Understory plant communities in the surroundings of the Joyuda Lagoon, Puerto Rico

by

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Abstract

Studies focused on the distribution of understory species associated with mangrove forests are very scarce. This research provides a detailed description of the understory community and their environmental requirements at a basin mangrove forest and an abandoned coconut plantation at the western edge of Joyuda Lagoon. A non-systematic survey, a 70-plot sample and a 40-plot sample were conducted. Understory and tree seedling percent cover were measured at the 70-plot sample. Tree canopy cover above the sampling site, pH, electrical conductivity, soil water content and total transmittance were measured at the 40-plot sample. Elevation was measured along the transects of the systematic survey. Species composition between the coconut plantation and the mangrove forest differed significantly. The environmental variables shown to be most significant and define understory species distribution were electrical conductivity, elevation and total transmittance. Mangrove dominated plots in contrast to the coconut plots were characterized by lower elevations, high salinity and light availability. These results suggest that if sea-level continues to increase mangrove forests and their associated understory will expand inland into the coconut plantation.

Resumen

Los estudios enfocados en la distribución de especies de sotobosques asociadas a manglares son escasos. Este estudio provee una descripción detallada de la comunidad de sotobosque y sus requisitos ambientales en un bosque de manglar de cuenca y una plantación de coco abandonada al borde occidental de la Laguna de Joyuda. Un estudio no-sistemático, un muestreo de 70-parcelas y un muestreo de 40-parcelas fueron conducidos. El por ciento de cobertura de sotobosque y de plántulas de arboles fueron medidos en el muestreo de 70-parcelas. El por ciento de cobertura de dosel sobre el lugar de muestreo, el pH, la conductividad eléctrica, el contenido de agua del suelo y la transmitancia total fueron medidas en el muestreo de 40-parcelas. La elevación fue medida a través de los transectos en el estudio sistemático. Composición de especies entre la plantación de coco y el bosque de manglar difirieron significativamente. Las variables ambientales que mostraron ser más significantes y definen la distribución de especies de sotobosque fueron conductividad eléctrica, elevación y transmitancia total. Parcelas dominadas por mangle al contrario de las parcelas de coco fueron caracterizadas por elevaciones bajas, alta salinidad y disponibilidad de luz. Estos resultados sugirieren que si el nivel del mar continua aumentando bosques de manglar y su sotobosque asociado se van a expandir tierra adentro hacia la plantación de coco.

Dedicatoria

A mi hermana, abuela y a mi adorado sobrino, por todo su apoyo y por hacer mi vida más feliz. A mi madre y padre por soportarme todos estos años, por todo su amor, por siempre escucharme y siempre estar ahí. Y finalmente a mi ángel de la guarda, mi abuelo.

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Introduction

The present study is aimed at understanding the understory vegetation of the forests surrounding the Joyuda Lagoon. Like other very low elevation coastal ecosystems in Puerto Rico, the vegetation surrounding the Joyuda Lagoon is likely to be impacted by changes associated with the rise in sea-level resulting from anthropogenic climate change. The rise in sea-level may already be modifying the hydrological regime of this ecosystem in similar ways as in other parts of the World (Nicholls et al., 2007). Such hydrological changes may be promoting the expansion of mangrove forest in this area by modifying the habitat both physically and chemically.

Studies of the understory of tropical mangrove forests are very scarce. Some studies have focused on particular species (e.g., Medina et al. 1990) while others have produced general descriptions of the herbaceous communities of coastal habitats closely associated with the mangrove forests (e.g. Gleason and Cook, 1928). Therefore, there is a need for a detailed description of this vegetation, its relationship with environmental factors, and an evaluation of its potential role in forecasting future trends in the coastal vegetation types as the expected climate change consequences unfold.

Literature Review

Mangroves are trees or shrubs that grow in the intertidal zone. Mangroves include 16 families, and 40 to 50 species (Feller and Sitnik, 1966). According to Tomlison (1994) a "true mangrove" must be exclusive to the following criteria: "1) Complete fidelity to the mangrove environment. 2) Major role in the structure of the community and ability to form pure stands. 3) Morphological specialization that adapts them to their environment 4) Physiological mechanism for salt exclusion so that they can grow in seawater. 5) Taxonomic isolation from terrestrial relatives." In Puerto Rico there are three "true mangroves", *Rhizophora mangle* (Rojo), *Avicennia germinans* (Negro) and *Laguncularia racemosa* (Blanco). A fourth species, *Conocarpus erectus* (Botón) can also be found, but do not follow all the requirements to be considered a "true mangrove" and is considered a transitional species.

The zonation patterns in mangroves often result in pure stands of species along the shoreline (Feller and Sitnik, 1996). These zonation patterns vary with geographical location and in some instances at local scale. For example in Florida and the Caribbean *R. mangle* occupies the seaward zone followed by *A. germinans* and *L. racemosa*; in Queensland, Australia is reverted by having *Avicennia* spp. in the seaward zone followed by *Rhizophora* spp. (Feller and Sitnik, 1996).

According to Smith (1992) there are different viable theories for these zonation patterns: 1) Land Building and Plant succession- this hypothesis is based in the idea that mangroves in the intertidal zone trap sediments creating new land for pioneer colonizers to invade and replace the original species. The process continues until the land is no longer intertidal, promoting plant succession and making this theory one of the most controversial and refuted hypothesis for the reason that most ecologists believe that mangroves respond rather than cause these processes. 2) Geomorphological influences- the theory of geomorphological influences is based in that mangrove zonation depends on topography and geomorphic factors, like sea-level rise. If sea-level rise is far greater than the ability of the mangroves to respond to that sea-level increase the area of mangroves will decrease. 3) Physico-chemical Gradients- this hypothesis is based in that zonation occurs by the different requirements of each species, like frequency of inundation, which incorporates other factors like salinity, soil water content, and other factors like nutrients, pH, etc. 4) Propagule dispersal- the theory that propagule dispersal creates the zonation patterns is based on “tidal sorting” of propagules, where position of the species along the pattern is related to the size of the propagule; smaller propagules are carried farther inland by the tides than bigger propagules. 5) Seed predation- this hypothesis is more important in certain regions and for certain mangrove species, for example mangroves in the Indo-Pacific region experience higher level of predation than in the Caribbean based on the species of predators present and their capabilities. 6) Competition- there is limited research that indicates that competition between mangrove species could influence zonation.

In Puerto Rico mangrove zonation is as previously described for Florida and the Caribbean zone. In zones more frequently flooded and with more water movement are areas dominated by *R. mangle*, for example the coastal forests found in the municipality of Ceiba and the community of Aguirre in Salinas, Puerto Rico. In areas with slow water movement and depressions where extreme salinity does not limits the growth and seedling survival, *A. Germinans* and *L. racemosa* dominates. Examples can be found in Piñones and Aguirre (Pool et al., 1977). Joyuda lagoon presents two types of Mangrove ecosystems, fringe forest dominated by *R. mangle* in the seaward zone and basin mangrove dominated by *A. germinans* (Lugo and Musa, 1993). In the basin forest some mixed stands of *L. racemosa* and *C. erectus* occur. Topography and hydrological conditions in the area define the zonation pattern found in Joyuda (Lugo and Musa, 1993).

Anthropogenic Disturbances

Around the globe a 35% reduction of the total mangrove area has been reported since 1980 (approx. 3000 km^2/yr) (Valiela et al., 2001). Most of this reduction is human induced principally by pollution, climate changes and destruction of the ecosystem. One of the principal pollutants affecting mangroves around the world are oil spills, causing mass mortalities like the ones observed in Galeta Island Pánama (Ellison and Farnsworth, 1996). In Puerto Rico two major oil spills have occurred. In the year 1962 the company “Argea Prima” spilled over 10,000 tons of oil southwest of Puerto Rico, practically destroying the mangrove ecosystem (Diaz-Piferrer, 1962), later in 1973 a second oil spill occurred once again southwest of Puerto Rico, (EPA, 1975), studies have shown that the oil spilled at both dates still persists in the sediments and may represent long-term negative effects on the mangroves (Corredor et al., 1990). Other pollutants are thermal pollution from power plant cooling systems, mercury contamination from mining, sewage, urban runoff, and pesticide runoff among others (Ellison and Farnsworth, 1996).

The effects of climate change in mangroves are an indirect anthropogenic effect. Higher temperatures represent soil warming, changes in weather patterns and sea-level rise (Ellison and Farnsworth, 1996). Soil warming and changes in weather patterns have not been well studied. Sea-level rise on the other hand has been widely discussed. Sea-level rise is caused by the melting of glaciers but principally by the warming and therefore expanding of the water (Tysban et al., 1990). During the 20th century mean sea-level rise was between the ranges of 1.0 to 2.0 mm/yr globally, and it is projected that a 0.11 to 0.77 m increase will occur between 1990 and 2100 (Church et al., 2001). This increase in sea-level could cause hydrological changes that can promote an inland expansion of a saline environment around the world. High salinities affect principally the re-generation of terrestrial species more than the survival of mature trees (Williams et al., 1999) causing mangrove ecosystems to replace terrestrial ecosystems (Shearman, 2010). A rate of 1.24 mm/yr between 1955 and 1999 was reported at Magueyes island sea-level station, just 23 km from Joyuda Lagoon. Based on this rate of increase an estimated 9.55 cm increase between 1930 and 2007 should have occurred in Joyuda. (Zervas, 2001).

Destruction of the mangrove ecosystem for wood, agriculture and urban development is another anthropogenic effect. Clear-cutting of mangroves can have detrimental effects and may result in a slow or no recuperation of the mangrove ecosystem. The removal of mangroves can result in a rapid soil sulfide accumulation that can result in subsequent soil acidification, which can limit seedling regeneration (Ellison and Farnsworth, 1996). Also, mangrove forest re-establishment depends on the presence of propagules, meaning that in areas that were completely cleared of mangroves the rate of re-establishment will be slower than areas where propagules and adult individuals are near or present (Ferwerda et al., 2007). Even with the presence of propagules, re-establishment after clear cutting takes longer compared to re-establishment after a disturbance such as a hurricane. In contrast it has been shown that vegetation cover keeps increasing years after a complete recuperation has occurred in clear-cut areas, compared to a hurricane affected area that do not present much of an increase in cover after it achieves complete recuperation (Ferwerda et al., 2007).

Martinuzzi et al. (2009) identified four major periods of mangrove changes in Puerto Rico. The first period between 1800-1938 was identified as the agricultural period where mangroves were extensively used for fuel wood, and charcoal, the lands were drained and were converted into agriculture. During this period mangroves decreased 45% in area. The second period was between 1938 and 1959. It was a recovery period (12% increase), which marked the end of the agricultural era and the beginning of the industrial era. The industrial era (1959-1971) represented the third period and yet another decline of mangrove area due to urban development. The final period from 1971 to present has been characterized by an increase of 23% in mangrove extent. This increase was faster during the first years of recuperation. Mangroves at Joyuda lagoon like other mangrove forest in Puerto Rico were affected by farming practices, mostly clear-cutting for fuel, wood, and coconut planting (Figure 2). These practices have been almost completely abandoned in this area. Chinea and Agosto (2007) concluded that forest cover increased twice its area by comparing aerial photographs from 1930 and 1997.

Mangrove understory vegetation

Understory species associated with mangroves are herbaceous or semi-woody halophytes mostly belonging to the Chenopodiaceae, Cyperaceae, Aizoaceae, Pteridaceae, Orchidaceae and Boraginaceae (Snedaker and Snedaker, 1984). Generally they are found wherever there has been a habitat disturbance (Snedaker and Snedaker, 1984), an open canopy or where rainfall or freshwater runoff lowers the salinity levels (Feller and Sitnik, 1996).

Gleason and Cook (1928) described similar vegetation in south Puerto Rico. This vegetation consisted of mostly monospecific patches of *Sesuvium portulacastrum* and *Batis maritima* in a strip of land where mangrove development is not as successful and the climax forest (as they describe) cannot be established. The colonization of both species usually begins at the base of the mangrove trees, where the soil is slightly elevated, slowly moving inland avoiding dense canopies. Among their observations is that *S. portulacastrum* prefers lower salinities and for that reason extends much farther inland, and it also prefers higher and drier soils than *B. maritima*. Other species found near the Batis-Sesuvium association were *Boerhavia scandens*, *Heliotropium curassavicum*, *Portulaca quadrifida* and *Spurious virginicus*.

It has also been hypothesized that some of these understory species may serve as facilitators for the establishment of mangroves after a disturbance by promoting trapping and establishment of propagules, and enhancing their survivorship and growth (McKee et al., 2007). At various locations, species such as saltwort (*Batis maritima)*, sea blights (*Suaeda* spp.), glassworts (*Salicornia* spp.), sea oxeye (*Barricia* spp.) and sea-purslanes (*Sesuvium* spp.) may serve as facilitators for the colonization of *A. germinans* (Milbrandt and Tinsley, 2006).

As mentioned before the ecological aspects regarding the distribution of these species have not been studied very deeply. Variables such as residence time of water, salinity, and light among others may be influencing the distribution of understory species.

Residence time of water

Residence time of water can affect salinity and soil oxygen. Salinity increases in areas where the residence time of water is short and the evaporation rates are high. Soil oxygen decreases in areas where the residence time of water is higher, causing very significant chemical changes in the soil. In areas with low oxygen, anaerobic bacteria tend to colonize using alternative oxidants for respiration, converting Mn^{4+}, NO_3^-, Fe^{3+} and SO_4^{-2} into their reduced state Mn^{2+}, N_2, Fe^{2+} and S^{-2} respectively, until the soil eventually reaches a high anaerobic state where reduction of carbon dioxide to methane occurs (Snedaker and Snedaker, 1984). The rate at which this last process takes place depends on the depth of the flooding and the amount of time the soil remains flooded. These changes in the redox state of Mn, NO_3^- and Fe can have an effect on plant growth by making these nutrients unavailable, as for example nitrogen that can only be used in an inorganic form (NO_3^-, NH_4^+) (Snedaker and Snedaker, 1984). Significant losses of nitrogen occur in flooded soil via denitrification. The development of understory species in the mangrove community depends on their environmental preference and resistance to these stressors.

The chemistry of sulfur is of great importance. In highly anaerobic flooded soils sulfate is reduced to sulfide. High levels of sulfide particularly H_2S is common in coastal forests where the concentration of sulfates is high. As H_2S is produced it tends to accumulate in the roots of the mangrove trees inhibiting oxygen transport (Kathiresan and Bingham, 2001). Toxicity caused by high levels of sulfide can lead to high mortality rates and growth decrease of mangroves. Sulfur can also have an effect in controlling the mobility of many important elements. High concentrations of sulfide along with iron pyrite (that is formed by iron redox reaction) become aerated, and jarosite $KFe_3^{III}(SO_4)_2(OH)_6$ begins to form, until it hydrolyses to form sulfuric acid and thus creating a very acidic soil. At low pH many metals exhibits greater solubility, which in response have an effect on phosphate release (Snedaker and Snedaker, 1984).

Decomposition also tends to be slow on anaerobic soils making key nutrients like nitrogen unavailable (Mitsch and Gosselink, 2007).

Salinity

According to Lugo et al. (1981) salinity constitutes the main stressor and regulator in the development of the mangrove forests. The distribution of mangrove species depends mainly on their tolerance to salinity. Mangrove responses to salinity stress include changes in sap osmotic pressure, changes in leaf size or tree height, salt exclusion at the root, and salt excretion trough the leaves (Lugo et al., 1981).

In well-drained soils under humid conditions soil salinity is practically non-existent because soluble salts are leached and carried downward into the ground water and eventually the ocean. In arid regions, where there is less rainfall to leach the salt but there are high evaporation rates, salts tend to concentrate in the soil and surface water (Poljakoff-Mayber and Gale, 1975). Because the residence time of water is shorter far from the lagoon, the evaporation rates are higher; therefore the highest soil salinities should occur more inland (Lugo and Musa, 1993).

Light

According to Janzen's (1985) hypothesis plants need to have an adequate amount of light to meet their metabolic demands. An example is the mangrove fern (*Acrostichum* spp.), which requires direct sunlight to be fully reproductive (Janzen, 1985). In contrast Medina et al. (1990) found that *Acrostichum aureum* is a shade tolerant plant that takes advantage of the lower evaporation rates produced by the shading, but to acquire full development and reproductive capacity they require full sun exposure.

Disturbances such as hurricanes can affect light availability by influencing canopy cover. Baldwin et al. (2001) reported an increase in understory species cover shortly after hurricane Andrew passed through the coast of Florida and their subsequent reduction four years later. Also, in a recent study, Sharpe, J.M. (2010) found that *A. danaeifolium* showed higher fertility rates after Hurricane George passed through Jobos Bay. Although Sharpe (2010) did not correlate canopy openness after the disturbance with higher fertility rates, Janzen's (1985) and Medina et al. (1990) theory could explain Sharpe's findings.

Objectives

1) To describe the understory community in the surroundings of the Joyuda lagoon.

2) To correlate the distribution of understory species with environmental factors.

Methods

Study area

The Joyuda Lagoon is a natural conservation area located near latitude 18º 8' 00" and longitude 67º 10' 30", southwest of Mayagüez, Puerto Rico (Figure 1). It lies within the Subtropical Moist Forest life zone (Ewel and Whitmore, 1973). It is believed that the lagoon was formed after the segregation of a small bay that was protected by a small barrier of sand (Comer, 1969). A coconut plantation was established in the western edge of the lagoon and most of its mangrove forests were cut for wood (Chinea and Agosto, 2007). The study area lies at the west side of the reserve, which is composed of a basin forest and an abandoned coconut plantation (Figure 1). According to Musa (1986) the mangrove forest of Joyuda Lagoon is believed to be more than 50 years old. The species of mangrove present are *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle* and are classified as "North coast mangroves" (Lugo and Musa, 1993). Elevation ranges from sea level to 2 m (USGS, 1966). Average annual temperature range between the years 1971-2000 was 19.8°C - 31.5°C at Mayagüez City station, located approximately 7.5 kilometers from the study area. For the same years and same station annual average precipitation was 1,744 mm (NOAA, 2011).

