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Functional study of resistance and resilience in mangrove ecosystems in the Dominican Republic.

Thesis submitted for consideration by the Education Division and the Graduate Program as a requirement for the degree of

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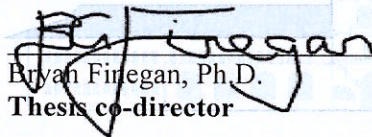
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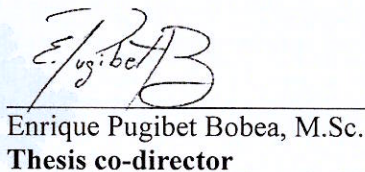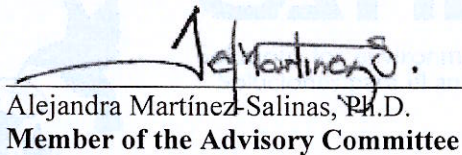
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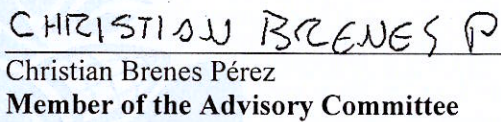
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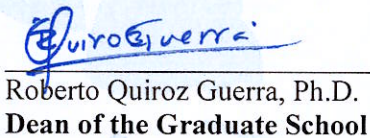
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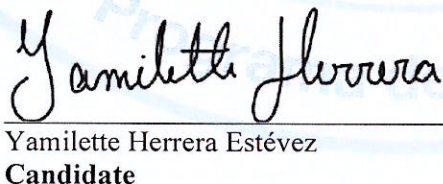**Thesis co-director**

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II

Dedication:

To my parents and sisters.
To my classmates in the master's degree.

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List of acronyms, abbreviations, and units
CATIE: Tropical Agricultural Research and Higher Education Center
UASD: Autonomous University of Santo Domingo
Ha-Hectare
Km^2-Square kilometer
IPCC- Intergovernmental Panel on Climate Change
DBH-Diameter at breast height
Mg mm^{-3}-Milligram by cubic millimeter
M-Meter
M^2 kg^{-1}-Square meter by kilogram
Mm-Millimeter
Mg-Milligram
TH-Total height
SLA-Specific leaf area
LA-Leaf area
LS-Succulence
SS-Seed size
WD-Wood density
LDMC-Leaf dry-matter content
RT-Root type
OECS-EAST Caribbean State Organization
PES-Plant Economic Spectrum

LES-Leaf Economic Spectrum
CIFOR- Center for International Forestry Research
PNUD- United Nations Development Program
USAID- United States Agency for International Development
GEF-Global Environment Facility
FW-Fresh weight
DW-Dry weight
CWM-Community weighted mean
PCA-Principal component analysis
AIC- Akaike information criterion
BIC- Bayesian information criterion

Functional study of resistance and resilience in Mangrove ecosystems in the Dominican Republic.

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Abstract:
Mangroves are coastal ecosystems restricted to tropical and subtropical regions of the world. In the Caribbean, four plant species dominate these ecosystems: *Rhizophora mangle, Laguncularia racemosa, Avicennia germinans and Conocarpus erectus.* The resilience and resistance of Caribbean mangroves have been poorly studied, despite these systems high vulnerability to drought events, hurricanes, and tropical storms. Considering current predictions showing increases in the intensity of extreme events and long-term temperature increments, it is crucial to study various aspects affecting longevity of these ecosystems. In this study we seek to characterize functional traits at the community level to quantify mangrove resilience and resistance and to explore the relationship of community level functional traits to disturbance, salinity, and microtopography in two sites located on the north-west coast of the Dominican Republic. Our results show that salinity is the main driver of differences in functional trait values, followed by disturbance. Community Weighted Mean (CWM) traits such as leaf area, specific leaf area, total height, and species with intermediate dispersal potential decrease with higher salinities, while leaf dry matter content and salt secretor species increase. CWM leaf succulence and leaf area decrease with higher levels of disturbance, while density of species with salt tolerant mechanisms, high dispersal potential and prop roots increase. We conclude that mangrove ecosystems are more resistant to hurricanes, sea level rise and tropical storms than to drought, and that sites dominated by R. mangle would have low resilience to long-term temperature increases due to the salt tolerance mechanism of this species

Resumen:
Los manglares son ecosistemas costeros restringidos a las regiones tropicales y subtropicales del mundo. En el Caribe, cuatro especies vegetales dominan estos ecosistemas: *Rhizophora mangle, Laguncularia racemosa, Avicennia germinans* y *Conocarpus erectus*. La resiliencia y la resistencia de los manglares del Caribe han sido poco estudiadas, a pesar de la alta vulnerabilidad de estos sistemas a los eventos de sequía, huracanes y tormentas tropicales. Teniendo en cuenta

las predicciones actuales que muestran un aumento en la intensidad de los eventos climáticos extremos y de la temperatura a largo plazo, es crucial estudiar varios aspectos que afectan a la longevidad de estos ecosistemas. En este estudio buscamos caracterizar los rasgos funcionales a nivel de comunidad para cuantificar la resiliencia y resistencia de los manglares y explorar la relación de los rasgos funcionales a nivel de comunidad con las perturbaciones, la salinidad y la microtopografía en dos sitios ubicados en la costa noroeste de la República Dominicana. Nuestros resultados muestran que la salinidad es el principal impulsor de las diferencias en los valores de los rasgos funcionales, seguido de las perturbaciones. Los rasgos de la media ponderada de la comunidad (CWM), como el área foliar, el área foliar específica, la altura total y las especies con potencial de dispersión intermedio, disminuyen con las salinidades más altas, mientras que el contenido de materia seca foliar y las especies secretoras de sal aumentan. La CWM de suculencia y área foliar disminuyen con niveles más altos de perturbación, mientras que la densidad de las especies con mecanismos de tolerancia a la sal, alto potencial de dispersión y raíces fúlcreas aumentan. También encontramos que los ecosistemas de manglares son más resistentes a los huracanes, al aumento del nivel del mar y a las tormentas tropicales que, a la sequía, y que los sitios dominados por *R. mangle* tendrían una baja resistencia a los aumentos de temperatura a largo plazo debido al mecanismo de tolerancia a la sal de esta especie.

Keywords: resilience, resistance, functional ecology, mangroves, drought, hurricanes, temperature increments.

Introduction:

Trait-based ecology has advanced considerably in the last two decades. Due to its generalizable and flexible methods, it can be widely applied to any ecosystem by quantifying the functional traits that regulate ecosystem processes and organism response to environmental variation (Laughlin 2014; Pan et al., 2020). This approach is based on the use of traits, which are organism characteristics capable of predicting organism response to or effect on the environment and its functioning (Díaz & Cabido, 2001; Salgado-Negret, 2016). Traits can be classified into response and effect. Response traits are characteristics that respond to the abiotic and biotic environment, while effect traits are those having significant effects on the dominant ecosystem processes (Díaz & Cabido, 2001).

It has been theorized that some trait combinations are viable and successful whereas others are not, with the degree of success being dependent on the environmental conditions present in any given ecosystem (Cannicci et al., 2021; Díaz et al., 2016; Funk et al., 2008). The effect of environmental changes on ecosystem processes can be direct when the selected response traits also affect ecosystem processes. This is the case, for example, for the effect of drought on dense woods, which is a direct determinant of plant resistance to water scarcity (Salgado-Negret, 2016).

Empirical and theoretical evidence is accumulating demonstrating that functional dynamic might affect short-term ecosystem resource dynamic and long-term ecosystem stability (Díaz & Cabido, 2001). Ecosystem resistance (short-term) is the degree of change shown by a variable following a disturbance. (Pimm, 1984; Rejmánek, 1996). Ecosystem complexity correlates with greater resistance- both theoretically and in field studies (Pimm, 1984). This result holds true

when modelling ecosystems with few plant species, but more connectivity, that is, greater interspecific interaction between species (Isbell et al., 2015; Pimm et al., 2019). Data from various experiments indicate that greater biodiversity often stabilizes ecosystem productivity, productivity-dependent ecosystem services and biodiversity, and increases resistance to climatic events (Isbell et al., 2015).

