

Intraspecific functional variability associated to mangrove forest zonation in West-Central Mexico

Judit Torres Fernández del Campo

Centro Ecológico de Cuyutlan

Miguel Olvera-Vargas (✉ molvera@cucsur.udg.mx)

Universidad de Guadalajara <https://orcid.org/0000-0002-7290-1639>

Blanca L. Figueroa-Rangel

University of Guadalajara: Universidad de Guadalajara

Ramón Cuevas-Guzmán

University of Guadalajara: Universidad de Guadalajara

Fernando Casanoves

Centro Agronomico Tropical de Investigacion y Ensenanza

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Abstract

Functional diversity and the contribution of functional traits in mangrove ecosystems dynamics in western México remain unknown. In this study, we assessed intraspecific trait variation in three different mangrove zones. We developed and tested the following hypothesis: i. mangrove species vary along trait axes associated with plant size and leaf economics. ii. there is intraspecific trait variation (ITV) in leaf traits related to economic aspects of plant function among mangrove zones. iii. the presence of functional variation in plant traits among mangrove zones is related to physicochemical ground-water gradients. We used 65 permanent plots, distributed across three contrasting mangrove zones to assess morphological functional traits: leaf area, specific leaf area (SLA), leaf dry-matter content (LDMC), tree height (H) and wood density; salinity, dissolved oxygen, pH and temperature were recorded in each plot. Principal Component Analysis (PCA) examined how mangrove and mangrove-associated species were assembled in the functional trait space; General Linear Models (GLM) to compare mean trait values for each species among mangrove zones and Redundancy Analysis (RDA) to identify the interstitial water variables explaining functional composition. *Laguncularia racemosa* and *Rhizophora mangle* were mainly explained by SLA, LDMC and H; both species were associated to a bigger tree height, great leaf dry matter content, and small SLA values. GLM suggested ITV among mangrove zones with spatial patterns related to interstitial water variables. Our findings suggested mangrove species exhibited significant ITV mainly in SLA and H; salinity and pH were relevant to the functional ecology in mangrove ecosystems.

Introduction

Mangrove ecosystems represent a unique botanical community comprised of a number of distinctive growth forms (Krauss and Osland 2020); they are wetlands located along sheltered intertidal zones, between mean sea level and the highest spring tide (Ma et al. 2020) of tropical, subtropical and some temperate coastal regions across the globe, resulting in functionally diverse tree communities (Friess et al. 2019; Rovai et al. 2021). Mangrove forests are well known for exhibiting spatial variation in plant species composition and abundance, tree sizes and total biomass production across intertidal zones; therefore, different species inhabit distinctive niches along elevation gradients (Wang et al. 2019). This phenomenon is termed zonation which is the joint result of the potential dispersion of seedlings, the response of species to environmental factors (microtopography, tidal inundation geographical locations, soil texture and salinity) and to inter- and intra-specific competition (Rani et al. 2018; Pimple et al. 2022). At local scales, zonation is exhibited along well-defined fertility gradients, productivity levels and carbon sequestration rates in response to presses (e.g., tidal cycle) or pulses (storm surge) flooding regimes (He et al. 2021). Most of the previous studies on zonation in mangrove forests have been qualitative descriptions of species abundance (Sreelekshmi et al. 2020), species distribution patterns in the intertidal zone (Ma et al. 2020); some of these studies have attempted to quantify the relationships between surface elevation and mangrove species distributions. However, to understand community assembly and the causal mechanisms underlying species coexistence, it has been suggested to focus on the analysis of changes in plant traits rather than in species abundance (Damgaard 2021). This approach is relevant