The study area lies on two types of soils: Cataño sands and a composition of Joyuda, Atolladero and Bajura soils (USDA, 2010). The Cataño sands series, the predominant soil at the abandoned coconut plantation, is a well drained soil that is formed from beach sand deposits derived from shell fragments, quartz grains and igneous rocks. While the Joyuda, Atolladero and Bajura soils series composition are very poorly drained soils that can be found principally in areas dominated by mangroves. The Joyuda series is an organic material derived soil composed principally by muck and mucky peat; the Atolladero series is beach sand derived composed by mucky loam and loamy sands; and the Bajura soils is derived from alluvium, composed principally by clay. For 2010 in the Mayagüez city station the period of high tides was observed between the months of July to November (NOAA, 2011).

Sampling design

For this study three sampling types: a survey, a 70-plot sample and a 40-plot sample were conducted. The survey was non-systematic floristic inventory that consisted of collecting understory species by walking through the study area. The systematic sampling of 70-plots and 40-plot sample consisted of five permanently marked parallel transects, running roughly at 10° from North were started near a fringe mangrove and ending inside the abandoned coconut plantation (Figure 1). Four transects were 85 m long, and the fifth transect was 125 m long, because the mangrove area there was more extensive. The distance between each transect was roughly 40 m.

A total of 51 sampling sites were selected initially as a preliminary sample. These sites were located in a scheme of 5, 10 or 15 m from each other. That sample was considered insufficient, therefore additional sampling sites were used to obtain a more balanced and representative sample. The final sample size included 70 sampling sites (referred as the 70-plot sample). At each of those sites understory and tree seedling percent cover were measured. Of this 70-plot sample 40 plots were selected to measure tree canopy cover above the sampling site, pH, electrical conductivity, gravimetric soil water content and total transmittance (these plots will be referred as the 40-plot sample). Elevation was measured all along the transects.

Vegetation Survey

A floristic inventory was conducted at the beginning of this study. This inventory was performed by walking through the study area and collecting species found in the understory. It was conducted mainly for assembling a list of the species found within the study area.

A more thorough sampling was conducted to determine the relative abundance of the species within the study area. Initially, the understory vegetation was sampled using a rectangular quadrat (1 m x 0.5 m) at 5, 10 or 15 m from each other (locations where the poles for determinations of ground elevations were established). The elevations of these initial sampling sites missed part of the elevation range of the study area, therefore 19 samples were added at randomly chosen locations among the missed elevations, for a total of 70 plots (70-plot sample). Species in each quadrat were noted and voucher specimens were collected outside but near each quadrat. Aerial pictures covering the entire area of each quadrat were obtained from an elevation of 1.4 m above the quadrats with an Olympus Camedia C-3040Zoom. Each image was registered using ArcGIS 9.3 and a 10 cm x 10 cm grid was drawn on each picture. Percent cover of each understory species was estimated from the pictures at each 10 cm x 10 cm sections, the percent cover values at each section were then summed and divided by 50 (total number of 10 cm x 10 cm sections in each quadrat) to obtain the percent cover of each species per quadrat. Of the 70-plot sample 33 plots had understory species and/or mangrove seedlings, these 33 plots plus 7 additional plots conforms the 40-plot sample. In addition to the understory vegetation, percent cover of canopy species growing over the quadrats was visually estimated in the 40-plot sample. The floristic inventory was conducted on three different dates July, 24, August 25 2008 and February 2009. The 70-plot sample and 40-plot sample survey was conducted between September 2009 and May 2010. Tree canopy cover values were estimated in February 2011. Nomenclature of vascular plants after Axelrod (2011).

Environmental Variables

Elevation- Ground elevation of the very level terrain of the surroundings of the Joyuda Lagoon should be highly correlated with the inundation regime of the study area. Prior to vegetation sampling ground relative elevation was measured at one meter intervals along each transect. Two poles were temporarily placed at each end of 5, 10 or 15 m intervals (depending on visibility). One end of a Zircon® water level was set at an arbitrary height in the first pole as the reference for measuring ground elevation; that reference was extended to the following pole using the other end of the water level. A fine cotton thread was extended between the two poles at the leveled reference elevations. Ground relative elevation was determined by measuring at 1 m intervals the distance between the cotton thread and the ground. Elevation measurements were taken during the months of July–August 2009. Elevation error was assessed when the study area was inundated by a heavy rainstorm in July 15, 2010 by measuring the distance from the water surface to the ground at several previously measured portions of the transects. The average error was 0.67 cm (ranges between 0 – 6 cm).

Electrical conductivity, pH and soil water content- Soil electrical conductivity (EC, an index of soil salinity), pH and soil water content were measured in the 40-plot sample. Three soil cores of approximately 0.30 m were extracted at randomly chosen locations within each quadrat, placed in a zipper plastic bag and immediately placed in a cooler. All the three soil cores obtained at each plot were later group into one sample for each plot for a total of 40 soil samples. Both pH and EC were determined by the saturated paste method as described in Rhoades et al. (1999), using 200 g of the preserved soil of each plot. EC and pH of the filtrate were measured with a YSI Model 31 Conductivity Bridge and a Fisher Accumet pH meter Model 800, respectively. To check the accuracy of the cell constant and conductivity bridge, a 0.01 mol KCL solution was used. The following equations were used: f(t)= ideal value/actual value, where f(t) represents the temperature-coefficient, the ideal values can be found in EPA (1983) and the actual EC value obtained at t temperature for the KCL; $ECe=f(t)*EC_t$, where ECe is the electrical conductivity traditional index of the filtrate, f(t) the temperature coefficient and EC_t is the electrical conductivity at temperature t.

Soil water content was measured with the Thermogravimetric oven-drying method as described in Topp and Ferré (2002) using 15 g of the preserved soil. Equations used can also be found in Topp and Ferré (2002). Soil samples were taken and processed in August 2010.

Light – The amount of light energy reaching over each quadrat was estimated with hemispherical photography using a Pentax ZX-50 camera with a Sigma 8 mm F4 fisheye lens. Each photo was taken from a tripod at approximately 0.75 m from the ground, focused at infinity, leveled horizontally looking up. The film used was color 200 ISO film. Each picture was processed using Gap Light Analyzer software to obtain percent of total transmittance. Description and information of the GLA software can be found at Frazer et al. (1999). Light measurements were taken in the same plots as EC, pH and soil water content measurement were taken (40-plot sample). The photos were taken and processed on November 2010.

Statistical Analysis

Non-metric multidimensional scaling procedures (NMS), using the “slow and through” autopilot mode of PC-ORD, were used for the ordinations. The distance measure used was Sorensen’s index. The procedure used 250 runs with real data and

250 runs with randomized data for the Monte Carlo test, and the stability criterion for accepting the best solution was 0.00000, with 500 iterations (McCune and Grace, 2002). Species with occurrences in less than 5% of the sampling units were considered rare species and were removed from the matrix prior to the ordination. The ordination used percent cover of species as the abundance measure of canopy and understory species found at the 40-plot sample. Environmental variables were superimposed on the ordination using joint plots. To assess diversity Shannon's diversity index ($H' = -\Sigma\, p_i \ln(p_i)$) and its equivalent in number were used.

Results

Species by sampling types

A total of 62 plant species were observed in the study area (Table 1). Of those 62 species 33 were understory species, 18 were tree species and 11 could not be identified because they were too immature. Forty species were found in the 70-plot sample. Of those 40 species, 17 were understory species, 12 were tree seedlings, and 11 species could not be identified. At the 40-plot sample 17 understory species, 12 tree seedlings, 11 species that could not be identified and 14 adult trees in the canopy were found.

Species abundance and distribution

The understory species with the highest cover in the study area was *Batis maritima*, but the highest frequency was that of *Scleria lithosperma* (Table 2). The tree species with highest seedling cover was *Calophyllum antillanum*, while the most frequent tree seedling was *Swietenia* spp.

Using the values of percent cover of canopy species, the plots were divided into mangrove dominated and coconut dominated plots. Of the 70-plots 24 were mangrove dominated and 46 were coconut dominated. The only two understory species found in the mangrove dominated plots were *Batis maritima* and *Sesuvium portulacastrum*. *Batis maritima* had the highest cover. Only three tree seedling species were found at these plots, and these seedlings corresponded to the three “true mangrove” species of Puerto Rico; they were not found within the coconut plantation.

Fifteen understory species were found in the plots within the coconut plantation, *Acrostichum aureum* had the highest cover followed by *Fimbristylis cymosa*. Both *B. maritima* and *S. portulacastrum* were absent from the coconut plantation plots. A total of nine tree species were found as seedlings, *Calophyllum antillanum* had the highest cover followed by *Swietenia* spp. The unidentified species were found only within the coconut plantation.

At the canopy stratum *Cocos nucifera* and *Avicennia germinans* showed the highest values of cover and frequency (Table 4). The four mangrove species were found as canopy species in the mangrove forest plots. While at the coconut plantation 12 of the 14 canopy species were found (Table 4). Two plots dominated by *C. nucifera* had *A. germinans* and *L. Racemosa* in the canopy (these plots will be referred as the canopy transition plots).

Batis maritima, *Acrostichum aureum,* and *Ernodea littoralis* were found growing at the lowest average elevations within the study area while *Nephrolepis rivularis* and *Jasminum fluminense* were growing at the highest average elevations (Table 2). The tree seedlings growing at the lowest elevations were *Rhizophora mangle* and *Avicennia germinans*. *Erithalis fruticosa* and *Morinda citrifolia* seedlings were growing at the highest elevations.

Species richness

An average of one understory species per plot was found at the 40-plot sample (Table 3). Both, overall species richness (Understory + tree seedlings + unknown species) and understory species richness were significantly different ($t = 4.53$, $df = 34$, $p < 0.001$ and $t = 3.45$, $df = 38$, $p = 0.001$, respectively) between the mangrove area and the coconut plantation. Understory species richness was higher in coconut plots (mean = 1.5) than in mangrove plots (mean = 0.4) (Table 3).

Ordination results

The best solution for the NMS was a 2-dimentional solution (final stress = 13.225, number of iterations = 42). Species present in two or fewer plots were removed from the original 40 plots x 54 species matrix; a total of 31 species (including all 11 unidentified species) were removed leaving a final matrix of 40 x 23. Two outliers, a species and a plot (<2.3 s.d.) were detected but were not excluded because they had little effect on the final ordination. The variability in communities explained by axis 1 was 64% and by axis 2 was 22%.

Plots in ordination space formed three main groups according to the tree species dominating the canopy above these plots: the coconut group, the *Conocarpus* group, and the true mangrove group (Figure 4A and B). The true mangrove group and *Conocarpus* group were separated from the coconut group along axis 1. Another group of 2 plots with a mixture of coconut and mangrove species in the canopy is located between the coconut and true mangrove groups.

Axis 1 was highly correlated with electrical conductivity (Spearman's rank correlation $r = 0.918$, $df = 38$, $p < 0.0001$)(Figure 4A). Other variables that were moderately correlated with axis 1 were canopy cover ($r = -0.734$, $df = 38$, $p < 0.0001$) and total transmittance ($r = 0.731$, $df = 38$, $p < 0.0001$). The remaining variables had weaker relationships with the axis.

The true mangroves group and the coconut group were separated from the *Conocarpus* group along axis 2. The true mangrove group seems to separate itself into two subgroups by dominant canopy species: *Avicennia-Laguncularia* group, and *Rhizophora* group. The variable with highest correlation with this axis was soil water content ($r = 0.601$, $df = 38$, $p < 0.0001$).

Differences among variables

Areas dominated by either mangroves or coconut differed significantly in several of the measured environmental and structural variables. Relative elevation was higher at coconut plots (mean = 50.9 cm) than at mangrove plots (mean = 16.1 cm); ($t = 10.15$, $df = 38$, $p < 0.001$). Electrical conductivity was higher at mangrove plots (mean = 23.1 dS/m) than at coconut plots (mean = 3.0 dS/m); ($t = 10.99$, $df = 17$, $p < 0.001$). Canopy cover was higher at coconut plots (mean = 114.6 %) than at mangrove plots (mean = 54.7 %); ($t = 7.24$, $df = 34$, $p < 0.001$). Overall richness (including tree seedlings) was higher at coconut plots (mean = 3.25) than at mangrove plots (mean = 1.25); ($t = 4.53$, df= 34, $p < 0.001$). Total transmittance was higher at mangrove plots (mean = 39.8 %) than at coconut plots (mean = 19.7 %); ($t = 4.99$, df = 16, $p < 0.001$). Understory species richness was higher at coconut plots (mean = 1.5) than at mangrove plots (mean = 0.4); ($t = 3.45$, df = 38, $p = 0.001$). Canopy richness was higher at coconut plots (mean = 2.54) than at mangrove plots (mean = 1.56); ($t = 3.75$, df = 38, $p = 0.001$). Also, pH was higher at coconut plots (mean = 8.27) than at mangrove plots (mean = 8.04); ($t = 2.84$, df = 31, $p = 0.008$) and soil water content was higher in mangrove plots (mean = 92.17 g) than in coconut plots (mean = 39.79 g); ($t = 2.15$, df = 15, $p = 0.049$). However, the following variables did not show significant differences between mangrove and coconut plots: understory cover ($t = 0.27$, df = 21, $p = 0.791$), overall cover ($t = 0.38$, df = 37, $p = 0.709$), seedling cover ($t = 0.47$, df = 29, $p = 0.644$) and seedling richness ($t = 1.74$, df = 38, $p = 0.089$).

Understory species richness was positively correlated with elevation ($r = 0.581$, df = 38, $p < 0.0001$). It also showed a negative correlation with EC ($r = -0.520$, df = 38, $p = 0.0006$). A negative and lower correlation was found between understory species richness and soil water content ($r = -0.369$, df = 38, $p = 0.019$). Correlations between understory species richness and total transmittance ($r = -0.263$, df = 38, $p = 0.101$), and with pH ($r = 0.055$, df = 38, $p = 0.736$) were not significant.

There were environmental intercorrelated variables (Table 5). Electrical conductivity and elevation had a high but negative correlation ($r = -0.849$, df = 38, $p < 0.0001$). Electrical conductivity and elevation were positively correlated with total transmittance ($r = 0.690$, $df = 38$, $p < 0.0001$ and $r = -0.528$, $df = 38$, $p = 0.001$ respectively). Moderate correlations were found for the following variables: elevation and soil water content ($r = -0.481$, $df = 38$, $p = 0.002$); EC and pH ($r = -0.455$, $df = 38$, $p = 0.003$); and elevation and pH ($r = 0.440$, $df = 38$, $p = 0.005$).

Discussion

Comparisons of Floristic Inventories

In 1981 Pérez et al. conducted a species inventory of the surroundings of the Joyuda Lagoon. They reported a total of 112 plant species that included understory and canopy species (Table 6). There are considerable differences between their species list and the full list of species observed in this study. The most appropriate comparison would be within a similar inventoried area. Table 6 includes the partial list of species they found on the western portion of the surroundings of the Joyuda Lagoon, where they found a total of 61 plant species. Forty-one of those species were not found in this study: 36 understory species, three tree species, and two additional species (name and growth form could not be corroborated with Axelrod's (2011) list). This study found 24 understory species and seven tree species that were not found by Pérez et al. (1981).

One of the species not listed in their study was *Batis maritima,* the understory species with the highest cover and highest frequency in this study. It is a species found in areas of mangrove die-off and hydrologic disturbances (Milbrandt and Tinsley, 2006). The absence of *B. maritima* in their study could mean that the species has colonized the study area recently. However, it is also possible that they failed to distinguish this species from *S. portulacastrum*, which is morphologically similar to *B. maritima* and tend to co-occur. In this study accurate identification of these species was achieved after they flowered. Two other understory species with high frequencies in this study that were not found in Pérez et al. (1981) inventory were *Scleria lithosperma* and *Nephrolepis rivularis*. However, they reported the genus *Scleria* sp., therefore, *S. lithosperma* may have been present then but not identified to species level. It is possible that *N. rivularis* was mistaken for *N. exaltata*, a species reported by Pérez et al. (1981).

Some of the differences among the canopy species found in both studies are worth discussing. *Albizia lebbeck*, *Chrysophyllum oliviforme* and *Chrysobalanus icaco* were not found at the west side of the lagoon, while *Erithalis fruticosa, Morinda citrifolia, Swietenia macrophylla* and *Swietenia mahagoni* were not found anywhere during their survey. Chinea and Agosto (2007) found 14 canopy species among which nine species were also found in the present study, including *Swietenia mahagoni*. Moreover, Chinea and Agosto (2007) observed two canopy species not included in Perez et al. (1981) or in this study: *Thespesia populnea* and *Delonix regia*.

Other than possible misidentifications, the two most likely explanations for these differences in species lists are: different sampling efforts or changes in species composition due to changes in habitat conditions. Sampling efforts were not the same in these studies. Pérez et al. (1981) apparently covered the whole area surrounding the lagoon but it is very unlikely that they were able to find all species living in this area. Moreover, this study covered a small portion of the west side of the lagoon, so the higher number of species found by Pérez et al. (1981) was not unreasonable. What is not compatible with the sampling effort explanation is the large number of species found in this study but not found by Pérez et al. (1981). Habitat changes may explain such difference.

The establishment of a coconut plantation in the study area dates back to the start of the 20th century (though probably earlier), as aerial photos of 1930 shows a very sparse canopy of what seem to be coconut palms planted in a regular pattern (Figure 2A). Aerial photos of more recent years show a very closed canopy dominated by coconut palms, suggesting abandonment of the maintenance of the plantation (Figure 2C). Closing of the canopy likely resulted in habitat changes affecting the persistence of several understory and canopy species. Possible habitat changes could have been reduced light availability, reduced temperatures and increased soil moisture as the canopy closed after its abandonment. After the abandonment of the plantation it is likely that pioneer species like *Psidium guajava* an exotic species commonly found in abandoned agricultural lands in Puerto Rico (Aide, et al., 2000) and reported by Pérez et al. (1981) modified the habitat to be later replaced by other species. In the 1977 aerial photograph (Figure 2B), a few years before Pérez et al. (1983) study, evenly spaced trees (most likely coconut), with a canopy more dense than in previous photos, but with sparse open patches can be observed. This trend in conditions is likely to lead to the replacement of pioneer sun-loving species with shade-tolerant species.

