is defined most simply as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (Gann et al. 2019 p. S7). It requires knowledge and understanding of the ecological relationships that existed within a degraded ecosystem to inform the most appropriate ways to recreate those relationships. Mangals, as inherently complex ecosystems, comprise many biotic and physicochemical components that must be understood in relation to each other before any restoration project is attempted.

Globally, a recognized limitation of mangrove restoration is the mismatch between the species planted and the mangal's hydrology and edaphology (Van Loon et al. 2016; Kodikara et al. 2017), as species for planting are often chosen out of convenience rather than ecological appropriateness. A review of mangrove restoration efforts in Sri Lanka (Kodikara et al. 2017) found that the disparate survival rates of planted mangroves were correlated with inappropriate planting conditions—including hydrology, edaphology, topography, and disturbance—where species were planted at elevations too high or too low to allow proper tidal inundation, and subsequently suffered from disturbances related to their positioning (e.g., trampling by livestock or entanglement with algae). The majority of seedlings planted in Sri Lanka were *Rhizophora* spp., which represents only a small percentage of the available seedling stock (Kodikara et al. 2017), and this undoubtedly contributed to the low success rates observed there. Similar failures have been observed at some sites in Grenada where only red mangroves have been planted to date (Grenada Fund for Conservation, unpublished reports). This monospecific approach limits the success of restoration attempts because no one species can be perfectly suited to the full range of environmental conditions throughout a restoration site.

Major questions remain in the field of mangrove restoration regarding whether mangroves should be planted at all, as R.R. Lewis, often considered the 'father of mangrove restoration', promotes the restoration of environmental conditions to allow natural recolonization of mangroves, with manual planting done only as a last resort (Lewis 2009). However, where mangroves are to be planted, Lewis considers the hydrology of the system to be the "single most important" consideration (2001 p. 9); arguably, edaphology is equally important as the two factors are interrelated and cannot be considered in isolation.

The steps required for successful mangrove restoration (Lewis & Marshall 1997; Lewis & Streever 2000; Lewis 2001, 2009) include:

1. Understand the autecology of each mangrove species
2. Understand the hydrology (and edaphology) of the system
3. Determine what is preventing natural recovery or succession of the system
4. Restore the hydrology (and edaphology) and allow natural recruitment
5. Plant mangroves (only if necessary)

Past failures in Grenada stem from the very first step of the above process, as there are significant knowledge gaps around the autecology of Caribbean mangrove species. Furthermore, studies on the local conditions within mangals are lacking, which limits the application of site-appropriate restoration measures. Restoration must be informed by the general hydrology and edaphology of mangal ecosystems, the local conditions, the local species, and their specific zonation requirements. In Grenada, much of this knowledge is non-existent, and this study aims to fill part of the knowledge gap on the autecology and zonation of the white mangrove species to facilitate restoration on the island.

2.7.1 Contributions to mangrove restoration

Understanding where and why white mangroves grow is expected to improve restoration in the following ways. Firstly, it will allow for the diversification of the plant stock used in restoration; mangrove restoration success in Grenada is currently limited by the exclusive use of red mangrove propagules, which are preferred because their large size facilitates easy collection and they are simple to propagate and plant (Moore 2014). Including white mangrove seedlings will increase the likelihood that the species planted will match the environmental conditions, and will likely improve survival rates. White mangroves also have a much faster growth rate than the other species once established, and can more quickly recolonize an area and stabilize the soil after a disturbance (Ball 1980; Fickert & Grüninger 2010). Secondly, understanding and applying white mangrove autecology will increase the cost-effectiveness of restoration projects, an incredibly important consideration as there are limited funds for projects of this nature (Lewis 2001); higher survival and success rates will translate to greater value derived from each dollar spent on mangrove restoration. Lastly, as future environmental conditions are uncertain due to anthropogenic climate change, white mangroves can provide more flexible options for restored mangal communities. Climate change-induced sea level rise will reduce the land available for mangroves along the coast and/or significantly alter the water table and hydroperiod within surviving mangals (Jennerjahn et al. 2017); the phenotypic plasticity of the white mangrove may allow it to survive in these changing conditions where more specialized species may suffer. Considering this, the white mangrove may be the most appropriate species to plant when restoring for resilience, i.e., in anticipation of uncertain future conditions (Suding 2011; Crow 2012).

3 Manuscript: The plasticity of white mangroves (*Laguncularia racemosa*) in Grenada, West Indies contributes to zonation literature and restoration planning

3.1 Introduction

Mangrove community structure and zonation may be determined by a number of biotic and abiotic factors (Tomlinson 1986; Ye & Cao 2008). Disparate settlement and establishment rates of mangrove propagules (Sousa et al. 2007; Fickert & Grüninger 2010), preferential herbivory by mangal inhabitants like crabs (Hogarth 1999), and species-specific tolerances to environmental gradients of salinity, hydroperiod, and elevation (Tomlinson 1986; Ellison et al. 2000; Hogarth 2015) may all contribute to the distribution of mangrove species within a mangal. Furthermore, unequal responses to both chronic disturbances like pollution (da Souza et al. 2014) and episodic disturbances like hurricanes (Piou et al. 2006) can shift zonation in favour of the most resilient species. In Grenada, the white mangrove (*Laguncularia racemosa* [L]. Gaertn. f.) has been observed occupying various positions throughout the mangal, despite its classification as a "back mangal" species (Tomlinson 1980) expected to be found inland of the red and black mangroves (*Rhizophora mangle* and *Avicennia germinans*, respectively). White mangroves are suspected to have a high degree of phenotypic plasticity, as evidenced by their diverse growth forms and morphological features in different areas of the mangal (personal observation). This suggests that intraspecific variation, in the form of trait plasticity, may also be a contributor to zonation. Thus, zonation within the mangal is likely a complex interplay of environmental gradients, species' tolerances, interspecific competition, and possibly intraspecific plasticity, resulting in forest "mosaics" that may deviate from the expected patterns (Tomlinson 1986 p. 16).

Phenotypic plasticity can be defined as any variability in physical characteristics or traits that is "environmentally induced", or broadly, the potential for variability under different environmental conditions (Richards et al. 2006; Arrivabene et al. 2014). Thus, plasticity is a response to environmental heterogeneity across spatial scales, e.g., within intertidal environments (Hays 2007), and temporal scales, e.g., under changing climatic conditions (Nicotra et al. 2010), in both cases contributing to the resilience of the species exhibiting trait plasticity (Budd et al. 2022). Phenotypic plasticity also contributes to ecological niche breadth, i.e., the range of resources that are usable or conditions that are tolerable by a species, as phenotypic plasticity allows individuals to acclimate to and exploit heterogenous environments (Richards et al. 2006; Sexton et al. 2017). A species with a high degree of trait plasticity, like the white mangrove, may therefore occupy a wider ecological niche than less plastic or more specialized species.

Few, if any, studies have yet made an explicit link between plasticity and zonation. If community zonation is a compromise of species' tolerances or niches (Hogarth 2015), and if plasticity contributes to niche expansion (Richards et al. 2006; Sexton et al. 2017), it follows then that plasticity may confer a species the ability to occupy multiple zones within an ecosystem or community. For instance, in mangrove forests in Kenya, *Avicennia marina* was found to have a bimodal zonation along both the seaward and landward fringes of the forest, and importantly, to exhibit significant plasticity in morphological traits and vegetation structure between the two zones (Dahdouh-Guebas et al. 2004). Although described in the literature as a landward-fringe (or back mangal) species, *A. marina* was not only present but thriving in the seaward zone outside of where it was expected (Dahdouh-Guebas et al. 2004), similar to the observations of white mangroves in Grenada. Thus, the white mangrove's defiance of expected zonation patterns may be attributed, at least in part, to the phenotypic plasticity of several traits, allowing it to be widely distributed throughout the mangal.

Mangrove trees of the same species can vary in morphological traits such as tree height, leaf size, and root form, and plasticity in these traits has been documented in several species (e.g., Dahdouh-Guebas et al. 2004, Lira-Medeiros et al. 2010, Arrivabene et al. 2014). White mangrove height and size are subject to salinity gradients, with taller and larger trees observed in low salinity conditions, such as riverine forests, compared to more saline sites (Lira-Medeiros et al. 2010). As these two parameters vary, the ratio of tree height to diameter at breast height, known as slenderness, may likewise vary; slenderness is a metric of tree stability, with slenderer trees (higher ratios) being more susceptible to wind damage (Wonn 1998; Pommerening 2007). While this relationship is well-documented for coniferous trees and has not yet been proven for mangroves, post-hurricane findings from Belize, Martinique, and Guadeloupe suggest that taller and/or slenderer mangroves did sustain greater damage from the storms (Piou et al. 2006; Imbert 2018). This phenomenon may also contribute to structural zonation, wherein smaller, dwarf trees are often found at the seaward edge of a mangal where they experience the greatest exposure to strong winds, and tree height and size increase toward the landward edge (Piou et al. 2006).

White mangrove leaf characteristics also change with environmental conditions, particularly salinity. Leaves can be significantly smaller (Lira-Medeiros et al. 2010) and more succulent (Sobrado 2005) in saline conditions, and they may also be prompted to secrete salt, at a rate directly linked to soil salinity (Sobrado 2004). Although white mangroves are classed as salt secreters (Tomlinson 1986), secretion is an entirely facultative function, and so its expression can be used as a metric of environmental salinity. Interestingly, white mangroves do not secrete from their petiolar glands analogous to salt glands in other species but rather from the epidermal surface of the leaf (Tomlinson 1986; Parida & Jha 2010).

Lastly, mangroves may express plasticity in root form, by facultatively producing aerial roots to aid in oxygenation during tidal inundation (Tomlinson 1986). The two main types of aerial roots are pneumatophores—negatively geotropic vertical roots that emerge from shallow cable roots and are most common in mudflat-occupying *Avicennia* mangroves (Hogarth 2015)—and adventitious roots—structural and aerating prop roots that radiate from the stem and are most associated with *Rhizophora* mangroves (Steffens & Rasmussen 2016). White mangroves, although generally described as not possessing any aerial roots, may develop pneumatophores and/or adventitious roots depending on their environmental conditions (Fig. 1); the former has been documented for decades (Tomlinson 1986), but the latter is a relatively new observation and literature suggests that its presence may be considered a sign of hydrologic or other stress (Alongi 2015; Radabaugh et al. 2021).

Figure 1: Aerial roots expression by white mangroves in Grenada: A–B) pneumatophores; and C–D) adventitious roots.

This ability to express phenotypic plasticity and survive in multiple zones of the mangal may have positive implications for the use of white mangroves for mangrove restoration. As mangrove losses worldwide continue due to unsustainable harvesting, deforestation, natural disasters, and climate change (FAO 2007; Jennerjahn et al. 2017), significant restoration is required just to achieve “no-net-loss” of these critical ecosystems (Lewis 2009 p. 787). However, restoration efforts have been limited in their success rates because of inappropriate species selections that are not compatible with the hydrology and/or edaphology of the restoration sites (Van Loon et al. 2016; Kodikara et al. 2017). Efforts in Grenada, led mainly by the Grenada Fund for Conservation, Inc., have had similarly inconsistent success rates because of the organization's sole reliance on red mangroves for restoration (preferred for their ease of collection and propagation; Moore 2014), which are not always suited to the conditions where they are planted. Mangrove restoration planning in Grenada and the wider Caribbean will benefit from a better understanding of the native mangrove species' ecology and the adoption of a multi-species approach.

This study aimed to investigate the occurrence and zonation of white mangroves in mangals in Grenada and identify any relevant links to its environment, to help fill the knowledge gap on the autecology of this species. I also explored the factors influencing the plasticity of tree characteristics—especially tree height and size, slenderness, pneumatophore and adventitious root production, leaf size and thickness, and leaf salt secretion—to identify possible triggers for white mangrove variations. These findings can be applied to inform and improve restoration practices through a better understanding of mangal zonation, natural hydrological and edaphic ranges, and the characteristics of less-employed species like the white mangrove.

I studied this in two forest types on Grenada, one basin forest (Conference) and one fringe forest (Westerhall; Fig. 2). Within the 298 ha of mangrove forest across Grenada and its Grenadines, five mangal types are represented, namely basin, fringe, littoral, scrub, and riverine forests (Lugo & Snedaker 1974; Moore et al. 2015). The dominant mangal type is basin forests (181 ha), followed by fringe forests (65 ha); together, these two forest types compose 83% of the total mangrove extent (Moore et al. 2015). It is important to study these forest types not only because they dominate Grenada's mangrove extent, but also because they are both uniquely vulnerable to climate change. Anticipated climate change effects like sea level rise (Jennerjahn et al. 2017) will encroach upon available fringe habitat and more severe storms may decimate these areas, which were found to be most impacted by previous storms including Hurricanes Ivan and Emily (Moore et al. 2015). Basin mangroves, though generally considered more stable, are also at risk, particularly from storm surges that may alter coastal topography and significantly change the hydrology of the sites (Moore et al. 2015). The forest types likely also differ in physical characteristics (like topography) and ecological characteristics (like species composition), both of which are important to consider for conservation or restoration planning. Thus, understanding the community characteristics of each type of mangal will aid in developing more site-specific management and restoration actions.

I hypothesized that mangal zonation and white mangrove plasticity are influenced by both site-level (i.e., mangal type) and plot-level factors (i.e., edaphology and hydrology). If mangal zonation and species composition are determined by mangal type, then the distribution and prevalence of white mangroves should differ between the basin and fringe forests. If the occurrence of white mangroves outside of the expected back mangal zone is related to the species' plasticity, then more plastic characteristics should be expressed where the species is present outside of this zone. I also tested whether white mangrove plasticity is influenced by environmental characteristics such as location within the mangal (distance from shore, zone, elevation), edaphology (e.g., bulk density, soil oxygenation), and/or hydrology (e.g., salinity, pH).

3.2 Methods

3.2.1 Site description

These data were collected in collaboration with the Gaea Conservation Network in April–July 2020 and 2021. Of the mangrove sites on Grenada (12°06'N, 61°41'W) previously identified and mapped by Moore et al. (2015), two sites were selected along the south- and north-eastern coasts of the island. These sites were selected because of their size (larger than 10 ha), accessibility (can be accessed via minor roads), composition (contain all three mangrove species), and the variability in their species organization (from preliminary surveys).

The two sites are the Conference and Westerhall Bay wetlands, located at approximately 12°09'26"N, 61°36'33"W and 12°01'01"N, 61°42'09"W respectively (Fig. 2). The sites differ in size, shape, mangal type, and level of anthropogenic activity. Conference is the larger of the two sites at 27 ha and has two ponds within the mangal. Conference is separated from the sea by a barrier beach (which has one major gap where the mangal and sea may meet at high tide) and extends several hundred meters inland with a basin-like topography; thus, Conference can be considered a basin forest (per Lugo & Snedaker 1974; Moore et al. 2015). The surrounding land is used for agriculture and the nearest community is sparsely distributed; however, a rum factory has recently been built inland of the mangal. Westerhall is a narrow 14-ha strip of mangal whose inland boundary is a sugarcane plantation; there is a densely populated community to the north, west, and east of the mangal, and it receives effluent from a nearby rum factory. Unlike Conference, Westerhall is a low-elevation mangal with direct connection to the sea along a sheltered shoreline, and can therefore be classified as a fringe forest (per Lugo & Snedaker 1974; Moore et al. 2015). Because of these distinct differences (shown in Fig. 3), Conference and Westerhall are ideal candidates for the comparison of mangal community structure and zonation in Grenada, as basin and fringe forests respectively.

A third site, Mt. Hartman (12°00'27"N, 61°45'00"W), was also surveyed in 2020, but due to leasing of the land and wetlands adjacent to the Mt. Hartman National Park for development in mid-2020, our access to the site was revoked. A helpful overview of the development is provided by BirdsCaribbean (2020) and Buckmire et al. (2022). Thus, Mt. Hartman was not included in any of the 2021 surveys and was removed from the analysis.

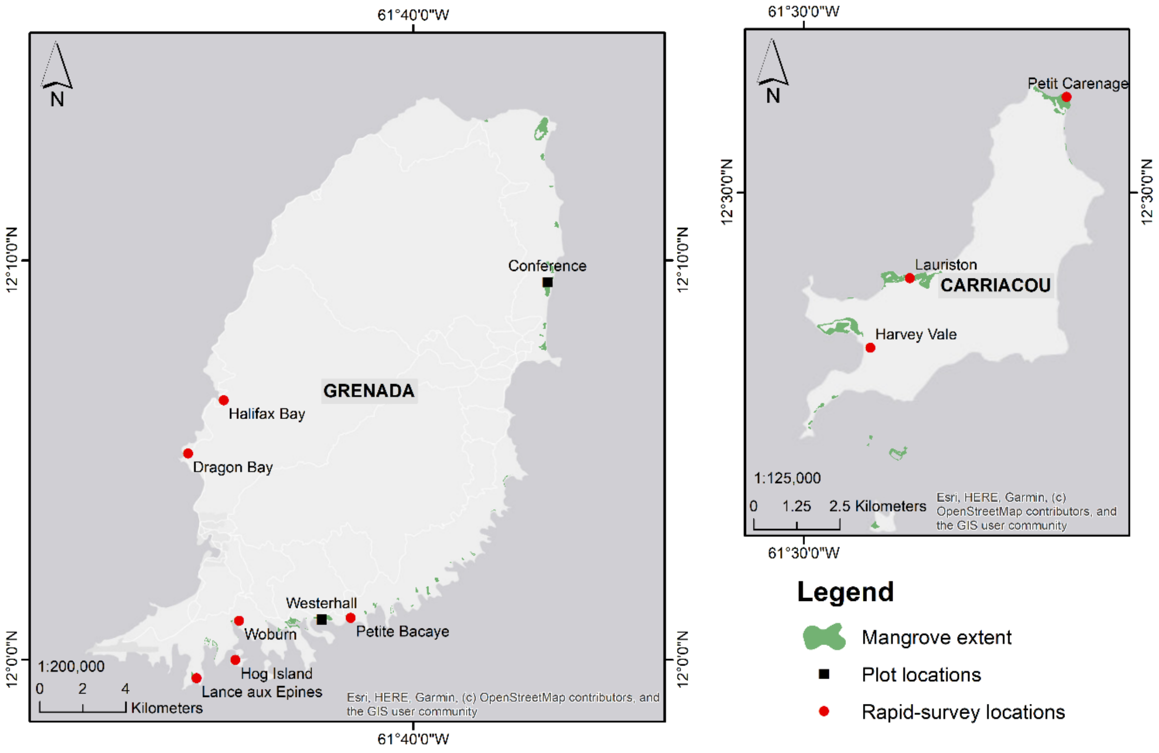

Figure 2: Map of Grenada showing the locations of the two main study sites (in black; Conference the basin forest in the northeast and Westerhall the fringe forest in the southeast) and nine additional rapid-surveyed sites (in red). The main island of Grenada is shown on the left and second largest island Carriacou is on the right. Created with ArcGIS Desktop 10.8.2.