Ecosystem resilience (long-term), on the other hand, is the speed at which variables return to a dynamic equilibrium after a disturbance (Pimm, 1984). The resilience approach to ecosystem analysis centers on the understanding that the natural state of a system is one of change (Pimm, 1984). Consequently, systems must be managed for flexibility rather than maintaining stability (Nelson et al., 2007).

High instability- equilibrium- in ecosystems allows them to possess high resilience, although this can depend on factors such as connectivity, number of species, and species composition (Holling, 1973; Isbell et al., 2015; Pimm, 1984). Also, a resilient ecosystem may not have high resistance. Therefore, some systems may persist overtime, not for their ability to withstand external factors, but for their capacity to recover quickly after the stability has been disturbed (Pimm et al., 2019).

Resistance and resilience to many environmental conditions can be studied with the use of functional ecology, some suggest it is also the best approach to analyze the future impacts of climate change on forests (De Battisti, 2021). Working in tropical dry forests, Paz et al., (2018) suggest that traits such as plant height, wood density, tree slenderness and specific leaf area are important predictors of storm effects on resistance. Similarly, De Battisti (2021) and Pérez-Harguindeguy et al., (2016) suggest using traits such as dispersal potential, seed germination, vegetative regrowth and seed size when studying ecosystem resilience since these traits provide a better insight into the future of ecosystems.

Few studies on the relationship between functional traits and environmental changes and their short and long-term effects have been focused on wetland ecosystems. Funk et al., (2008) analyzed ways to restore and assembly ecosystem function considering the trait combinations of native and exotic species (Laughlin, 2014; Timmermann & Baattrup-pedersen, 2015) and considered the functional approach to measure success in ecosystem restoration sites. Others considered the importance of choosing the right traits for ecosystem analysis, in which they concluded that Specific Leaf Area (SLA) was the best indicator of resource use in succulent species (Vendramini et al., 2002).

Pan et al., (2020) found that the Leaf Economic Spectrum (LES) does exist in wetland plants, but with weaker and often shifting trait-trait associations relative to the non-wetland LES, which suggest that stressors in these ecosystems, such as hydric stress and nutrient availability, have a bigger influence on their trait association.

Some studies have seen the need to fill the gap of information related to ecosystem function in wetlands, but some, like mangroves, are still understudied (De Battisti, 2021). Mangroves are intertidal ecosystems that exist in tropical and subtropical zones all around the world (Herrera Silveira et al., 2022). They are highly valued for the ecosystem services they provide to

communities and ecosystems adjacent to them, such as their high capacity for carbon storage and erosion protection. Economic valuation of ecosystem services from mangroves suggests values ranging between US$200,000 and $900,000 per hectare (FAO, 2007; Kauffman et al., 2014; Wells et al., 2018).

Although highly valued, mangrove ecosystems are vulnerable to a wide range of disturbances, including unsustainable fishing, land use change, expansion of agricultural areas and salt mines (CATIE et al., 2019; FAO, 2020; Kauffman et al., 2014). The vulnerability they are subject to makes it even more relevant to assess their resilience and resistance to short- and long-term disturbances (De Battisti, 2021).

Caribbean mangrove ecosystems are composed by four plant species: *Rhizophora mangle, Laguncularia racemosa, Avicennia germinans and Conocarpus erectus* (OECS & USAID, 2009). These areas are highly vulnerable due to their geographical characteristics, which make them highly vulnerable to rising temperatures, hurricanes and tropical storms (IPCC, 2021; Taylor et al., 2012). In a study carried out after Hurricane George passed in the Dominican Republic, mangroves showed an average tree mortality rate of 47.7% with *L. racemosa* experiencing the lower mortality rate (26%) followed by *R. mangle* (50%) and *A. germinans* (64%) (Sherman et al., 2001).

In the Colombian Caribbean, a study showed that mangroves reaction to increasing temperatures can be related to their ability to resist salinity. Mangrove forests dominated by *R. mangle* can cope with wave strength and salinities close to those of sea water (about 35%), those dominated by *A. germinans* can tolerate and develop under salinity conditions of 60–65% and sandier substrates, while those dominated by L. racemosa can cope similarly to R. mangle but need more open canopy (Sobrado & Ewe, 2006; Villate Daza et al., 2020).

Some studies have used trait-based ecology to differentiate between true mangroves and mangrove associates, ecosystem types that differed in leaf traits and osmotic properties (Wang et al., 2011). Arrivabene et al., (2014) concluded that mangroves possess leaf morpho-anatomical plasticity, which shows how mangrove species tend to have wide adaptability. Although this may not apply to all mangrove species, experiments show that in some, trait composition is relatively constant, while others are more adaptable to changes, such as gradients of soil nutrients. In an experimental greenhouse study with seedlings, *L. racemosa* showed strategies that are more competitive over slow-growing species in nutrient-rich soils through changing in adaptive strategies (Wei et al., 2022).

Given that the range and the values of functional traits carried by plants are strong drivers of ecosystem processes, and furthermore, mangroves show adaptive geographic trait distribution (Arrivabene et al., 2014; Díaz & Cabido, 2001), our objectives were to characterize functional traits at the community level to quantify mangrove resilience and resistance and to determine the relationship of community level functional traits to disturbance, salinity, and microtopography in two sites on the north-west coast of the Dominican Republic.

We tested the hypothesis that community weighted means of mangrove functional traits would respond to the salinity gradient, with lower influence of disturbance and microtopography. We also predicted that functional traits at community level would decrease for leaf traits like SLA, LA and LS as salinity increased while sites with higher levels of disturbance would affect WD and LDMC. We reasoned that our functional study would permit the inference that mangrove ecosystems will be highly resistant to extreme climate events, but not very resilient to long-term gradual climate change.

Materials and methods:

Study area

The sites for this study are located on the northwest coast of the Dominican Republic. The first site is the Manglares de Estero Balsa National Park situated in coordinates UTM, zone 19Q: North 2196046 M, South 2178350 M, East 2196646 M, West 208774 M., the second is El Morro National Park located in coordinates UTM, zone 19Q: North 2203772, South 2198793, East 234112, West 221541.

Estero Balsa covers a total area of 5,654 ha, with a 3,000- h a buffer zone, while El Morrooccupies a total area of 1,849 ha. Both are open for visitation and possess agreements for sustainable fishing with local fishing communities. The area has a mean annual temperature of 26.4 ℃ and a mean annual rainfall of 677 mm (Ministerio de Medio Ambiente y Recursos Naturales, PNUD, and GEF 2009, 2014).

Hurricanes, urban development, salt mines and unsustainable agricultural practices have affected the coast. Currently, ecological flows have been altered in addition to downstream water supply, increased erosion and pollution of the coastal strip, which have affected the edge of the mangrove ecosystems (CATIE et al., 2019).

Field data

We established 32 10 m radius circular vegetation plots, 20 in Estero Balsa and twelve in El Morro. Plots were systematically placed along transects perpendicular to the coastal edge of the forests. Each transect had between 1 and 3 plots depending on transect length. The plots were placed at 1 to 1.5 km linear distance from each other, however, because of accessibility issues three plots had to be placed closer, with an average distance of 0.8 km (Cifuentes et al., 2018; Rahman et al., 2021; Sherman et al., 2001). All data was collected from January to May 2022.

Physical and biological parameters

Salinity and microtopography were assessed on each of the 32 vegetation plots. Salinity was evaluated via the analysis of water samples using a Digital salinity tester Ciztada, model LD-203. Microtopography was assessed via the "Level hose" method as explained by Rodríguez-Zúñiga et al., (2018). Measurements were taken on the first and last 5 m of all vegetation plots in the direction of the coast (Cifuentes et al., 2018).