Species and environmental differences between mangrove and coconut forests

Species composition differed drastically between the mangrove forest and the coconut plantation. There were no shared understory species between abandoned coconut plantation and the mangrove forest. Only species at the canopy stratum were shared between both areas (canopy transition plots), which is congruent with Chinea and Agosto (2007) of a clear distinction of species composition at both areas. This difference in composition can be attributed to the environmental conditions of each site.

The variables that showed higher correlations with the distribution of species were elevation, EC, canopy cover and total transmittance. These environmental variables measured showed a significant difference between the plots in the mangrove forest and the coconut plantation, meaning that these two forests are two completely different habitats with different environmental qualities and species. This is congruent with Lugo and Musa's (1993) conclusion that environmental variables define the vegetation profile in Joyuda. One of the few variables showing similar values in these areas was pH. Consistent with Musa's (1986) findings of alkaline pH in basin forests soils without tributaries.

From the EC values obtained, we can conclude that the soils of the mangrove forest are saline soils. There are few species like *B. maritima* and *S. portulacastrum* that can tolerate these saline environments. It is important to mention that *Bacopa monnieri* and *Acrostichum aureum* were found in the preliminary survey as associates of the mangrove forest. Other understory species reported by Gleason and Cook (1928) as associates with *B. maritima* and *S. portulacastrum* were not present in this study.

B. maritima and *S. portulacastrum* are both succulent halophytic species that tolerate high salinities by accumulating salts in their leaves (Lonard, et al., 2011; Lonard and Judd, 1997). They require high sunlight and avoid dense canopy (Lonard, et al., 2011; Lonard and Judd, 1997). Both species were found at plots with high EC, low elevations, high total transmittance (light) and low canopy cover. Both are also affected by the frequency of inundation and avoid high inundation rates (Lonard, et al., 2011). This is why they are found in more inland plots in the mangrove forest, dominated either by *A*. *germinans* or *C. erectus*, and avoiding plots that are dominated by *R. mangle*. From their ecological requirements it is expected that *B. maritima* and *S. portulacastrum* will disappear from plots where canopy cover is increasing and will migrate inland upon sea-level increase.

In general, the abandoned coconut plantation group was characterized by high elevations, low EC, high canopy cover and low total transmittance. There appear to be few clear distribution patterns among the understory species at the coconut plantation. *Abrus precatorius*, *Passiflora suberosa* and *Scleria lithosperma* were a species found far from the mangrove area in the highest elevations and lowest EC values, when compared to the average values found in the plantation. The higher EC values in the coconut plantation were for the canopy transition plots. At these plots *A. aureum*, *F. cymosa* and an unknown species were found. For the remaining understory species a clear pattern could not be established, either because the environmental patterns were not clear or the species was found in 2 or less plots. The same assumption as with canopy trees compositional changes can be applied to understory species at the coconut plantation. Light availability, temperature and soil moisture can affect the composition of these species. During the 1930's when the coconut plantation was active it is probable that these understory species were constantly cleared for maintenance of the plantation.

After the abandonment it is likely that sun-loving species colonized the area to be later replaced by shade-tolerant species.

Because of the correlation between elevation and species dominance, and the relationship of elevation with sea-level it is likely that an increase in sea-level will modify this ecosystem. Chinea and Agosto (2007) compared aerial photographs from 1930 and 1997 and concluded that forest cover doubled its area in the surroundings of the Joyuda Lagoon. This increase included an expansion of fringe mangrove forest as well as a replacement of the coconut plantation with additional coconut growth and colonization by other trees species. A closer inspection of the areas dominated today by mangroves suggests that basin forest, dominated by *Avicennia germinans*, has encroached into the abandoned coconut plantation (Figure 2A and 2C). This basin mangrove expansion may be due to sea-level increase as predicted by the sea-level rise hypothesis. An expected increase of 9.55 cm between 1930 and 2007 should have occurred in Joyuda based on a trend estimate by Zervas (2001). This sea-level increase most likely modified the environment by expanding the flooded area and moving further inland the highly saline soils. This modification of the environment is likely the cause of coconut palm die-off observed in the transition zone between mangroves and the coconut plantation in the study area, and will likely inhibit the regeneration of terrestrial species. If the increase rate in sea level of 0.124 cm/yr continues it is likely that lagoon water will enter several meters inland due to the leveled slopes of the study area (Figure 3). Therefore, creating a more intertidal system with higher salinities and frequent inundation regime that will allow the establishment of mangroves and their understory associates. It is likely that these saline conditions will continue to cause the retreat of the coconut plantation and their associated understory species, promote mangrove expansion and inland movement of mangrove associated understory species. Future monitoring is highly recommended.

Conclusions

1) Species composition on the west side of Joyuda seems to be changing. These changes are likely due to the abandonment of the coconut plantation and the environmental changes associated with this process.
2) The mangrove and abandoned coconut plantation are two distinct habitats that vary in species composition and environmental variables.
3) Electrical conductivity, elevation, total transmittance were the most significant environmental variables and are the variables that define the distribution of the species.
4) There were no shared understory species between the mangrove forest and the coconut plantation, except for species at the canopy stratum.
5) *Batis maritima* and *Sesuvium portulacastrum* were the only understory species found in the mangrove forest.
6) *Abrus precatorius, Acrostichum aureum, Blechum pyramidatum, Capraria biflora, Desmodium incanum, Ernodea littoralis, Fimbristylis cymosa, Jasminum fluminense, Nephrolepis rivularis, Oeceoclades maculata, Paspalum laxum, Passiflora suberosa, Psilotum nudum, Scleria lithosperma,* and *Vigna luteola* were the understory species found in the coconut plantation.
7) The plots in the mangrove forest were characterized by high salinities, high light and low elevations. Meaning that *B. maritima* and *S. portulacastrum* requires

areas that are dominated by mangroves, with high salinities, lots of light and low elevations.

8) The plots in the coconut plantation were characterized by low salinities and light; and high elevations.

9) Comparison between the mangrove species indicates that in average the lowest elevation and highest soil water content values were found in plots dominated by *R. mangle*. While the highest elevation, lowest EC, soil water content and total transmittance was found for the *C. erectus* plot. *A. germinans* plots had the highest EC, total transmittance and canopy cover and the lowest pH.

10) Mangrove forest expansion into the coconut plantation is most likely due to sea-level increase. If the reported sea-level increase continue it is likely that the coconut plantation will continue to retreat and mangrove forest expand.

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Tables

Table 1. List of all the plant species found in the study area divided by the sampling type where they were found. Species found at each sampling type are marked with an X.

Growth form	Family	Species name	Sampling types		
			Preliminary survey	70-plot sample	40-plot sample
Understory Species					
fern-like	Pteridaceae	*Acrostichum aureum*		X	X
fern-like	Pteridaceae	*Acrostichum danaeifolium*	X		
fern-like	Lomariopsidaceae	*Nephrolepis rivularis*	X	X	X
forb/herb	Psilotaceae	*Psilotum nudum*		X	X
herb	Amaranthaceae	*Alternanthera ficoidea*	X		
herb	Plantaginaceae	*Bacopa monnieri*	X		
herb	Bataceae	*Batis maritima*		X	X
herb	Acanthaceae	*Blechum pyramidatum*		X	X
herb	Scrophulariaceae	*Capraria biflora*		X	X
herb	Fabaceae-Faboideae	*Crotalaria retusa*	X		
herb	Fabaceae-Faboideae	*Desmodium incanum*		X	X
herb	Euphorbiaceae	*Euphorbia cyathophora*	X		
herb	Cyperaceae	*Fimbristylis cymosa*		X	X
herb	Cyperaceae	*Fimbristylis dichotoma*	X		
herb	Cyperaceae	*Fimbristylis spadicea*	X		
herb	Orchidaceae	*Oeceoclades maculata*	X	X	X
herb	Poaceae	*Paspalum laxum*	X	X	X
herb	Cyperaceae	*Scleria lithosperma*		X	X

herb	Aizoaceae	*Sesuvium portulacastrum*	X	X	X
herb	Asteraceae	*Sphagneticola trilobata*	X		
herb	Verbenaceae	*Stachytarpheta strigosa*	X		
herb	Asteraceae	*Synedrella nodiflora*	X		
herb	Poaceae	*Zoysia matrella*	X		
herb/shrub	Euphorbiaceae	*Argythamnia candicans*	X		
shrub	Rubiaceae	*Ernodea littoralis*		X	X
vine	Fabaceae-Faboideae	*Abrus precatorius*		X	X
vine	Vitaceae	*Cissus verticillata*	X		
vine	Cucurbitaceae	*Doyerea emetocathartica*	X		
vine	Oleaceae	*Jasminum fluminense*		X	X
vine	Asteraceae	*Mikania micrantha*	X		
vine	Passifloraceae	*Passiflora suberosa*	X	X	X
vine	Fabaceae-Faboideae	*Teramnus labialis*	X		
vine	Fabaceae-Faboideae	*Vigna luteola*		X	X
	Tree species				
shrub/tree	Chrysobalanaceae	*Chrysobalanus icaco*		X	X*
shrub/tree	Celastraceae	*Crossopetalum rhacoma*		X	X
shrub/tree	Rubiaceae	*Erithalis fruticosa*		X	X
shrub/tree	Rubiaceae	*Morinda citrifolia*		X	X
tree	Fabaceae-Mimosoideae	*Albizia lebbeck*			X*
tree	Fabaceae-Faboideae	*Andira inermis*		X	X
tree	Acanthaceae	*Avicennia germinans*		X	X*
tree	Burseraceae	*Bursera simaruba*		X	X*
tree	Clusiaseae	*Calophyllum antillanum*		X	X*
tree	Sapotaceae	*Chrysophyllum oliviforme*			X*

tree	Arecaceae	*Cocos nucifera*	X	X*
tree	Combretaceae	*Conocarpus erectus*		X*
tree	Combretaceae	*Laguncularia racemosa*	X	X*
tree	Rhizophoraceae	*Rhizophora mangle*	X	X*
tree	Arecaceae	*Sabal causiarum*		X*
tree	Meliaceae	*Swietenia macrophylla*		X*
tree	Meliaceae	*Swietenia mahagoni*		X*
tree	Meliaceae	*Swietenia spp*	X	X
tree	Combretaceae	*Terminalia catappa*		X*
Unknown species				
		sp1	X	X
		sp2	X	X
		sp3	X	X
		sp4	X	X
		sp5	X	X
		sp6	X	X
		sp7	X	X
		sp8	X	X
		sp9	X	X
		sp10	X	X
		sp11	X	X

*Tree species found as canopy species.

Table 2. List of all the species found in the 70-plot sample with their respective average cover, frequency and the average cover of each species within the mangrove, coconut/mangrove and coconut plantation dominated plots. Average elevation corresponds to the average elevation of all the plots where the species was found.

Species	**Acronym**	**Average cover (%)**	**Frequency (%)**	**Average cover (%)**			**Average Elevation (cm)****
				Mangrove	**Coconut/ Mangrove***	**Coconut plantation**	
Understory species							
Abrus precatorius l.	*abr pre*	0.064	4.286	0.000	0.000	0.098	60.200
Acrostichum aureum	*acr aur*	0.410	1.429	0.000	14.350	0.624	27.400
Batis maritima	*bat mar*	1.306	7.143	3.808	0.000	0.000	25.760
Blechum pyramidatum	*ble pyr*	0.034	1.429	0.000	0.000	0.052	48.600
Capraria biflora	*cap bif*	0.011	2.857	0.000	0.000	0.017	48.600
Desmodium incanum	*des inc*	0.060	1.429	0.000	0.000	0.091	48.600
Ernodea littoralis	*ern lit*	0.137	1.429	0.000	0.000	0.209	27.400
Fimbristylis cymosa	*fim cym*	0.352	5.714	0.000	0.060	0.535	36.650
Jasminum fluminense	*jas flu*	0.027	1.429	0.000	0.000	0.041	62.800
Nephrolepis rivularis	*nep riv*	0.211	5.714	0.000	0.000	0.322	62.850
Oeceoclades maculata	*oec mac*	0.026	2.857	0.000	0.000	0.039	62.600
Paspalum laxum	*pas lax*	0.113	2.857	0.000	0.000	0.172	54.300
Passiflora suberosa	*pas sub*	0.184	4.286	0.000	0.000	0.280	62.000
Psilotum nudum	*psi nud*	0.037	4.286	0.000	0.000	0.057	50.133
Scleria lithosperma	*scl lit*	0.312	10.000	0.000	0.000	0.475	61.400

Sesuvium portulacastrum	*ses port*	0.277	2.857	0.808	0.000	0.000	27.600
Vigna luteola	*vig lut*	0.004	1.429	0.000	0.000	0.007	61.800
Seedlings of woody species							
Andira inermis	*and ine*	0.040	2.857	0.000	0.000	0.061	39.900
Avicennia germinans	*avi ger*	0.479	7.143	1.396	0.000	0.000	17.980
Bursera simaruba	*bur sim*	0.171	17.143	0.000	0.000	0.261	42.983
Calophyllum antillanum	*cal cal*	0.906	10.000	0.000	0.000	1.378	49.914
Chrysobalanus icaco	*chr ica*	0.140	5.714	0.000	0.000	0.213	48.450
Cocos nucifera	*coc nuc*	0.073	2.857	0.000	0.000	0.111	46.700
Crossopetalum rhacoma	*cro rha*	0.144	4.286	0.000	0.000	0.220	45.333
Erithalis fruticosa	*eri fru*	0.003	1.429	0.000	0.000	0.004	61.200
Laguncularia racemosa	*lag rac*	0.627	8.571	1.829	0.000	0.000	19.000
Morinda citrifolia	*mor cit*	0.011	1.429	0.000	0.000	0.017	57.000
Rhizophora mangle	*rhi man*	0.211	4.286	0.617	0.000	0.000	10.600
Swietenia spp.	*swi spp*	0.360	21.429	0.000	0.000	0.548	50.200
Unknown species							
sp1	sp1	0.029	1.429	0.000	0.000	0.043	68.000
sp2	sp2	0.002	1.429	0.000	0.000	0.003	59.800
sp3	sp3	0.001	1.429	0.000	0.000	0.002	59.800
sp4	sp4	0.050	1.429	0.000	0.000	0.076	59.800
sp5	sp5	0.003	1.429	0.000	0.000	0.004	61.800
sp6	sp6	0.023	1.429	0.000	0.000	0.035	27.400
sp7	sp7	0.024	1.429	0.000	0.000	0.037	27.400
sp8	sp8	0.006	1.429	0.000	0.000	0.009	57.000
sp9	sp9	1.289	1.429	0.000	45.100	1.961	31.000

sp10	sp10	0.001	1.429	0.000	0.000	0.002	61.800
sp 11	sp11	0.003	1.429	0.000	0.000	0.004	62.800

*These values corresponds to the canopy transition plots.
**The reference value was 0 cm.

Table 3. Average species richness and species diversity separated by species categories and canopy dominance groups for the 40-plot sample.

Group (sample size)	Average species richness (S.D.)	Shannon's diversity index	Exp Shannon
Overall (40)			
Understory species	1.1 (1.30)	0.201	1.223
Tree Seedlings	1.1 (1.24)	0.166	1.181
Understory species + unknown species	1.4 (1.45)	0.249	1.283
Canopy dominance (40)			
Mangrove			
Understory + tree seedlings + unknown	1.2 (1.71)	0.193	1.213
Understory	0.4 (1.55)	0.062	1.064
Coconut Plantation			
Understory + tree seedlings + unknown	3.2 (1.74)	0.728	2.071
Understory	1.5 (1.14)	0.294	1.342

Table 4. Average cover and frequency of the 14 tree species found as canopy species at the 40-plot sample, plus the average cover of each specie at the mangrove dominated plots and coconut dominated plots.

Species	Acronym	Average cover (%)	Frequency (%)	Average cover (%)	
				Mangrove	Coconut plantation
Albizia lebbeck	alb leb'	1.000	2.500	0.000	1.667
Avicennia germinans	avi ger'	13.250	32.500	29.375	2.500
Bursera simaruba	bur sim'	0.125	2.500	0.000	0.208
Calophyllum antillanum	cal cal'	6.250	22.500	0.000	10.417
Chrysophylum oliviforme	chr oli'	0.125	2.500	0.000	0.208
Cocos nucifera	coc nuc'	39.500	60.000	0.000	65.833
Conocarpus erectus	con ere'	1.875	5.000	4.688	0.000
Chrysobalanus icaco	chr ica'	3.125	10.000	0.000	5.208
Laguncularia racemosa	lag rac'	3.750	20.000	8.750	0.417
Rhizophora mangle	rhi man'	4.750	10.000	11.875	0.000
Sabal causiarum	sab cau'	1.250	5.000	0.000	2.083
Swietenia macrophylla	swi mac'	1.250	7.500	0.000	2.083
Swietenia mahagoni	swi mah'	12.250	20.000	0.000	20.417
Terminalia catappa	ter cat'	1.875	12.500	0.000	3.125

Table 5. Intercorrelation values based on Pearson's correlation coefficient for the environmental variables at the 40-plot sample. Correlation coefficients in bold were significant at $p < 0.05$. Environmental variables are: pH, EC= electrical conductivity (salinity), SWC= soil water content and total transmittance (light availability).

	pH	EC	SWC	Total transmittance
Elevation	**0.440**	**-0.849**	**-0.481**	**-0.528**
pH	1.000	**-0.455**	-0.050	**-0.392**
EC		1.000	**0.348**	**0.690**
SWC			1.000	0.062

Table 6. Comparison of the species found by Pérez et al. (1981) and the current research.