Figure 3: Side-by-side comparison of the two main study sites using aerial imagery (from Gaea Conservation Network). A) Basin forest (Conference) and B) fringe forest (Westerhall).

Data collection was done in April–July of both years during the transition from dry to rainy season. Because the surveys were spread throughout this transition period and we recognized the potential variability of water chemistry, soil chemistry analyses were added in 2021 as a more stable measure of the long-term conditions in the mangal.

3.2.2 Field methods

Community surveys

In 2020, vegetation surveys were done at each of the sites to quantify their species composition. Transects were laid perpendicular to the shore, on a sea-to-land gradient from the shoreline to the inland boundary of the mangal, spaced about 150 m apart. As the sites are shaped differently, the number of transects differed by site; there were two transects at Conference and four at Westerhall. Along each transect, we established equidistant plots of 10 m × 10 m; the distance between plots varied from about 30 m on the shortest transect to 125 m on the longest. Again, because of the dissimilar shapes of the sites, the number of plots at each site differed, with 4 plots per transect at Conference and 3 plots per transect at Westerhall. The plots closest to the sea were designated as the “seaward zone”, those at the inland edge were designated “landward zone”, and the intermediate plots “interior zone”. Equidistant plots were chosen instead of regularly spaced plots to account for the differences in site shape and ensure that the same amount of data were collected along each transect (and for each zone) within each site. A total of 20 plots were established across the two sites at a gradient of distances from the shore (0–365 m).

Relative elevation within each site was determined using water depth measurements at high tide; the depth at both the seaward and landward edge of each plot was measured to construct a relative elevation model and determine the natural tidal boundaries of each mangal. The depth to the apparent Redox Potential Discontinuity layer (aRPD), which is the depth where there is a visible change from the well-aerated topsoil to anaerobic subsoil (Gerwing et al. 2015), was also found by digging until there was a noticeable colour change in the sediment.

We made note of any seedlings within the plot, and their relative abundance by species based on percentage ground cover. We then classed every adult mangrove tree by species and by circumference as measured at breast height (1.5 m) with a measuring tape. The five size classes were 0–3.18 cm, 3.19–7.96 cm, 7.97–31.82 cm, 31.83–63.65 cm, and > 63.65 cm in circumference, corresponding to diameters at breast height (DBH) of 0–10 mm, 10–25 mm, 25–100 mm, 100–200 mm, and >200 mm (World Bank 2019a). These methods were adapted to Grenada's local conditions from established mangrove sampling methods (Cintrón-Molero & Schaeffer-Novelli 1984; World Bank 2019a). The community survey data were used to describe mangal composition and to calculate the Importance Value Index (IVI)—a compositive measure of the relative density, frequency, and basal area of each species—to quantify their structural role in the different zones of the ecosystem.

White mangrove surveys

Based on the data from the 2020 vegetation survey, I selected only plots with white mangroves present for additional surveys. We revisited 6 plots at Conference and 7 at Westerhall. There was some discrepancy between the white mangrove abundances recorded in 2020 and 2021, with some of the revisited plots having more or fewer white mangroves than observed in the previous survey; these differences were likely due to tree mortality, blow-downs, and new growth between the two survey periods. In the plots where these discrepancies were observed, the updated (2021) survey numbers were used for the analysis.

Within each of these plots, we surveyed all adult white mangroves present, visually estimating their height and measuring circumference at breast height with a measuring tape. All trees with a DBH larger than 5 cm (circumference > ~15 cm) were tagged with aluminium tree tags to facilitate future monitoring. We also recorded the overall growth form of each white mangrove (tree or dwarf [i.e., plants with abnormal or stunted growth, generally < 3 m tall; Reef et al. 2010]) and the presence of any aerial roots (pneumatophores or adventitious roots). Three leaves each were retrieved from five randomly selected trees, and their length, width, and thickness were measured using a digital calliper; they were also examined for the presence of visible salt crystals on the leaf surface. Other measures like quantity of salt secreted, leaf mass, and species leaf area could not be obtained as we did not have access to laboratory equipment to process the leaves further. The leaf sample may be slightly skewed as they could not be randomly chosen due to the varying heights of the trees; the team climbed trees to pick leaves from various heights where possible, but there were some plots where no leaves were within reach and the slenderness of the tree precluded climbing.

Additional soil chemistry measurements were taken; we took soil samples between 5 and 15 cm deep from a subset of the plots for processing by the Produce Chemists' Laboratory. The samples were taken using a stratified design, with one per site, per mangal zone, and per treatment (white mangroves present or not); thus, a total of nine samples were taken: five at Conference (*n* = 2 seaward, 2 interior, 1 landward) and four at Westerhall (*n* =

1 seaward, 2 interior, 1 landward). Soil samples were all collected during a two-week period (27 April–8 May 2021) to minimize seasonal variability. The parameters measured were pH, nitrate, phosphate, conductivity, moisture content, organic matter, chloride content (a proxy for salinity with a conversion factor of 1.65[1]), and bulk density of the soil, using various established laboratory methods (Appendix A).

To obtain a larger sample size of white mangrove features around Grenada and extend my inferences on plasticity outside of the two main study sites, we also conducted a rapid survey of white mangroves trees at several additional sites. We measured the same vegetation parameters as above (tree height, DBH, root form, growth form, leaf size, leaf thickness, and salt secretion) and extracted porewater samples from the rhizosphere of select white mangroves at 20–30 cm deep using a porewater sipper. The pH, redox potential, and salinity of these porewater samples was measured in-situ with an Orion 290A+ multimeter and a refractometer respectively, and the soil type was visually classified. The general qualitative soil types were “sand” for large-grained light-coloured sediment, “silt” for medium-grained black/dark sediment, “clay” for very fine reddish brown sediment, and “mix” as appropriate for mixtures of the three above types. We sampled nine additional sites and an average of 3 trees per site. These sites were Halifax Bay, Dragon Bay, Woburn Bay, Lance aux Epines, and Petit Bacaye on Grenada; Lauriston Point, Harvey Vale, and Petit Carenage on Carriacou; and Hog Island (Fig. 2). Calivigny, Marlmount Bay, Long wall, and Levera on Grenada and Tyrrel Bay on Carriacou were also visited, but we were unable to successfully collect data at these sites for a number of reasons (unfavourable weather, difficulty extracting samples due to the density of the sediment, and/or equipment failures in the field).

The white mangrove survey data were used to relate white mangrove plasticity to the environmental conditions within each zone. The additional vegetation and porewater data, which were collected outside of the established plots, were used to identify any correlations between white mangrove plasticity and porewater chemistry.

3.2.3 Data analysis

All statistical analyses were done in R 4.1.1 (R Core Team 2021). I first calculated several derived variables such as the relative elevation (difference in water depth between each plot and the seaward plot in that transect), N:P ratio (ratio of nitrate to phosphate), tree slenderness (ratio of tree height to diameter; Pommerening 2007), basal area ($\pi[DBH^2]/40000$), leaf area ($\pi\left[{}^{Length}/_{2}\right]\left[{}^{Width}/_{2}\right]$), root frequency (% of trees with

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[1] Based on the ratio of molar masses between Cl^- ions and NaCl.

aerial roots in each plot), and Importance Value Index (IVI). The IVI (per Cintrón-Molero & Schaeffer-Novelli 1984) is a measure of the relative importance of different species within a community and is calculated as the sum of the relative density, frequency, and basal area out of a total of 300 (Fickert & Grüninger 2010). I calculated the IVI of each species at several scales: overall, by site, by mangal zone, and by plot within each site. For the IVI calculations for each plot, I used only a sum of relative density and basal area, producing plot-level IVI out of a total of 200.

I compared site-level conditions using two sample *t*-tests (Student's or Welch depending on the ratio of variances) and identified correlations among the environmental variables with Pearson's correlation tests. As several of the soil parameters were strongly correlated, I performed Principal Components Analysis to eliminate multicollinearity and reduce the dimensions of the explanatory variables; this was done using singular-value decomposition with the *prcomp* function in R and the variables were each scaled and centred. The first four principal components captured 95.7% of the variance in these variables and were not correlated with each other, so these axes (principal components) were used in the models for further analyses.

Generalized Linear Mixed Models (GLMMs) were used to account for non-normal data distributions, levels of nesting within the data, and both numerical and categorical explanatory variables. Numerical data were modelled with a *Gaussian* distribution, and binomial and beta distributions were used for binary and proportion variables respectively. All models were produced with the package *glmmTMB* 1.1.2.3 (Brooks et al. 2017) and I used AIC$_c$ (small-sample adjusted Akaike's Information Criterion) for model selection in package *bbmle* 1.0.24 (Bolker & R Development Core Team 2021). Where necessary, I averaged the top models (all within 2 AIC$_c$ units) using the package *MuMIn* 1.44.3 (Barton 2021) and interpreted the full averages (or zero method averages) as recommended by Grueber et al. (2011) to determine the relative strength of the predictors and to avoid biasing the parameters away from zero.

For the established plots, my response variables of interest were tree height, tree size (DBH), slenderness, aerial root presence, aerial root frequency, leaf size (area), and leaf thickness. I first ran preliminary models for each response variable to determine the most appropriate predictor(s) for location: continuous distance, categorical zone, and/or relative elevation. The best location predictor(s) differed for each response variable, so the model suite was tailored to each variable. I also checked for any important interactions between the location variable(s) and site. The model suite for each response variable included a null, site only model, location model, soil model (using the four principal components), and a global model, for a total of 5 models (Appendix B1); all models besides the null included site as a variable. Leaf variable model suites also included vegetation parameters and pairwise combinations of location, vegetation, and soil, for a total of 9 models (Appendix B2). All tree-level and leaf-level variables were nested within plot as a random variable.

In addition to the models, I calculated response variable means and ranges using the full dataset (*n* = 144 trees). This was done to account for the data excluded by the models, as the models were computed using a subset of the data that included both white mangrove and soil sample information (*n* = 6 out of 20 plots). Within these plots (and analysed by the models) were 53 trees, just over one-third of the 144 trees sampled in total. Thus, to account for the data excluded by the models and to provide a more accurate account of white mangrove characteristics, I used the full dataset of 144 trees to calculate summary statistics and identify important correlations to explanatory variables such as depth to aRPD.

These GLMM analyses were repeated for the data collected at additional sites during the rapid survey. These sites lacked plot-level metadata so there were no location predictors. The key response variables here were tree height, tree size, slenderness, aerial root presence, aerial root frequency, leaf size, and leaf thickness. Independent variables included site and environmental parameters (salinity, pH, redox potential, and soil type). The model suites had 5 models for tree-level variables and 9 models for leaf-level variables (Appendix C).

3.3 Results

3.3.1 Site characteristics

The main study sites differed in their physical characteristics. Relative elevation of the inland plots was significantly different between sites (df = 18, $p < 0.001$), averaging -9.5 (± 14.6) cm in the basin mangrove forest and 18.1 (± 14.8) cm in the fringe forest compared to the seaward plot in each transect (Fig. 4). The seaward plots in the fringe forest are at sea level and the mean elevation of the plots increases naturally towards the landward edge; thus, there was a significant positive correlation between distance and relative elevation in the fringe forest ($r(10) = 0.58$, $p = 0.046$). By contrast, the seaward plots in the basin forest are located on an elevated sand bank ~1 m above sea level that is separated from the sea by a strip of sandy beach > 10 m wide; the sand bank itself is at least 15 m wide and gently slopes towards the lower elevation swamp in the interior of the mangal. Because of this topography, the basin mangal had no clear correlation between distance and relative elevation ($r(6) = -0.42$, $p = 0.305$), and the interior plots were lower in elevation than the seaward plots.

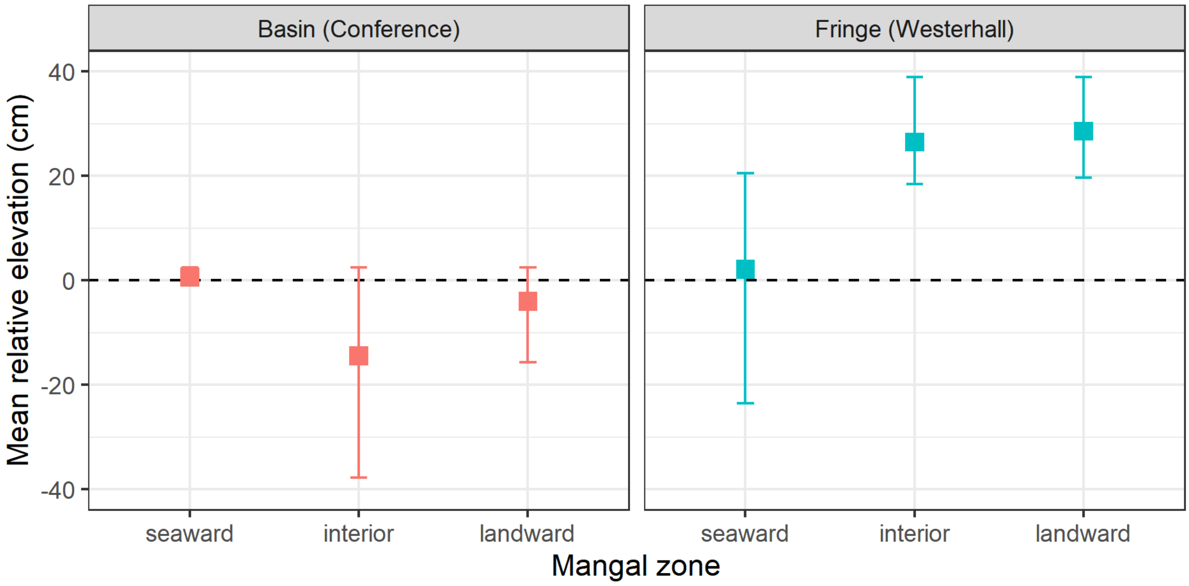

Figure 4: Mean relative elevation recorded within established plots at a basin and fringe mangrove forest on Grenada, 2021, across the three zones of the mangal (seaward, interior, and landward). Sample sizes for each site are: basin forest $n = 8$ plots (2 seaward, 4 interior, and 2 landward); fringe forest $n = 12$ plots (4 seaward, 4 interior, and 4 landward). Error bars show the minimum and maximum relative elevation measured within each zone at each site. Dashed horizontal line represents 0 cm, the reference point at the seaward edge of each transect. Basin forest values are shown in pink and fringe forest values are shown in blue.

This difference in the topography and connectivity of the mangals affected the physicochemical characteristics at each site (Fig. 5). Sediment bulk density within the fringe forest had a small range (0.942–1.254 g/mL) whereas it varied substantially within the basin forest (0.706–1.756 g/mL) and decreased with distance from shore (1.410 ± 0.494 g/mL at the seaward edge, 0.977 ± 0.383 g/mL in the interior, and 0.801 g/mL at the landward edge). Organic matter was strongly correlated with bulk density ($r(7) = -0.92$, $p < 0.001$), with high density sandy soils having less organic matter than low density clayey soils. Bulk density and moisture content were also strongly correlated ($r(7) = -0.87$, $p = 0.002$), with sandy soils having less moisture. A few soil parameters differed by zone within the mangal with opposing trends by site, including moisture content, organic matter, and the ratio of nitrogen to phosphorous (Fig. 5). N:P ratio was variable in the basin forest (0.40–0.87) and peaked in one of the interior plots, whereas in the fringe forest, the ratio was lower overall but had a positive relationship with distance from shore (0.38 at the seaward edge, 0.46 ± 0.02 in the interior, and 0.63 at the landward edge).

Of the soil parameters measured (Table 1), only pH and depth to aRPD were significantly different between sites. The soil in the fringe forest was more acidic with a much shallower aRPD than that in the basin forest (Table 1). The effect of site on the depth to aRPD was also apparent in the model parameter estimate of -62.03 ± 12.73 cm ($p < 0.001$) for the fringe forest compared to the basin forest, as was the effect of zone with model parameter estimates of 53.96 ± 19.44 cm ($p = 0.006$) and 45.02 ± 20.78 cm ($p = 0.030$) for interior and landward zones respectively compared to the seaward zone.