Functional traits

We chose a set of seven functional traits for measurement due to their relevance to the objectives of our study (Table 1 and 2 in supplementary material). We measured Total Height (TH) of all trees present at the plot using a clinometer, and visually inspected and estimated the percentage of trees showing signs of disease or disturbance based on criteria defined by Sherman et al., (2001). We also measured the diameter at breast height (DBH) for all trees with DBH ≥ 2.5 cm. For plants below 1.3 m in height, diameter was measured at 30 cm. (Cifuentes et al., 2018; Yanagisawa et al., 2010). Foliage samples were taken in each plot using tall pruners from at least five fully sun-exposed or partially exposed canopies of individuals from each species present in the plot (Pérez-Harguindeguy et al., 2016; Wang et al., 2011). Samples were taken from *R. mangle, L. racemosa* and *A. germinans.*

After collection, leaves were rehydrated and leaf area (LA) was measured using imageJ (Salgado-Negret, 2016), then we obtained Fresh Weight (FW) using an Ohaus analytical scale (model EX124). Leaves were oven-dried at 70° C for 24 hours and reweighed to obtain Dry Weight (DW) (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2016; Wang et al., 2011).

Specific Leaf Area (SLA) (cm^2 g^{-1}), was calculated as the area of a fresh leaf (cm^2), divided by its oven-dry weight (g) (Pérez-Harguindeguy et al., 2016).

$$SLA = \frac{LA}{DW}$$

Leaf Succulence (LS) (g dm^{-2}) was calculated using the formula proposed by Mantovani (1999):

$$LS = \frac{FW\text{-}DW}{(LA)}$$

Leaf Dry Matter content (LDMC) (mg g^{-1}) was calculated as the oven-dry weight (mg) of a leaf, divided by its fresh wight (g).

$$LDMC = \frac{DW}{(FW)}$$

Wood samples of five individuals of all species on each plot were collected using wood corers and oven-dried at 70° C for 72 hours, then Wood Dry Mass (WDM) (mg) and Wood Dry Volume (WDV) (mm^3) were measured to calculate Wood density (WD) (mg mm^{-3}) (Williamson & Wiemann, 2010):

$$WD = \frac{WDM}{WDV}$$

We also collected a minimum of five seeds from fruiting species. All seeds were oven-dried and weighted to obtain Seed Size (SS) (g) (Pérez-Harguindeguy et al., 2016). Finally, we considered categorical traits: Root type (RT), fulcrum or pneumatophores, high and intermediate dispersal potential (DP) and salt resistance mechanisms (tolerant, secretor and excluder) (Allen, 2013; Eisner, 2017; Kattge et al., 2020; Pagad, 2007; Parida & Jha, 2010).

Numerical traits were analyzed using Community Weighted Means (CWM)- which is the expected trait value of a randomly selected individual. We used basal area as the weighting variable. For all traits, CWM values were calculated using the FDiversity software (Salgado-Negret, 2016). Regarding categorical traits, we used the tree density of the species possessing said traits by plot.

Statistical analysis
We performed Principal Component Analysis (PCA) for descriptive visualizations of mangrove functional composition, considering the Community weighted means (CWM) of the functional traits weighted by basal area for species and plots. We used the InfoStat software and the R-function 'princomp' (Chain-Guadarrama et al., 2018; Díaz et al., 2016; Mardia et al., 1979; Venables and Ripley, 2002).

We used Linear Mixed Models (LMMs) to explore the bivariate relationships between trait CWM and the physical parameters. We considered the traits and physical parameters (salinity, disturbance and microtopography) as fixed effects and sites, transects and plots as random effects. We used the AIC (Akaike Information Criterion) and BIC (Bayesian Information Criterion) to guide best model selection (Casanoves, Pla, & Di Rienzo, 2011; Chain-Guadarrama et al., 2018). Also, we performed multiple linear regression models considering salinity, disturbance and microtopography as regressor variables to visualize the relationship between the CWMs and physical parameters (Rahman et al., 2021)

Results
We measured 1,244 trees belonging to three species and three families. *R. mangle* was the most abundant with 60% of all individuals measured across all plots, followed by *A. germinans* (35%) and *L. racemosa* (5%). These species and families are typical of Caribbean mangrove ecosystems. Salinity was measured for 31 plots because one plot was dry, while microtopography was measured in all 32 plots. Salinity ranged from 0 to 55 ppt and microtopography varied from 1.89 to 19.81 across both sites. Leaf, seed, and wood samples were taken and measured for 215 individuals: 115 (53%) *R. mangle*, 75 (35%) *A. germinans* and 25 (12%) *L. racemosa*.

TRAITS	ESTERO BALSA	EL MORRO
WD (mg mm^{-3})	2.55 ±1.31	2.25 ±1.35
LS(g dm^{-2})	1.84 ±1.15	1.52 ±0.88
TH(m)	7.56 ±3.58	5.345 ±2.34
LA (cm^2)	37.43 ±22.78	25.75 ±14.1
SS(g)	1.92 ±0.53	1.56 ±0.38
SLA (cm^2 g^{-1})	65.27 ±45.67	44.94 ±30.91
LDMC (mg g^{-1})	0.32 ±0.07	0.41 ±0.08

Table 1. Functional traits individual means and standard deviation in value across sites (n=215). Wood density (WD), leaf succulence (LS), tree height (TH), leaf area (LA), seed size (SS), specific leaf area (SLA), and leaf dry matter content (LDMC).

Variable 1	Variable 2	r	P-value
Specific leaf area	WD	0.30	***0.0012***
	LS	0.29	***0.0234***
	TH	0.52	0.1479
	LA	0.44	***0.0018***
	SS	0.24	0.6245
	LDMC	-0.77	***<0.0001***
Wood density	LS	-0.54	***0.0465***
	TH	-0.20	0.9642
	LA	-0.46	0.2758
	SS	-0.20	0.5321
	LDMC	-0.25	0.3552
Leaf succulence	TH	0.52	0.0984
	LA	0.96	***<0.0001***
	SS	0.51	0.1306
	LDMC	-0.29	0.3553
Total height	LA	0.60	***0.0040***
	SS	0.40	0.3673
	LDMC	-0.21	0.5589
Leaf Area	SS	0.47	***0.0061***
	LDMC	-0.29	0.3074
Seed size	LDMC	-0.11	0.5994

Table 2. Pearson coefficients (r) and P-values of correlations between community weighted means (CWM) of wood density, leaf succulence, total height, leaf area, seed size and specific leaf area of mangrove communities sampled in Estero Balsa and El Morro, Dominican Republic. Significant P-values (<0.05).

Specific leaf area showed significant positive correlations with wood density (P= 0.0012), Leaf succulence (P=0.0234) and leaf area (P=0.0018) and a negative correlation with leaf dry matter content (P<0.0001) (Table 2). Wood density marginally correlated with leaf succulence (P=0.0465), while leaf succulence had a positive correlation with leaf area (P<0.0001). Total height had a positive correlation with leaf area (P=0.0040) and leaf area was positively correlated with seed size (P=0.0061).

Table 1 shows the results of functional traits measured in field, in both sites; all functional traits possess a wide interspecific variability. Communities in Estero Balsa show higher values on all functional traits, but only specific leaf area (P=0.0038) and leaf area (P=0.0257) showed significant differences, both being higher in Estero Balsa.