Growth form	Family	Species name	Current Research	Pérez et al. (1981) west inventory	Pérez et al. (1981) full inventory
fern-like	Pteridaceae	*Acrostichum aureum*	X	X	X
fern-like	Pteridaceae	*Acrostichum danaeafolium*	X	X	X
herb	Cyperaceae	*Fimbristylis cymosa*	X	X	X
herb	Cyperaceae	*Fimbristylis dichotoma*	X	X	X
herb	Poaceae	*Paspalum laxum*	X	X	X
herb	Aizoaceae	*Sesuvium portulacastrum*	X	X	X
herb	Asteraceae	*Sphagneticola trilobata*	X	X	X
shrub	Rubiaceae	*Ernodea littoralis*	X	X	X
shrub/tree	Celastraceae	*Crossopetalum rhacoma*	X	X	X
tree	Fabaceae-Faboideae	*Andira inermis*	X	X	X
tree	Acanthaceae	*Avicennia germinans*	X	X	X
tree	Burseraceae	*Bursera simaruba*	X	X	X
tree	Clusiaceae	*Calophyllum antillanum*	X	X	X
tree	Arecaceae	*Cocos nucifera*	X	X	X
tree	Combretaceae	*Conocarpus erectus*	X	X	X
tree	Combretaceae	*Laguncularia racemosa*	X	X	X
tree	Rhizophoraceae	*Rhizophora mangle*	X	X	X
tree	Arecaceae	*Sabal causiarum*	X	X	X
tree	Combretaceae	*Terminalia catappa*	X	X	X
vine	Fabaceae-Faboideae	*Vigna luteola*	X	X	X

herb	Plantaginaceae	*Bacopa monnieri*	X	X
shrub/tree	Chrysobalanaceae	*Chrysobalanus icaco*	X	X
tree	Fabaceae-Mimosoideae	*Albizia lebbeck*	X	X
tree	Sapotaceae	*Chrysophyllum oliviforme*	X	X
fern-like	Lomariopsidaceae	*Nephrolepis rivularis*	X	
forb/herb	Psilotaceae	*Psilotum nudum*	X	
herb	Amaranthaceae	*Alternanthera ficoidea*	X	
herb	Bataceae	*Batis maritima*	X	
herb	Acanthaceae	*Blechum pyramidatum*	X	
herb	Scrophulariaceae	*Capraria biflora*	X	
herb	Fabaceae-Faboideae	*Crotalaria retusa*	X	
herb	Fabaceae-Faboideae	*Desmodium incanum*	X	
herb	Euphorbiaceae	*Euphorbia cyathophora*	X	
herb	Cyperaceae	*Fimbristylis spadicea*	X	
herb	Orchidaceae	*Oeceoclades maculata*	X	
herb	Cyperaceae	*Scleria lithosperma*	X	
herb	Verbenaceae	*Stachytarpheta strigosa*	X	
herb	Asteraceae	*Synedrella nodiflora*	X	
herb	Poaceae	*Zoysia matrella*	X	
herb/shrub	Euphorbiaceae	*Argythamnia candicans*	X	
shrub/tree	Rubiaceae	*Erithalis fruticosa*	X	
shrub/tree	Rubiaceae	*Morinda citrifolia*	X	
tree	Meliaceae	*Swietenia macrophylla*	X	
tree	Meliaceae	*Swietenia mahagoni*	X	
vine	Fabaceae-Faboideae	*Abrus precatorius*	X	

vine	Vitaceae	*Cissus verticillata*	X		
vine	Cucurbitaceae	*Doyerea emetocathartica*	X		
vine	Oleaceae	*Jasminum fluminense*	X		
vine	Asteraceae	*Mikania micrantha*	X		
vine	Passifloraceae	*Passiflora suberosa*	X		
vine	Fabaceae-Faboideae	*Teramnus labialis*	X		
fern-like	Lomariopsidaceae	*Nephrolepis exaltata*		X	X
herb	Poaceae	*Andropogon bicornis*		X	X
herb	Poaceae	*Axonopus compressus*		X	X
herb	Asteraceae	*Bidens pilosa*		X	X
herb	Malvaceae	*Corchorus hirsutus*		X	X
herb	Fabaceae-Faboideae	*Crotalaria incana*		X	X
herb	Fabaceae-Faboideae	*Crotalaria pallida*		X	X
herb	Cyperaceae	*Cyperus ligularis*		X	X
herb	Cyperaceae	*Cyperus polystachyos*		X	X
herb	Poaceae	*Dichanthium annulatum*		X	X
herb	Cyperaceae	*Eleocharis geniculata*		X	X
herb	Asteraceae	*Emilia coccinea*		X	X
herb	Euphorbiaceae	*Euphorbia heterophylla*		X	X
herb	Euphorbiaceae	*Euphorbia hypericifolia*		X	X
herb	Poaceae	*Eustachys petraea*		X	X
herb	Cyperaceae	*Fimbristylis ferruginea*		X	X
herb	Poaceae	*Paspalum virgatum*		X	X
herb	Phyllanthaceae	*Phyllanthus urinaria*		X	X
herb	Asteraceae	*Pluchea odorata*		X	X

herb	Cyperaceae	*Scleria sp.*	X	X
herb	Fabaceae-Faboideae	*Sesbania sericea*	X	X
herb	Poaceae	*Spartina patens*	X	X
herb	Rubiaceae	*Spermacoce verticillata*	X	X
herb	Poaceae	*Sporobolus indicus*	X	X
herb	Poaceae	*Sporobolus virginicus*	X	X
herb	Verbenaceae	*Stachytarpheta jamaicensis*	X	X
herb	Turneraceae	*Turnera ulmifolia*	X	X
shrub	Asteraceae	*Chromolaena odorata*	X	X
shrub	Verbenaceae	*Lantana camara*	X	X
shrub	Verbenaceae	*Lantana involucrata*	X	X
shrub	Malvaceae	*Waltheria indica*	X	X
shrub	Asteraceae	*Chromolaena corymbosa*	X	X
shrub/tree	Apocynaceae	*Rauvolfia nitida*	X	X
tree	Annonaceae	*Annona glabra*	X	X
shrub/tree	Myrtaceae	*Psidium guajava*	X	X
vine	Fabaceae-Faboideae	*Centrosema pubescens*	X	X
vine	Convolvulaceae	*Ipomoea tiliacea*	X	X
vine	Passifloraceae	*Passiflora foetida*	X	X
vine	Malpighiaceae	*Stigmaphyllon emarginatum*	X	X
	Malvaceae	*Hibiscus sp.*	X	X
		Trichachne insularis	X	X
herb	Fabaceae-Faboideae	*Aeschynomene americana*		X
herb	Apocynaceae	*Asclepias curassavica*		X
herb	Asteraceae	*Conyza canadensis*		X

herb	Poaceae	*Cynodon dactylon*	X
herb	Cyperaceae	*Cyperus odoratus*	X
herb	Cyperaceae	*Cyperus surinamensis*	X
herb	Cyperaceae	*Eleocharis elegans*	X
herb	Cyperaceae	*Eleocharis interstincta*	X
herb	Cyperaceae	*Fuirena umbellata*	X
herb	Cyperaceae	*Kyllinga brevifolia*	X
herb	Poaceae	*Leersia hexandra*	X
herb	Onagraceae	*Ludwigia octovalvis*	X
herb	Poaceae	*Megathyrsus maximus*	X
herb	Fabaceae-Mimosoideae	*Mimosa pudica*	X
herb	Poaceae	*Pennisetum purpureum*	X
herb	Cyperaceae	*Rhynchospora ciliata*	X
herb	Poaceae	*Saccharum officinarum*	X
herb	Fabaceae-Caesalpinioideae	*Senna occidentalis*	X
herb	Malvaceae	*Sida acuta*	X
herb	Poaceae	*Steinchisma laxa*	X
herb	Poaceae	*Stenotaphrum secundatum*	X
herb	Fabaceae-Faboideae	*Tephrosia cinerea*	X
herb	Bromeliaceae	*Tillandsia utriculata*	X
herb	Orchidaceae	*Tolumnia variegata*	X
herb	Typhaceae	*Typha domingensis*	X
herb	Malvaceae	*Urena lobata*	X
herb	Poaceae	*Urochloa mutica*	X
shrub	Solanaceae	*Solanum torvum*	X

shrub/tree	Anacardiaceae	*Comocladia dodonaea*	X
shrub/tree	Fabaceae-Mimosoideae	*Leucaena leucocephala*	X
shrub/tree	Rubiaceae	*Randia aculeata*	X
shrub/tree	Rubiaceae	*Rondeletia inermis*	X
shrub/tree	Fabaceae-Mimosoideae	*Senegalia riparia*	X
tree	Malpighiaceae	*Byrsonima lucida*	X
tree	Salicaceae	*Casearia sylvestris*	X
tree	Verbenaceae	*Citharexylum spinosum*	X
tree	Clusiaceae	*Clusia rosea*	X
tree	Polygonaceae	*Coccoloba michrostachya*	X
tree	Bignoniaceae	*Crescentia cujete*	X
tree	Clusiaceae	*Mammea americana*	X
tree	Anacardiaceae	*Mangifera indica*	X
tree	Polygalaceae	*Polygala penaea*	X
tree	Arecaceae	*Roystonea borinquena*	X
tree	Fabaceae-Caesalpinioideae	*Stahlia monosperma*	X
tree	Bignoniaceae	*Tabebuia heterophylla*	X
vine	Dennstaedtiaceae	*Pteridium caudatum*	X
		Fuillantus urinaria	X

Figures

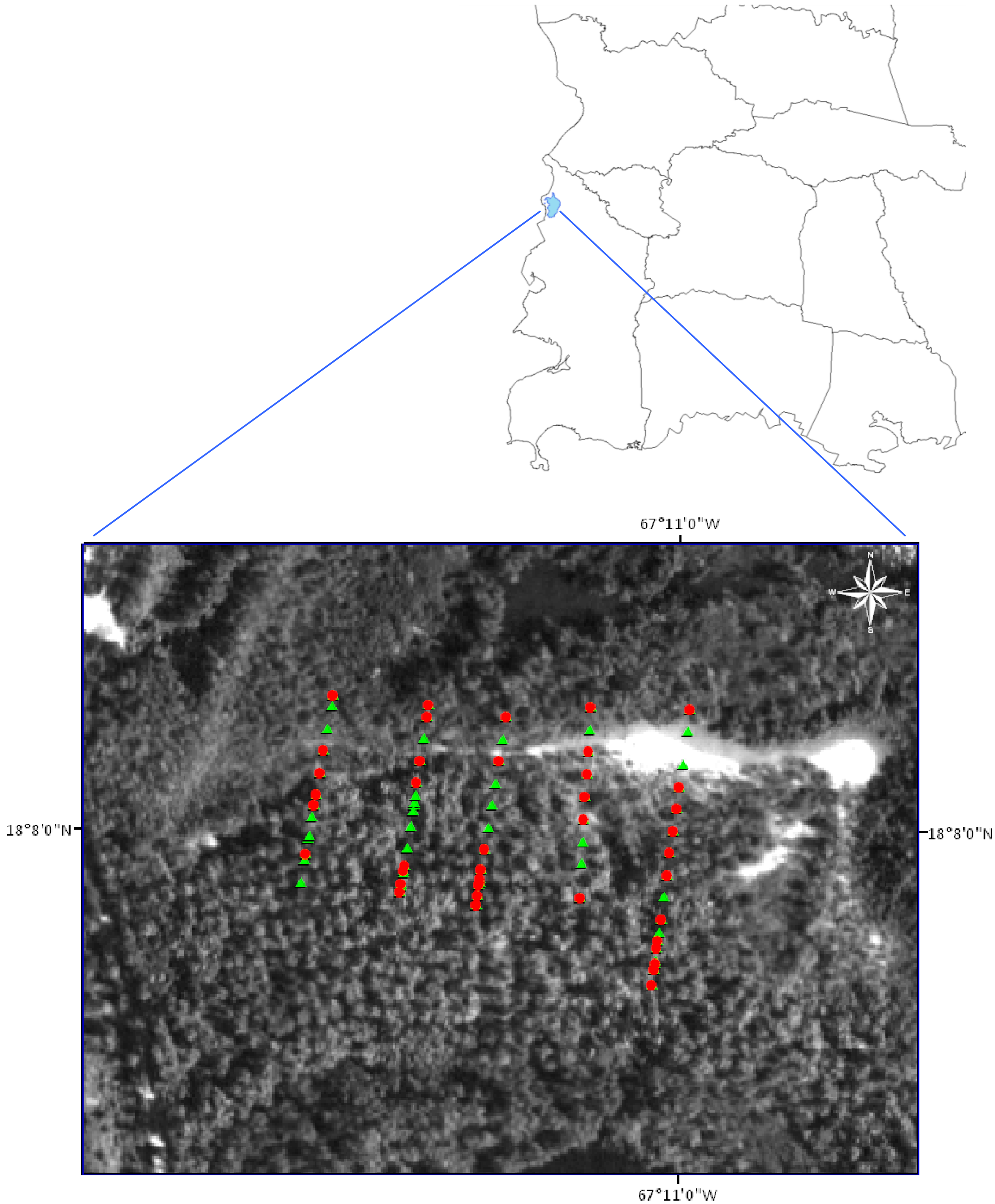
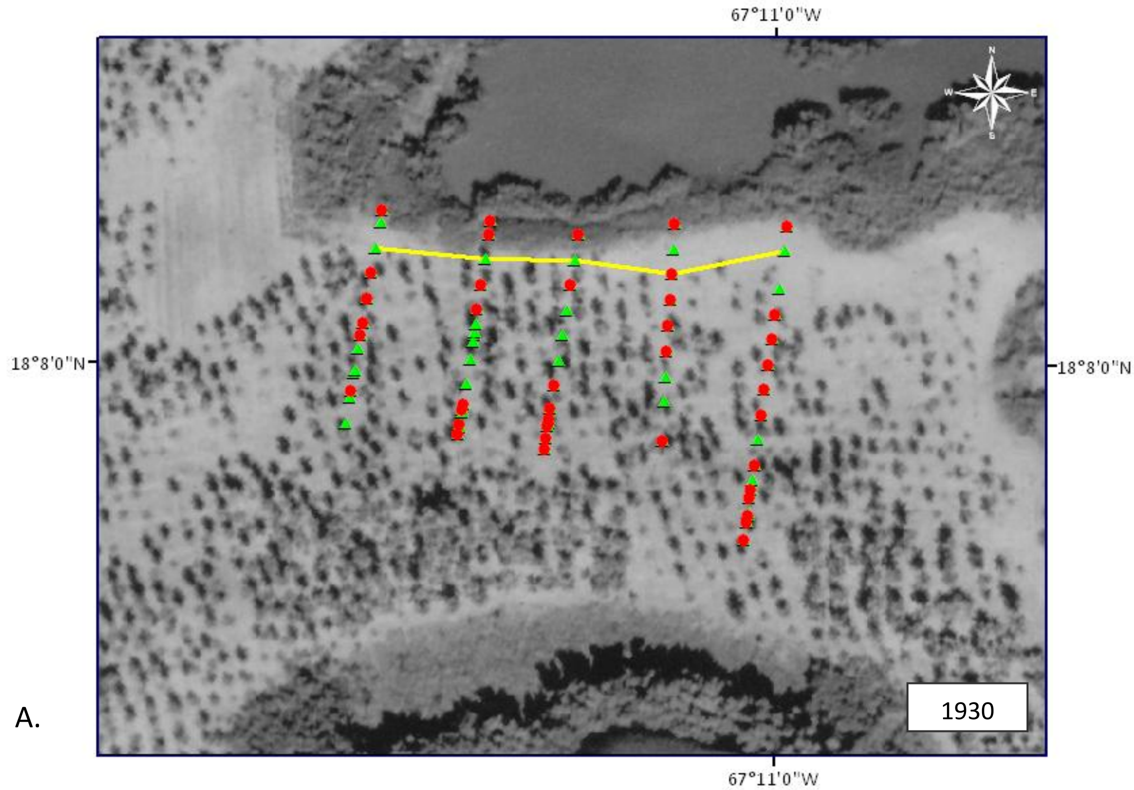
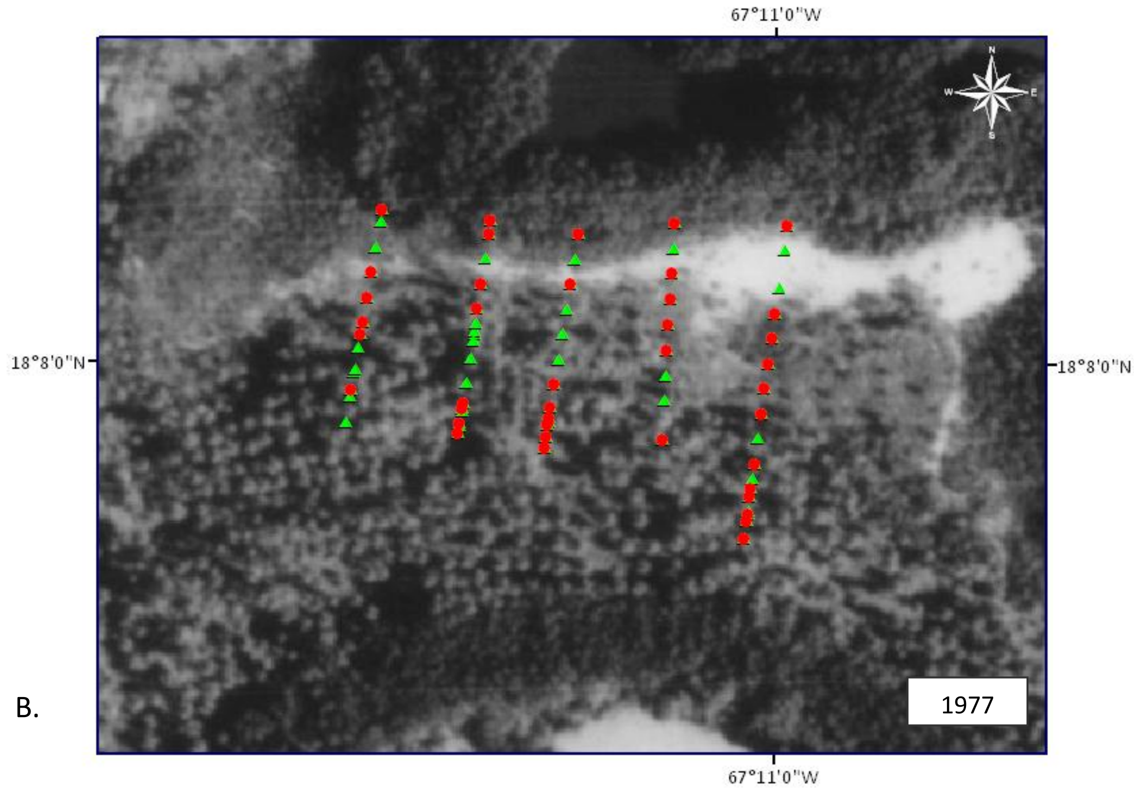


Figure 1. Map of southwest Puerto Rico; the Joyuda Lagoon is highlighted in blue. Aerial photograph of 2004; the study area lies at the west side of the Joyuda Lagoon, just north of Atolladero Lagoon. Red dots and green triangles mark the 70-plot sample at the study area. Red dots are the 40-plot sample where environmental variables were measured.