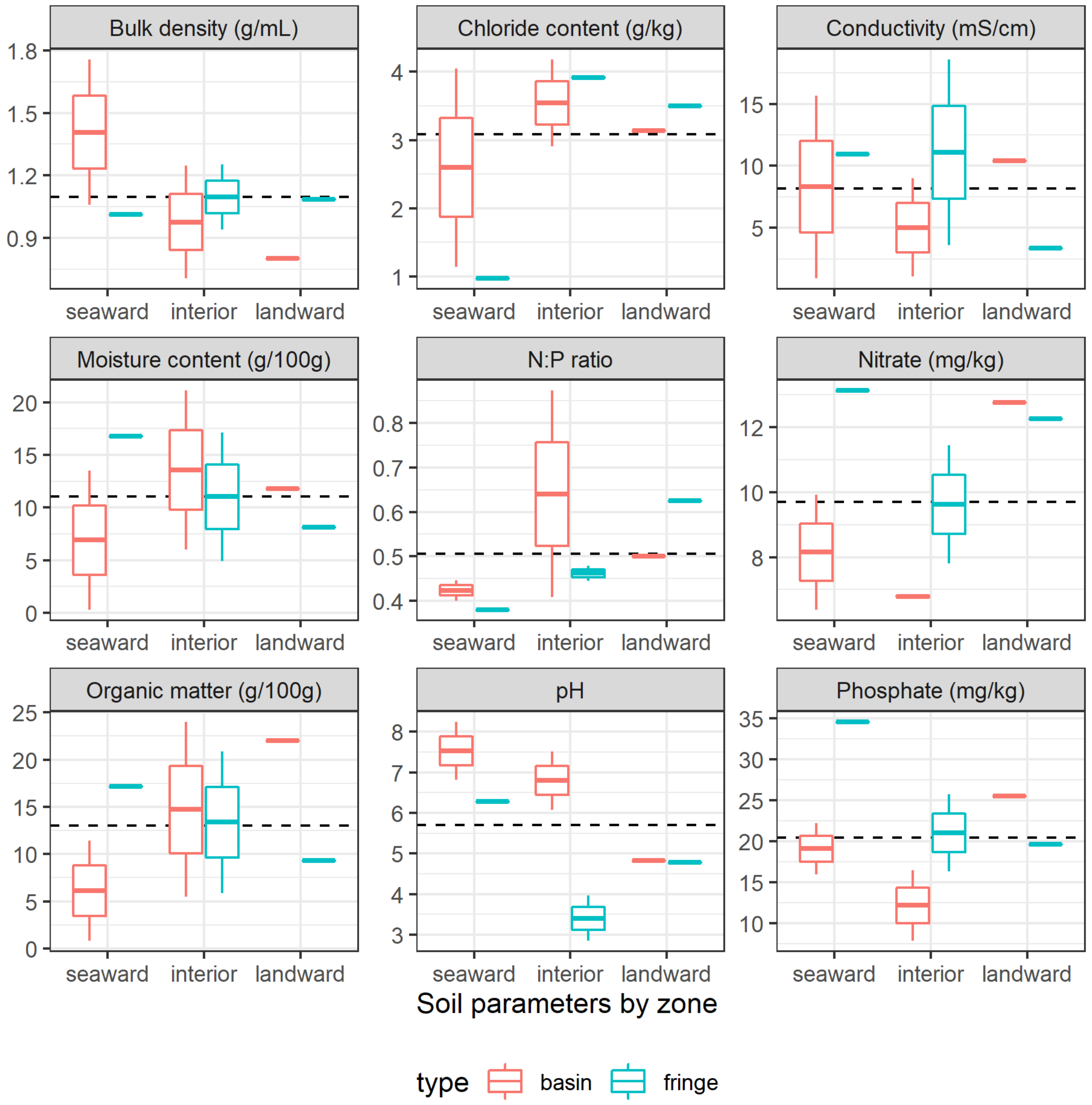

Figure 5: Boxplots for nine physicochemical parameters measured within established plots at a basin and fringe mangrove forest on Grenada, 2021, across the three zones of the mangal (seaward, interior, and landward). Dashed horizontal line shows the overall mean for each parameter (*n* = 9 soil samples). Basin forest values are shown in pink and fringe forest values are shown in blue.

Table 1: Soil parameter means (± SD) across all plots and by site, for soil samples taken within established plots at a basin and fringe mangrove forest on Grenada, 2021. $n = 9$ for all parameters except for Depth to aRPD ($n = 16$[a]). Final column shows p of two-sample t-tests comparing sites for each soil parameter ($\alpha = 0.05$, significance denoted with *).

Parameter	**Overall**	**Basin forest (Conference; $n = 5, 8$[a])**	**Fringe forest (Westerhall; $n = 4, 8$[a])**	p
Bulk density (g/mL)	1.096 (± 0.307)	1.114 (± 0.418)	1.073 (± 0.134)	*0.859*
Chloride content (g/kg)	3.082 (± 1.223)	3.085 (± 1.217)	3.077 (± 1.418)	*0.993*
Conductivity (mS/cm)	8.176 (± 6.367)	7.409 (± 6.363)	9.135 (± 7.206)	*0.714*
Depth to aRPD[a] (cm)	30 (± 39)	56 (± 42)	5 (± 5)	*0.012**
Moisture content (g/100g)	11.07 (± 6.76)	10.53 (± 7.87)	11.74 (± 6.17)	*0.810*
N:P ratio	0.51 (± 0.16)	0.53 (± 0.20)	0.48 (± 0.10)	*0.709*
Nitrate (mg/kg)	9.70 (± 2.79)	8.53 (± 2.76)	11.16 (± 2.34)	*0.173*
Organic matter (g/100g)	13.00 (± 8.32)	12.75 (± 10.12)	13.31 (± 6.90)	*0.928*
pH	5.70 (± 1.74)	6.69 (± 1.32)	4.47 (± 1.44)	*0.047**
Phosphate (mg/kg)	20.47 (± 7.65)	17.61 (± 6.77)	24.04 (± 8.02)	*0.232*

Table 2: Correlation coefficient values among eight explanatory soil variables from soil samples taken within established plots at a basin and fringe mangrove forest on Grenada, 2021. *n* = 9 samples of each variable. Highly correlated values (>|0.6|) are shown in bold.

	Bulk density (g/mL)	Chloride content (g/kg)	Conductivity (mS/cm)	Moisture content (g/100g)	Nitrate (mg/kg)	Organic matter (g/100g)	pH	Phosphate (mg/kg)
Bulk density (g/mL)	1.00	-0.31	-0.34	**-0.87**	-0.48	**-0.92**	0.42	-0.15
Chloride content (g/kg)		1.00	0.33	0.04	-0.08	0.04	-0.44	-0.27
Conductivity (mS/cm)			1.00	0.42	0.52	0.37	-0.14	**0.67**
Moisture content (g/100g)				1.00	0.39	**0.91**	-0.19	0.22
Nitrate (mg/kg)					1.00	0.49	-0.40	**0.83**
Organic matter (g/100g)						1.00	-0.33	0.24
pH							1.00	-0.13
Phosphate (mg/kg)								1.00

Principal Components Analysis was used to account for the correlations among several of the soil parameters (Table 2), and the first four components captured 95.7% of the variance in these variables (Table 3). The first component was loaded by moisture content and organic matter with bulk density in an opposing direction, i.e., principal component 1 (PC1) increased as soil moisture content and organic matter increased and as bulk density decreased. This component represents organic richness, describing soil texture and retention of both moisture and organic matter. Principal component 2 (PC2) was loaded by chloride content and phosphate in opposing directions, increasing as chloride increased and phosphate decreased. This component was more strongly associated with phosphate and thus represents soil nutrients. The third component was also loaded by chloride content and pH, increasing as chloride increased and pH decreased; chloride had a larger loading on this component and is a proxy for salinity, so PC3 represents soil salinity. Lastly, principal component 4 (PC4) was loaded strongly by both conductivity and pH, increasing as either increased; PC4 thus represents the ionic properties of the soil.

Table 3: Eigenvector values for the eight explanatory soil variables captured by the first four components (PCs) produced by Principal Components Analysis. Soil samples were taken within established plots at a basin and fringe mangrove forest on Grenada, 2021. Only values > |0.4| are shown. Each PC is shown with its variance explained in brackets and name below in quotation marks.

Soil parameters	**PC1 (47.9%) "Organic richness"**	**PC2 (21.3%) "Nutrients"**	**PC3 (16.2%) "Salinity"**	**PC4 (10.3%) "Ions"**
Bulk density (g/mL)	-0.44528			
Chloride content (g/kg)		0.472659	0.60411	
Conductivity (mS/cm)				0.595897
Moisture content (g/100g)	0.424507			
Nitrate (mg/kg)				
Organic matter (g/100g)	0.445853			
pH			-0.45411	0.649636
Phosphate (mg/kg)		-0.6081		

The relevant principal components form four axes against which the plots are redistributed. In terms of soil organic richness and nutrients (principal components 1 and 2 respectively), the plots were widely spread (Fig. 6). The interior plots at both sites were generally high in nutrients but varied greatly in organic richness; the plot with the most organic-rich soil was in the interior of the fringe forest. Outliers included the seaward plots at both sites, where the seaward fringe plot had organic-rich but nutrient-poor soil, and one of the seaward basin plots was very poor in both soil organic matter and nutrients (i.e., it had a loose, dry, low-nutrient soil). In terms of the salinity and ionic properties of the soil (principal components 3 and 4 respectively), the plots were also widely distributed (Fig. 7). The seaward and interior basin plots had the highest pH whereas the interior and landward fringe plots had the lowest pH. Another outlier was one interior basin plot, which was lowest in salinity.

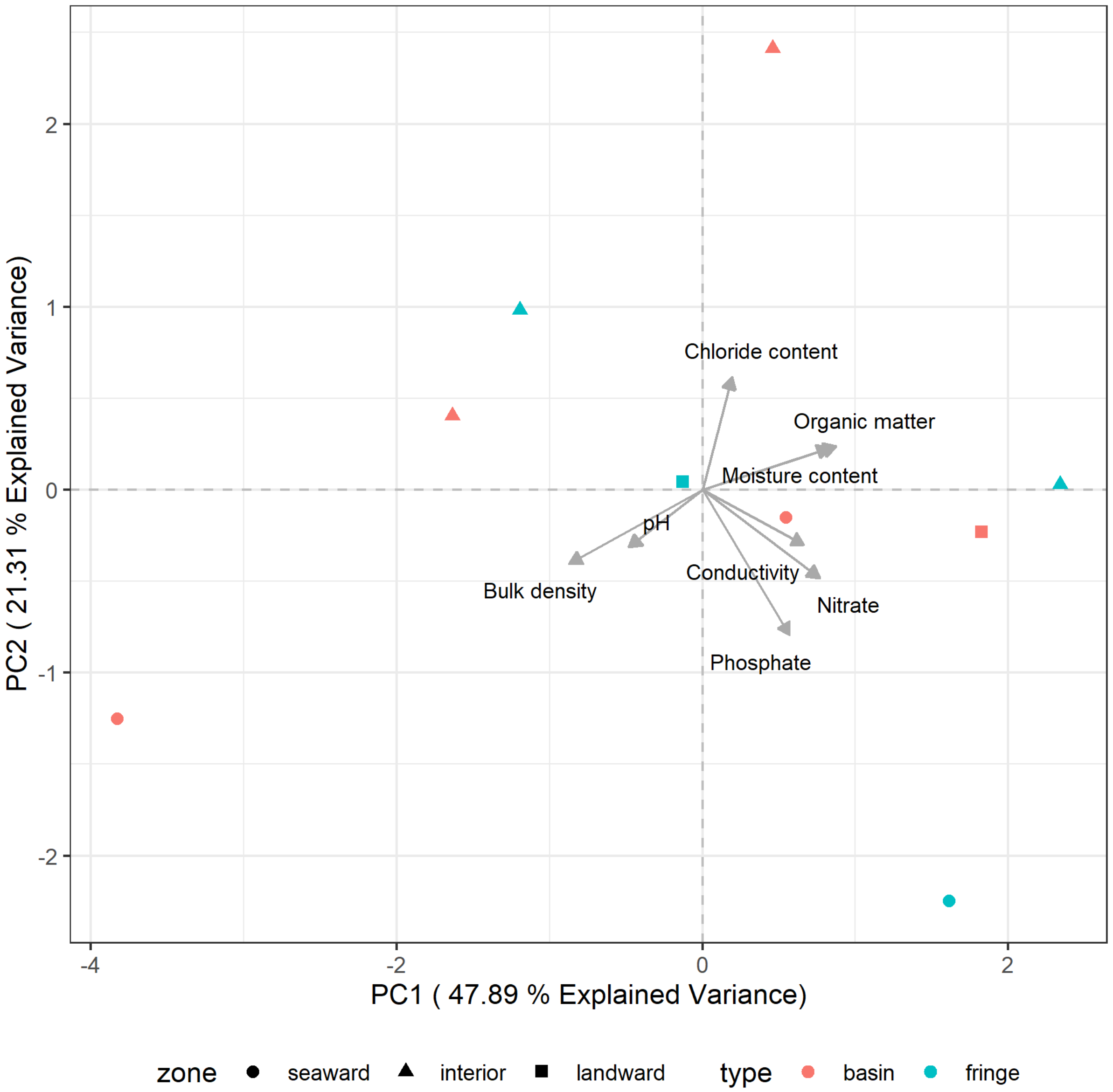

Figure 6: Results of the Principal Components Analysis showing the eigenvectors of the soil parameters plotted against the first two principal components (axes). PC1 represents soil organic richness and PC2 represents soil nutrients. Soil samples were taken within established plots at a basin and fringe mangrove forest on Grenada, 2021. The distribution of the plots along these axes is also shown by site and zone: seaward plots are circles, interior plots are triangles, and landward plots are squares; basin forest plots are coloured pink and fringe forest plots are blue.

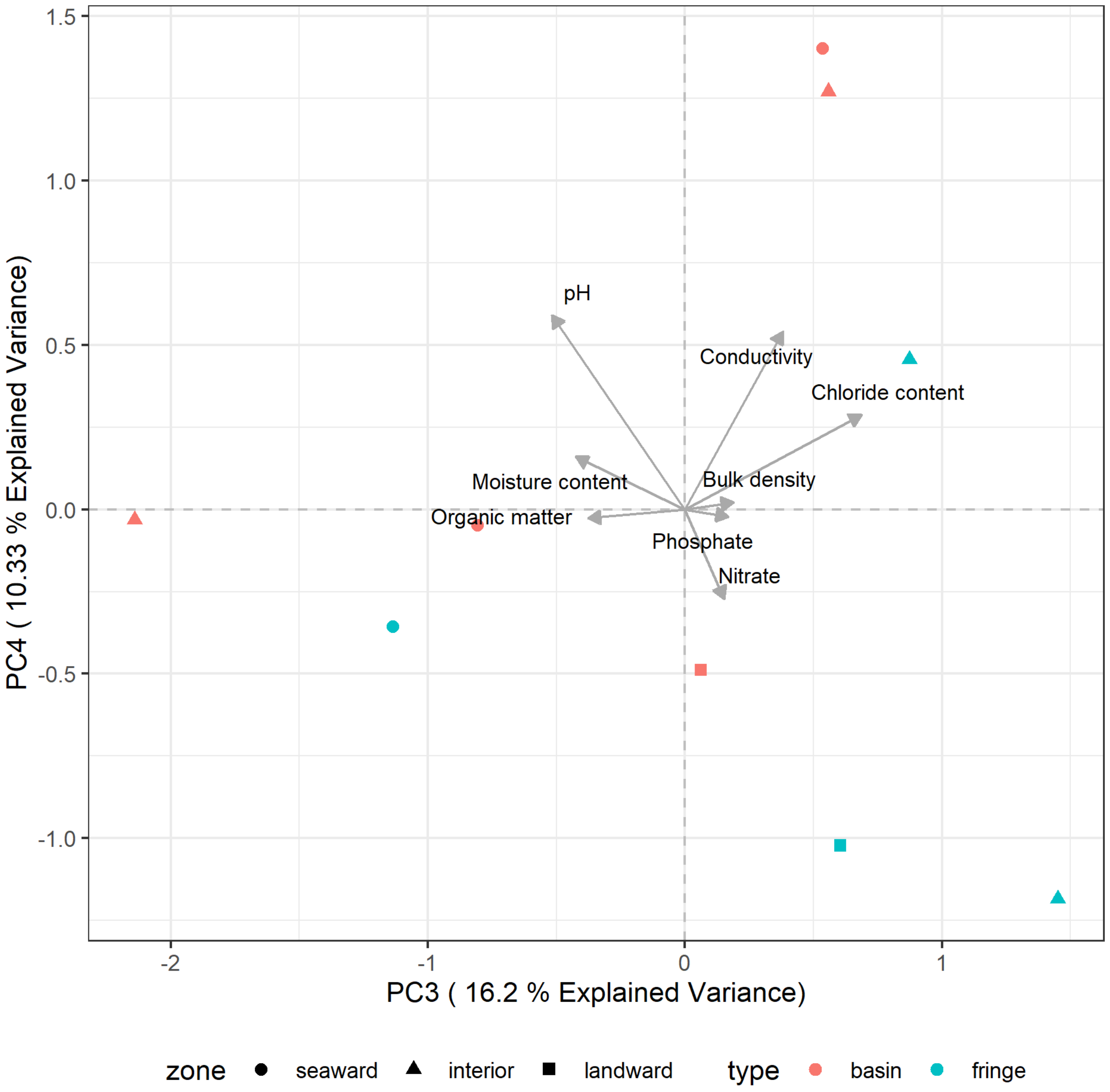

Figure 7: Results of the Principal Components Analysis showing the eigenvectors of the soil parameters plotted against the third and fourth principal components (axes). PC3 represents soil salinity and PC4 represents soil ions. Soil samples were taken within established plots at a basin and fringe mangrove forest on Grenada, 2021. The distribution of the plots along these axes is also shown by site and zone: seaward plots are circles, interior plots are triangles, and landward plots are squares; basin forest plots are coloured pink and fringe forest plots are blue.

3.3.2 Best location predictor

Table 4: Most informative location predictor(s) for each response variable from preliminary models*. Data were collected within established plots at a basin and fringe mangrove forest on Grenada in 2020 and 2021.