for mexican mangrove ecosystems which display particular features that challenge their functional ecology assessment: their species richness is extremely low, they are able to tolerate stressful abiotic environments, mainly driven by physicochemical ground-water properties and show a high inter and intraspecific forest stand structural complexity along different zones (Torres-Fernández del Campo et al. 2018). Considering the relevance of the functional-based approach has acquired over the last decades in the assessment of plant community assembly (McGill et al. 2006; Mouillot et al. 2011; Spasojevic and Suding 2012), the focus of the present research relies in the evaluation of functional traits, defined as any morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival (*sensu* Violle et al. 2007); functional traits have been extensively used to understand important ecosystem functioning processes and to define groups and ranks of species according to their functions (Albert et al. 2010a; Albert et al. 2010b). A number of studies (Carmona et al. 2015; Fajardo and Siefert 2018; Li et al. 2018; Salazar et al. 2018) revealed that functional traits vary considerably at intraspecific level, making it relevant to assess intraspecific trait variation (ITV), particularly in species-poor communities where ITV is more likely to account for a large proportion of total community functional diversity (Violle et al. 2012; Siefert et al. 2015). To account for differences in mangrove functional composition along zonation, the so-called 'community-weighted mean trait values' (CWMs) method developed by Garnier et al. (2004) is one of the most appropriate technique which quantifies shifts in mean trait values due to environmental selection for certain functional traits (Ricotta and Moretti 2011); it consists in the mean trait value for a given species, weighted by its relative abundance within the community, then summed across all species (Garnier et al. 2004). Accordingly, Wright et al.. (2004) compiled a suite of leaf traits to produce the *leaf economics spectrum* (LES) with plants placed along a universal axis, from "slow" to "fast" resource uptake and use strategies; one extreme of the spectrum being represented by species with acquisitive resource use and the other by species with conservative resource use. Subsequently, Díaz et al. (2016) expanded the LES view, describing a two-dimensional global spectrum of plant form and function, where one major dimension reflects plant size and the other dimension represents LES. While extensive research is available on global mangrove tree diversity, there is no information for functional diversity for mangrove forests in west-central Mexico; therefore, aiming to fill this gap, we synthesize our research aims as follows: *i*) to identify the resource use and life strategies of mangrove and mangrove-associated species based on Díaz et al. (2016). We expect mangrove species be at the end of the spectrum, defined as those species with conservative resource traits such as low specific leaf area (SLA), which is one of the most important traits that synthesizes light capture dimension (Carlucci et al. 2015); *ii*) to assess intraspecific trait variation (ITV) across mangrove zones according to their proximity to the seashore. Hence, we expect to find ITV among mangrove zones in leaf traits related to economic aspects of plant function, such as SLA and leaf dry matter content (LDMC); *iii*) to assess differences in functional composition among mangroves in response to four ground-water gradients (salinity, dissolved oxygen, pH and temperature); we expect to find inter-mangrove zones functional variation in species traits along those gradients, according to the LES and the global spectrum of plant form and function.

Materials And Methods

Study area

This study was conducted in the Cuyutlán Lagoon, a large low-relief coastal lagoon of approximately 7,200 ha situated between: 18° 56' - 19° 03'N, 104° 00' - 104° 19' W in west-central Mexico. This is the fourth largest coastal wetland in Mexico with *Rhizophora mangle* and *Laguncularia racemosa* as the two most dominant mangrove species; its utmost north-western portion is connected to the Pacific Ocean by a 250 m-wide mouth called Canal Tepalcates and by a 80 m-wide mouth called Canal Ventanas (Torres and Quintanilla-Montoya 2014). The depth of the lagoon diminishes from north-western to south-eastern, with less than 1 m in its shallowest parts (Mellink and de la Riva 2005). Climate is sub-wet and semidry-warm with summer rains. Average annual temperature is 26 °C, with a maximum of 28 °C and a minimum of 22°C. The average annual precipitation ranges from 800 to 1,200 mm (García 2004).

Lagoon zonation

The lagoon was divided in three mangrove zones according to their proximity to the seashore: mouth, central and inner zone (Fig. 1). The mouth zone is impacted daily with flooding by tidal flushing. In contrast, flooding in the central and inner zones depends on seasonal runoff. Water surface salinity also varies in each of the three zones: in the mouth zone, water salinity is higher than in the two other zones due to its proximity to the sea; the central zone is a flat plain area where water evaporation produces high salinity conditions; the inner zone is an estuary with inputs of occasional freshwater from the Armeria River, water salinity in this zone is generally low compared with the other two zones (Torres-Fernández del Campo et al. 2018).