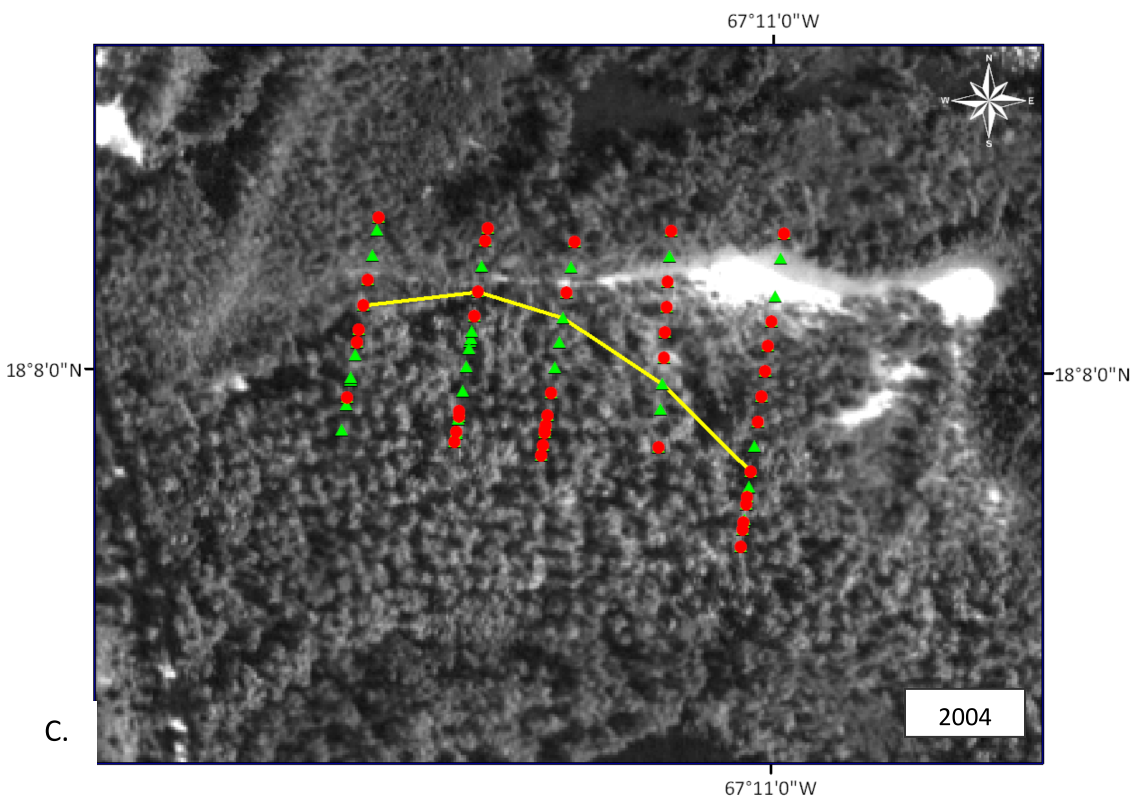


A.

Figure 2. Aerial photographs of the study area on three different dates. Red dots and green triangles are the 70-plot sample, the red dots are the 40-plot sample, the yellow line represents the limit of the coconut plantation. A. Study area during the 1930 shows evenly spaced vegetation indicating that the area was an active coconut plantation. B. Image of 1977 shows even distributed vegetation with a denser canopy and vegetation-free gaps result of a recent abandonment of the coconut plantation. C. Aerial photograph during the 2004 shows a denser canopy and coconut retreat. Maps were created using ArcGIS 10; GPS points were obtained with a Magellan MobileMapper with sub-meter accuracy.


67°11'0"W
18°8'0"N
18°8'0"N
67°11'0"W
1977

B.


67°11'0"W
18°8'0"N
18°8'0"N
67°11'0"W
2004

C.

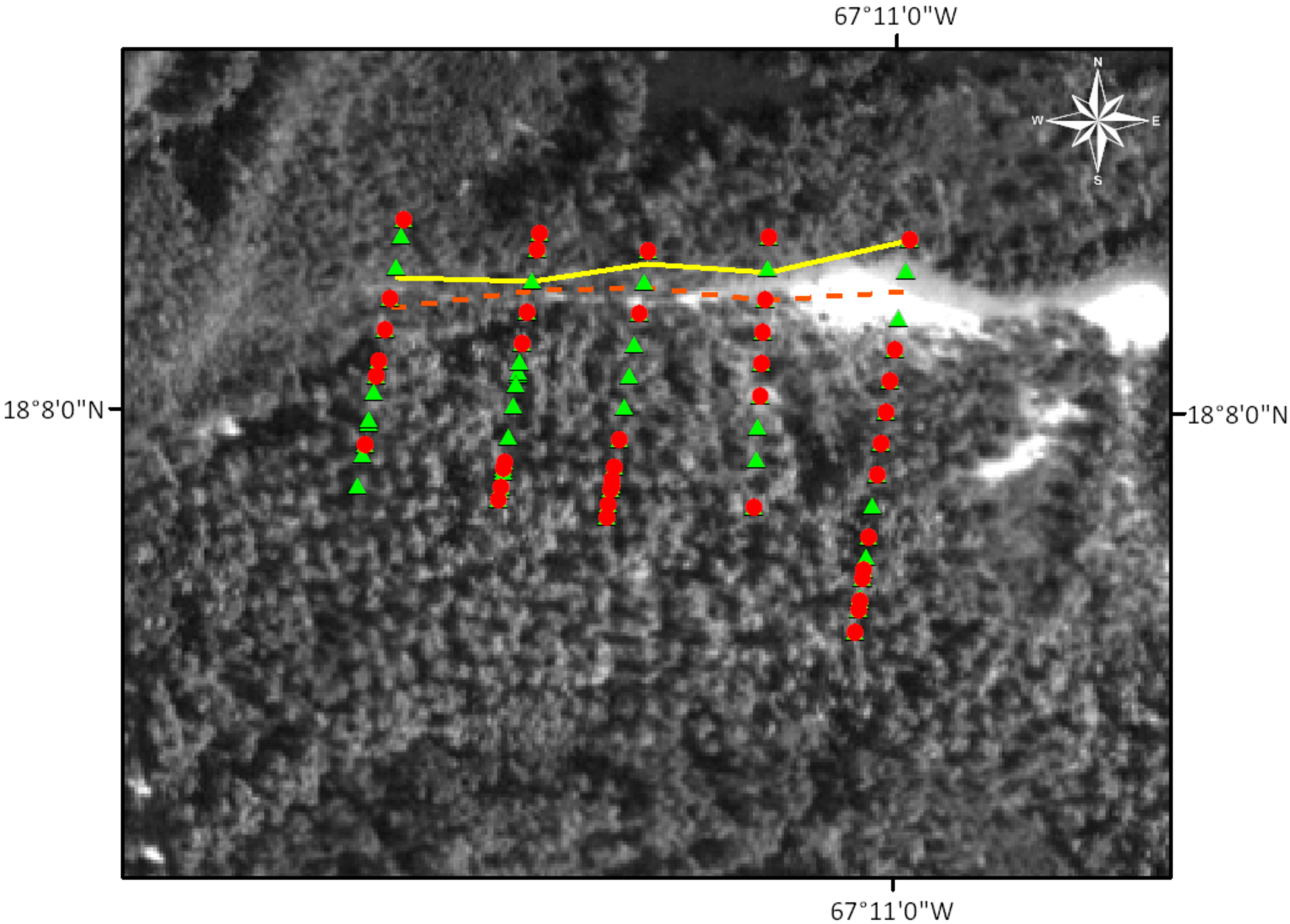


Figure 3. Aerial photograph of 2004, yellow solid line represents current sea-level based on a reference elevation of 11.7 cm, red dashed line represents sea-level increase for 2050 at a rate of .12 cm/yr.

A.

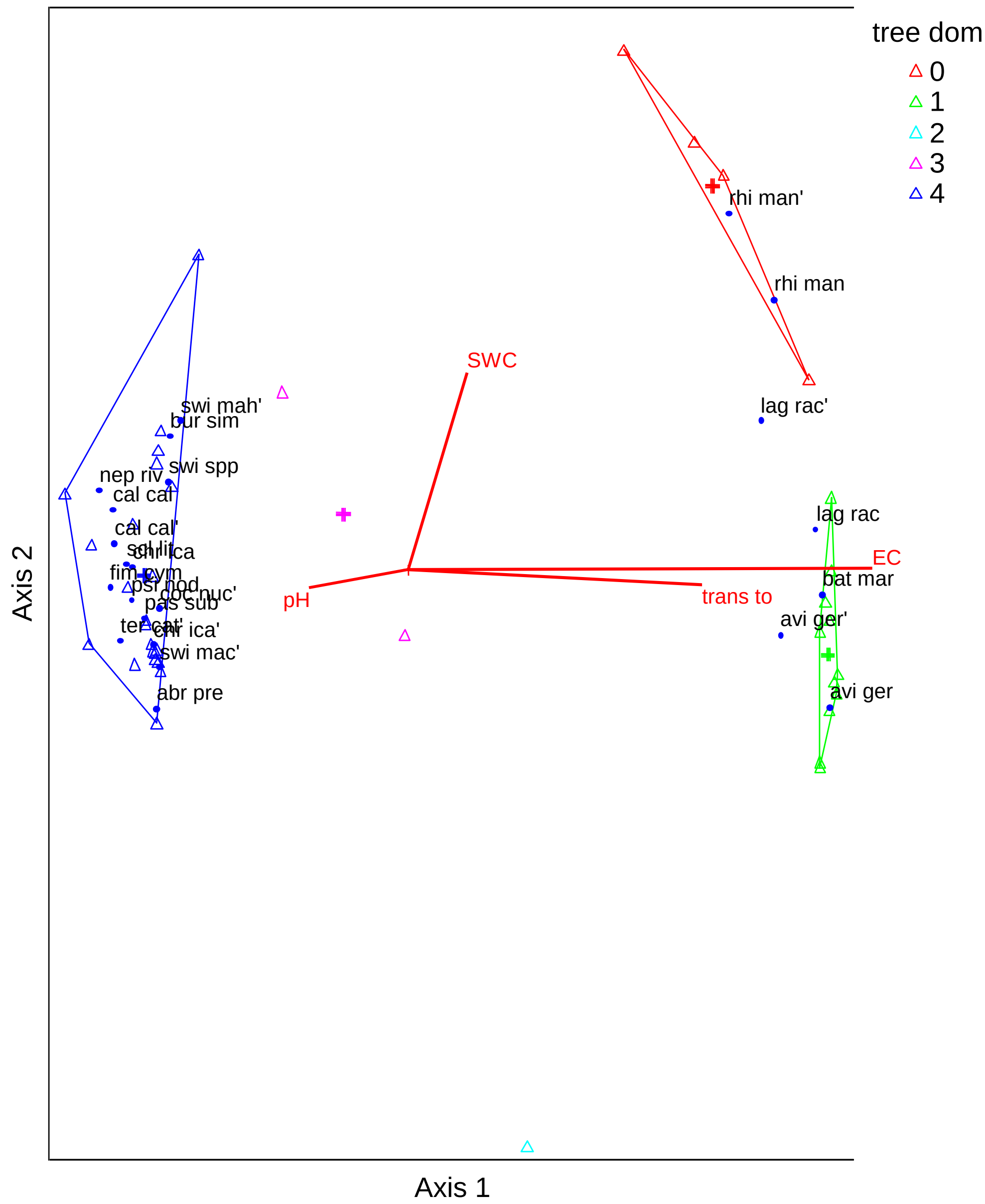
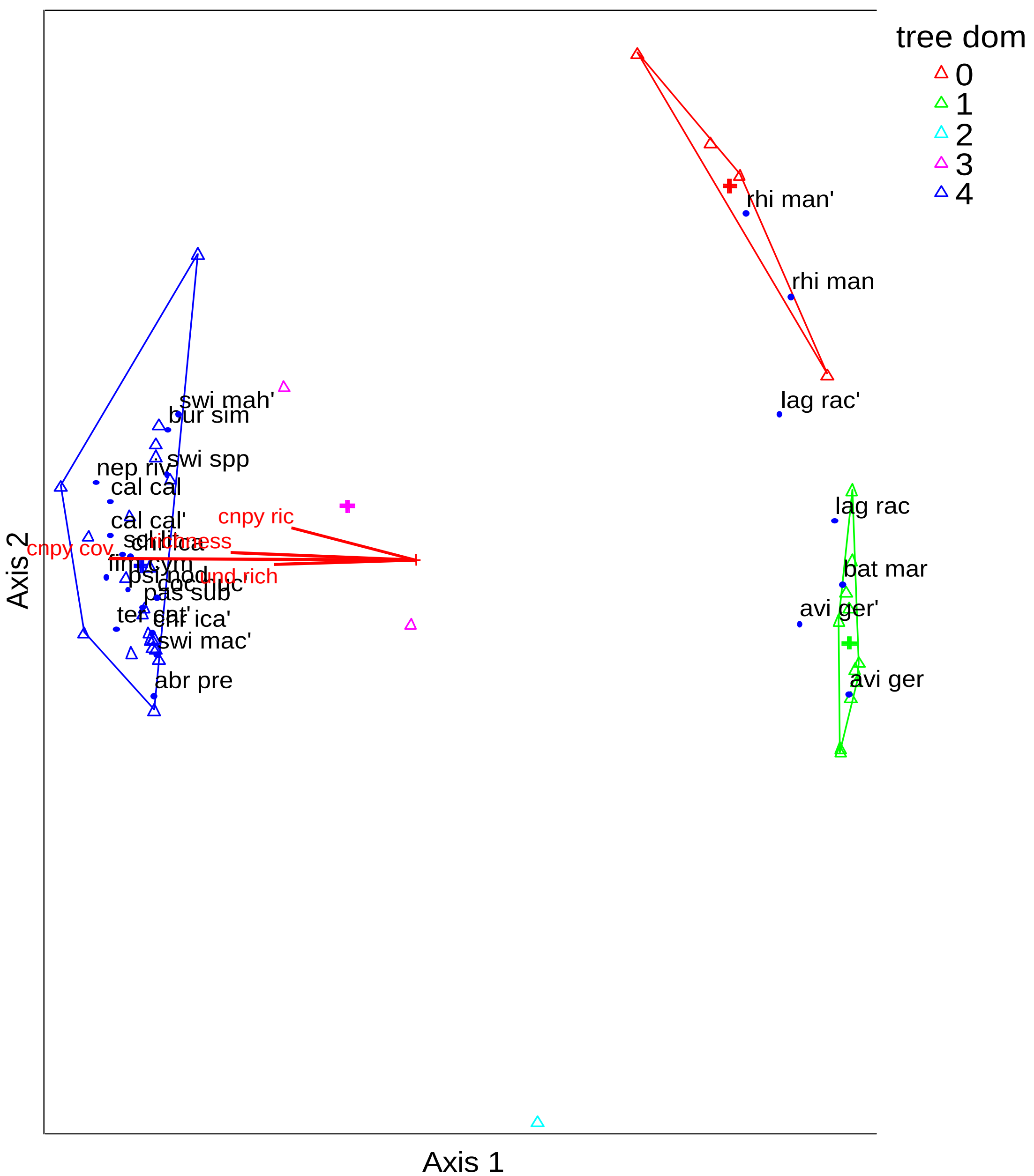


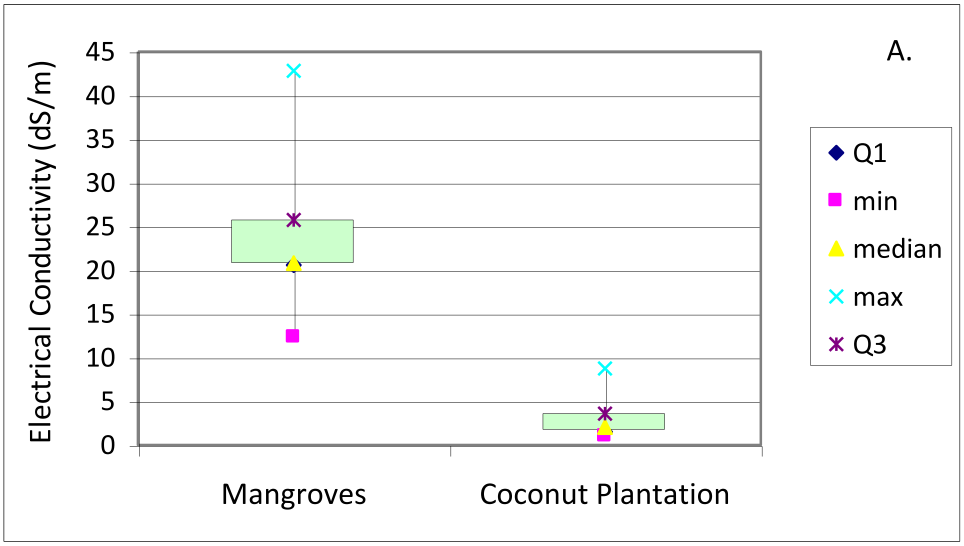
Figure 4. Non-metric multidimensional scaling ordination graphs. Tree dominance is as follow: red triangles=*R. mangle*, green triangles=*A. germinans* and/or *L. racemosa*, light blue triangle=*C. erectus*, pink triangles= canopy transition plots and blue triangles=*C. nucifera*. A. NMS with a joint plot of environmental variables. The environmental variables are as follow: SWC= soil water content, EC= electrical conductivity, trans tot= total transmittance and pH. B. NMS with structural variables. The environmental variables are as follow: cnpy ric= canopy richness, richness= overall richness, cnpy cov= canopy cover and und rich= understory richness. Species acronyms can be found in table 2 and 4.