Response variables	**Distance**	**Elevation**	**Zone**
White mangrove presence	✓	✓	
White mangrove IVI	✓	✓	
Black mangrove IVI	✓	✓	
Red mangrove IVI	✓	✓	
Tree height		✓	
Tree size	✓	✓	✓
Slenderness	✓	✓	✓
Pneumatophore presence	✓	✓	
Pneumatophore frequency	✓	✓	✓
Leaf area	✓	✓	✓
Leaf thickness	✓	✓	✓

*The location predictors were selected by AIC_c model selection from a full model suite containing each location predictor and combinations thereof; these predictors were then used in the final models for each response variable. Distance represents numerical distance of the plot from the shoreline, elevation represents numerical elevation of the plot relative to the seaward edge of the mangal, and zone represents the categorical position of the plot within the mangal (seaward, interior, or landward).

Preliminary models selected different location predictors as most relevant for each of the response variables (Table 4). All community-level characteristics, i.e., white mangrove presence and individual species' IVI, were best explained by distance and elevation but not zone. Most vegetation characteristics, like tree size and leaf thickness, were influenced by a combination of all three location predictors. Only tree height had a single best location predictor, namely elevation. Elevation was the most important location predictor overall and had an effect on all of the response variables measured.

3.3.3 Community structure

Within the plots there was a total of 447 trees of all three mangrove species, with well over half (*n* = 278) being white mangroves (Table 5). Tree abundance averaged 22 ± 27 trees per plot, equal to a density of 0.224 trees/m^2 or 2,235 trees/ha. The most trees were found in one of the seaward basin plots with 115 trees total (105 white, 4 red, and 6 black mangroves), almost twice as many as in the second most dense plot (a landward fringe plot with 66 trees). Overall, however, tree abundance, density, and basal area were higher in the fringe forest than the basin forest (Table 5). The basal area of the trees totalled 2.82 m^2 or 14.1 m^2/ha (Table 5) and ranged 0.001–0.469 m^2 per plot. White mangroves had the highest abundance, density, and basal area of the three species, but red mangroves occurred most frequently (in 80% of plots; Table 5).

Table 5: Community structure statistics for three mangrove species within established plots at a basin and fringe mangrove forest on Grenada, 2021. *n* = 20 plots; plots were 10 m × 10 m for a total surveyed area of 2000 m^2 or 0.2 ha across the 20 plots. Importance Value Index (IVI; Cintrón-Molero & Schaeffer-Novelli 1984) was calculated as the sum of the relative abundance, relative basal area, and relative frequency of each species.

	Abundance (total no. of trees)	Density (trees/ha)	Basal area (m^2)	Basal area (m^2/ha)	Frequency (% occurrence)	IVI
Overall	447	2235	2.82	14.10	-	-
By species:						
Black mangrove	21	105	0.14	0.70	0.35	28.96
Red mangrove	148	740	1.11	5.55	0.80	116.78
White mangrove	278	1390	1.58	7.90	0.65	154.26
By site:						
Basin forest (*n* = 8 plots)	163	2038	0.97	12.13	-	-
Fringe forest (*n* = 12 plots)	284	2367	1.85	15.42	-	-

White mangroves were present in 13 of the 20 plots (65% of plots; Table 5). This proportion was higher in the basin (6/8 or 75%) than the fringe forest (7/12 or 58%). While the basin forest had white mangroves in all zones (seaward, interior, and landward), the seaward plots in the fringe forest were completely devoid of the species. Plots where the species was present had between 2 and 105 trees each (mean = 14 ± 27 trees). White mangrove seedlings were present in most plots where adults were present (*n* = 11/13 plots), with relative abundances ranging 1–55% of ground cover. Across all 20 plots, white mangrove seedlings were more abundant than seedlings of red and black put together at the time of sampling (mean percentage ground cover = 7% ± 16% white mangroves versus 2% ± 4% red and black mangroves).

Comparing IVI across all plots at both sites (Table 5; Fig. 8A), the white mangrove was the most structurally important species overall with an IVI of 154. Red mangroves were second most important (IVI 117) while black mangroves were least important (IVI 29). The species composition at the two sites was very different (Fig. 8B). While white mangroves were notably more important in the basin forest, with an IVI more than twice that of the second most important species (red), white and red were near equal in the fringe forest. IVI of all species also varied with elevation, as shown in Fig. 8C.

The global model with site, location, and soil variables was selected for all species' IVI (Table 6). White mangrove IVI increased with higher organic richness and elevation (Fig. 8C) and decreased with soil nutrients and ions; the species was more structurally important in the basin than the fringe forest. Only salinity (PC3) was not influential to white mangrove or any species' IVI. Red mangrove IVI increased with higher distance, soil nutrients, and ions (PC2 and PC4 respectively) and decreased with elevation (Fig. 8C) and organic richness (PC1). Site was again a very influential variable and red mangroves were more structurally important in the fringe forest than the basin forest. Black mangrove IVI did not differ by site or distance but did decrease with higher elevation (Fig. 8C). Soil nutrients and ions (PC2 and PC4 respectively) were both very influential on black mangrove IVI, with nutrients having a positive effect and ions having a negative effect.

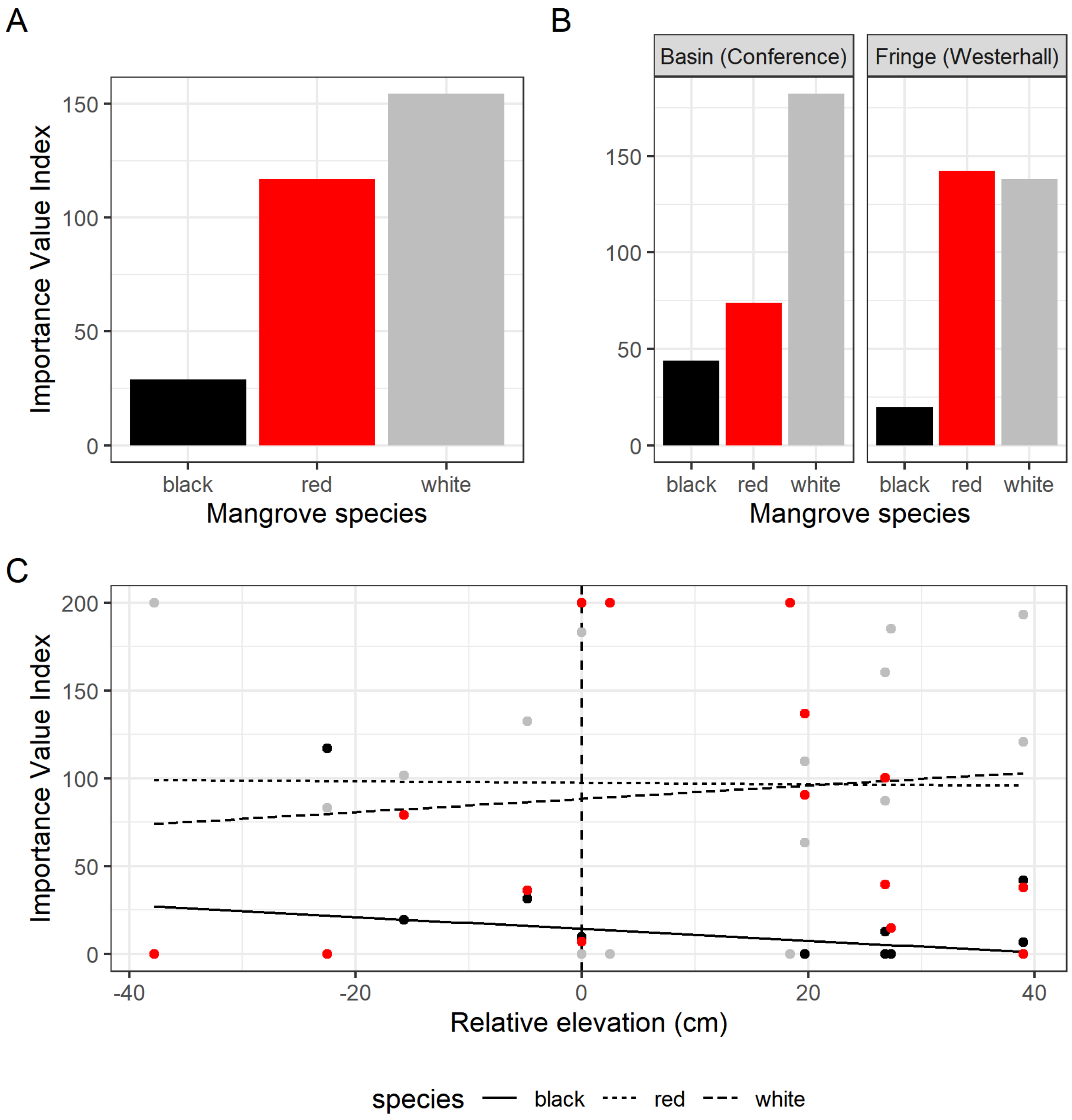

Figure 8: Importance Value Index (IVI) for three mangrove species within surveyed plots at one basin and one fringe mangrove forest in Grenada, 2021. A) Overall IVI calculated for all plots across both sites (*n* = 20 plots). B) IVI by site (*n* = 8 plots in basin forest and 12 plots in fringe forest). C) IVI by elevation across both sites (*n* = 20 plots), with each point representing the IVI of one species within one plot. Black mangroves are shown in black, red mangroves in red, and white mangroves in grey. The dashed vertical line represents the reference elevation of 0 cm at the seaward edge of each transect. The additional lines are the smoothed conditional means for a linear model between IVI and elevation; the solid line represents black mangroves, the short-dashed line represents red mangroves, and the long-dashed line white mangroves. See Table 6 for parameter estimates.

Species composition also differed by zone, but this effect was determined by site (Fig. 9). In the basin forest, white mangroves dominated in the seaward plots and decreased in importance towards the landward edge, while red mangroves were in the minority in the seaward plots and increased in importance towards the landward edge. By contrast, in the fringe forest, red mangroves dominated the seaward plots and white the landward plots. Thus, the structural importance of these two species was inversely related and site-dependent. Black mangroves were the least important species regardless of site or zone, but the species' IVI was highest in the interior of the basin forest.

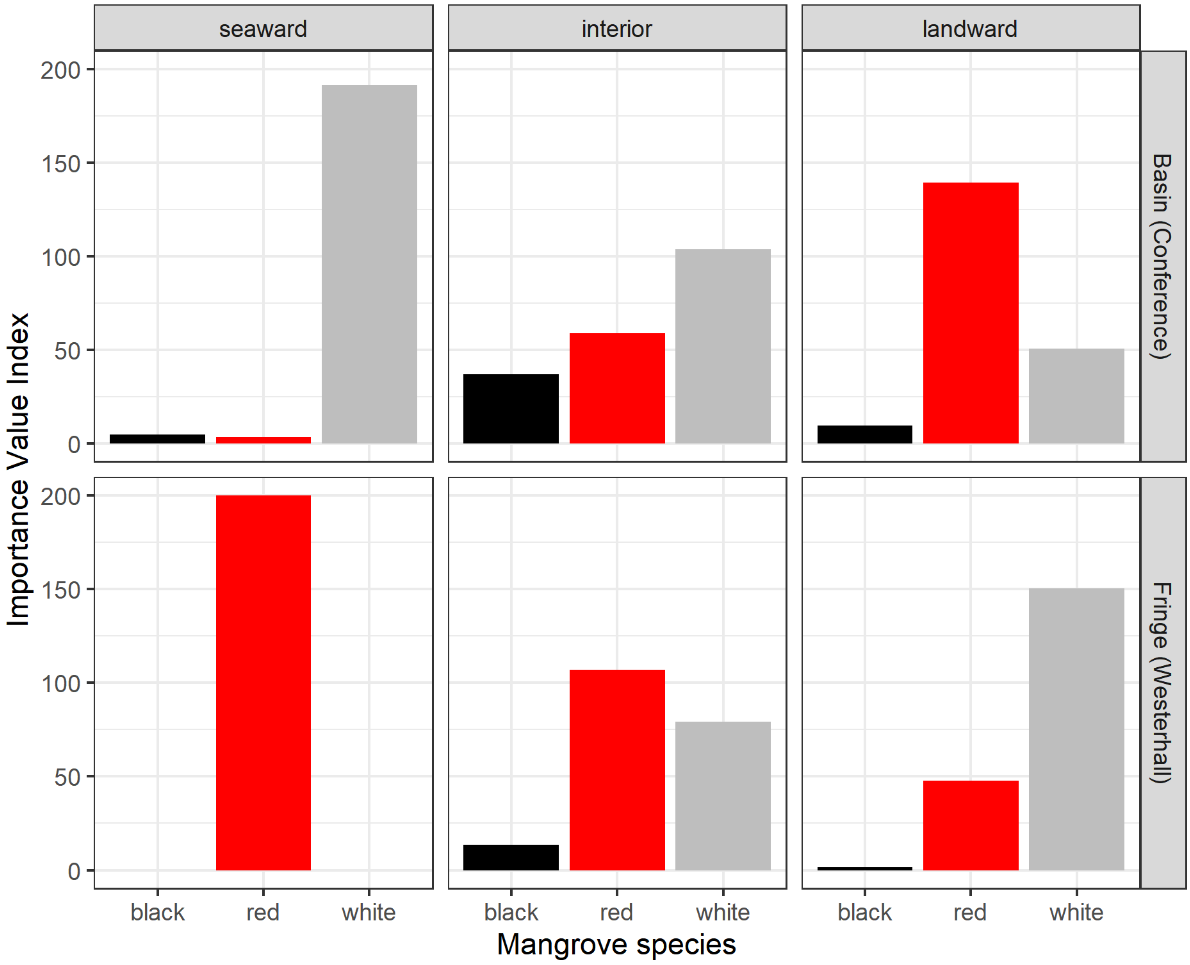

Figure 9: Importance Value Index (IVI) for three mangrove species by site (basin and fringe forest) and zone (seaward, interior, and landward) in Grenada, 2021. The basin mangrove is at the top and the fringe mangrove at the bottom; from left the right, the mangal zones are seaward (*n* = 2 plots in basin, 4 in fringe), interior (*n* = 4 in basin, 4 in fringe), and landward (*n* = 2 in basin, 4 in fringe). Black mangroves are shown in black, red mangroves in red, and white mangroves in grey.

Table 6: AIC$_c$-selected model results for community-level response variables (white mangrove IVI, black mangrove IVI, and red mangrove IVI) within established plots at a basin and fringe mangrove forest on Grenada, 2021. Parameter estimates are shown with 95% confidence intervals in brackets and *p* under the estimates in italics. *n* = 9 plots for these community-level variables. Response variables for which the null model was selected as the best model are not included in this table. Note that the explanatory variable zone (with factors "interior" and "landward") was not included in any of the best models and was excluded from the table.

	White mangrove IVI	**Black mangrove IVI**	**Red mangrove IVI**
Best location predictor[a]	Distance and elevation	Distance and elevation	Distance and elevation
Best model	Global: ~ site + location + soil	Global: ~ site + location + soil	Global: ~ site + location + soil
Family	*Gaussian* (identity)	*Gaussian* (identity)	*Gaussian* (identity)
Intercept – Basin forest (Conference)	370.121 (368.336–371.905) *< 0.001*	13.278 (6.576–19.980) *< 0.001*	-183.399 (-191.885– -174.912) *< 0.001*
Fringe forest (Westerhall)	-682.813 (-686.704– -678.922) *< 0.001*	2.126 (-12.490–16.742) *0.776*	680.686 (662.179– 699.193) *< 0.001*
Elevation	14.905 (14.769–15.042) *< 0.001*	-0.735 (-1.247– -0.223) *0.005*	-14.170 (-14.819– -13.522) *< 0.001*
Distance	-0.681 (-0.689– -0.672) *< 0.001*	-0.019 (-0.051–0.013) *0.248*	0.700 (0.659–0.741) *< 0.001*
Soil organic richness (PC1)	69.198 (68.675–69.721) *< 0.001*	-0.553 (-2.517–1.410) *0.581*	-68.645 (-71.131– -66.159) *< 0.001*
Soil nutrients (PC2)	-66.061 (-66.677– -65.446) *< 0.001*	6.76634 (4.454–9.078) *< 0.001*	59.295 (56.367–62.223) *< 0.001*

Table 6 continued.

	White mangrove IVI	**Black mangrove IVI**	**Red mangrove IVI**
Soi salinity (PC3)	-0.434 (-1.290–0.421) *0.320*	0.291 (-2.923–3.505) *0.859*	0.1431 (-3.927–4.213) *0.945*
Soil ions (PC4)	-148.125 (-149.127– -147.123) *< 0.001*	-8.002 (-11.766– -4.239) *< 0.001*	156.127 (151.361–160.893) *< 0.001*

[a] Best location predictor variable(s) for each response variable as determined by preliminary models. See Table 4 for more details.

Table 7: AIC_c-selected model results for vegetation response variables (tree height, DBH, and slenderness, pneumatophore presence and frequency, and leaf area and thickness) of white mangrove trees sampled within established plots at a basin and fringe mangrove forest on Grenada, 2021. Parameter estimates are shown with 95% confidence intervals in brackets and *p* under the estimates in italics. Response variables for which the null model was selected as the best model are not included in this table.

	Tree-level variables (*n* = 53)					**Leaf-level variables (*n* = 84)**
	Height (m)	**DBH (cm)**	**Slenderness***	**Pneumatophore presence**	**Pneumatophore frequency**	**Thickness (mm)***
Best location predictor[a]	Elevation	Distance, elevation, and zone	Distance, elevation, and zone	Distance and elevation	Distance, elevation, and zone	Distance, elevation, and zone
Best model	Location: ~ site + location	Soil: ~ site + soil	Averaged model; Location: ~ site + location Soil: ~ site + soil	Location: ~ site + location	Soil: ~ site + soil	Averaged model; Site: ~ site Soil: ~ site + soil
Family	*Gaussian* (identity)	*Gaussian* (identity)	*Gaussian* (identity)	binomial (logit)	beta (logit)	*Gaussian* (identity)
Intercept – Basin forest (Conference), seaward zone	3.725 (1.981–5.469) *< 0.001*	7.475 (3.628–11.321) *< 0.001*	-32.286 (-386.517–321.944) *0.858*	-2.392 (-3.976– -0.808) *0.003*	-0.774 (-0.774– -0.774) *< 0.001*	0.964 (0.831–1.098) *< 0.001*

Table 7 continued.