Our Principal components analysis (Figure 1) shows all plots in the trait space as defined by PC1 and PC2, having PC1 explaining 46.5% of the variation and PC2 explaining 26.3%. PC 1, the most important axis of variation in the data, represents a spectrum of plot functional composition from plots with a high representation of pneumatophores, relatively high wood density and drop-shaped seeds (positive scores on PC1). Contrasting with plots with lower values of these traits and stronger representation of pyriform seeds, fulcrum roots and relatively large seeds (negative
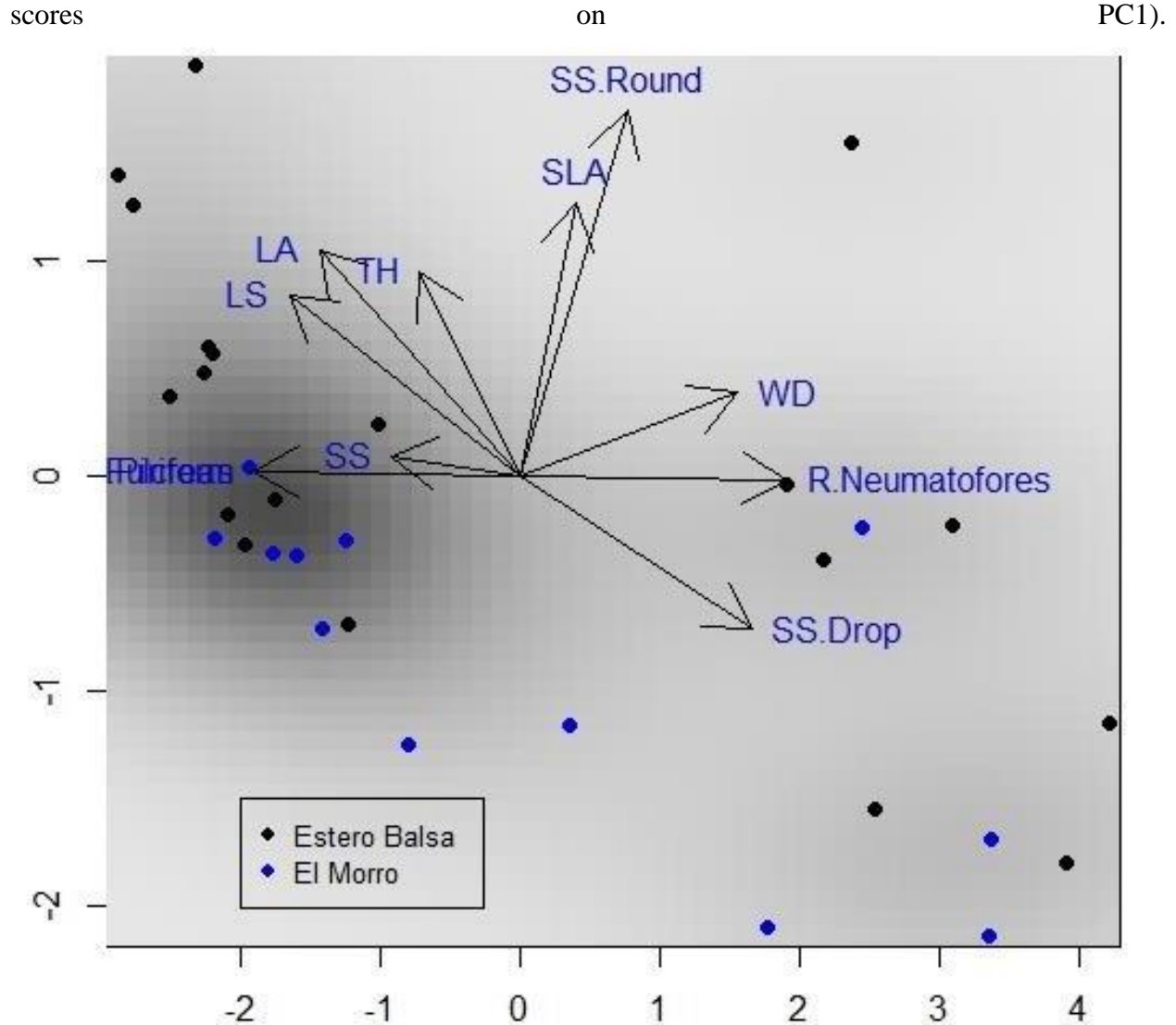
Figure 1. Biplot indicating the distribution of the scores from the Principal Component Analysis. Projection of plots (dots) on the plane defined by principal component axes PC1 (46.5%of variance explained) and PC2 (26.3%), dot color indicates site- Estero Balsa (Black) and El Morro (Blue). Solid arrows indicate direction and weighting of vectors representing traits. Background color gradient indicates regions of highest (dark) to lowest (clear) occurrence probability defined by PC1 and PC2.

PC2 is a spectrum of functional composition from plots with high CWM specific leaf area associated with round seeds, height and to a lesser extent, leaf area and succulence (positive scores on PC 2) and with negative scores, plots with the opposite characteristics.

In an additional PCA where species were considered (Figure 1. in supplementary material), *L. racemosa* and *A. germinans* both show greater relationship with leaf dry matter content and wood density, while *R. mangle* was further correlated with leaf area, tree height, specific leaf area and leaf succulence. It is important to note that the abundance of *L. racemosa* was not high enough to be conclusive.

Relationship of functional traits with physical parameters

Linear mixed models indicated significant negative relationships of CWM specific leaf area (P=0.0005), tree height (P=0.0076) and leaf area (P=0.0498) with salinity, while CWM leaf dry matter content showed a positive relationship with salinity (Figure 2). For categorical traits, intermediate dispersal potential was negatively related with salinity (P=0.0248), while salt secretor species showed a positive relationship (P=0.0248) (Figure 2).