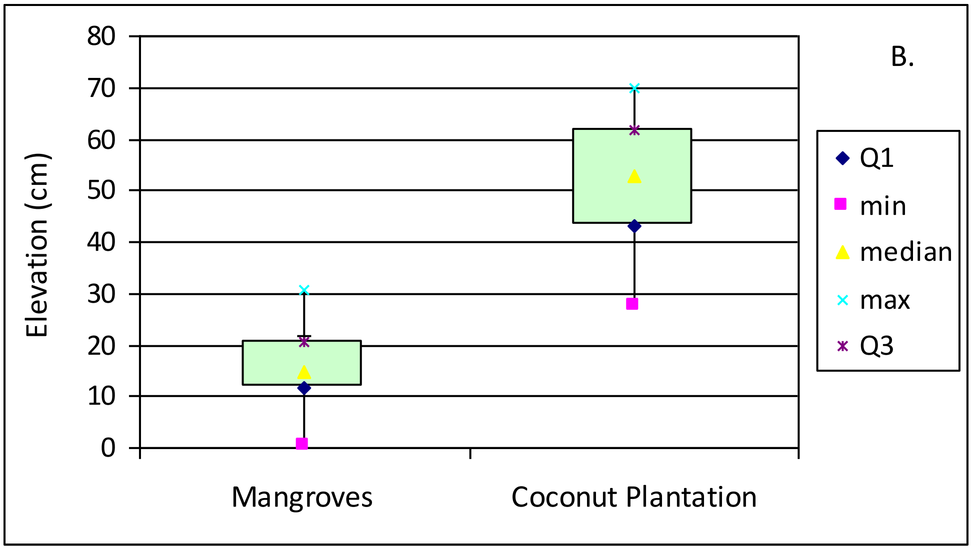
B.

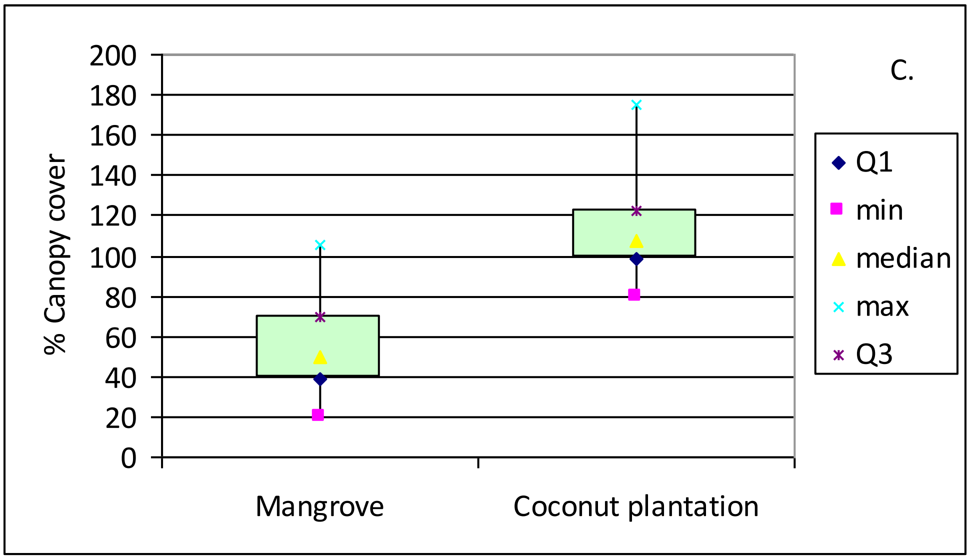

tree dom
0
1
2
3
4
rhi man'
rhi man
lag rac'
lag rac
bat mar
avi ger'
avi ger
swi mah'
bur sim
swi spp
nep riv
cal cal
cal cal'
cnpy ric
cnpy cov
swi mac'
abr pre
und rich
Axis 1
Axis 2

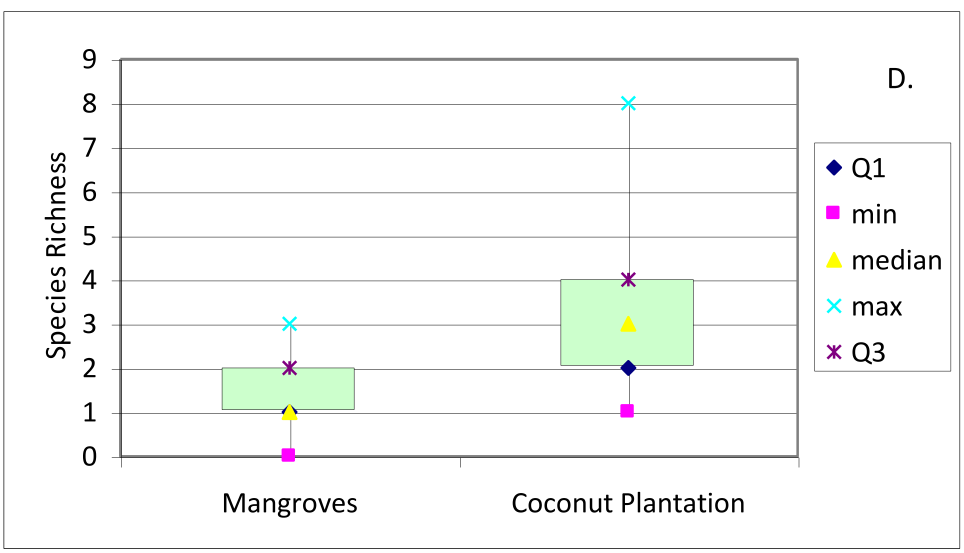
Appendices

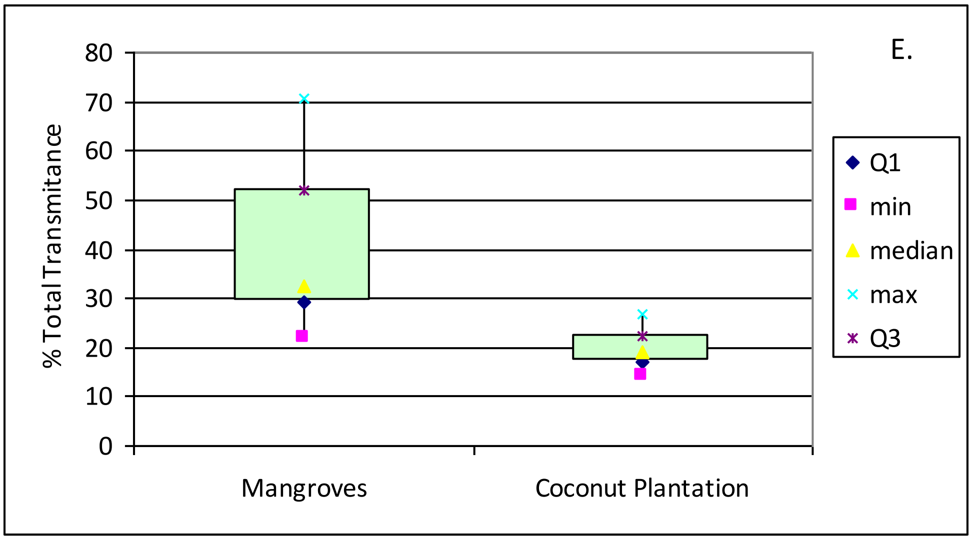
Appendix 1. Comparison of the variables that showed significance between the mangrove forest and the coconut plantation for the 40-sample plots. Q1 represents the first quartile, Q3 the third quartile, min is the minimum value, max is the maximum value and the median of the data. A. Electrical conductivity, B. Elevation, C. Canopy cover, D. Overall species richness, E. Total transmittance, F. Understory species richness, G. Canopy richness, H. pH and I. Soil water content.

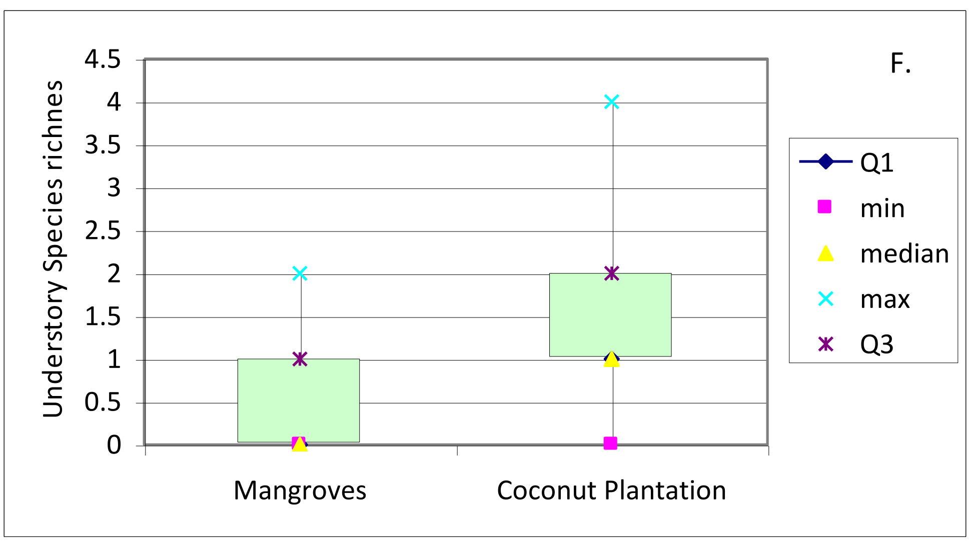


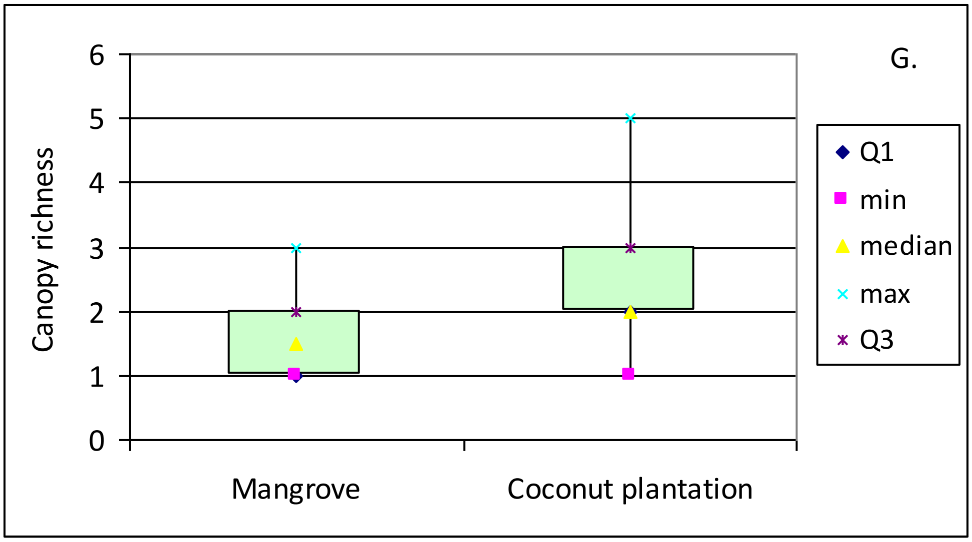


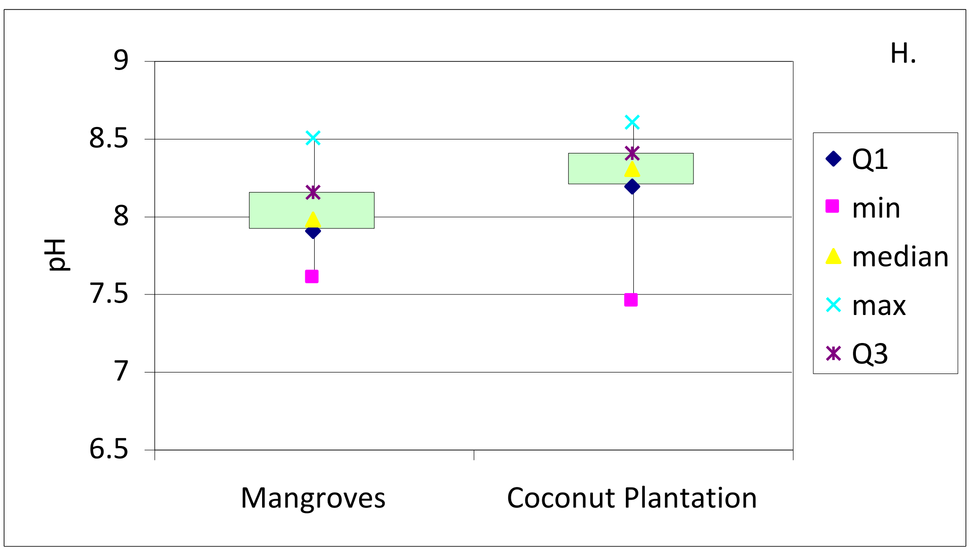

C.
% Canopy cover
200
180
160
140
120
100
80
60
40
20
0
Mangrove
Coconut plantation
Q1
min
median
max
Q3

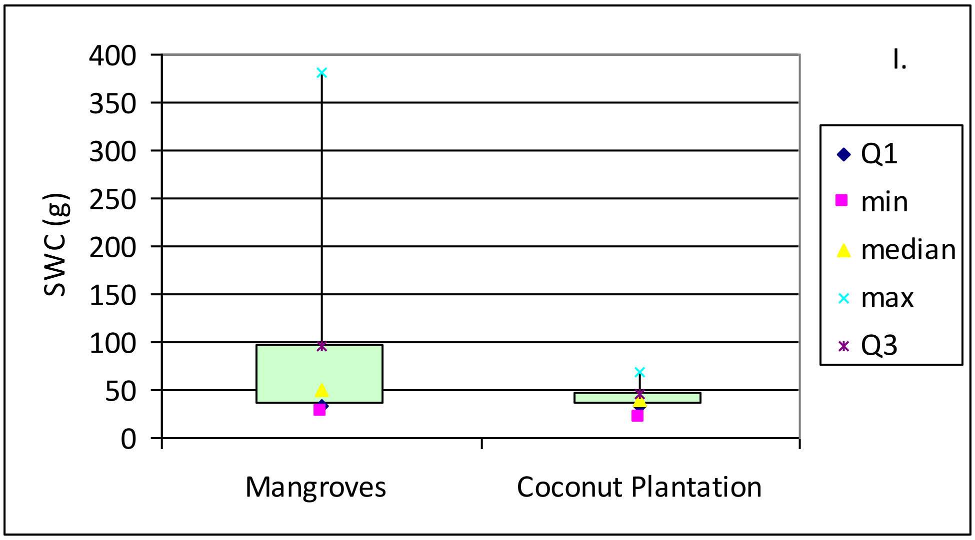

D.
Species Richness
9
8
7
6
5
4
3
2
1
0
Mangroves
Coconut Plantation
Q1
min
median
max
Q3


E.
% Total Transmitance
80
70
60
50
40
30
20
10
0
Mangroves
Coconut Plantation
Q1
min
median
max
Q3


F.
Understory Species richnes
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
Mangroves
Coconut Plantation
Q1
min
median
max
Q3

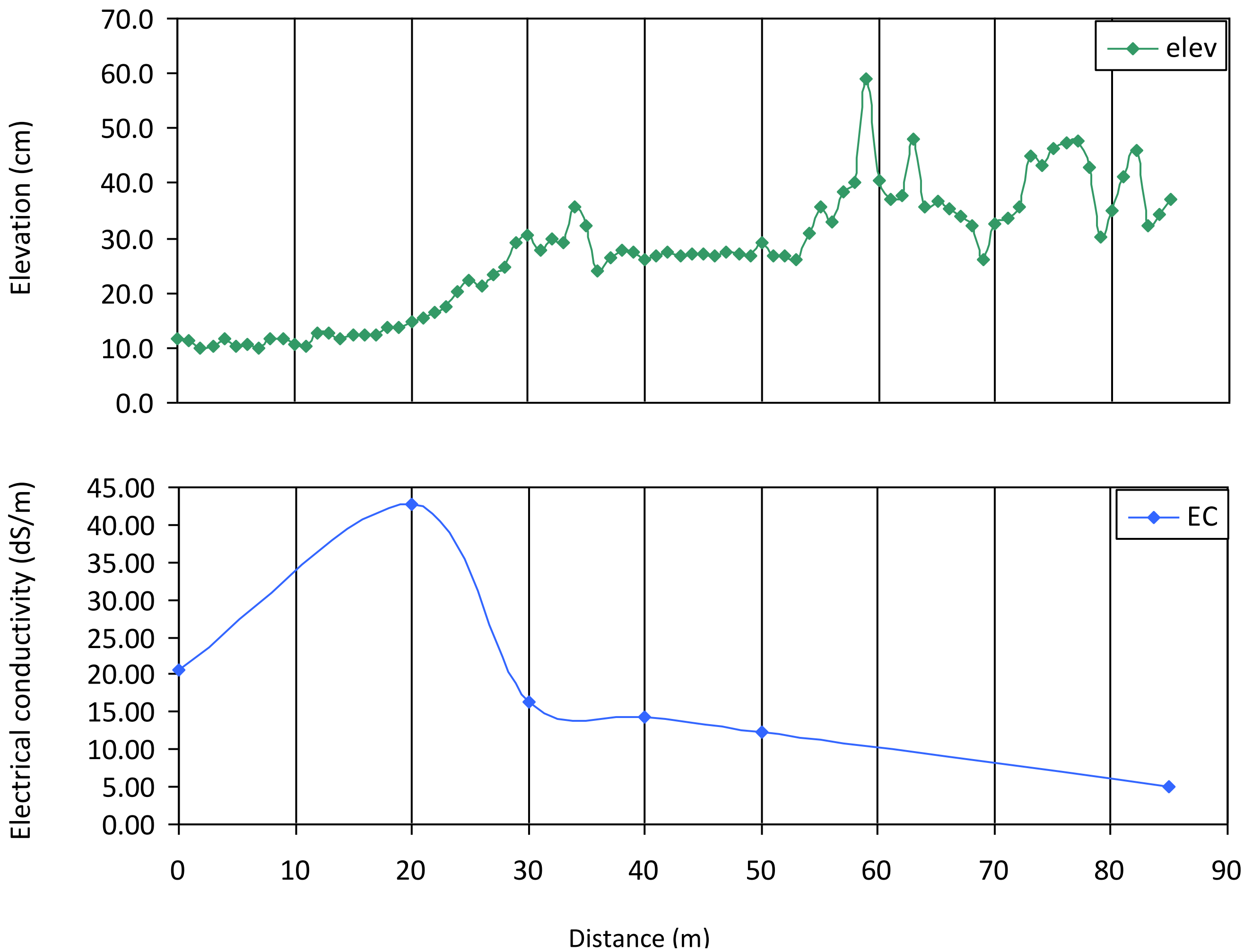

G.
Canopy richness
6
5
4
3
2
1
0
Mangrove
Coconut plantation
Q1
min
median
max
Q3

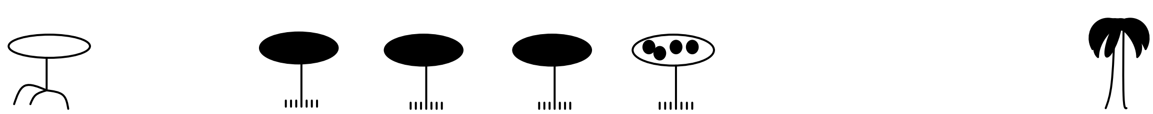

H.
pH
9
8.5
8
7.5
7
6.5
Mangroves
Coconut Plantation
Q1
min
median
max
Q3


I.
SWC (g)
400
350
300
250
200
150
100
50
0
Mangroves
Coconut Plantation
Q1
min
median
max
Q3

Appendix 2. Elevation (cm), electrical conductivity (dS/m), tree dominance and understory species present in each transect. Distance is the distance from the starting point in the transect.