	Height (m)	**DBH (cm)**	**Slenderness***	**Pneumatophore presence**	**Pneumatophore frequency**	**Thickness (mm)***
Fringe forest (Westerhall)	36.682 (29.127–44.237) *< 0.001*	26.097 (13.326–38.869) *< 0.001*	-6147.649 (-18918.241–6622.942) *0.345*	24.276 (1.606–46.946) *0.036*	1.110 (1.110–1.110) *< 0.001*	-0.578 (-0.910– -0.246) *< 0.001*
Zone – Interior			544.699 (-623.134–1712.531) *0.361*			
Zone – Landward			154.355 (-198.851–507.561) *0.392*			
Elevation	-1.206 (-1.434– -0.978) *< 0.001*		198.624 (-225.699–622.980) *0.359*	-0.691 (-1.429–0.047) *0.066*		
Distance			8.611 (-9.708–26.929) *0.357*	-0.018 (0.049–0.0125) *0.245*		
Soil organic richness (PC1)		4.846 (3.271–6.422) *< 0.001*	-4.378 (-15.282–6.527) *0.431*		1.167 (1.167–1.167) *< 0.001*	-0.016 (-0.076–0.043) *0.589*

Table 7 continued.

	Height (m)	DBH (cm)	Slenderness*	Pneumatophore presence	Pneumatophore frequency	Thickness (mm)*
Soil nutrients (PC2)		-6.990 (-9.989– -3.991) *< 0.001*	8.010 (-12.253–28.274) *0.438*		0.793 (0.793–0.793) *< 0.001*	0.030 (-0.083–0.144) *0.598*
Soi salinity (PC3)		-8.436 (-12.426–-4.445) *< 0.001*	16.959 (-20.398–54.316) *0.374*		0.905 (0.905–0.905) *< 0.001*	-0.001 (-0.096–0.095) *0.990*
Soil ions (PC4)		0.607 (-4.350–5.564) *0.810*	-38.222 (-116.075–39.632) *0.336*		-1.149 (-1.149– -1.149) *< 0.001*	0.034 (-0.098–0.166) *0.613*

*The values shown for these response variables were produced by averaging the top models (within 2 AIC_c units) with package *MuMIn* in R. The full average (or zero-method average) and full confidence intervals are shown.

[a] Best location predictor variable(s) for each response variable as determined by preliminary models. See Table 4 for more details.

Table 8: AIC$_c$-selected model results for vegetation response variables (tree DBH, pneumatophore and adventitious root frequency, leaf area, and leaf thickness) for white mangrove trees rapid-surveyed at nine additional sites across Grenada, 2021. Parameter estimates are shown with 95% confidence intervals in brackets and *p* under the estimates in italics. Response variables for which the null model was selected as the best model are not included in this table. Note that the explanatory variables soil type and redox potential were not included in any of the best models and so were excluded from the table.

	Tree-level variables (*n* = 28)			**Leaf-level variables (*n* = 87)**	
	DBH (cm)	**Pneumatophore frequency**	**Adventitious root frequency**	**Leaf area (mm^2)**	**Thickness (mm)**
Best model	Site: ~ site	Site: ~ site	Site: ~ site	Water : ~ site + water	Site: ~ site
Family	*Gaussian* (identity)	beta (logit)	beta (logit)	*Gaussian* (identity)	*Gaussian* (identity)
Intercept – Lance aux Epines	16.073 (12.763–19.382) *< 0.001*	1.386 (1.386–1.386) *< 0.001*	-6.907 (-6.907– -6.907) *< 0.001*	2791.929 (-2838.155–8422.012) *0.331*	0.307 (0.201–0.413) *< 0.001*
Site – Dragon Bay	-6.827 (-13.019– -0.634) *0.031*	1.386 (1.386–1.386) *< 0.001*	6.897e-05 (-9.827e-05–2.362e-04) *0.419*	-1762.043 (-2667.654– -856.432) *< 0.001*	-0.207 (-0.405– -0.008) *0.041*
Site – Halifax Bay	5.676 (0.271–11.080) *0.039*	5.520 (5.520–5.520) *< 0.001*	2.639e-06 (-1.262e-04–1.315e-04) *0.968*	-1194.800 (-1931.356– -458.244) *0.001*	-0.118 (-0.291–0.055) *0.183*

Table 8 continued.

	DBH (cm)	Pneumatophore frequency	Adventitious root frequency	Leaf area (mm^2)	Thickness (mm)
Site – Harvey Vale	-10.439 (-16.632– -4.247) *< 0.001*	5.520 (5.520–5.521) *< 0.001*	-2.275e-05 (-1.726e-04–1.271e-04) *0.766*	-51.846 (-1882.223–1778.531) *0.956*	0.377 (0.178–0.575) *< 0.001*
Site – Hog Island	-7.231 (-11.912– -2.550) *0.002*	5.520 (5.520–5.521) *< 0.001*	-6.127e-05 (-1.929e-04–7.040e-05) *0.362*	-595.108 (-2116.837–926.621) *0.443*	0.120 (-0.030–0.270) *0.117*
Site – Lauriston	-5.856 (-11.261– -0.451) *0.0337*	-8.293 (-8.2931– -8.2931) *< 0.001*	13.813 (13.813–13.813) *< 0.001*	474.216 (-1399.775–2348.207) *0.620*	0.327 (0.168–0.486) *< 0.001*
Site – Petit Carenage	-11.219 (-17.411– -5.027) *< 0.001*	5.520 (5.520–5.521) *< 0.001*	-3.121e-05 (-1.830e-04–1.206e-04) *0.687*	-1692.895 (-3662.701–276.910) *0.092*	-0.140 (-0.400–0.120) *0.291*
Site – Petite Bacaye	-11.129 (-16.534– -5.724) *< 0.001*	5.520 (5.520–5.521) *< 0.001*	6.214 (6.214–6.214) *< 0.001*	-2270.435 (-3067.598–-1473.272) *< 0.001*	-0.057 (-0.216–0.102) *0.485*
Site – Woburn	-11.383 (-16.788– -5.978) *< 0.001*	5.521 (5.520–5.521) *< 0.001*	1.115e-06 (1.277e-04–1.300e-04) *0.986*	-1047.255 (-1823.415–-271.094) *0.008*	0.849 (0.676–1.022) *< 0.001*

Table 8 continued.

	DBH (cm)	**Pneumatophore frequency**	**Adventitious root frequency**	**Leaf area (mm^2)**	**Thickness (mm)**
pH				297.412 (-487.992–1082.815) *0.458*	
Salinity				-28.912 (-52.549– -5.274) *0.017*	

3.3.4 White mangrove features

Within the plots, white mangrove tree height ranged from 1.2 to 30.5 m (*n* = 144, mean = 9.7 ± 6.0 m) and decreased as elevation increased (Table 7). The trees were taller on average in the fringe forest than the basin forest (Fig. 10A); however, the tallest trees (30.5 m) were found in the landward zone of the basin forest.

Tree size (DBH) ranged from 0.6 to 54.7 cm (*n* = 144, mean = 9.5 ± 7.6 cm) and was also higher on average in the fringe forest than the basin forest (Table 7; Fig. 10B). Tree size increased with higher organic richness (PC1) and decreased with higher nutrients and salinity (PC2–3); salinity was the most influential soil variable with an effect size of -8.436 (Table 7).

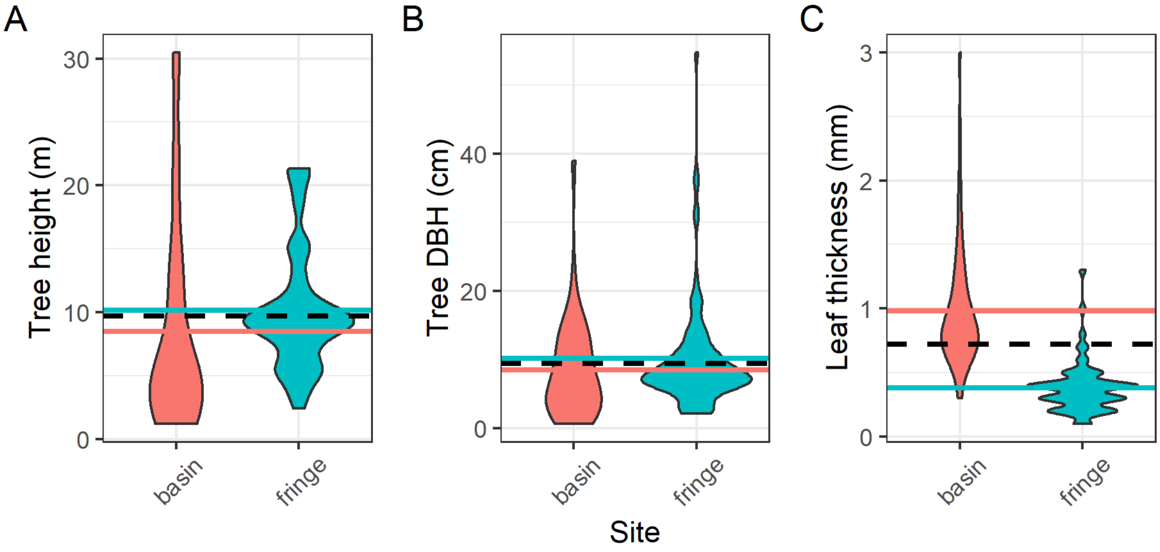

Figure 10: Tree and leaf characteristics (*n* = 144 each) for trees sampled within established plots at a basin and fringe mangrove forest on Grenada, 2021, contrasted by site (only the response variables for which site was influential). A) Tree height. B) Tree size (DBH). C) Leaf thickness. The basin forest is shown in pink and the fringe forest in blue; the coloured solid lines represent the mean within each site and the black dashed line the overall mean.

The ratio of tree height to diameter (i.e., slenderness) was very variable, ranging from 12.4 to 287.3 (*n* = 144, mean = 122.2 ± 51.8). Slenderness was unique in that the top two models—namely models 2 (Location) and 3 (Soil)—had equal AIC$_c$ values and model weights (AIC$_c$ = 577.8, weight = 0.48) so these two models were averaged. None of the individual variables were influential in the averaged model (Table 7), but cumulatively both location and soil had an effect on tree slenderness as AIC$_c$ determined these models to have a much better fit to the data than the null model.

Leaf size ranged from 569 to 8461 mm^2 (n = 144, mean = 3069 ± 1265 mm^2) but did not clearly differ by site or any other explanatory variable that was measured (null model selected as best fit to the data). The thickness of the leaves also varied greatly from 0.1 to 3.0 mm (n = 144, mean = 0.7 ± 0.5 mm). Leaf thickness was higher in the basin forest than the fringe forest (Fig. 10C) and was also affected by soil characteristics, though none of the latter variables were individually influential (Table 7). Of the 144 leaves sampled, none had visible salt crystals.

White mangrove aerial root presence differed by site. Adventitious roots were only present in one plot in the basin forest (an interior plot with a relative elevation of -37.8 cm; Appendix D1) and were completely absent in the fringe forest; however, the data were insufficient to run conclusive models for this root type. Pneumatophores were present at both sites but more common in the fringe forest; location variables, namely elevation and distance, were also included in the best fit model but were not individually influential (Table 7). In the fringe forest, pneumatophores were present in every plot containing white mangroves (n = 7) and were associated with 96 of the 104 trees surveyed. In the basin forest, they were less common, observed in half of the 6 plots containing white mangroves and associated with 11 of the 40 trees surveyed. Pneumatophores were observed in plots with water depth ranging 0–15.7 cm and adventitious roots in a water depth of 37.8 cm; the two aerial root types did not co-occur on any trees within the plots.

The frequency of pneumatophore expression (% of trees with these roots in each plot) was influenced by site and soil chemistry (Table 7). Higher pneumatophore frequencies were found in the fringe forest and were associated with organic-rich, nutrient-rich, and saline soils (PC1–3) and lower soil ions (PC4); of the soil variables, organic richness had the largest effect size on pneumatophore frequency (1.167). Pneumatophore frequency was also inversely correlated with aRPD depth ($r(11) = -0.74$, $p = 0.004$), meaning pneumatophores were more common where the aRPD was close to the surface.

3.3.5 Porewater chemistry and white mangrove features at rapid-surveyed sites

The nine additional rapid survey sites differed in their environmental parameters (Fig. 11A). pH ranged from 5.04 to 7.85 (mean = 6.41 ± 1.04) but had a clear division by location; the sites on mainland Grenada had much higher pH (mean = 7.23 ± 0.36) than those on Carriacou or Hog Island (mean = 5.26 ± 0.26). Redox potential varied greatly across the sites, from -370 to 173 mV (mean = -131 ± 148 mV); despite this large range, most samples (79%) had a negative redox potential, indicating very reductive soil conditions. Salinity ranged from brackish to hypersaline (5–60 psu; mean = 27 ± 17 psu), with the hypersaline extreme found at Lauriston Point, a flow-restricted site on Carriacou (Fig. 2). Of the four general soil types documented, silt was most common followed by sand and sand/clay mix, then sand/silt mix. The porewater chemistry was also related to the soil type, with redox potential being notably different among types; redox potential was lowest in silty soils, intermediate in the sediment mixes, and much higher (and mostly positive) in sandy soils (Fig. 11B).

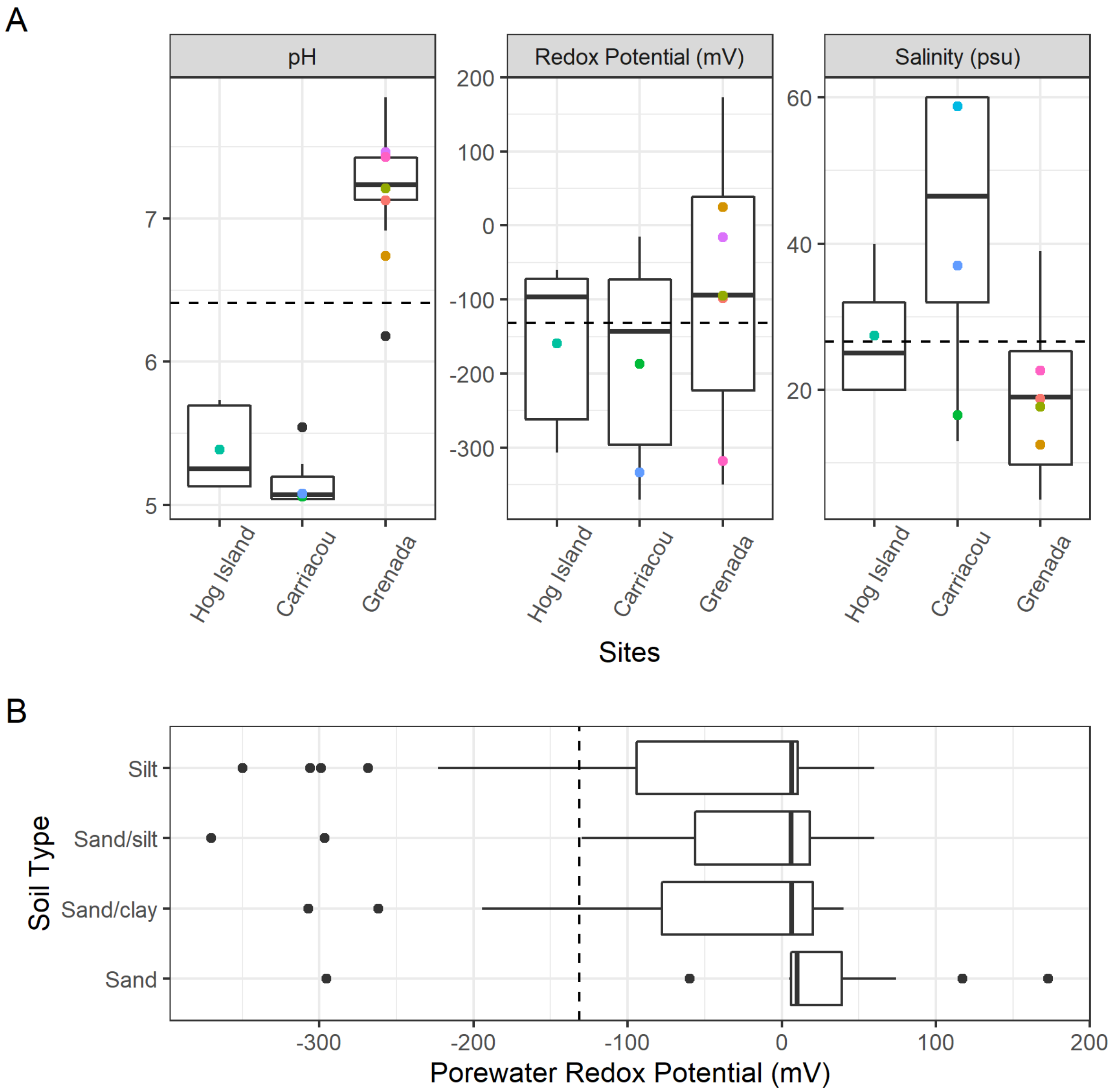

Figure 11: Porewater parameters (pH, redox potential, and salinity) for nine additional sites sampled during a rapid survey across three islands in the country of Grenada, 2021. A) Medians and ranges for all three parameters on each of islands, shown in ascending order of size (Hog Island, Carriacou, and mainland Grenada); points overlaid on the boxplots are the individual site means on each of the islands. B) Values for porewater redox potential in relation to the four soil types recorded (silt, sand/silt mix, sand/clay mix, and sand). Dashed lines represent the means for each soil parameter.

The full range of environmental conditions in which white mangroves were found growing, both within the established plots and at the nine additional sites, is provided below (Table 9).

Table 9: Range of environmental parameters associated with live white mangrove trees in this study across 11 mangal sites across Grenada, 2021.