CWM for leaf succulence (P=0.0446), and leaf area (P=0.0337) were related with disturbance. Both decreased as disturbance increased as shown in Figure 3. For categorical traits, high dispersal potential (P<0.0001), prop roots (P=0.0007) and salt tolerant species (P=0.0007) were positively related to disturbance (Figure 3). No significant tendencies were observed for wood density, seed size, and other categorical traits (Figure 2 and 3 in supplementary material).
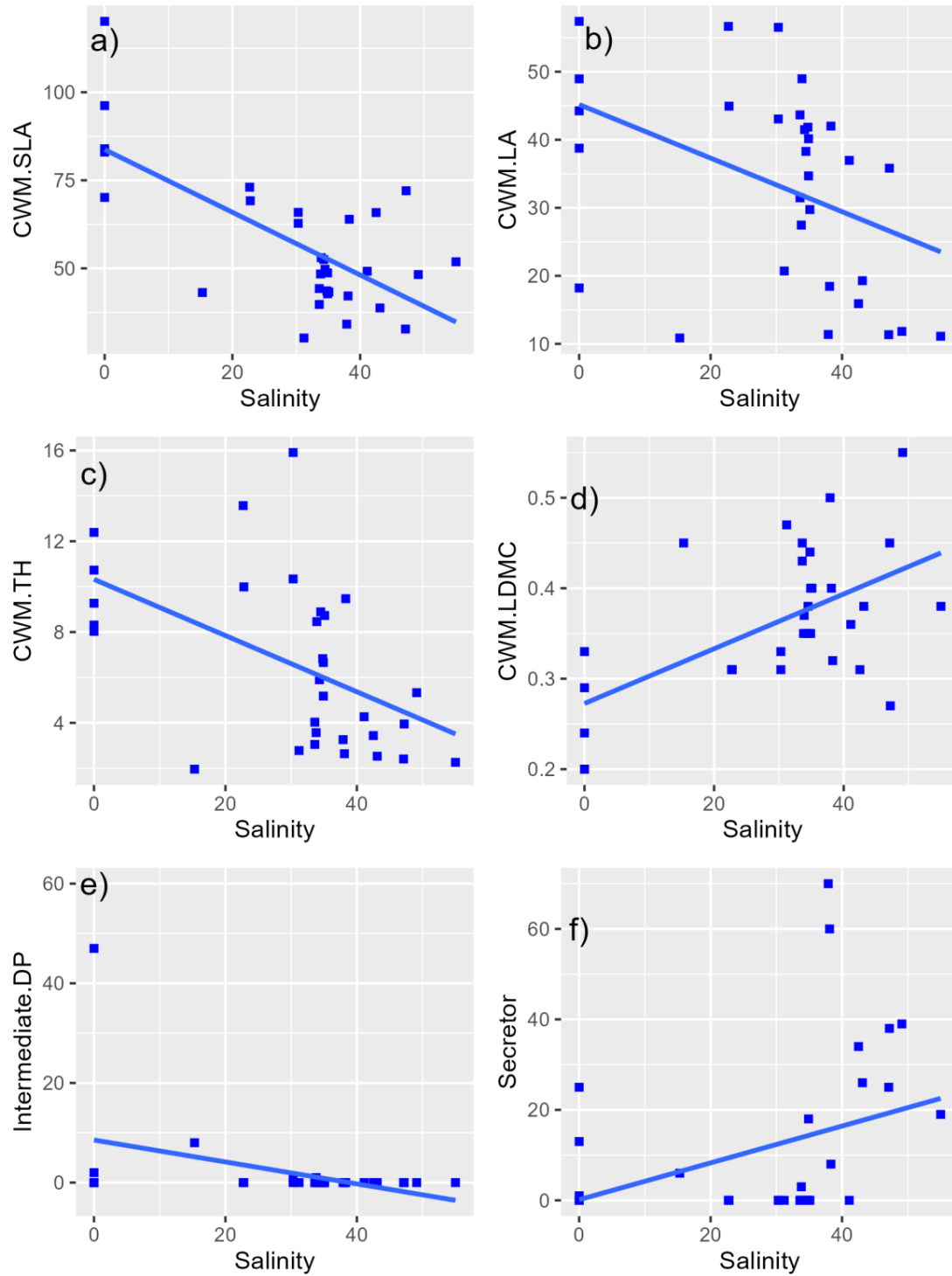
Figure 2. Linear regressions. Salinity versus a) CWM Specific Leaf Area (SLA, cm² g⁻¹), b)CWM Leaf Area (LA, cm²), c) CWM Leaf Dry Matter Content (LDMC, mg g⁻¹), d) CWM Total Height (TH, m),relative abundance of trees with e) Intermediate Dispersal Potential, and f) Salt secretor species.
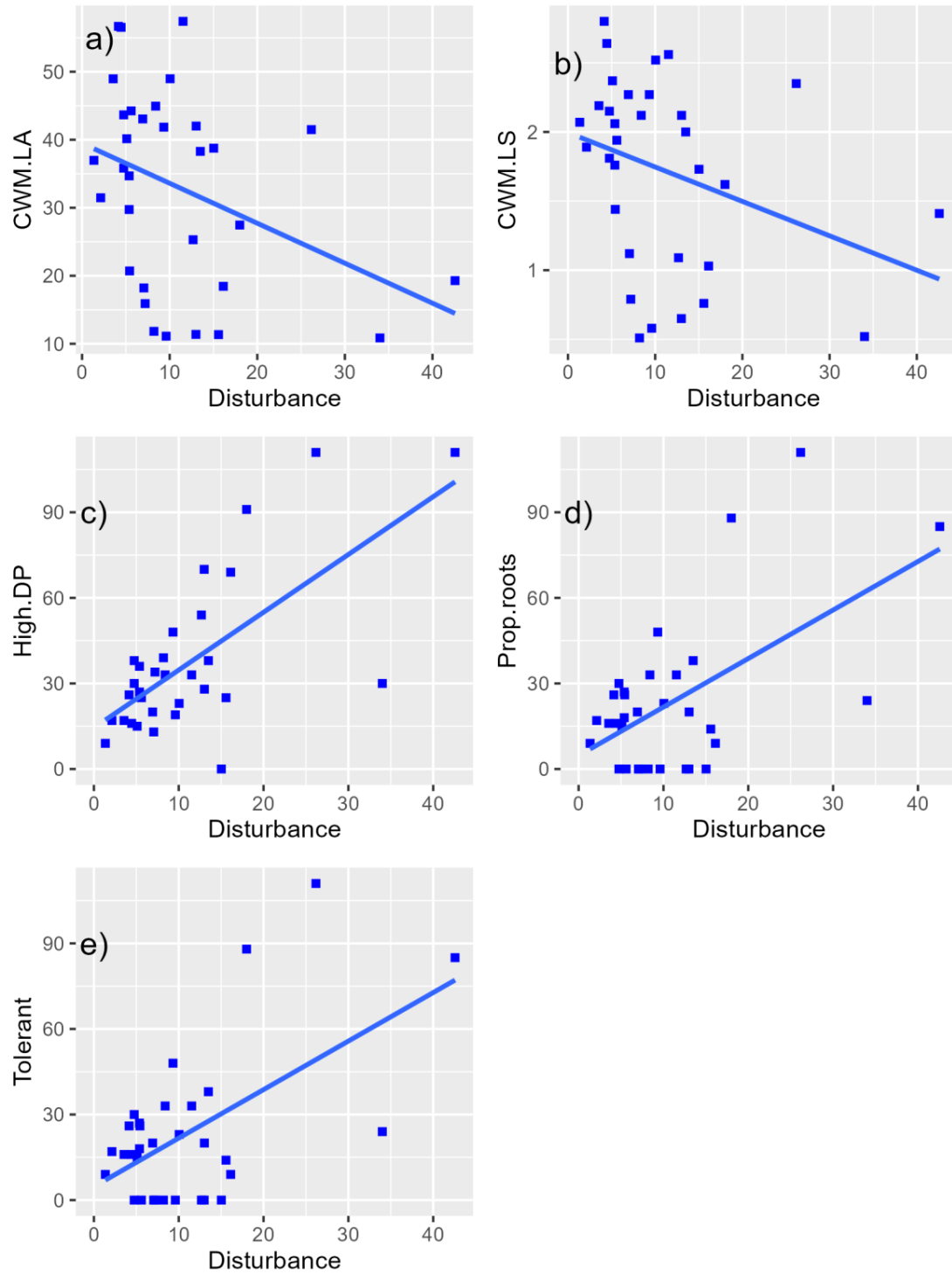
Figure 3. Linear regressions. Disturbance versus a) CWM Leaf succulence (LS, g dm^{-2}), b) CWM Leaf area (LA, cm^2), relative abundance of tree species with c) High Dispersal Potential, d) Prop roots, and e) Salt tolerance species.

Discussion

Mangroves provide coastal communities with erosion protection, sediment accretion, carbon storage and many more ecosystem services, yet few studies seek to understand resilience and resistance in Caribbean mangroves. It is critical to apply modern approaches such as functional ecology to better comprehend the capacity to withstand changing conditions of these highly valuable forests. In the present study, we seek to determine how traits differ with environmental gradients present in mangroves and how functional traits might help us understand the resilience and resistance of these ecosystems to climate change.

Relationship of community weighted means with physical parameters.

Plant height showed significant variation between plots, this is explained by the salinity gradient, as a notable decline was present as salinity increased. This is consistent with previous studies that show the effect of salinity in mangrove species. For example, *R. mangle* showed a decrease in tree size as higher salinities were present, which has been explained by salinity inhibiting tree growth (Flowers & Colmer, 2008; Peel et al.,2017).

Different studies have shown that salinity stress can inhibit growth in mangrove species (Peel et al., 2017). Species studied in the Venezuelan Caribbean, including the ones found in Montecristi, responded to this stress with a reduction in leaf area expansion agreeing with our findings. The stress may be derived from drought, nutrients, salinity or pollution (Medina & Francisco, 1997). The decrease is caused by low rates of water loss from leaves for surviving under hypersaline growth conditions, which limits carbon gain, as a result "scrub mangroves" develop under higher salinities (Villate Daza et al., 2020). Furthermore, all species show the same decrease as salinity increases, which further confirms how they use the adaptability of these traits as a response to the environmental gradients in the ecosystem (Arrivabene et al., 2014; Wei et al., 2022).

Leaf traits such as specific leaf area and leaf area have been argued to decrease due to high salinity values, but studies show that it is possible that this stress can be caused by drought as hydric stress increases (Medina & Francisco, 1997; Peel et al., 2017). Higher levels of leaf succulence protect the photosynthetic tissue, as well minimizing transpiration (Merzlyak et al., 2003). Some possible causes for low succulence include water deficit, high solar radiation and low soil nutrient content (Poorter et al., 2009)

Resistance
Temperature and drought

In the Caribbean, temperatures and drought are expected to increase in the future (IPCC, 2021). These events act on short- term scales (days to months) and can be considered as a pulse disturbance as they vary throughout the year. The Dominican Republic has very marked dry (December to April) and wet (May/June to November) seasons (De Battisti, 2021; Easterling, Evans, et al., 2000).