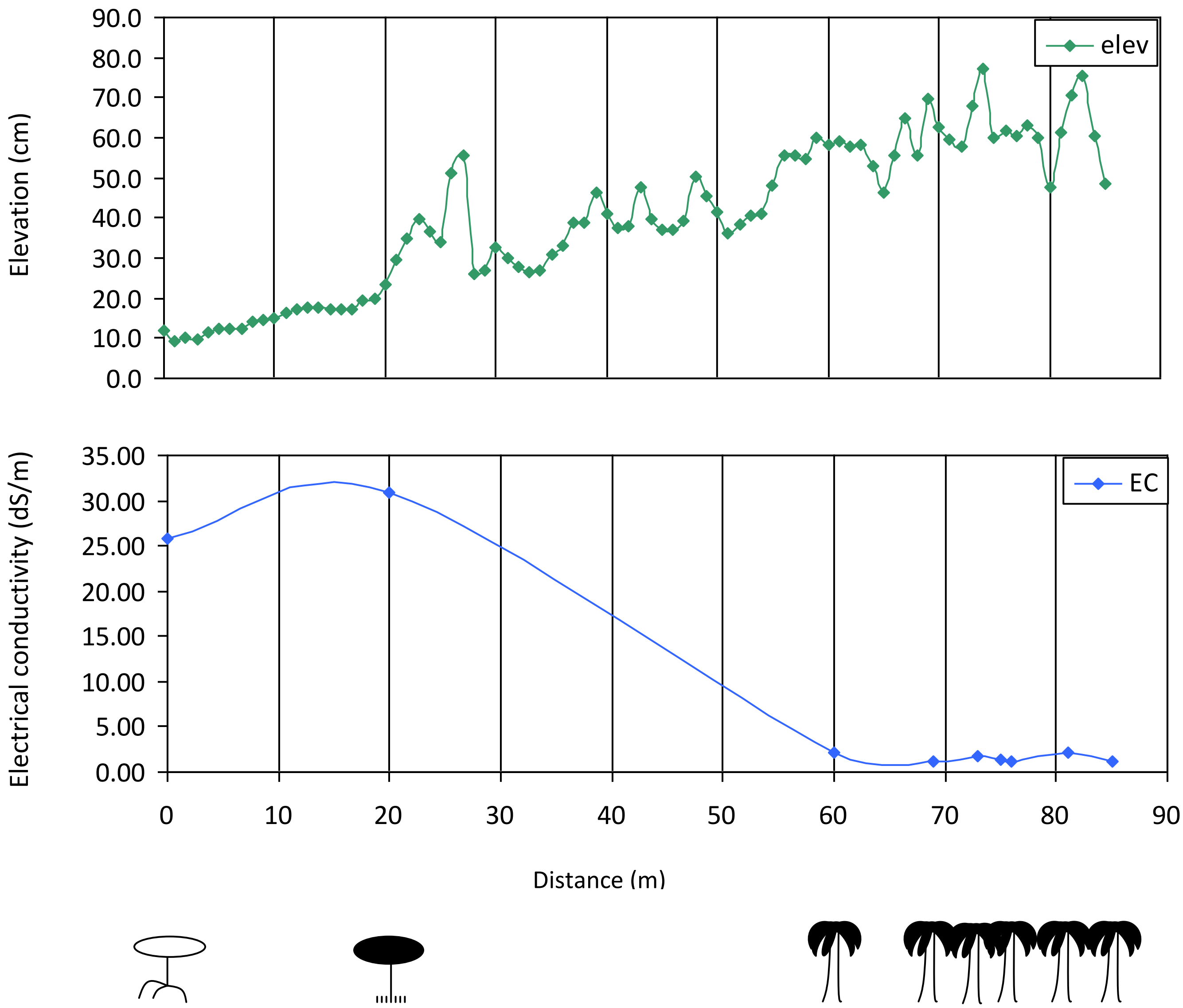
Transect I





B. maritima	x	x	x
S. portulacastrum		x	x

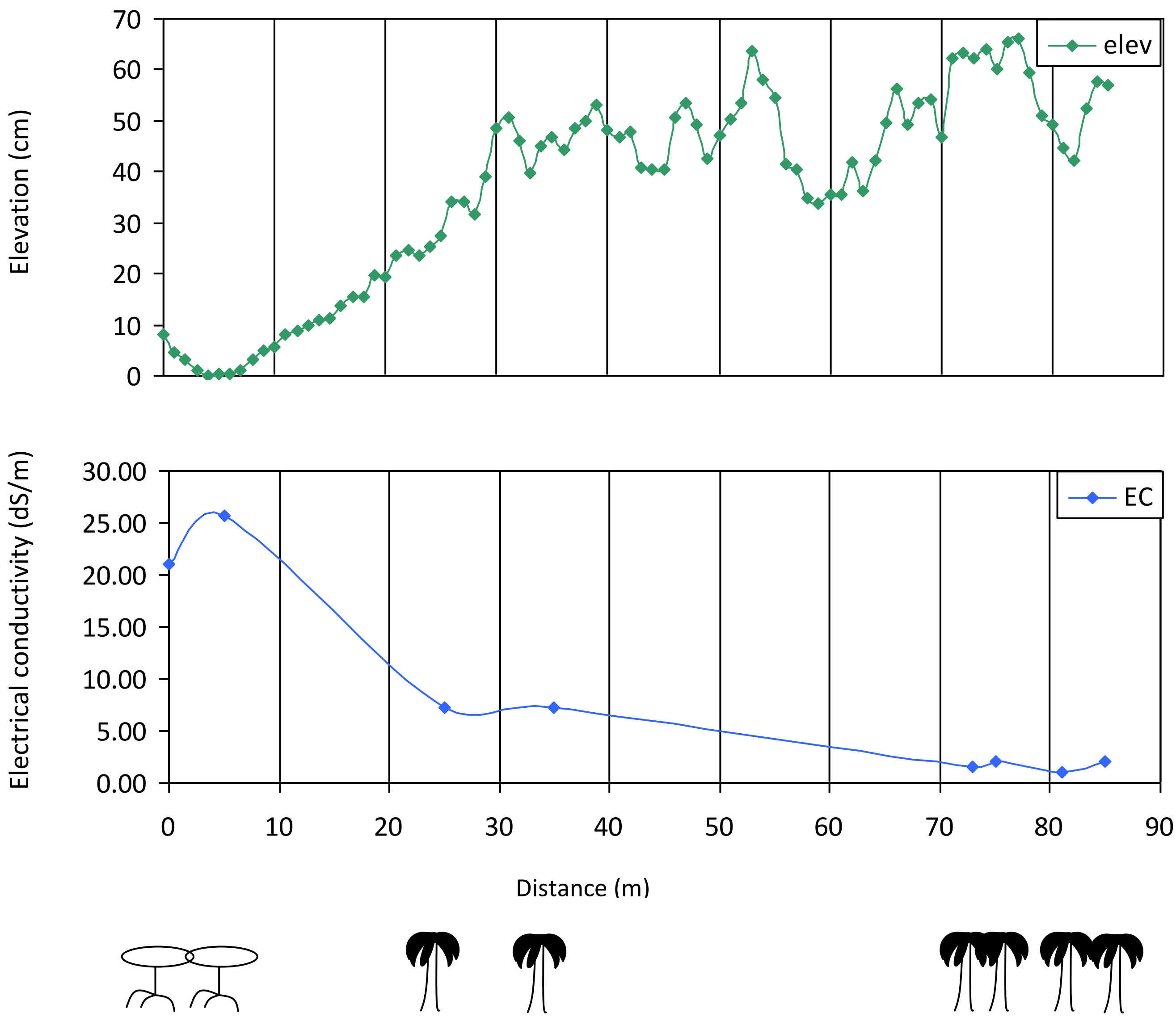
Transect II



A. precatorius		x			
B. maritima	x				
B. pyramidatum					x
C. biflora			x		
D. incanum					x
F. cymosa					x
N. rivularis				x	
P. laxum				x	

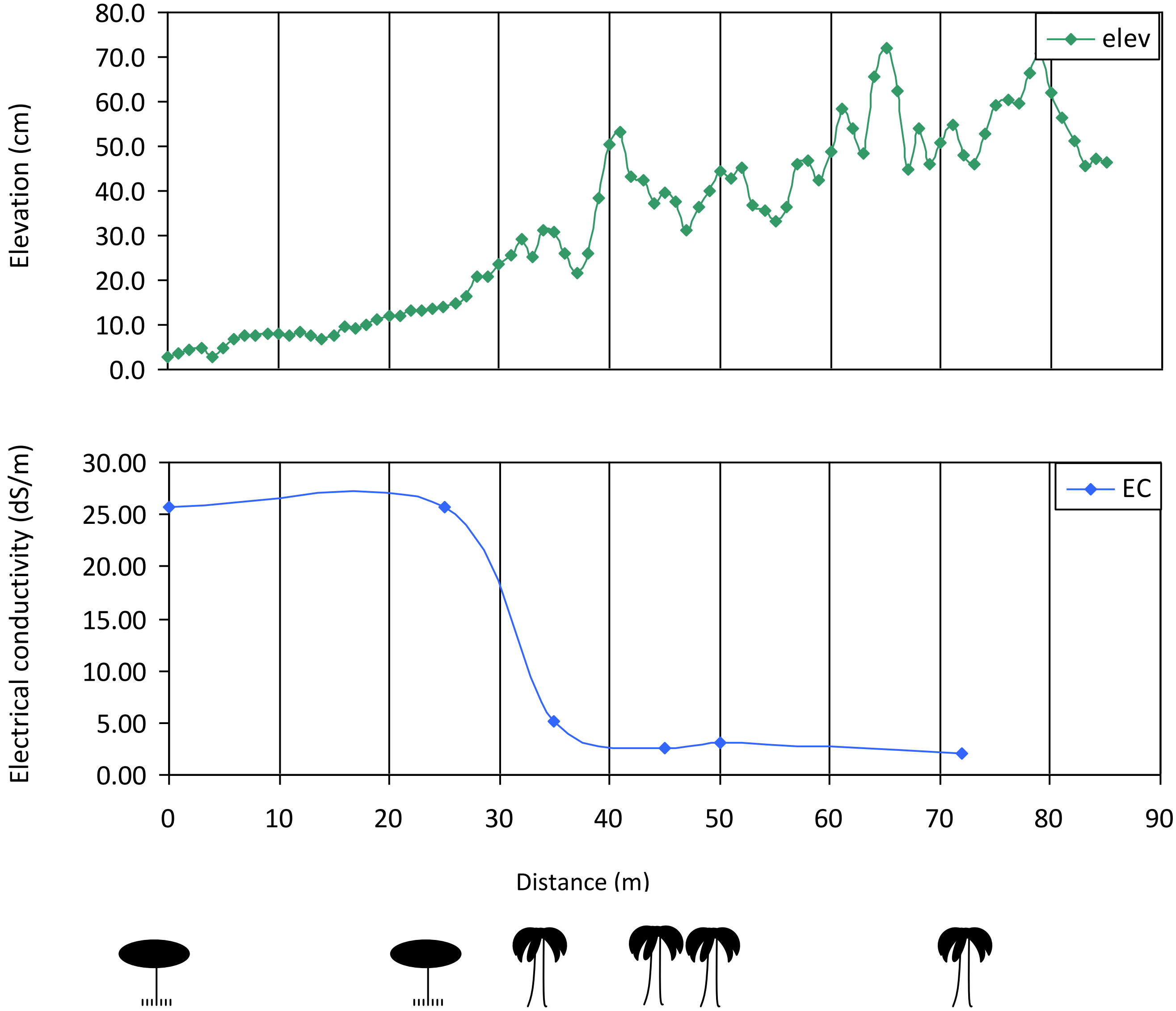
P. nudum					x
P suberosa	x	x	x		
S. lithosperma			x	x	x
Sp1		x			
Sp2			x		
Sp3			x		
Sp4			x		
Sp5				x	
V. luteola				x	

Transect III



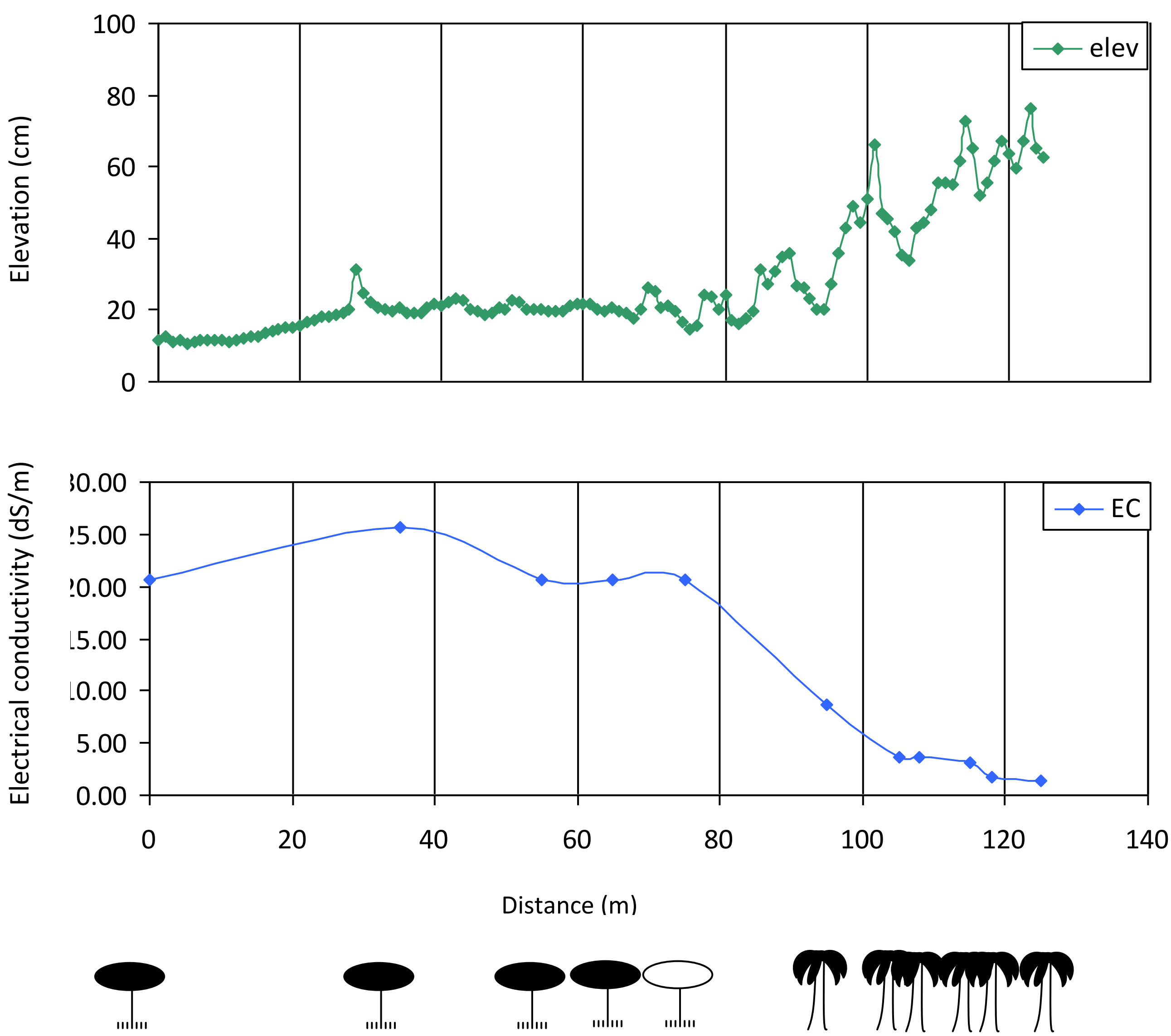
A. precatorius			x	x		
C. biflora	x					
E. littoralis	x					
F. cymosa	x					
O. maculata			x			
P. laxum		x				
P. nudum					X	
S. lithosperma			x	x		
Sp6	x					
Sp7	x					
Sp8						x

Transect IV



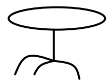
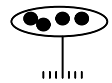
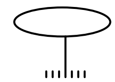
F. cymosa x x
Sp9 x

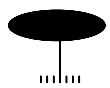
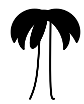
Transect V



A. aureum		x				
B. maritima	x					
J. fluminense						X
N. rivularis				x	x	X
O. maculata						X
P. nudum			x			
S. lithosperma						
Sp10					x	X
Sp11					x	X

Legend:

R. mangle  *C. erectus*  *L. racemosa* 

A. germinans  *C. nucifera* 

Appendix 3. Understory species found at each plot, within the 40-plot sample. Row titles correspond to the plot. Column titles are the acronym of the species. Acronyms can be found in Table 2.