	Minimum recorded values	**Maximum recorded values**
Bulk density (g/mL)	0.706	1.756
Chloride content (g/kg)	1.145	4.050
Conductivity (mS/cm)	0.927	15.68
Depth to aRPD (cm)	0.0	21.2
Moisture content (g/100g)	0.29	21.10
N:P ratio	0.40	0.87
Nitrate (mg/kg)	6.38	12.76
Organic matter (g/100g)	0.81	24.00
pH	2.85	8.24
Phosphate (mg/kg)	7.85	25.52
Redox potential (mV)	-370	173
Relative elevation (cm)	-37.8	39.0
Salinity (psu)	5	60

A total of 30 trees were sampled at the additional sites. Tree height ranged from 2.7 to 12.2 m (mean = 7.2 ± 2.7 m) and did not clearly differ in relation to site or soil parameters. DBH differed greatly by site (Table 8), from 2.1 to 22.3 cm (mean = 10.2 ± 6.7 cm); a noteworthy outlier was Halifax Bay with the largest trees (> 20 cm), without which the other sites averaged 8.9 (± 5.7) cm. Despite differences by site, tree size was not clearly related to any of the quantified soil and porewater parameters. The height/diameter ratio (slenderness) was also calculated (mean = 97.1 ± 54.8), but the models did not identify any clear influences by the environmental variables measured.

Leaf size and thickness also varied, influenced by site and porewater chemistry (Table 8). Leaf area averaged 3134 mm^2 (± 1189 mm^2; range 997–7087 mm^2), and particularly large leaves (> 4000 mm^2) were found at Lance aux Epines; leaf size also decreased with higher salinity (effect size -28.912). Leaf thickness averaged 0.5 mm (± 0.4 mm; range 0.1–1.6 mm), with the thickest leaves (mean = 1.2 ± 0.3 mm) found at Woburn (Table 8). None of the 87 leaves sampled had visible salt crystals.

The presence of pneumatophores and adventitious roots was not related to any of the environmental variables measured, but the frequency of both roots was. Pneumatophores were very common overall (found on 83% of trees surveyed) and were equally likely to occur at most sites (Table 8). Adventitious root frequency was also influenced primarily by site, with the highest probability of occurring at Lauriston and Petite Bacaye, the only two sites where they were observed (Table 8). The effect size was larger for Lauriston (twice that of Petite Bacaye), where the majority of the adventitious roots were observed (4 out of 4 trees surveyed there); this is possibly due to an association with the hypersaline conditions at that site, but porewater salinity was not included in the best model and so this cannot be confirmed. The two aerial root types were strongly negatively correlated ($r(7) = -0.80$, $p = 0.010$) and only rarely co-occurred (2 out of 30 trees surveyed).

For all the trees put together ($n = 174$), pneumatophores and adventitious roots were also negatively correlated, though not as strongly ($r(172) = -0.32$, $p < 0.001$), only co-occurring on the 2 trees mentioned above.

3.4 Discussion

White mangroves within Grenadian mangals differed in their occurrence and zonation between mangal forest types, and the trees also exhibited varying degrees of trait plasticity both between forest types and within each forest. My findings support my overall hypotheses that mangal zonation and white mangrove plasticity are influenced by both site-level (i.e., mangal type) and plot-level factors (i.e., edaphology and hydrology). Location within mangals was partitioned into continuous distance from shore, categorical zone, and relative elevation to the seaward edge. In doing so, I was able to decouple the effects of elevation from zone *per se* and reveal that white mangrove distribution was primarily determined by elevation and the interior topography of the mangal, which in turn is mediated by forest type. The species dominated the landward zone of the fringe forest, as expected, but instead dominated the seaward zone of the basin forest. From this, I found that the white mangrove does not prefer back mangal habitat *per se*, but simply higher-elevation habitat with a limited hydroperiod, which can be found at different locations within the mangal depending on forest type. White mangroves exhibited trait plasticity in tree height, diameter, leaf size, and root form in response to several plot-level environmental variables. Plasticity in root form was most interesting, particularly the expression of pneumatophores, adventitious roots, and rarely both by the same tree; pneumatophores were associated with reductive soil conditions (acidic organic-rich soils and shallow water), as were adventitious roots to a more extreme degree (deep water). The latter were most prevalent in sites under chronic inundation or hydrologic stress and likely were produced after pneumatophores were buried or submerged, highlighting the incredible plasticity of white mangroves to produce not one, but two types of aerial roots under different environmental conditions. This plasticity of various white mangrove traits likely contributes to the expansion of the species' ecological niche and its widespread distribution in the mangal; however, its realized niche is probably mediated by competition from red mangroves, leading to a low white mangrove prevalence in low-elevation or otherwise non-ideal zones. This paper presents a first description of white mangrove plasticity, particularly the expression of aerial roots, across several sites in Grenada and incorporates trait plasticity into our understanding of mangal community zonation.

3.4.1 Describing the mangal environment

Mangrove communities are often organized from the ground up, influenced most directly by site edaphology and hydrology (Hogarth 2015), both of which were very variable among the sites surveyed. Correlations among variables such as soil moisture, organic matter, and bulk density were expected as bulk density describes the size and arrangement of the sediment particles and their subsequent ability to hold moisture and matter (Brown & Wherrett 2021). Low-density substrate tends to be waterlogged and associated with higher organic matter content (Brown & Wherrett 2021), so it follows that the most organic-rich and low-density soils were found in the waterlogged interior at both main study sites. The soil type and degree of waterlogging also led to variations in porewater redox potential—where sandy high-density soils were only moderately reductive (i.e., redox potential was positive but less than 300 mV; Hogarth 2015)—and the depth to the aRPD (Gerwing et al. 2015)—with the aRPD being much shallower in the fringe forest, likely due to more frequent inundation restricting oxygen availability to the very top sediment layer (Hogarth 2015). Extreme values of both pH and salinity were recorded (Table 9) but did not constitute cause for concern as they were both still within tolerable ranges for mangroves; for pH in particular, values of 3 and lower have been recorded in mangrove systems elsewhere (Hossain & Nuruddin 2016), so these extreme values are not erroneous and are simply indicative of the highly reductive nature of some mangal soils in Grenada. The N:P ratio was also exceptionally low, not exceeding 1:1 within the plots (mean = 0.51 ± 0.16; Table 9), substantially lower than the optimal ratios for plant growth (8–15:1; McDonald et al. 2003). This suggests severe N limitation within Grenadian mangals; nutrient limitation is common in mangrove soils, but the scarcity of either N or P varies between and within mangals (Feller et al. 2003; McDonald et al. 2003; Reef et al. 2010; Hogarth 2015). Here, I found that although it was extremely low in all the plots sampled, the N:P ratio in the fringe forest had a positive relationship with distance from shore with the seaward zone being more nitrogen-limited than the landward zone, similar to Feller et al.'s (2003) findings in Belize. The delicate balance between N and P availability in mangrove sediment is believed to be driven largely by tidal inundation and nutrient exchange (Feller et al. 2003; Reef et al. 2010), explaining these observations in the tidally influenced fringe forest; the N:P ratio in the basin forest had no clear patterns and so the dynamics of nutrient availability in other forest types warrants further investigation.

Location within the mangal community can be described in several ways, and in this study, was partitioned into continuous distance from shore, categorical zone, and relative elevation. The best location predictor(s) differed by response variable (Table 4), which is an important consideration as they each contain different information about the mangal community and the way it is organized. Sites can be shaped differently, such as in this study where the basin forest extends much further inland than the fringe forest, and this difference is captured by continuous distance from shore. However, each mangal is still divided into categorical zones with seaward and landward edges flanking an interior zone, and the forest type and shape will determine the location of these zones relative to the shore, e.g., one interior basin plot and two landward fringe plots were at the same distance from shore (~70 m). Relative elevation adds an additional layer of information not captured by the former two, as the topography of the mangal also differs by forest type. In this case, the fringe forest was characterized by positive elevation changes along the sea-to-land gradient, whereas the basin forest had a lower interior elevation relative to the sand bank at its seaward edge. Thus, the three location predictors are complementary and should all be considered in a given study, as analysis can reveal more insight into the mechanisms behind different community and vegetation features.

Structural importance (IVI) of the three mangrove species was best explained by distance and elevation but not zone. This is a critical finding, as it shifts the focus from zone as the main determinant of community structure to include measures like elevation which may vary with forest type. The white mangrove, for instance, is considered a back mangal or landward fringe species (Tomlinson 1986), but it was observed here dominating the seaward basin plots. The inclusion of elevation explains both the occurrence and prevalence of the species in these unexpected areas because although this zone was closest to the sea, the topography of the basin forest provided higher elevation habitat along its seaward edge for white mangroves. Relative elevation in this study was derived from water depth, so it follows that these findings are supported by the theory of inundation class-based zonation (*sensu* Watson 1928; Chapman 1944; Friess 2017). Red mangroves are better suited to deeper inundation classes, i.e., lower elevation habitat, by dint of their sturdy and nearly ubiquitous prop roots, whereas white and black mangroves are more often found in shallower inundation classes, i.e., higher elevation habitat, where their pneumatophores experience only periodic flooding (Tomlinson 1986; Hogarth 1999, 2015; Fickert & Grüninger 2010; Friess 2017). However, while tidal inundation is a clear driving force in the fringe forest (Urrego et al. 2009), rainfall and freshwater retention may be more important in the basin forest, which has no clear permanent connection to the sea (Fig. 3). Indeed, Watson's findings were based on a gently sloping fringe forest similar to the one in this study, but his scheme can still be applied, albeit with caution, to other forest types with differing topography by focusing on surface elevation rather than frequency of inundation (Friess 2017). Thus, relative elevation and water depth are critical at both sites, but not necessarily driven by tidal inundation in the basin forest.

In terms of white mangrove features, most were explained by a combination of all three location predictors, although elevation was the only predictor common to all of the measured traits. For instance, pneumatophore presence was explained by distance and elevation, as expected due to the link between elevation and hydroperiod (Hossain & Nuruddin 2016)—i.e., lower elevations remain flooded for longer periods—prompting the development of pneumatophores for oxygenation (Tomlinson 1986; Hogarth 2015). Given the complexity of white mangrove expression and the various environmental cues that can contribute to plasticity (Valladares et al. 2007), it is not surprising that distance, zone, and elevation all have to be considered.

3.4.2 Considerations for mangal composition and zonation

The species composition within the sites was generally as expected based on previous surveys and maps (Appendix E). White mangroves were the most important overall, particularly in the basin forest where they were twice as dominant as red mangroves. In the fringe forest, the two species were much closer in structural importance, likely due to the level of connectivity to the sea and water depth providing ideal habitat for the red mangroves through most of the site (Friess 2017) while white mangroves dominated in the landward zone. Black mangroves were the least structurally important species overall, which was expected due to their relatively low abundance across Grenada (Appendix E); the species has only been recorded in significant numbers at a few sites, including Mt. Hartman where they are co-dominant with white mangroves (unpublished data). Of all the parameters measured, soil salinity (chloride content) was the only edaphic factor that did not influence species composition or zonation in this study (Table 6), confirming that although salinity is an important hydrological challenge of the mangal environment, it does not make or break species distribution, a distinction that has been previously suggested (Lugo & Snedaker 1974; Hogarth 2015).

White mangrove distribution and prevalence were starkly different between the two forest types surveyed, supporting my hypothesis that mangal composition can be influenced at the site level by forest type. Forest type can be considered a composite measure that captures not only the location of the mangal along the coast, but also the degree of connection to the sea, presence or magnitude of freshwater inputs, direction of physicochemical gradients, and the internal topography of the site (Lugo & Snedaker 1974; Moore et al. 2015); in this study, internal topography emerged as the main differentiating factor between the study sites, with a significant impact on species distribution. The fringe forest's topography with the lowest elevation at the seaward edge produced a species zonation similar to that predicted by the literature: red mangroves at the seaward edge, mixed species—including black—in the interior, and white at the landward edge (Fig. 12; Hogarth 2015; Friess 2017).

However, deviations from this zonation pattern were evident in the basin forest with its barrier beach, elevated seaward sand bank, and lower interior elevation; there, white mangroves were dominant at the seaward edge, with a mixed-species assemblage in the interior and red mangroves dominating at the landward edge (Fig. 12). This inverse distribution pattern of white mangroves between sites, along with the exclusion of zone as an important predictor for the species' IVI (as discussed in section 3.4.1), suggest the true mechanisms behind white mangrove zonation. Based on my findings, the white mangrove does not prefer back mangal habitat *per se* as the literature suggests (e.g., Tomlinson 1986), but higher-elevation habitat where its hydroperiod is limited (Friess 2017). The simple difference between my two sites was that the elevation was highest at the landward edge in the fringe forest versus the seaward edge in the basin forest; published zonation patterns (e.g., Hogarth 2015) therefore refer only to fringe forests and do not account for the varying topography of other mangal types. Here I provide an updated zonation diagram for the Caribbean region that accounts for these differences, contrasting the fringe and basin forests (Fig. 12); over time, this should be expanded to include the other forest types as well.

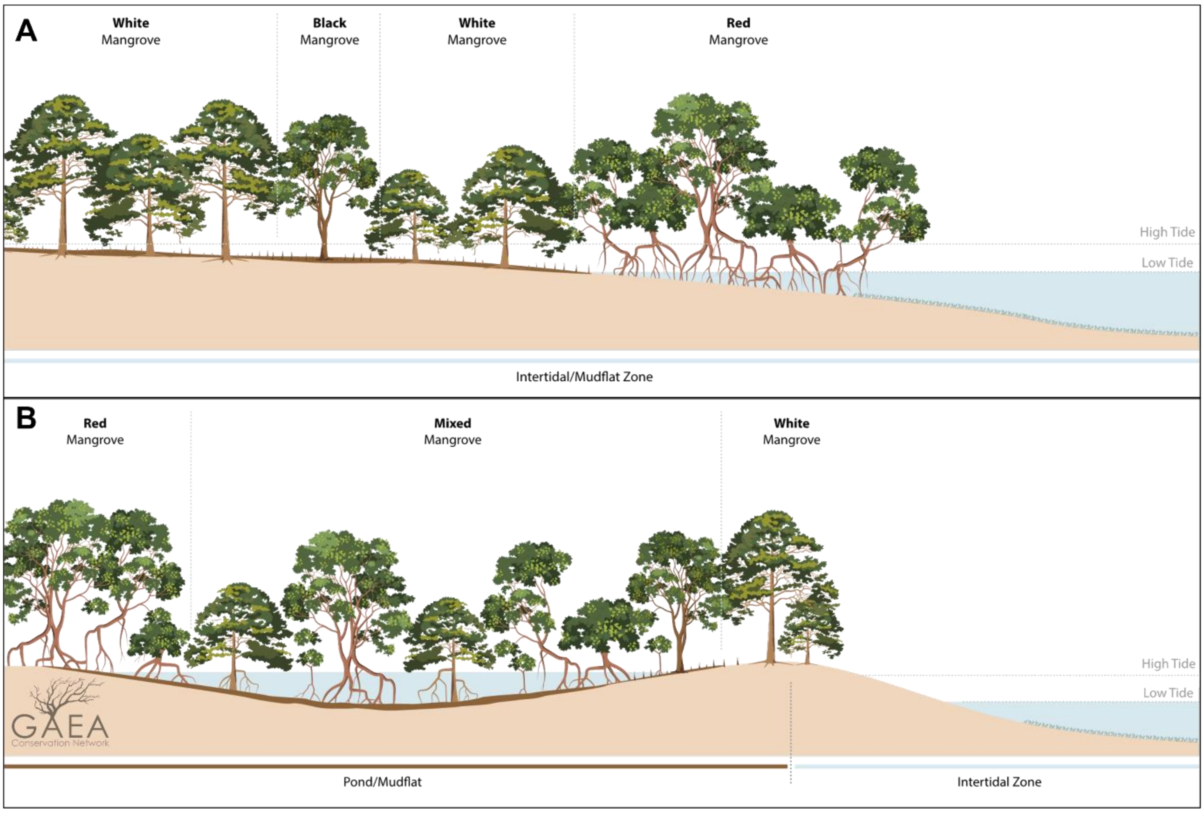

Figure 12: Zonation pattern diagrams for mangrove forests in the Caribbean composed of red (*Rhizophora mangle*), black (*Avicennia germinans*), and white mangroves (*Laguncularia racemosa*). Two forest types are shown: A) fringe forest, and B) basin forest. Created by the Gaea Conservation Network using the data from this study.

3.4.3 Observed white mangrove plasticity

Plasticity was observed in several white mangrove traits including tree size, leaf size, and root form along different environmental gradients of hydrology and edaphology. On average, trees were taller in the fringe forest, and the association between tree height and elevation was explained by the stark elevational differences between the sites (Fig. 4). Trees were also larger (in diameter) in the fringe forest and were associated with organic-rich soils and lower nutrient contents and salinity; the trees likely benefitted from the low-salinity conditions as they were able to prioritize growth and productivity over salt management, which is energetically costly (Hossain & Nuruddin 2016). Despite these differences in tree height and size, slenderness was not clearly influenced by any of the parameters measured (Table 7), as tree height and size generally varied together. Nevertheless, some structural zonation was observed, with inland trees being generally more slender than those at the seaward edge, which is likely an adaptation to increase stability and prevent wind damage along the exposed seaward edge (Wonn 1998; Piou et al. 2006). Particularly low ratios, i.e., shorter thicker trees, were recorded at one of the seaward plots in the basin forest, where mature trees were growing with their trunks nearly horizontal, producing a dense canopy low to the ground; these were classified as dwarf plants, which are most resistant to wind damage (Piou et al. 2006). One possible reason for this growth form could be that these trees were blown down by the strong winds along the coast, and subsequently continued growing from their fallen position; either way, the structural zonation observed in the basin forest can likely be attributed to the strong winds along the exposed Atlantic coast where the site is located (Conference; Fig. 2).