As temperature increases, salinity is expected to concentrate even further as water evaporates (De Battisti, 2021). As found in our results, SLA, AF and plant size show a significant decrease

with salinity (Arrivabene et al., 2014; Medina & Francisco, 1997; Peel et al., 2017). These results suggest that traits related to resistance to salinity might underpin the ability to resist drought (De Battisti, 2021). *R. mangle* probably has the lowest resistance to higher salinities as its mechanism is salt tolerance, while *A. germinans* probably has the highest resistance with secretion as its mechanism.

Species in coastal ecosystems such as marshes and dunes adopted succulent leaves for maintaining osmotic balance under water deficit or saline conditions (Flowers & Colmer, 2008). This suggests that species with higher succulence resist better to drought occurrence, our results show that sites with low disturbance possess higher levels of succulence, which means that sites that already have high disturbance levels are more vulnerable to increases in saline conditions, while sites with low disturbance will have more resistance.

Sea level rise

For the Caribbean, sea level rise predictions are insignificant (IPCC, 2021) and even if sea levels were to increase higher than expected, mangrove ecosystems can withstand high rates of sea-level rise if enough sediment for accretion is supplied (Krauss et al., 2014). In mangroves, sediment accretion is strongly tied to root types, in our study sites, species possess two types of roots; *R. mangle* has prop or fulcrum roots and *L. racemosa* and *A. germinans* have pneumatophores (OECS & USAID, 2009). In a study carried out in Micronesia, prop roots facilitated sediment accretion (11.0 mm year^{-1}) more than pneumatophores (mean, 8.3 mm year^{-1}) (Krauss et al., 2003).

In Estero Balsa, the relative abundance of *R. mangle* is 56%, while in El Morro is 65%, which suggests the forests potentially have high sediment accretion rates. Although not at the same rate, *L. racemosa* and *A. germinans* still contribute to sediment accretion. This indicates that these ecosystems may have high resistance to sea level rise.

Hurricanes and tropical storms

The Caribbean is a hotspot for hurricanes and tropical storms; they are the source for major damage to mangrove ecosystems (OECS & USAID, 2009). Sherman et al., (2001) found that after hurricane George in 1998 only about 15% of plants of the species *L. racemosa* and *A. germinans* presented less than 25% of canopy loss, while *R. mangle* had over 60%, and had a higher mortality rate. Studies show that some functional traits have a significant effect on the resistance of trees to storms. For a tropical dry forest, for example, Paz et al., (2018) explain how increased wood density, specific leaf area, tree slenderness and tree height, seem to increase the likelihood of trees experiencing damage by winds, while De Battisti (2021) showed how plant density is a key aspect of erosion resistance. This suggests, in general, that tall, light-acquisitive fast-growing species may experience a higher risk of severe damage (Paz et al., 2018). Although Sherman et al., (2001) found no clear patterns emerging between canopy height and tree damage in Dominican mangroves, which further indicates how the Plant economic spectrum (PES) may differ between wetland and dryland ecosystems.

Our data shows that CWM SLA and mean plot TH are negatively related to salinity and plant density, which suggests that areas where vegetation has low SLA and TH values would be less resistant to hurricanes and tropical storms, while sites with higher values would have higher resistance. WD possess positive correlations with salinity and plant density, this combination of high WD and plant density may allow for higher resistance to wind and waves caused by storms, allowing sites with higher values to resist them, while areas with low values may be more vulnerable.

At Montecristi *R. mangle* traits suggest it is relatively fast-growing, while *L. racemosa* and *A. germinans* have slow-growing traits. Considering that *R. mangle* is the most abundant species in both sites, this may decrease the resistance of the ecosystem.

On the other hand, root type may offer a significant advantage for resistance to erosion and damage by waves caused by storms, which gives an edge to *R. mangle* with its prop roots. Mangrove forests can reduce shore erosion up to 15 times in comparison with unvegetated shores thanks to species with prop roots (Sánchez-Núñez et al., 2019). This indicates that although this species may be less resistant because of its fast-growing qualities, its root type will help it contain and resist the effect of stronger waves, making sites dominated by *R. mangle* more resistant to storms.

Resilience
Long-term temperature increments

Temperature increments in the Caribbean have been observed since 1981, and models suggest that these increases will continue in the future (IPCC, 2021). Long-term temperature increases have various effects on ecosystem composition (Gedan et al., 2011), this can affect the resilience of forests considering the strategies used by different plant species as environmental gradients change.

As temperature increases, salinity levels in wetlands are expected to increase (De Battisti, 2021). In marshes, salt-tolerant plants have expanded at the expense of intolerant species, these plants have traits unsuitable to resist other types of disturbance like waves or storms (Watson & Byrne, 2009). *R. mangle* is highly resistant to waves and wind due to its prop roots, it is also the least tolerant to higher salinity levels, being located closest to the shore, where salt is more diluted (OECS & USAID, 2009). With higher abundance, and colonization of *R. mangle*, the ecosystem may be less resilient to temperature and salinity increments in the future.

As salinity levels spike, the sites dominated by salt tolerant species like R. mangle, may be at risk, and seedlings will have a hard time developing as hypersaline conditions limit carbon gain, inhibiting growth of newer plants and seed germination (Sobrado & Ewe, 2006; Villate Daza et al., 2020).

Recovery
An ecosystem's ability to recover from disturbance is of the utmost importance for its resilience, a resistant ecosystem may not last if it can't recover from extreme conditions (Pimm, 1984). The

main mechanisms of recovery in mangroves are seed dispersal, germination and vegetative regrowth (De Battisti, 2021).

Water is the main type of dispersal for mangrove species (Ariel, 2002). Mangrove species possess viviparous seeds, which means seeds sprout while still attached to the plant. Seedlings, like the ones of *R. mangle*, possess adaptations that allow them to float and to implant themselves in the right direction when moved by water. This allows for better seed germination and gives the species the ability to colonize clear patches with greater ease than the others (OECS & USAID, 2009).

Temperature increases may affect timing of leaf emergence and success of reproduction (Gilman et al., 2008). If this is the case, areas where salinity may increase with temperature increments to intolerable levels for mangrove species, will also suffer from low rates of germination success. Although salinity is not a universal driver, experiments show that reduced salinity levels enhance the establishment success of mangrove seedlings in saltmarshes (Manea et al., 2020).

Vegetative regrowth in mangrove ecosystems hasn't been widely studied, and findings suggests that most recovery in this ecosystem is done by very successful seedling strategies and natural rehabilitation is usually recommended for restoration efforts (Herrera Silveira et al., 2022; Kamali & Hashim, 2011). The dependency of the mangrove ecosystem on seed germination may decrease its resilience significantly, as this ability is limited with the conditions expected to occur in the future.

Conclusions

Salinity may increase with gradual climate change; we infer that it would increase the conservative (slow growing) character of mangroves in Montecristi. Extending hypersaline conditions would enlarge the distribution of dwarf mangrove, while a gradual increase in disturbance may lead to a decrease in succulence and leaf area.

Mangrove ecosystems are inferred to show high resilience to sea level rise, hurricanes, and storms due to *R. mangle* dominance and tree density. On the other hand, disturbance decreases succulence, which may decrease resistance to drought. Gradual increases in temperature will likely lead to increases in salinity, making sites dominated by *R. mangle* less resilient. Long-term monitoring is vitally important to verify the inferences made from this functional study.