	abr pre	acr aur	bat mar	ble pyr	cap bif	des inc	ern lit	fim cym	jas flu	nep riv	oec mac	pas lax
t100	0	0	0	0	0	0	0	0	0	0	0	0
t120	0	0	0	0	0	0	0	0	0	0	0	0
t130	0	0	58.3	0	0	0	0	0	0	0	0	0
t140	0	0	16.8	0	0	0	0	0	0	0	0	0
t150	0	0	1.5	0	0	0	0	0	0	0	0	0
t185	0	0	0	0	0	0	0	0	0	0	0	0
t200	0	0	0	0	0	0	0	0	0	0	0	0
t220	0	0	14.6	0	0	0	0	0	0	0	0	0
t260	0.2	0	0	0	0	0	0	0	0	0	0	0
t269	0	0	0	0	0.1	0	0	0	0	0	0	0
t273	0	0	0	0	0	0	0	0	0	0	0	0
t275	0	0	0	0	0	0	0	0	0	0	0	0
t276	0	0	0	0	0	0	0	0	0	8.4	0	5.3
t281	0	0	0	0	0	0	0	0	0	0	0	0
t285	0	0	0	2.4	0	4.2	0	20.52	0	0	0	0
t300	0	0	0	0	0	0	0	0	0	0	0	0
t305	0	0	0	0	0	0	0	0	0	0	0	0
t325	0	0	0	0	0.7	0	9.6	2.7	0	0	0	0
t335	0	0	0	0	0	0	0	0	0	0	0	2.6
t373	3.7	0	0	0	0	0	0	0	0	0	1	0
t375	0.6	0	0	0	0	0	0	0	0	0	0	0
t381	0	0	0	0	0	0	0	0	0	0	0	0
t385	0	0	0	0	0	0	0	0	0	0	0	0
t400	0	0	0	0	0	0	0	0	0	0	0	0
t425	0	0	0	0	0	0	0	0	0	0	0	0
t435	0	0	0	0	0	0	0	1.2	0	0	0	0
t445	0	0	0	0	0	0	0	0.2	0	0	0	0
t450	0	0	0	0	0	0	0	0	0	0	0	0
t472	0	0	0	0	0	0	0	0	0	0	0	0
t500	0	0	0	0	0	0	0	0	0	0	0	0
t535	0	0	0	0	0	0	0	0	0	0	0	0
t555	0	0	0.2	0	0	0	0	0	0	0	0	0
t565	0	0	0	0	0	0	0	0	0	0	0	0
t575	0	0	0	0	0	0	0	0	0	0	0	0
t595	0	28.7	0	0	0	0	0	0	0	0	0	0
t5105	0	0	0	0	0	0	0	0	0	0	0	0
t5108	0	0	0	0	0	0	0	0	0	0	0	0
t5115	0	0	0	0	0	0	0	0	0	0.9	0	0
t5118	0	0	0	0	0	0	0	0	0	2.4	0	0
t5125	0	0	0	0	0	0	0	0	1.9	3.1	0.8	0

	pas sub	psi nod	scl lit	ses por	sp1	sp2	sp3	sp4	sp5	sp6	sp7	sp8
t100	0	0	0	0	0	0	0	0	0	0	0	0
t120	0	0	0	0	0	0	0	0	0	0	0	0
t130	0	0	0	0	0	0	0	0	0	0	0	0
t140	0	0	0	8.2	0	0	0	0	0	0	0	0
t150	0	0	0	11.2	0	0	0	0	0	0	0	0
t185	0	0	0	0	0	0	0	0	0	0	0	0
t200	0	0	0	0	0	0	0	0	0	0	0	0
t220	0	0	0	0	0	0	0	0	0	0	0	0
t260	1.3	0	0	0	0	0	0	0	0	0	0	0
t269	0	0	0	0	0	0	0	0	0	0	0	0
t273	11.3	0	0	0	2	0	0	0	0	0	0	0
t275	0.3	0	6.44	0	0	0.14	0.1	3.5	0	0	0	0
t276	0	0	1.8	0	0	0	0	0	0.2	0	0	0
t281	0	2.1	2.8	0	0	0	0	0	0	0	0	0
t285	0	0	0	0	0	0	0	0	0	0	0	0
t300	0	0	0	0	0	0	0	0	0	0	0	0
t305	0	0	0	0	0	0	0	0	0	0	0	0
t325	0	0	0	0	0	0	0	0	0	1.6	1.7	0
t335	0	0	0	0	0	0	0	0	0	0	0	0
t373	0	0	4.7	0	0	0	0	0	0	0	0	0
t375	0	0	0.6	0	0	0	0	0	0	0	0	0
t381	0	0.2	0	0	0	0	0	0	0	0	0	0
t385	0	0	0	0	0	0	0	0	0	0	0	0.4
t400	0	0	0	0	0	0	0	0	0	0	0	0
t425	0	0	0	0	0	0	0	0	0	0	0	0
t435	0	0	0	0	0	0	0	0	0	0	0	0
t445	0	0	0	0	0	0	0	0	0	0	0	0
t450	0	0	0	0	0	0	0	0	0	0	0	0
t472	0	0	0	0	0	0	0	0	0	0	0	0
t500	0	0	0	0	0	0	0	0	0	0	0	0
t535	0	0	0	0	0	0	0	0	0	0	0	0
t555	0	0	0	0	0	0	0	0	0	0	0	0
t565	0	0	0	0	0	0	0	0	0	0	0	0
t575	0	0	0	0	0	0	0	0	0	0	0	0
t595	0	0	0	0	0	0	0	0	0	0	0	0
t5105	0	0	0	0	0	0	0	0	0	0	0	0
t5108	0	0.3	0	0	0	0	0	0	0	0	0	0
t5115	0	0	0	0	0	0	0	0	0	0	0	0
t5118	0	0	5.3	0	0	0	0	0	0	0	0	0
t5125	0	0	0.2	0	0	0	0	0	0	0	0	0

	sp9	sp10	sp 11	vig lut
t100	0	0	0	0
t120	0	0	0	0
t130	0	0	0	0
t140	0	0	0	0
t150	0	0	0	0
t185	0	0	0	0
t200	0	0	0	0
t220	0	0	0	0
t260	0	0	0	0
t269	0	0	0	0
t273	0	0	0	0
t275	0	0	0	0
t276	0	0	0	0.3
t281	0	0	0	0
t285	0	0	0	0
t300	0	0	0	0
t305	0	0	0	0
t325	0	0	0	0
t335	0	0	0	0
t373	0	0	0	0
t375	0	0	0	0
t381	0	0	0	0
t385	0	0	0	0
t400	0	0	0	0
t425	0	0	0	0
t435	90.2	0	0	0
t445	0	0	0	0
t450	0	0	0	0
t472	0	0	0	0
t500	0	0	0	0
t535	0	0	0	0
t555	0	0	0	0
t565	0	0	0	0
t575	0	0	0	0
t595	0	0	0	0
t5105	0	0	0	0
t5108	0	0	0	0
t5115	0	0	0	0
t5118	0	0.1	0	0
t5125	0	0	0.2	0

Appendix 4. Tree seedlings found at each plot, within the 40-plot sample. Row titles correspond to the plot. Column titles are the acronym of the species. Acronyms can be found in Table 4.

	and ine	avi ger	bur sim	cal cal	chr ica	coc nuc	cro rha	eri fru	lag rac	mor cit	rhi man	swi spp
t100	0	0	0	0	0	0	0	0	6.30	0	3.3	0
t120	0	0	0	0	0	0	0	0	0	0	0	0
t130	0	0	0	0	0	0	0	0	0.6	0	0	0
t140	0	0	0	0	0	0	0	0	0	0	0	0
t150	0	0	0	0	0	0	0	0	0	0	0	0
t185	0	0	0.4	0	0.3	0	0	0	0	0	0	0
t200	0	0	0	0	0	0	0	0	0	0	9.4	0
t220	0	0	0	0	0	0	0	0	10.9	0	0	0
t260	0	0	0	0	0	1.7	0	0	0	0	0	0
t269	0	0	0	0	0	0	0	0	0	0	0	0
t273	0	0	0	0	0	0	0	0	0	0	0	0
t275	0	0	0	18.4	0	0	0	0	0	0	0	0
t276	0	0	0	8.1	0	0	0	0	0	0	0	0
t281	0	0	0.9	0	0	0	0	0.2	0	0	0	0
t285	0	0	0	10.2	0	0	0	0	0	0	0	0
t300	0	0	0	0	0	0	0	0	0	0	2.1	0
t305	0	0	0	0	0	0	0	0	0	0	0	0
t325	0	0	1.9	0.9	0	0	0	0	0	0	0	3
t335	0	0	0.4	0	0	0	4.6	0	0	0	0	1.4
t373	0	0	0	0	0	0	0	0	0	0	0	1.8
t375	0	0	0	0	0	0	0	0	0	0	0	0.6
t381	0.2	0	0	0.3	2.6	0	0	0	0	0	0	0
t385	0	0	0	0	0	0	0	0	0	0.8	0	0
t400	0	0	0	0	0	0	0	0	0	0	0	0
t425	0	0	0	0	0	0	0	0	2.9	0	0	0
t435	0	0	0	0	0	0	0	0	0	0	0	0
t445	0	0	1.4	0	0	0	5.1	0	0	0	0	2.2
t450	0	0	0	0	0	0	0	0	0	0	0	0.7
t472	0	0	0.2	20.8	0	0	0	0	0	0	0	0.9
t500	0	5.7	0	0	0	0	0	0	0	0	0	0
t535	0	8.4	0	0	0	0	0	0	0	0	0	0
t555	0	14.1	0	0	0	0	0	0	9.5	0	0	0
t565	0	1.5	0	0	0	0	0	0	0	0	0	0
t575	0	0	0	0	0	0	0	0	13.7	0	0	0
t595	0	0	0	0	0	0	0	0	0	0	0	0
t5105	2.6	0	0	0	0	3.4	0	0	0	0	0	0
t5108	0	0	0	0	0	0	0	0	0	0	0	0
t5115	0	0	0	0	0	0	0	0	0	0	0	0
t5118	0	0	0	0	0	0	0	0	0	0	0	2.3
t5125	0	0	0	0	6.5	0	0	0	0	0	0	0

Appendix 5. Environmental variables found at each plot, within the 40-plot sample. Row titles correspond to the plot. Column titles are the environmental variable measured: elev= elevation (cm), pH= pH, EC= electrical conductivity (dS/m), SWC= soil water content (g), trans tot= total transmittance (%) and tree dom= tree dominance (0= *R. mangle*, 1= *A. germinans* and/or *L. racemosa*, 2= *C. erectus*, 3= canopy transition plots, 4= *C. nucifera* plots)

	elev	pH	EC	SWC	trans tot	tree dom
t100	11.6	7.65	20.58	212.5	30.04	0
t120	14.8	7.95	42.80	33.33333	62.21	1
t130	30.6	8.15	16.46	29.05983	41.37	1
t140	26.2	7.9	14.41	40.18692	63.64	1
t150	29	8.3	12.35	26.89076	21.89	2
t185	37.2	8.3	5.15	41.1215	16.03	4
t200	12	8.15	25.73	194.1176	24.75	0
t220	23.2	8	30.87	42.45283	23.13	1
t260	58.2	8.55	2.06	39.42308	19.84	4
t269	69.8	8.5	1.23	36.36364	26.32	4
t273	68	8.6	1.75	40.56604	21.74	4
t275	59.8	8.25	1.44	33.62832	23.11	4
t276	61.8	8.2	1.18	27.9661	22.21	4
t281	61.2	8.4	2.06	27.35043	20.59	4
t285	48.6	8.4	1.13	54.08163	16.87	4
t300	8.2	8.5	20.98	380.6452	33.85	0
t305	0.4	7.9	25.73	151.6667	29.52	0
t325	27.4	7.45	7.20	33.92857	18.5	4
t335	46.8	8.5	7.20	44.23077	23.88	4
t373	62.4	8.25	1.54	31.30435	19.12	4
t375	60	8.15	2.06	37.61468	18.55	4
t381	44.6	8.4	1.03	48.51485	24.26	4
t385	57	8.4	2.06	38.53211	17.01	4
t400	2.6	8.15	25.73	72.41379	31.44	1
t425	14.2	7.6	25.73	77.38095	50.67	1
t435	31	8.4	5.15	39.81481	26.94	3
t445	39.6	8.3	2.57	50	19.34	4
t450	44.4	8	3.09	42.85714	19.37	4
t472	48	8.35	2.06	49.50495	14.28	4
t500	11.7	7.95	20.58	56.25	31.23	1
t535	19.2	7.95	25.73	29.05983	70.74	1
t555	19.8	8.1	20.58	33.62832	55.82	1
t565	19.6	7.85	20.58	56.25	37.8	1
t575	14.6	8.5	20.58	38.88889	28.05	2
t595	27.4	8.45	8.75	35.45455	18.49	3
t5105	35.2	8.15	3.60	68.53933	15.62	4

t5108	44.6	8.2	3.60	47.05882	17.17	4
t5115	65	8	3.09	39.81481	15.9	4
t5118	61.8	8.2	1.75	26.27119	15.53	4
t5125	62.8	8	1.44	20.96774	22.39	4

Appendix 6. T-test results for the level of significance of the elevation values (cm) obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	16.10625	50.94167
Variance	74.6499583	170.9999
Observations	16	24
Hypothesized Mean Difference	0	
df	38	
t Stat	-10.145015	
P(T<=t) one-tail	1.1424E-12	
t Critical one-tail	1.68595307	
P(T<=t) two-tail	2.28E-12	
t Critical two-tail	2.02439423	

Appendix 7. T-test results for the level of significance of the electrical conductivity values (dS/m)(salinity) obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	23.0870625	3.007681
Variance	50.2924922	4.644164
Observations	16	24
Hypothesized Mean Difference	0	
df	17	
t Stat	10.99223602	
P(T<=t) one-tail	1.90168E-09	
t Critical one-tail	1.739606432	
P(T<=t) two-tail	3.80E-09	
t Critical two-tail	2.109818524	

Appendix 8. T-test results for the level of significance of the pH values obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	8.0375	8.266667
Variance	0.065167	0.058841
Observations	16	24
Hypothesized Mean Difference	0	
df	31	
t Stat	-2.8371	
P(T<=t) one-tail	0.003978	
t Critical one-tail	1.695519	
P(T<=t) two-tail	0.007955	
t Critical two-tail	2.039515	

Appendix 9. T-test results for the level of significance of the soil water content values (g) obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	92.17030761	39.78789
Variance	9463.258915	104.4678
Observations	16	24
Hypothesized Mean Difference	0	
df	15	
t Stat	2.146015742	
P(T<=t) one-tail	0.024320334	
t Critical one-tail	1.753051038	
P(T<=t) two-tail	0.048640668	
t Critical two-tail	2.131450856	

Appendix 10. T-test results for the level of significance of the total transmittance values (%) (light availability) obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	39.759375	19.71083
Variance	250.1312063	12.27873
Observations	16	24
Hypothesized Mean Difference	0	
df	16	
t Stat	4.989606109	
P(T<=t) one-tail	6.68205E-05	
t Critical one-tail	1.745884219	
P(T<=t) two-tail	0.000133641	
t Critical two-tail	2.119904821	

Appendix 11. T-test results for the level of significance of the values in overall species richness obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	1.25	3.25
Variance	0.733333333	3.586957
Observations	16	24
Hypothesized Mean Difference	0	
df	34	
t Stat	-4.525745769	
P(T<=t) one-tail	3.50749E-05	
t Critical one-tail	1.690923455	
P(T<=t) two-tail	7.01498E-05	
t Critical two-tail	2.032243174	

Appendix 12. T-test results for the level of significance of the values in understory species richness obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	0.4375	1.5
Variance	0.529167	1.478261
Observations	16	24
Hypothesized Mean Difference	0	
df	38	
t Stat	-3.45326	
P(T<=t) one-tail	0.000687	
t Critical one-tail	1.685953	
P(T<=t) two-tail	0.001375	
t Critical two-tail	2.024394	

Appendix 13. T-test results for the level of significance of the values in seedling richness obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	0.8125	1.291666667
Variance	0.429166667	1.172101449
Observations	16	24
Hypothesized Mean Difference	0	
df	38	
t Stat	-1.742015685	
P(T<=t) one-tail	0.044797823	
t Critical one-tail	1.685953066	
P(T<=t) two-tail	0.089595645	
t Critical two-tail	2.024394234	

Appendix 14. T-tests results for the level of significance for the values in canopy richness (%) obtained in the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	1.5625	2.541666667
Variance	0.395833333	1.041666667
Observations	16	24
Hypothesized Mean Difference	0	
df	38	
t Stat	-3.751008357	
P(T<=t) one-tail	0.000293331	
t Critical one-tail	1.685953066	
P(T<=t) two-tail	0.000586662	
t Critical two-tail	2.024394234	

Appendix 15. T-test results for the level of significance for the values of overall cover (%) obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	12.24375	14.325
Variance	233.833292	384.9531
Observations	16	24
Hypothesized Mean Difference	0	
df	37	
t Stat	-0.37590542	
P(T<=t) one-tail	0.35456698	
t Critical one-tail	1.68709448	
P(T<=t) two-tail	0.70913397	
t Critical two-tail	2.02619049	

Appendix 16. T-test results for the level of significance of the values of understory cover (%) obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	6.925	5.785833
Variance	242.0726667	68.17657
Observations	16	24
Hypothesized Mean Difference	0	
df	21	
t Stat	0.268726456	
P(T<=t) one-tail	0.395381268	
t Critical one-tail	1.720743512	
P(T<=t) two-tail	0.790762535	
t Critical two-tail	2.079614205	

Appendix 17. T-test results for the level of significance of the values of seedling cover (%) obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	5.31875	4.366666667
Variance	43.82429167	34.04144928
Observations	16	24
Hypothesized Mean Difference	0	
df	29	
t Stat	0.466942531	
P(T<=t) one-tail	0.322015142	
t Critical one-tail	1.699127097	
P(T<=t) two-tail	0.644030285	
t Critical two-tail	2.045230758	

Appendix 18. T-test results for the level of significance of the values of canopy cover (%) obtained at the mangrove dominated plots vs. the coconut dominated plots.

t-Test: Two-Sample Assuming Unequal Variances

	Mangrove	*Coconut*
Mean	54.6875	114.5833333
Variance	621.5625	710.6884058
Observations	16	24
Hypothesized Mean Difference	0	
df	34	
t Stat	-7.239010407	
P(T<=t) one-tail	1.11474E-08	
t Critical one-tail	1.690923455	
P(T<=t) two-tail	2.22947E-08	
t Critical two-tail	2.032243174	