Study plots and forest inventory

We established sixty-five 100 m² (10 x 10 m) permanent plots across the three mangrove zones. Within each mangrove zone, the permanent plots were established 50 m away from each other following a systematic sampling design. In the mouth zone we established 27 permanent plots, 25 in the inner zone and 13 in the central zone (Figure 1). The plots covered a wide-range of environmental, floristic and stand structural variation occupied by the mangrove ecosystem in the study area.

In each plot, all adult trees ≥ 2.5 cm diameter at breast height (DBH) and ≥ 1.3 m tall were tagged, enumerated and identified to species level and their DBH and total tree height were measured (the distance between the top of the crown and the base of the tree on the ground). DBH was measured to the nearest millimeter using a diametric tape; the tree height was measured to the nearest 10 centimeters using a Haga clinometer.

Interstitial water

We measured interstitial water variables such as temperature (°C), salinity (PSU), pH and dissolved oxygen (mg l⁻¹) at 30 – 40 cm depth in each permanent plot, twice a year, one in the dry season (April 2016) and one in the wet season (September 2016). For this purpose, we used an acrylic tube attached to

a syringe. In total, 145 interstitial water samples were collected and analyzed for interstitial water properties using a Multiparameter (Hanna HI 9828 model).

Functional traits measurement

We measured in each of the five species present in the permanent plots the following five functional traits: leaf area (LA) (cm^2); specific leaf area (SLA) ($\text{mm}^2 \text{mg}^{-1}$); leaf dry-matter content (LDMC) (mg g^{-1}) total tree height (H) (m) and wood density (WD) (g cm^{-3}) considering they are the most commonly traits to assess ecological strategies in forest species (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). In order to assess the range of functional trait variation by species in each mangrove zone, ten leaves per individual for each species were sampled and 50 individuals of each species were randomly selected for tree height measurements. For leaf sampling, we detached healthy leaves from all over the tree crown (from the base to the top of the crown); we kept the leaves in sealed plastic bags with wet paper in order to limit water loss or prevent their desiccation. We followed Pérez-Harguindeguy et al. (2013) approach to assess leaf area (the one-sided or projected area of an individual leaf), specific leaf area (the one-sided area of a fresh leaf, divided by its oven-dry mass) and leaf dry-matter content (oven-dry mass of a leaf, divided by its water-saturated fresh mass). Leaf area was measured in the laboratory with a CI-202 Portable Area Meter; wet and dry leaf weights were measured with a Kern PCB3500-2 digital balance. Wood density values of each species were compiled from the literature (Zanne et al. 2009).

Statistical analysis

We performed Principal Component Analysis (PCA) to examine how mangrove and mangrove-associated were assembled relative to each other in the functional trait space, based on the global spectrum of plant form and function (Díaz et al. 2016). To run PCA, we used a species by functional trait values matrix, containing five species and the five functional trait values of each of the species considered in this study. Prior to run PCA, in order to compare the traits which were measured at different scales, the traits values were standardized using the procedure of centering and standardizing and adjusted to standard deviate.

In order to identify ITV, we compared the mean functional trait values among mangrove zones for each species using general linear models (GLM), based on Maximum Likelihood estimates and considering the mangrove zone as a fixed effect. The analysis was performed in four of the five species present in the three zones (*Laguncularia racemosa*, *Rhizophora mangle*, *Prosopis juliflora* and *Guazuma ulmifolia*), due to *Ficus insipida* was only recorded in one zone. When the corresponding ANOVA null hypothesis was rejected, we used Fisher LSD ($\alpha=0.05$) to test for differences among means. The assumptions of normality and homogeneous variances were assessed through graphical inspection of residuals.