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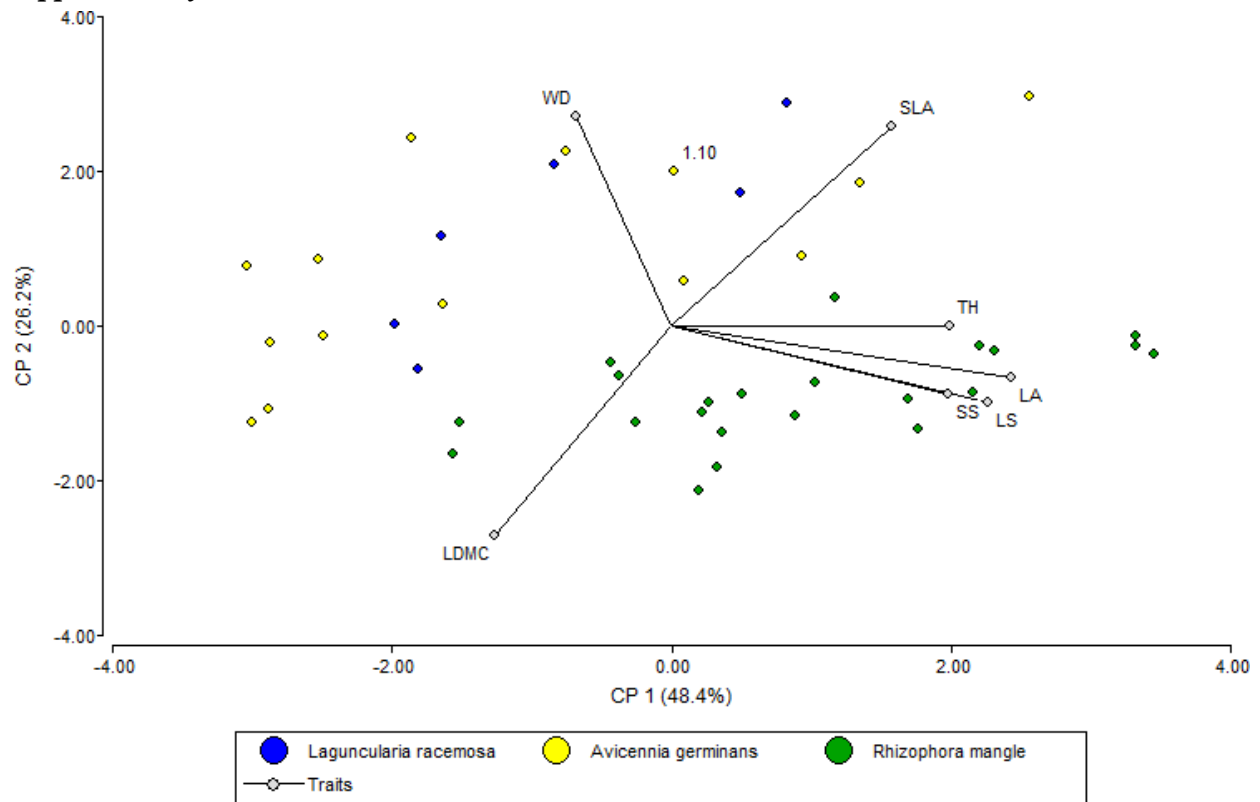
Figure 1. Biplot indicating the distribution of the scores from the Principal Component Analysis. Projection plots (dots) on the plane defined by principal component axes (PC) 1 (48.4%) and 2(26.2%). Dots color indicates the species. Arrows indicate direction and weighing of vectors representing traits.
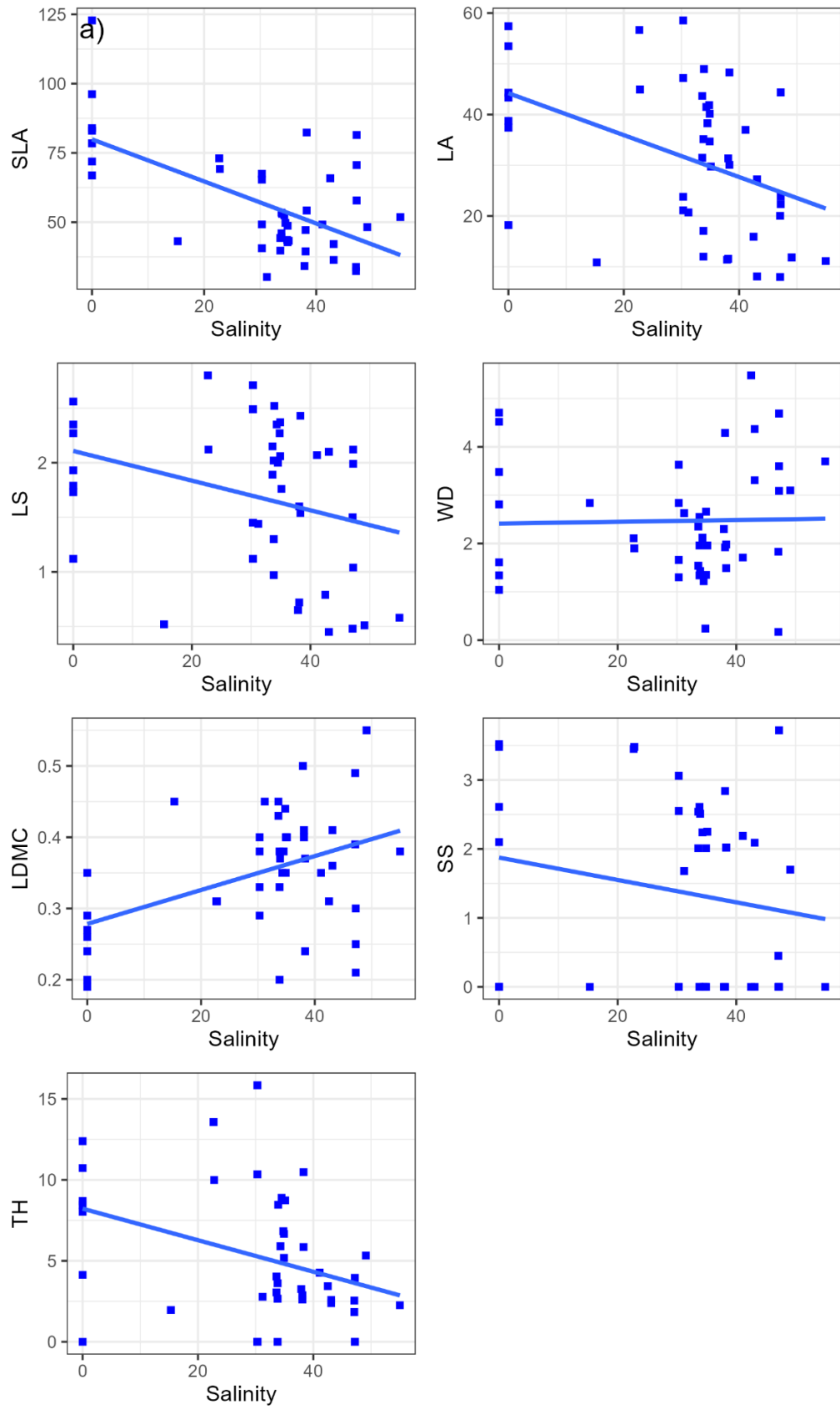
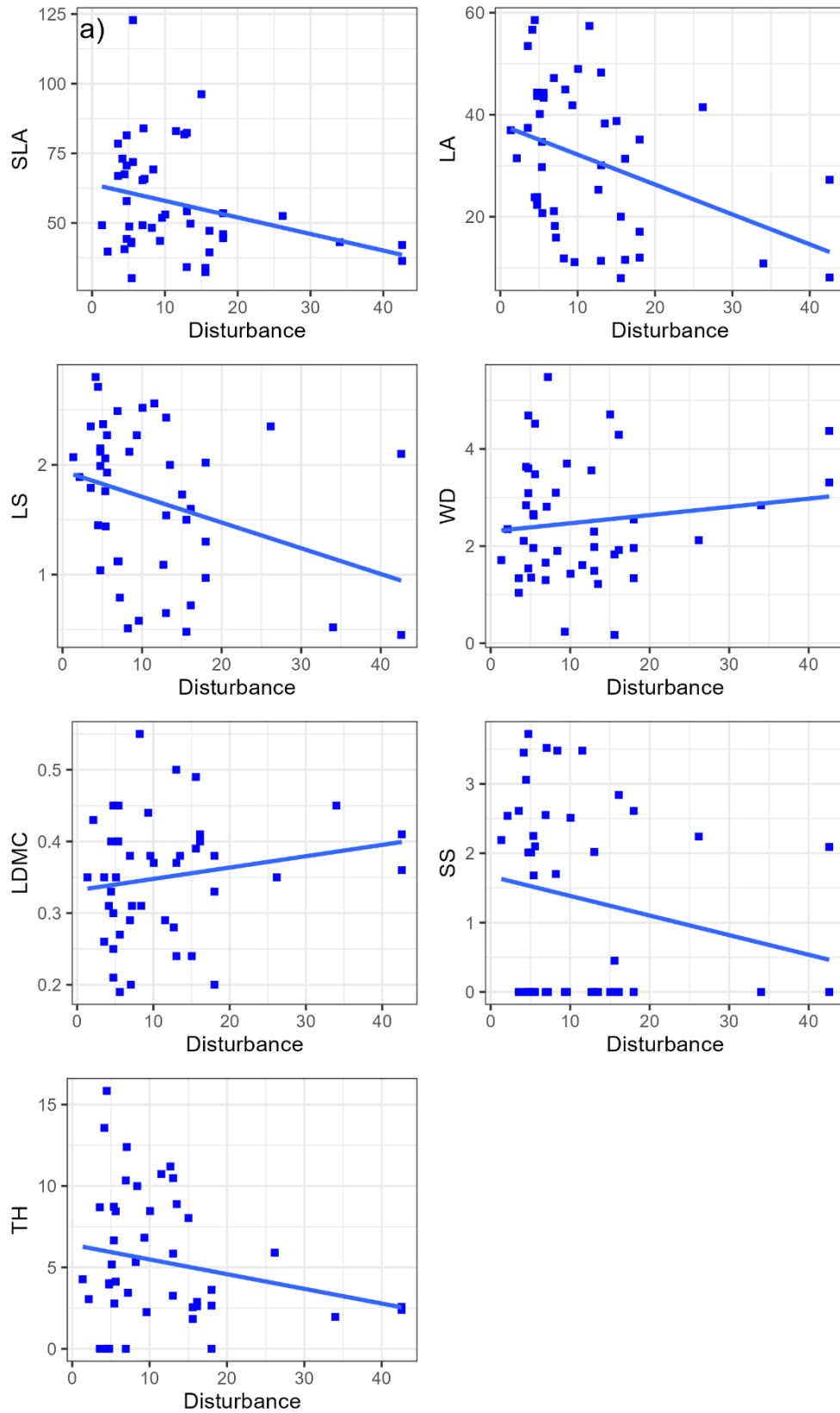*Figure 2. Linear regressions for traits and Salinity.*