Although leaf size and thickness varied substantially among the sites, the data did not reveal any clear environmental patterns for the latter. Only leaf size variation was linked to porewater salinity, with higher salinities producing smaller leaves as leaf growth is limited in these conditions (Lira-Medeiros et al. 2010); smaller leaves may also be an adaptation to reduce evaporation in saline conditions (Dahdouh-Guebas et al. 2004). As leaves are the sole photosynthetic surface of mangroves, plasticity in both leaf morphology and anatomy is a critical feature for maintaining productivity under different conditions (Khan et al. 2020). None of the 231 leaves sampled had visible salt crystals, though this does not rule out salt secretion completely; white mangroves have been described as extruding “chains” of salt crystals, presumably visible with the naked eye (Tomlinson 1986 p. 223; Parida & Jha 2010). However, salt secretion in this species has thus far only been quantified by Sobrado (2004), who retrieved and measured the salt using laboratory methods that were unfortunately outside of the scope of this study. Therefore, it is possible that at least the trees in the most saline sites, such as Lauriston Point, employed secretion as a salt-tolerance mechanism, but the crystals may have been too small to observe with the naked eye.

The highest degree of plasticity was observed in root form, with the facultative expression of either pneumatophores or adventitious roots under varying edaphic and hydrological conditions. Pneumatophores were associated with several variables that indicate reductive or anoxic conditions in the sediment, including low elevation and pH, shallow aRPD, and high salinity, nutrients, and organic richness. They are expressed under these conditions to allow aeration when there is limited oxygen available in the soil and during tidal inundation (Tomlinson 1986; Hogarth 2015). As the soil in the fringe forest was generally more reductive (shallower aRPD and more acidic soil; Table 1) than the basin forest, it follows that pneumatophore presence and frequency were higher at the former site.

Adventitious roots appear to be associated with high-stress or chronically inundated sites. Their presence in the basin forest at an extremely low-elevation plot (-37.8 cm) suggest that adventitious roots are a response to prolonged inundation, similar to the prop roots of *Rhizophora* (Tomlinson 1986). This is consistent with Radabaugh et al.’s (2021) description of adventitious roots as a response to inundation to increase oxygenation and a reliable sign of stress within mangals. The white mangrove trees expressing these roots in the basin forest were stunted, no more than 2.5 m tall (dwarf), and the roots resembled those of the nearby red mangroves but were thinner and denser (Appendix D1). Among the rapid-surveyed sites, adventitious roots were also associated with a high-stress site, namely Lauriston Point on Carriacou, which was found to be flow-restricted following hurricane damage in 2004 and 2005 (Layman et al. 2006). It is unclear whether tidal connection was ever restored at the site, and I observed it to be hypersaline (porewater salinity 55–60 psu), possibly due to restricted flow and excessive evaporation. Along the landward edge of the mangal, there were also bleached snags and the remains of adventitious roots (Appendix D2), though it is unclear whether the observed mortality is natural or anthropogenic. However, adventitious roots were also observed on one tree at Petite Bacaye that had low porewater salinity (10 psu) and only mildly reductive soil (redox potential 173 mV). Thus, adventitious roots may also be expressed by healthy or unstressed trees, as suggested by Radabaugh et al. (2021), and their frequency (100% expression in the basin forest plot and at Lauriston versus 25% at Petite Bacaye) should be used as a metric of stress, rather than simply presence/absence. Despite their association with stress conditions, the expression of adventitious roots allows white mangroves to persist in these environments and is thus a form of adaptive plasticity (Arrivabene et al. 2014).

The two aerial root types were almost mutually exclusive, only co-occurring on 2 of the 174 trees surveyed, which may be for a number of reasons. Because the functions of the aerial root types overlap (i.e., oxygenation; Tomlinson 1986) and they are energetically expensive to grow and maintain (Hogarth 2015), it may simply be redundant to express both and so trees may prioritize one or the other to maximize survival based on their environmental conditions. An alternative hypothesis is that pneumatophores are expressed first, as they are energetically cheaper, and if they are buried or submerged and thus unable to perform their function, then the formation of adventitious roots is prompted (Radabaugh et al. 2021); the burial or submergence of the shorter pneumatophores would also explain why they were so hard to observe on trees that also had adventitious roots. This theory is supported by experimental findings of root production under burial conditions in Kenya (Okello et al. 2020), where three mangrove species that typically possess aerial roots (*Avicennia marina, Ceriops tagal*, and *Rhizophora mucronate*) were prompted to produce more of their characteristic aerial root under partial burial (pneumatophores, knee roots, and prop roots respectively). What makes the white mangrove unique is its ability to produce multiple types of aerial roots (i.e., both pneumatophores and adventitious roots) to most appropriately acclimate to its environment; thus, plasticity is exhibited not just in the ability to produce aerial roots but also to choose one or the other.

At one additional site—Lance aux Epines, where my sampling was limited to the fringes due to inaccessibility of the interior at the time—pneumatophores and adventitious roots were later observed (in January 2022) co-occurring on several of the interior trees. This site is under severe hydrologic stress due to flow restriction by a road that dissects the mangal and has separated the larger part of the ecosystem from the sea. There, I observed both pneumatophores and adventitious roots on the majority of the interior trees (Appendix D4). The environmental influences responsible for this dual aerial root expression, beyond the apparent hydrologic stress, are unknown and warrant further investigation in Lance aux Epines and similar sites. What is obvious, however, is that this extensive stress response did not occur overnight and is likely the culmination of decades of hydrologic stress caused by the road construction and other factors; these more subtle signs of stress and ecosystem degradation must be recognized in order to prevent complete loss of ecosystems (Lewis et al. 2016). Adventitious root frequency may be a reliable early sign of hydrologic stress that can be used to inform timely management measures (Radabaugh et al. 2021).

Plasticity as a contributor to zonation

White mangroves were present throughout all three zones of the mangal, and this widespread distribution may be attributed to the species' phenotypic plasticity and wide ecological niche (Richards et al. 2006; Sexton et al. 2017). The species was present across a large range of environmental conditions (Table 9), revealing its wide ecological tolerances and therefore niche. Published ranges for most of the environmental parameters studied herein are rare, but even more extreme values for salinity (maximum 90 ppt; Smith 1992; Quadros & Zimmer 2017), bulk density (< 0.45 g/cm^3; Sánchez-Arias & Rodríguez 2010), and organic matter (maximum 37.0%; Urrego et al. 2014) have been recorded at sites with white mangroves. N:P ratios observed in Grenada were lower than those published elsewhere in the Caribbean (3–17:1; McDonald et al. 2003). Quadros and Zimmer (2017) also provide a dataset of white mangrove traits against which this study can be compared. Absolute maximum tree height (30 m) is on par with the tallest trees recorded in my plots, while both leaf area (5.69–84.61 cm^2) and leaf thickness (0.1–3.0 mm) recorded in Grenada exceeded the published ranges (27.4–48.6 cm^2 and 0.35–0.48 mm respectively; Quadros & Zimmer 2017), revealing even greater plasticity in these traits.

The link between white mangrove plasticity, niche breadth, and community zonation is evident when one considers, for instance, the expression of aerial roots. As discussed above, red mangroves dominated the lower-elevation plots at both main sites because of their characteristic prop roots whereas white mangroves were more prevalent in the higher-elevation, less-inundated plots. However, this is not to say that white mangroves were excluded from low elevations; when they were present in these conditions, they exhibited either pneumatophores or adventitious roots to facilitate oxygenation (Tomlinson 1986; Hogarth 2015), even at elevations as low as -37.8 cm (basin forest interior) where they grew alongside red mangroves. Furthermore, the ability of white mangroves to exhibit both types of aerial roots means that they are functionally able to grow throughout the range of elevations and water depths in a mangal, perhaps expressing no roots, pneumatophores, and then adventitious roots across the water depth gradient, as observed in this study (Fig. 13). Experimental studies have also found that white mangrove seedlings can grow and thrive in both high salinity and periodically flooded environments by expressing adaptive plasticity in leaf production and growth rate (Krauss et al. 2006; Bompy et al. 2014). The true distribution of the species, then, would be limited not by its own ecological tolerances but by competition from species like the red mangrove in deeper zones (Ball 1980; Fickert & Grüninger 2010). In other words, the fundamental niche of the white mangrove is wide due to trait plasticity, but its realized niche is limited by interspecific competition within the mangal (Ball 1980; Sexton et al. 2017).

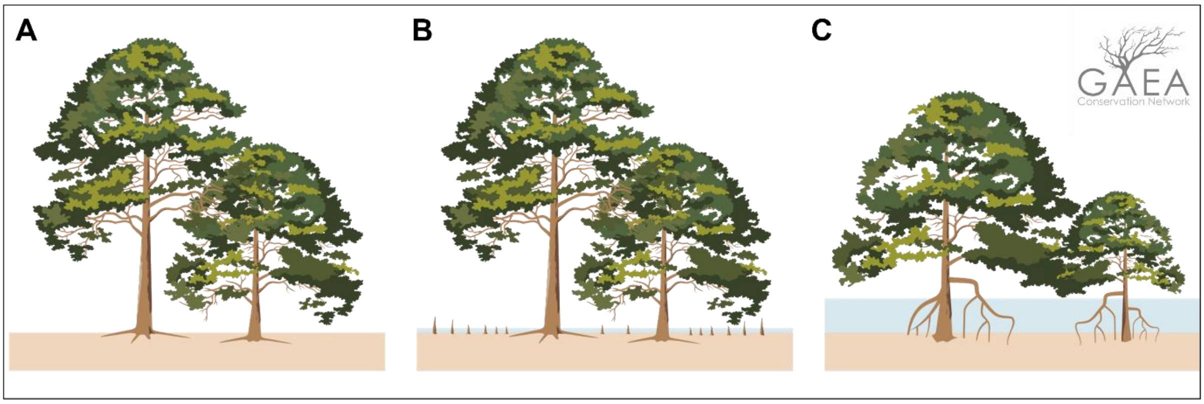

Figure 13: Diagram showing three conditions of aerial root expression by white mangroves: A) no roots; B) pneumatophores in shallow conditions; and C) adventitious roots in deeper conditions. Created by Gaea Conservation Network using the data from this study.

3.4.4 Implications for restoration

Overall, I found that white mangroves can exhibit significant phenotypic plasticity, allowing them to grow in many different locations within the mangal. Because of this wide ecological niche and prevalence throughout the mangal, I believe that white mangroves should be included in the seedling stock for restoration in the Caribbean. The species is also a recognized pioneer species (Tomlinson 1986) and can quickly recolonize an area and stabilize the soil after a disturbance (Ball 1980; Fickert & Grüninger 2010), creating the conditions necessary for other species to grow. Furthermore, because of the link between plasticity and resilience (Budd et al. 2022), white mangroves can act as a buffer to changing environmental conditions like hydroperiod with their ability to express not one but two types of aerial roots. This is especially important in the face of anthropogenic climate change (Nicotra et al. 2010), as sea level rise is expected to reduce the land available for mangroves along the coast and/or significantly alter the water table and hydroperiod within surviving mangals (Jennerjahn et al. 2017). Thus, the white mangrove’s plasticity affords it greater flexibility and makes it an appropriate choice when restoring for resilience, i.e., in anticipation of uncertain future conditions (Suding 2011; Crow 2012).

However, care must be taken not to treat white mangroves as a panacea for all restoration applications and indiscriminately plant them without regard for site-specific conditions; appropriate site assessments are still necessary to determine the most ecologically suited species for each site (Lewis 2001, 2009). These assessments may include the hydrology (water levels, hydroperiod, and sources of freshwater inputs), topography, edaphology (especially indicators of aeration like pH and redox potential), and the disturbance history of the site (Lewis 2009; Trench & Webber 2012; Van Loon et al. 2016); findings from this study suggest that forest type should also be considered, as forest type may shape topographical and hydrological factors at the site level. The best species to plant can then be selected based on the historic species composition and natural zonation patterns of the local ecosystem as well as individual species' tolerances (Trench & Webber 2012; Lewis & Brown 2014). Above all, a multi-species approach to restoration using a diversified seedling stock of all or most local species should be best practice.

The adoption of a multi-species approach will likely improve restoration success rates, with positive implications for both the cost-effectiveness and sustainability of efforts. A diversified seedling stock means that the most appropriate species can be planted within the restoration area, increasing the likelihood that the species will be matched to its environment (Lewis & Brown 2014); species-environment mismatch is one of the main reasons for restoration failure worldwide (Van Loon et al. 2016; Kodikara et al. 2017), so this is perhaps the most important advantage of a multi- versus single-species approach. The next important advantage is financial. Mangrove restoration is no cheap undertaking, with projects in the Caribbean costing an average of USD$28,500 per ha ($n = 4$ countries, range USD$14,000–45,000 in Grenada and Florida respectively; World Bank 2019b). Thus, cost-effectiveness is an important consideration as there are limited funds available for projects of this nature (Lewis 2001); higher survival and success rates will translate to greater value derived from each dollar spent on mangrove restoration, and may even be an attractant for funders who may prioritize restoration practitioners with an effective track record. Lastly, the sustainability of restoration efforts depends on the ability of restored mangals to adapt to uncertain future environmental conditions; a diverse mangal community with various species of different ecological tolerances will be best able to persist under climate change.

Restoration in Grenada: a case study

Restoration efforts in Grenada have been led mainly by the Grenada Fund for Conservation, Inc. (GFC), and over the last decade, the organization has recorded inconsistent success rates (GFC, unpublished reports). Heartening success stories, e.g., Woburn and Calivigny Bay, are mixed with reports of limited establishment and restoration "failure" in other areas (GFC, unpublished reports). To date, the organization has relied solely on red mangroves for reasons of convenience (ease of collection and propagation; Moore 2014), and this lack of diversity is likely responsible for the inconsistent results. Although red mangroves are hardy and have a proven track record of restoration throughout the Caribbean—including Jamaica (Trench & Webber 2012), Mexico (Tsuruda 2013), and several countries in the Eastern Caribbean (e.g., The Nature Conservancy n.d.)—they were not perfectly suited to every site where they were planted in Grenada, because no one species can be. A review of past restoration projects in the country reveals that red mangroves thrived where they were planted in the understory of mature vegetation like white mangroves (e.g., Telescope) or in regularly inundated areas (e.g., Woburn), but not where they were exposed to direct sunlight or heavy winds (e.g., Pearls; unpublished data). These results are explained by red mangroves being a late-successional, shade-tolerant species (Ball 1980), thus highlighting the importance of understanding species' autecology and planting them in the appropriate conditions (Lewis & Brown 2014).

The less-utilized species in Grenada, i.e., the black and white mangroves, also have strengths that can be used in restoration. Both species are pioneer species that establish easily in denuded areas and stabilize the soil (Tomlinson 1986; Lewis & Brown 2014); as pioneer species, they also germinate readily (Trench & Webber 2012), which may reduce their nursery preparation time and result in more rapid seedling turnover, thus improving the efficiency of restoration efforts. Of the two species, only black mangroves have previously been used in the country, in one project in 1998 at Petit Carenage, Carriacou (Moore 2004). There, the species was planted alongside red mangroves and in monospecific plots (~900 propagules total), but all plants died in the first year; however, natural black mangrove recruits from the surrounding vegetation established within the plots and had more than tripled the species' percentage cover over 6 years (Moore 2004). White mangroves, on the other hand, have never been planted in Grenada but exhibited a similar degree of natural recruitment at another restoration site; in Calivigny, a small quantity of red mangroves was planted in 2010, after which the white mangroves rapidly recolonized the site from surviving adult trees along the fringes (GFC, unpublished reports). Complete vegetation cover was achieved within a decade, now with a mixed stand of white and red mangroves (personal observation). These observations speak to the incredible colonization ability of both species, especially after disturbances like hurricanes, and suggest that they can be easily incorporated into restoration practices, whether before or alongside red mangroves. Exact species selections for each restoration project and site should of course depend on the local conditions and historic species composition; the relatively low abundance of black mangroves across Grenada (Appendix E) means that they may be excluded from most projects, but white and red mangroves will both likely be necessary in the majority of sites. Thus, a multi-species approach should be adopted in Grenada to fully exploit the strengths of each of the three local species.

This study revealed three other important considerations for mangrove restoration. Overall, mangrove forest density and basal area recorded in Grenada (2,235 trees/ha and 14.1 m^2/ha respectively) were much lower than those reported for elsewhere in the Caribbean region, e.g., Belize and Florida, which may be as high as 40,000 trees/ha and 78.6 m^2/ha respectively (Ball 1980; Feller et al. 2003). As no other papers have reported on stand density or basal area in Grenada (to my knowledge), it is unclear whether these low figures are common throughout the whole country; however, native stand density should be considered when planting mangroves to ensure that restored forests resemble the structure of natural forests. Furthermore, the sediment at the two main study sites was found to be extremely N-limited, with N:P values much lower than that recommended for optimal plant growth (McDonald et al. 2003). Mangroves are generally nutrient-limited (lacking either N or P depending on location; Feller et al. 2003; Hogarth 2015), so nutrient enrichment during mangrove restoration is not unheard of. Restoration manuals for the Caribbean (e.g., Bovell 2011; Trench & Webber 2012) suggest fertilization of seedlings in the nursery using various ratios of N-P-K fertilizer, and the same can be suggested for Grenada. However, nutrient enrichment can contribute to coastal eutrophication and negatively affect the plants' nutrient use efficiency and root:shoot allocation ratios, making the plants more susceptible to changes in sediment nutrient availability and salinity (Reef et al. 2010); thus, fertilization should be used sparingly and only when deemed necessary following soil assessments. This study also revealed that the degree of nutrient limitation varied within and between the forest types in Grenada, and so soil nutrient assessments are necessary within each forest and each zone where restoration is intended to ensure the most appropriate ratio of fertilizer (if any) is used. In addition to the differences in nutrient availability, the two forest types differed in overall topography and species composition, both factors that are critical to consider when restoring. Given the demonstrated preferences of the white and red mangroves for high- and low-elevation sites respectively, forest-type-specific restoration plans can be developed for Grenada. For instance, red mangroves can and should be planted along the seaward edge of fringe forests, as is common practice (GFC, unpublished reports), but are not recommended for use on the elevated seaward edge of basin forests; white mangroves should be planted in these areas instead. Thus, considerations of stand density, nutrient availability, and forest type should be incorporated into restoration planning. Improving methods for the effective restoration of mangrove forests is more important than ever, as climate change (Moore et al. 2015; Jennerjahn et al. 2017) and unsustainable development (e.g., Buckmire et al. 2022) continue to threaten and decimate these ecosystems in Grenada and the wider Caribbean region.