We examine differences in functional composition among mangrove zones by calculating Community-Weighted Means (CWM) of each plot (Spasojevic and Suding 2012; Cohen et al. 2014). CWM is a functional variability measure of a functional trait given by the mean trait value of each species, weighted by its relative abundance within the community (in our case the mangrove zones) and summed across all

species (Garnier et al. 2004). We calculated CWM values for each trait t and each plot p as (Muscarella and Uriarte 2016):

$$\text{CWM}_{tp} = \sum_{i=1}^S a_{ip} \times t_i$$

where: a_{ip} is the relative abundance of species i in plot p and t_i is the mean trait value of species i . From an ecological perspective, this metric is considered as defining the dominant traits in a community and is directly related to the mass ratio hypothesis which considers the traits of the most abundant species to largely determine ecosystem processes (Ricotta and Moretti 2011).

We also used a GLM to test for difference in CWM trait values among mangrove zones, considering mangrove zones as a fixed effect. When the ANOVA null hypothesis was rejected, we used Fisher LSD to test for differences among means. The assumptions of normality and homogeneous variances were assessed through graphical inspection of residuals.

In order to identify the interstitial water variables that better explain functional composition in each mangrove zone, we ran Redundancy Analysis (RDA) (Borcard et al. 2011). To perform RDA, we used the CWM trait values and interstitial water variables with the stepwise-forward selection procedure; significance was tested by 1000 Monte Carlo unrestricted permutations. PCA and GLM analyses were run in InfoStat v.2018 (Di Rienzo et al. 2019). RDA was carried out in QEco software (Di Rienzo et al. 2019).

Results

Species composition

In total, we recorded 1 969 individuals across the three mangrove zones; the species composition, in order of absolute abundance, was represented by five species: *Laguncularia racemosa* (L.) C.F. Gaertn. ($n = 1$ 725 individuals), *Rhizophora mangle* L. ($n = 213$), *Prosopis juliflora* (Sw.) DC. ($n = 24$), *Guazuma ulmifolia* Lam ($n = 6$) and *Ficus insipida* Willd ($n = 1$). In our study area, the first two species: *L. racemosa* and *R. mangle* corresponded to mangrove species, while the remaining three are considered as mangrove-associated species.

Intraspecific functional traits

Our PCA results based on the five species and the five functional traits showed that the principal component axes one and two accounted for 87.4% of the overall variation. Hence, our results suggested that PC1 was structured by a strong component (51.4% of the variance) in which *L. racemosa* and *R. mangle* were constrained by SLA and H dimensions across this axis (Fig. 2). Both species were associated to a greater tree height and smaller SLA values. Axis PC2 explained 36.0% of total variance

where *G. ulmifolia* was linked to a higher SLA and LDMC; *F. insipida* was linked to a greater LA and to a lower WD; *P. juliflora* was related to a higher WD (Fig. 2).

According to our GLM results, we also found intraspecific variability in functional traits among mangrove zones (Table 1). The most variable trait was SLA, which resulted significantly different among the zones; *G. ulmifolia* was recorded in the mouth and the inner zones, while *F. insipida* was only present in the mouth zone. Except for *L. racemosa*, H was the most homogeneous functional trait, with no significant differences among mangrove zones in any species. LDMC behaved differently depending on the zone and species: in *L. racemosa*, it was similar in the mouth and central zones and significantly different from the inner zone; for *R. mangle* LDMC was similar in the mouth and inner zones although both zones were significantly different from the central zone. Furthermore, the highest LDMC value always occurred in the central zone for every species. LA trait showed significant differences between mouth and central zones with low values in the central zone (Table 1).

Table 1

General Linear Models of functional trait testing for differences among individuals of the same species among mangrove zones. LA: leaf area (cm²); SLA: specific leaf area (mm² mg⁻¹); LDMC: leaf dry-matter content (mg g⁻¹); H: tree height (m). Means with a common letter are not significantly different (LSD: $p < 0.05$; *LSD: $p < 0.10$). (*F. insipida* analysis is missing since it was only found in mouth zone).