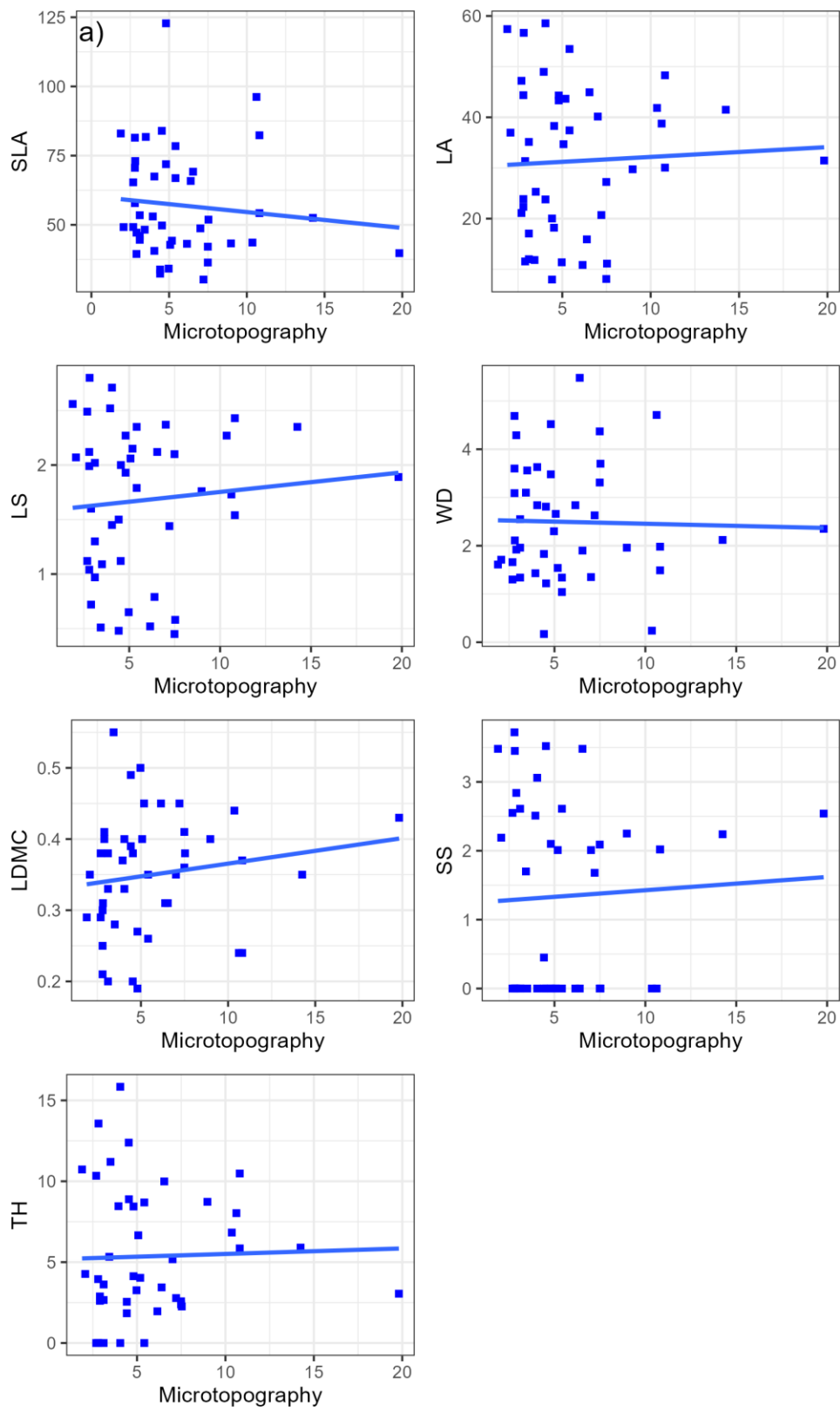*Figure 3. Linear regressions for traits and Disturbance.*

Figure 4. Linear regressions for traits and Microtopography.

Resistance	Drought	Succulence	Increases water retention
		Height	Inhibits growth
		SLA/LA	Inhibits growth Increases transpiration levels
	Hurricanes/ storms	Height	Increases damage risk
		Wood density	Decreases damage risk
		Root type	Anchors the plant to the ground
		Tree density	Increases wave resistance
		LDMC	Increases resistance to physical hazards
	Sea level rise	Root type	Increases sediment accretion

Table 1. Functional traits and their relationship to resistance to short-term climatic disturbances (Arrivabene et al., 2014; De Battisti, 2021; Easterling, Meehl, et al., 2000; Flowers & Colmer, 2008; IPCC, 2021; Krauss et al., 2014; Krauss et al., 2003; Medina & Francisco, 1997; Peel et al., 2017; Pérez-Harguindeguy et al., 2016).

Resilience	Temperature increments	SLA/LA	Inhibits growth Increases transpiration levels
		Succulence	Increases water retention
		Dispersal potential	Colonization of disturbed areas
		Salt resistance	Increases resilience
		Seed size	Probability of germination
	Recovery	Dispersal potential	Colonization of disturbed areas
		Salt resistance	Increases resilience Increases seed germination
		Seed size	Probability of germination

Table 2. Functional traits and their relationship to resilience to long-term climatic disturbances (De Battisti, 2021; Gedan et al., 2011; Gilman et al., 2008; Herrera Silveira et al., 2022; Kamali & Hashim, 2011; Manea et al., 2020; OECS & USAID, 2009; Pérez-Harguindeguy et al., 2016; Pimm, 1984; Sobrado & Ewe, 2006; Villate Daza et al., 2020; Watson & Byrne, 2009).