3.4.5 Limitations

Some queries that were outside the scope of this study include laboratory analyses to quantify salt secretion by white mangrove leaves (Sobrado 2004) and genetic analyses to determine the basis of the phenotypic plasticity observed and whether Lira-Medeiros et al.'s (2010) findings of epigenetic modification hold true in the Grenadian context. Plasticity in white mangrove traits was measured simply as variability in the quantitative morphological traits and as presence/absence of qualitative traits like aerial root form; however, the degree of plasticity was not formally quantified. A follow-up study could convert these observations into one or more of the available plasticity indices to allow comparison of white mangrove plasticity and responsiveness with other species and ecosystems (Valladares et al. 2006). I also would have liked to take absolute measurements of elevation within the mangal (i.e., elevation above sea level), but the density of the mangrove forest (> 2,000 trees/ha; Table 5) prevented more sophisticated GPS techniques such as real-time kinematic positioning (RTK) from being used to quantify elevation. Instead, we used simple measurements of water depth at high tide, and thus relative elevation was based on the water depth in each plot compared to the water depth in the seaward plot in each transect. Absolute elevation from RTK would have allowed me to make more inferences about tidal influences on community structure as it describes the site's position in relation to the sea, not just the interior topography of the site.

Sample sizes were limited by two things. First, due to financial limitations under this project, soil samples could only be obtained for 9 of the 20 plots; the sampling was stratified to ensure equal coverage across sites, zones, and treatments (white mangroves present or absent). However, this reduced the sample data available for the models to those plots with both soil sample and white mangrove data, capturing 53 of the 144 trees sampled in total. Thus, a lot of statistical power was lost from the analyses and the models were less informative than they could have been with more soil sample data and a larger inclusion of plots. Second, several sites—Calivigny, Levera, Long wall, Marlmount Bay, and Tyrrel Bay—were visited during the rapid survey but not sampled due to sampling difficulty, weather, and/or equipment failures on the day of the survey. Adventitious roots were observed at many of these sites (Appendix D), which could have provided more insight into the mechanisms behind this feature had we been able to complete a full survey at these sites.

Despite its limitations, this paper presents a first description of white mangrove plasticity and expression of adventitious roots at these sites. Having now documented the presence of adventitious roots in Grenada and recognizing their relationship to stress factors (Alongi 2015; Radabaugh et al. 2021), I recommend a more detailed follow-up study on the prevalence of adventitious roots that includes variables such as root density, height above substrate, and site history and stressors. Such a study would allow robust comparisons of adventitious root density among sites of varying environmental stressors, to hopefully reveal the main factors contributing to poor mangal health in Grenada; early detection of stresses is critical to ensure timely action and avoid the loss of entire mangrove forests (Lewis et al. 2016; Radabaugh et al. 2021). I also observed adventitious roots on several black mangrove trees at my sites (Appendix D)—which I did not quantify as it was not the focus of my study—but inclusion of this species in any future studies on adventitious root expression would add tremendously to our understanding of mangal stress and the physiological response of individual species.

3.4.6 Conclusion

This study combines observations of white mangrove plasticity and community zonation with a rich literature on both concepts that had not yet been considered together. White mangroves expressed phenotypic plasticity most notably in root form by producing pneumatophores and/or adventitious roots in deep-water conditions. Despite a demonstrated preference for high-elevation or shallow-water areas, white mangroves were able to persist in these deeper habitats through adaptive plasticity, thus expanding the species' ecological niche and defying expected zonation patterns. This contributes to our understanding of community zonation, not just as an interplay of environmental and interspecific influences, but as an even more complex phenomenon mediated by species plasticity and intraspecific variation. Studies on the link between plasticity and invasiveness are common (e.g., Richards et al. 2006), but inquiry should be extended into the 'invasiveness' of native species into other zones of their natural ecosystems, i.e., the ability of species with a high degree of trait plasticity to persist in multiple zones and under vastly different environmental conditions, thereby disrupting or shaping their community zonation. This will undoubtedly yield interesting findings on species traits, plant plasticity, and community dynamics, with implications for forest management of both mangroves and terrestrial plants.

Given the genetic similarity and high connectivity of the white mangrove population throughout the Caribbean (Hodel et al. 2018), these findings from Grenada should easily be extrapolated to other subpopulations in its range. Where the white mangrove co-occurs with the red and black mangroves, i.e., through most of the Caribbean Basin, community dynamics among the three species may be similar to those observed here. The importance of both plot-level (hydrology and edaphology) and site-level (forest type) environmental variables to white mangrove plasticity and zonation should prompt further investigation into the ecological differences among different forest types; from additional studies, we should also be able to visualize more forest-type-specific zonation patterns for the region (e.g., Fig. 12). One of the critical findings from this study was that white mangroves preferred not back mangal habitat but simply higher-elevation habitat, which was discovered by decoupling the effects of elevation from zone *per se*. Thus, the white mangrove should not be called a strictly back-mangal or landward-fringe species, as the location of its preferred high-elevation habitat is determined by forest type. Deepening our understanding of these mechanisms behind white mangrove plasticity and zonation in the context of Grenadian mangals will inform the conservation, management, and restoration of the species throughout the Caribbean region.

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Appendices

Appendix A: Soil parameters and respective analysis methods

Table A1: Soil parameters measured and their respective analysis methods and units, as provided by the Produce Chemists' Laboratory in St. George, Grenada. Established industry methods from Hoskins (1997) and Horwitz (2000) were used.

Parameter	Analysis Method	Unit
Bulk density	Pycnometric	g/mL
Chloride content	Titrimetric	g/kg
Conductivity	Conductimetric	mS/cm
Moisture content	Gravimetric	g/100g
Organic matter	Gravimetric	g/100g
Nitrate	Colorimetric	mg/kg
pH	Potentiometric	-
Phosphate	Colorimetric	mg/kg

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Appendix B: Model suites for within-plot variables

Table B1: Model suite composition for vegetation response variables (tree height, tree size [DBH], slenderness, aerial root presence, and aerial root frequency) within established plots at a basin and fringe mangrove forest on Grenada, 2021.

Model	**Variables**
Null	-
Site only	Site (Conference or Westerhall) + (1|plotID)
Location	Site + Location (distance, zone, and/or elevation) + (1|plotID)
Soil	Site + Principal Components 1–4 + (1|plotID)
Global	Site + Location + Principal Components 1–4 + (1|plotID)

Table B2: Model suite composition for leaf-level vegetation response variables (leaf size [area] and leaf thickness) within established plots at a basin and fringe mangrove forest on Grenada, 2021.

Model	**Variables**
Null	-
Site only	Site (Conference or Westerhall) + (1|plotID)
Location	Site + Location (distance, zone, and/or elevation) + (1|plotID)
Soil	Site + Principal Components 1–4 + (1|plotID)
Vegetation	Site + Vegetation (tree height and size) + (1|plotID)
Location and Soil	Site + Location + Principal Components 1–4 + (1|plotID)
Vegetation and Soil	Site + Vegetation + Principal Components 1–4 + (1|plotID)
Location and Vegetation	Site + Location + Vegetation + (1|plotID)
Global	Site + Location + Vegetation + Principal Components 1–4 + (1|plotID)

Appendix C: Model suites for additional rapid-surveyed variables

Table C1: Model suite composition for vegetation response variables (tree height, tree size [DBH], slenderness, aerial root presence, and aerial root frequency) at additional rapid-surveyed sites (*n* = 9) across Grenada, 2021.

Model	**Variables**
Null	-
Site only	Site
Water	Site + Water (pH and salinity)
Soil	Site + Soil (redox potential and soil type)
Global	Site + Water + Soil

Table C2: Model suite composition for leaf-level vegetation response variables (leaf size [area] and leaf thickness) at additional rapid-surveyed sites (*n* = 9) across Grenada, 2021.

Model	**Variables**
Null	-
Site only	Site + (1|tag)
Water	Site + Water (pH and salinity) + (1|tag)
Soil	Site + Soil (redox potential and soil type) + (1|tag)
Vegetation	Site + Vegetation (tree height and size) + (1|tag)
Water and Soil	Site + Water + Soil + (1|tag)
Vegetation and Soil	Site + Vegetation + Soil + (1|tag)
Water and Vegetation	Site + Water + Vegetation + (1|tag)
Global	Site + Water + Vegetation + Soil + (1|tag)

Appendix D: Evidence of adventitious roots on mangroves in Grenada

D1: Conference (basin forest), Grenada (detailed in text, see sections 3.3.4 and 3.4.3)

Photo description: (L) White mangroves adventitious roots in a flooded, low-elevation plot in the basin forest. (R) Red mangrove prop roots and white mangrove adventitious roots next to each other on trees just outside the plot boundary.

D2: Lauriston, Carriacou (detailed in text, see sections 3.3.5 and 3.4.3)

Photo description: (L) Dense white mangrove adventitious roots on live trees at Lauriston Point. (R) Dried adventitious roots and dwarf snags at the landward edge of the mangal, with new shoots emerging from the roots. (Bottom) Extent of dead vegetation (continuing into the distance all along the landward edge of the mangal) including bleached snags and adventitious roots. Mortality may be due to the hypersaline conditions or to clearing for visibility by the adjacent airport.

D3: Levera, Grenada (visited but not successfully sampled)

Photo description: White mangrove adventitious roots on several trees at Levera.

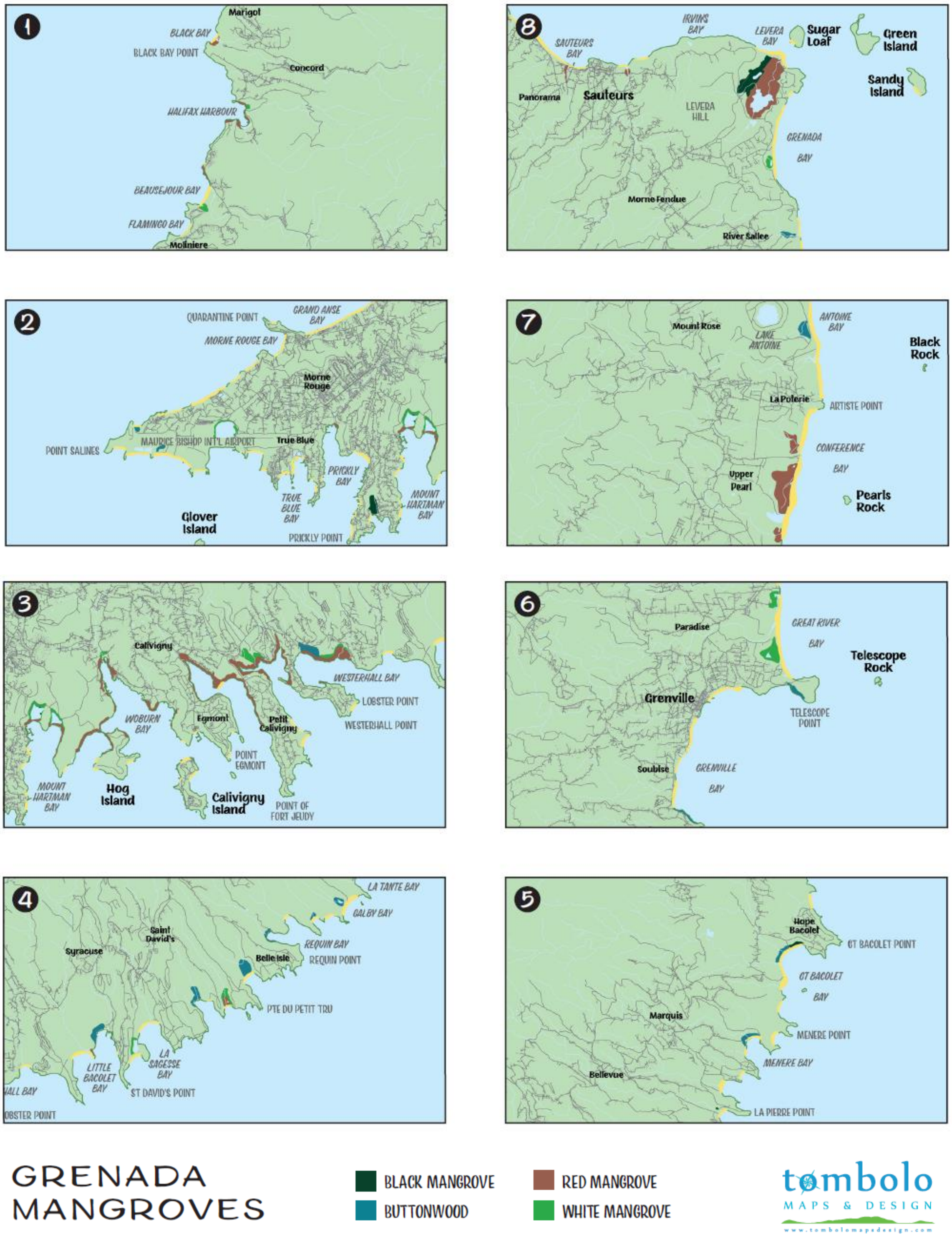
D4: Lance aux Epines, Grenada (visited but only successfully sampled on the forest fringes; detailed in text, see section 3.4.3)

Photo description: Various forms and densities of white mangrove adventitious roots at Lance aux Epines. (Bottom R) Pneumatophores also present on most trees within mangal, co-occuring with adventitious roots.

D5: Black mangroves

Photo description: Black mangrove adventitious roots at (Top) Conference (basin forest) and (Bottom) Pearls on Grenada. The two sites are very close together and may be considered to be part of the same extensive historical coastal forest in the Big Bay, St. Andrew area.

Appendix E: Map of species distributions in Grenada



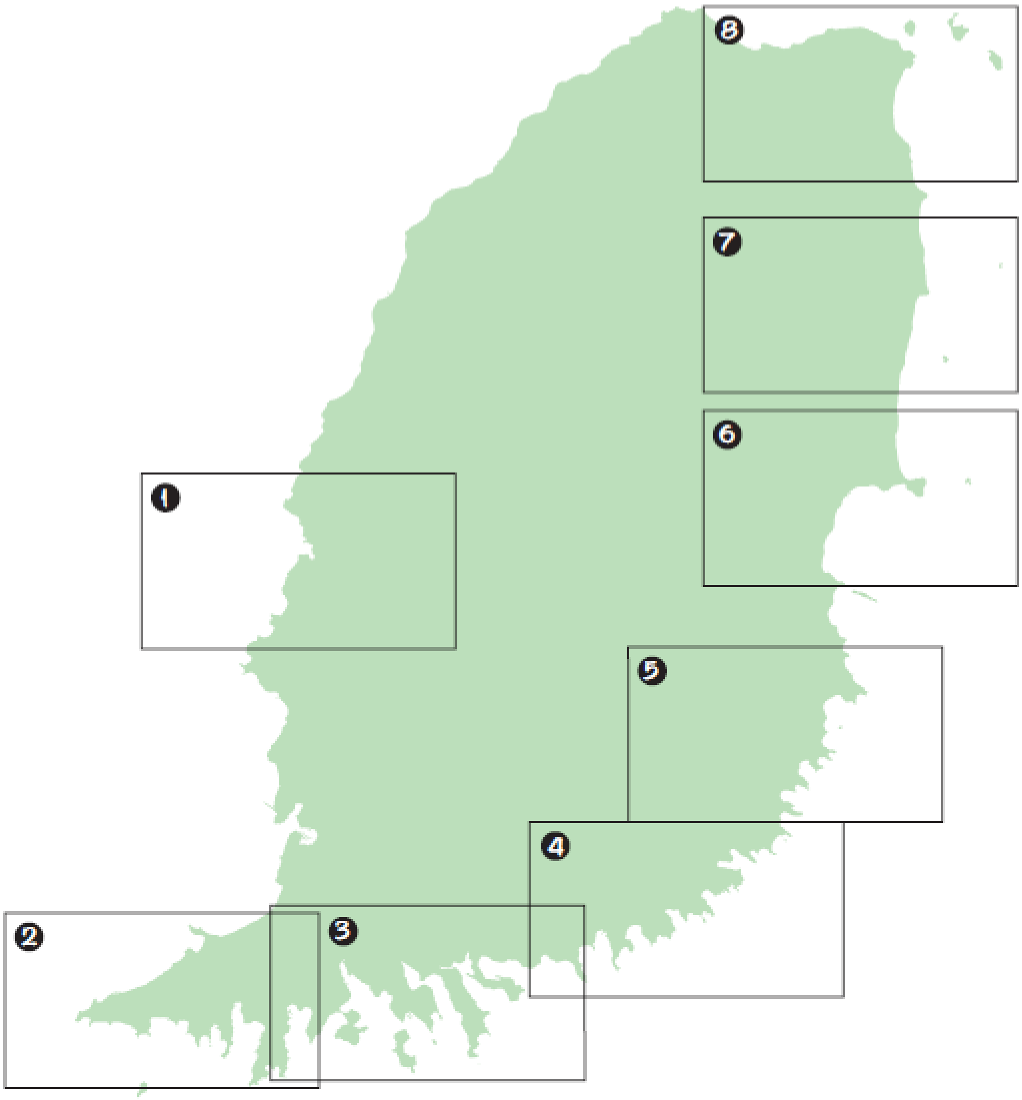


Figure E1: Map showing the general mangrove species distributions across sites on the main island of Grenada, West Indies. Produced by Tombolo Maps & Design for Gaea Conservation Network based on surveys by Moore et al. (2015).