Species	Trait	p	Mouth zone	Central zone	Inner zone
<i>Laguncularia racemosa</i>	LA	0.0525*	31.19 ± 1.09 A	26.62 ± 1.54 B	29.18 ± 1.09 AB
	SLA	< 0.0001	5.73 ± 0.25 C	6.93 ± 0.35 B	7.97 ± 0.25 A
	LDMC	0.0006	322.20 ± 12.62 A	347.39 ± 17.85 A	268.35 ± 12.62 B
	H	< 0.0001	14.92 ± 0.33 A	9.12 ± 0.47 C	13.03 ± 0.36 B
<i>Rizophora mangle</i>	LA	< 0.0001	93.23 ± 3.16 A	58.98 ± 4.47 B	65.41 ± 3.20 B
	SLA	< 0.0001	7.35 ± 0.21 B	6.33 ± 0.29 C	8.15 ± 0.21 A
	LDMC	0.0097	306.48 ± 9.94 B	351.10 ± 14.06 A	299.25 ± 10.04 B
	H	0.2065	8.86 ± 0.77 A	5.50 ± 3.00 A	10.23 ± 0.77 A
<i>Prosopis juliflora</i>	LA	< 0.0001	1.24 ± 0.06 B	0.56 ± 0.06 C	1.62 ± 0.04 A
	SLA	< 0.0001	17.49 ± 0.72 A	10.39 ± 0.72 B	14.70 ± 0.51 C
	LDMC	< 0.0001	295.83 ± 0.56 C	450.00 ± 0.56 A	424.70 ± 0.39 B
	H	0.3110	7.50 ± 3.58 A	5.83 ± 2.07 A	10.50 ± 1.79 A

Species	Trait	p	Mouth zone	Central zone	Inner zone
<i>Guazuma ulmifolia</i>	LA	0.0216	53.76 ± 3.77 B	-	69.14 ± 3.77 A
	SLA	0.0106	17.69 ± 1.27 B	-	23.36 ± 1.27 A
	LDMC	0.5197	423.06 ± 29.63 A	-	374.80 ± 29.63 A
	H	0.5598	5.50 ± 1.80 A	-	8.00 ± 3.12 A

Mangrove zones functional traits

CWM values showed significant differences among mangrove zones for all traits. The most dissimilar traits were SLA, LDMC and H, which revealed a complete disparity among the three zones (Table 2). CWM of SLA showed the highest value in the inner zone and the lowest in the mouth zone; H showed the highest value in the mouth zone and the lowest in the central. In turns, the highest value for LDMC occurred in the central zone while the lowest arose in the inner zone (Table 2).

Table 2
General Linear Models of CWM trait values among lagoon zones. LA: leaf area (cm²); SLA: specific leaf area (mm² mg⁻¹); LDMC: leaf dry-matter content (mg g⁻¹); H: tree height (m); WD: wood density (g cm⁻³). Values with a common letter are not significantly different (LSD: p < 0.05; *LSD: p < 0.10).

CWM traits	p	Mouth zone	Central zone	Inner zone
LA	0.0019	42.98 ± 2.49 A	26.75 ± 3.59 B	37.15 ± 2.59 A
SLA	< 0.0001	6.35 ± 0.13 C	6.99 ± 0.18 B	8.41 ± 0.13 A
LDMC	< 0.0001	324.26 ± 3.46 B	349.41 ± 4.99 A	279.38 ± 3.60 C
H	< 0.0001	13.73 ± 0.25 A	8.98 ± 0.36 C	12.20 ± 0.26 B
WD	0.0729*	0.66 ± 0.02 AB	0.61 ± 0.03 B	0.69 ± 0.02 A

Functional traits along environmental gradients

RDA results showed an evident spatial pattern among CWM traits in relation with interstitial water variables. The first axis accounted for 49% of the explained variance; this axis was mainly related to LDMC, close to the central zone and related to salinity of dry season (SalD); along the same axis but inversely related, SLA and H were the most significant traits close to the central and inner zones (Fig. 3). The second axis, which explained 24% of the variance, was related to WD, LA, H and SLA; the last two traits were related to pHW and pH_D. An interesting result was the clear separation of the central zone from the inner and the mouth zones, a result mainly attributed to the interstitial water variables (Fig. 3).

Discussion

Species adaptive strategies

According to the PCA results, there was an inverse relationship between tree height and SLA. These results supported our first hypothesis that “mangrove species should be attached to the height-SLA dimension in the spectrum”. *L. racemosa* and *R. mangle* were distributed over the height-SLA dimension, associated with high values in tree height and low values for SLA. This finding is in accordance with a well-established hypothesis (Díaz et al. 2016; Grime, 1998; Westoby, 1998) which suggest that adaptive specialization in plants arises from a trade-off between functional traits allowing rapid resource acquisition (‘acquisitive type’), with another set of functional traits that allows the maintenance of resources within well protected tissues (‘conservative type’). The maximum tree height attained by an individual plant, compared to others within the same community, is considered an important plant strategy, linked to light acquisition and competitive ability (Westoby 1998; Siefert et al. 2015). Freschet et al. (2010) using empirical data, in a sub-arctic flora, revealed the so-called “plant economics spectrum”; they claim that SLA is an indicator of resource-use strategies, with SLA low values associated with conservative strategies achieving greater leaf life span through extra structural strength. In harsh environments, mainly in low resource availability conditions (e.g. nutrients, humidity, sun-light), low SLA is favourable because it maximises the use of limited nutrients availability (Roche et al. 2004). Long-lived leaves accumulate greater leaf mass capturing high amount of light (Westoby et al. 2002). The resource-retaining strategies are favoured when resource availability is low (Cornwell and Ackerly 2009; Carmona et al. 2015), as occurs in mangrove environments. Hence, functional traits of mangrove and mangrove-associated species in our study area suggest a conservative resource-retaining strategy, as we also predicted in our first hypothesis

Intraspecific functional trait variation among zones

We found intraspecific variability in functional traits among the three mangrove zones, with the SLA as the most variable trait. This result confirms our second hypothesis which stated that “ITV in leaf traits among mangrove zones should be related to economic aspects of plant function, such as SLA and LDMC. Variation in functional traits commonly depict dissimilar adjustment to variation in environmental conditions representing niche differentiation among species (He et al. 2018). In line with similar studies (Freschet et al. 2010; Siefert et al. 2015), we found great variation within species traits. Li et al. (2018)

found substantial within and between species variability in leaf traits such as SLA in *Pinus koraiensis* and *Fraxinus mandshurica*, two dominant tree species along a latitudinal gradient in northeast China; Siefert et al. (2015) conducted a meta-analysis on the relative extent of ITV within and between plant communities worldwide; they concluded that, on average, ITV accounted for 32% of the total trait variation among communities. Our results also suggested that ITV could play an important role in driving shifts in SLA across contrasting environmental gradients (among mouth, central and inner zones) predicted by the LES (Wright et al. 2004; Fajardo and Siefert 2018). A particular trait confers different competitive ability depending on environmental conditions (Weiher et al. 1999). Depending on the mangrove zone, each species responded differently to environmental variability, suggesting that the three mangrove zones in our study area are functionally different. *L. racemosa* and *R. mangle*, both with conservative resource-retaining strategy, accounted for a different pattern in the variation of SLA among zones. *L. racemosa* maintained the lowest SLA value in the mouth zone, while *R. mangle* showed low SLA value in the central zone. In our study area, ITV could be the result of a species morphological adaptation, which may be expected to be rapid but likely without genetic transcendence. It could also be the result of a genetic change, an adaptive evolutionary response that may have greater significance (Siefert et al. 2015). This is an important issue which should be investigated in future research in our study area.

Functional composition along environmental gradients

Regarding significant differences among mangrove zones, our results with CWM values, confirmed our third hypothesis; “we would expect to find inter-zones variation in functional traits, according to the global spectrum of plant form and function along physicochemical ground-water gradients” (*sensu* Díaz et al. 2016). Variations in CWM among mangrove zones followed the same pattern of ITV for *L. racemosa* for SLA and H traits. According to the mass-ratio hypothesis, traits of the dominant species are the most meaningful elements of ecosystem functioning (Díaz et al. 2007; Grime, 1998); this fact is in accordance with our findings concerning CWM for SLA and H which could be primarily driven by ITV of *L. racemosa*, the most abundant species in our study area. This result is similar to those reported by Fajardo and Siefert (2018) who emphasize the importance of local environmental variation as a driver of functional trait diversity.

RDA on CWM showed that LDMC increased with a higher salinity (SalD) and lower pH (pHW and pH_D), while SLA and H decreased. Henceforth, salinity and pH were significant ground-water variables explaining mangrove functional variability in our study. Similar results have been found along environmental gradients in mountain ecosystems suggesting that SLA increased while LDMC decreased with precipitation, disturbance or soil nutrients (e.g. Schellenberger Costa et al. 2017). The relationship between functional traits and physicochemical variables support the plant economics spectrum, indicating higher acquisition in plants with less stressed soils (Díaz et al. 2016; Freschet et al. 2010; Wright et al. 2004). These traits–environment interactions can be inferred in terms of physiological trade-offs linked to the plant ability of resource acquisition in stressful conditions (Muscarella and Uriarte 2016). The more saline and acidic ground-water, the less optimal conditions for mangrove forest

development in our study area (Torres-Fernández del Campo et al. 2018); salinity affects mangrove tree growth (Méndez-Alonzo et al. 2012) while pH, due to its integration with other physiochemical parameters, has strong influence on abiotic factors such as macro- and micro-nutrient availability and salinity, but also with biotic factors such as soil-microbial community (Mendes and Tsai 2018). Hence, our mangrove floristic zonation suggested a sharper resource conservation plant response (low values in SLA and H, but high values in LDMC) in zones with higher salinity and lower pH. This occurred in the central zone of the Cuyutlán Lagoon which is a flat plain area where water evaporation produces high salinity conditions (Torres-Fernández del Campo et al. 2018); on the contrary, mangrove zones with a resource acquisition strategy (higher SLA and H) occurred in zones with fresher water inputs but mainly in the inner zone.

Conclusions

Results from the present research revealed that mangrove and mangrove-associated species in the Cuyutlan lagoon in west-central Mexico have significant ITV in the SLA trait, an important leaf economic trait. These findings could be interpreted as species adaptation to the local environment. However, environmental variability across the study area led to different responses in ITV among species, suggesting variation in the species competitive ability along environmental gradients conferring this community with a rapid colonization, together with a conservative resource-retaining strategy.

CWM values of H, SLA and LDMC led to significant functional differences among mangrove zones along physicochemical gradients, explained mainly by water salinity and pH. Salty and acidic ground-water conditions increased LDMC values but decreased H and SLA. On the contrary, zones with higher pH and fresh water availability showed a higher SLA and H. Physicochemical ground-water variables, particularly salinity and pH, seems to be remarkably relevant to the functional ecology of mangrove ecosystems supporting the plant economics spectrum. Nevertheless, we recommend a broaden evaluation regarding the effects of these physicochemical variables in the functional trait space on wetland ecosystems, particularly in a more diverse environmental and floristic conditions. This evaluation would expand our understanding on the functional composition of these important forest ecosystems globally impacted by human-induced activities and climate change.

Declarations

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Authors’ Contributions

Judit Torres-Fernández del Campo and **Miguel Olvera Vargas** conceived the original idea, designed methodology, collected and analysed the data and wrote the manuscript; **Blanca Lorena Figueroa-Rangel**

analysed the data and wrote the manuscript. **Ramón Cuevas Guzmán** contributed with writing and reading the manuscript; **Fernando Casanoves** analysed the data and contributed with writing and reading the manuscript. All authors contributed critically to the drafts, discussed the results and commented on the manuscript and gave final approval for publication.

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Code Availability: not applicable.

Ethics Approval: not applicable

Consent to Participate: yes

Consent for Publication: yes

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Figures



Figure 1

Cuyutlan Lagoon in west-central Mexico showing the sampled zones including their GPS derived position (Map modified from INEGI 2013).

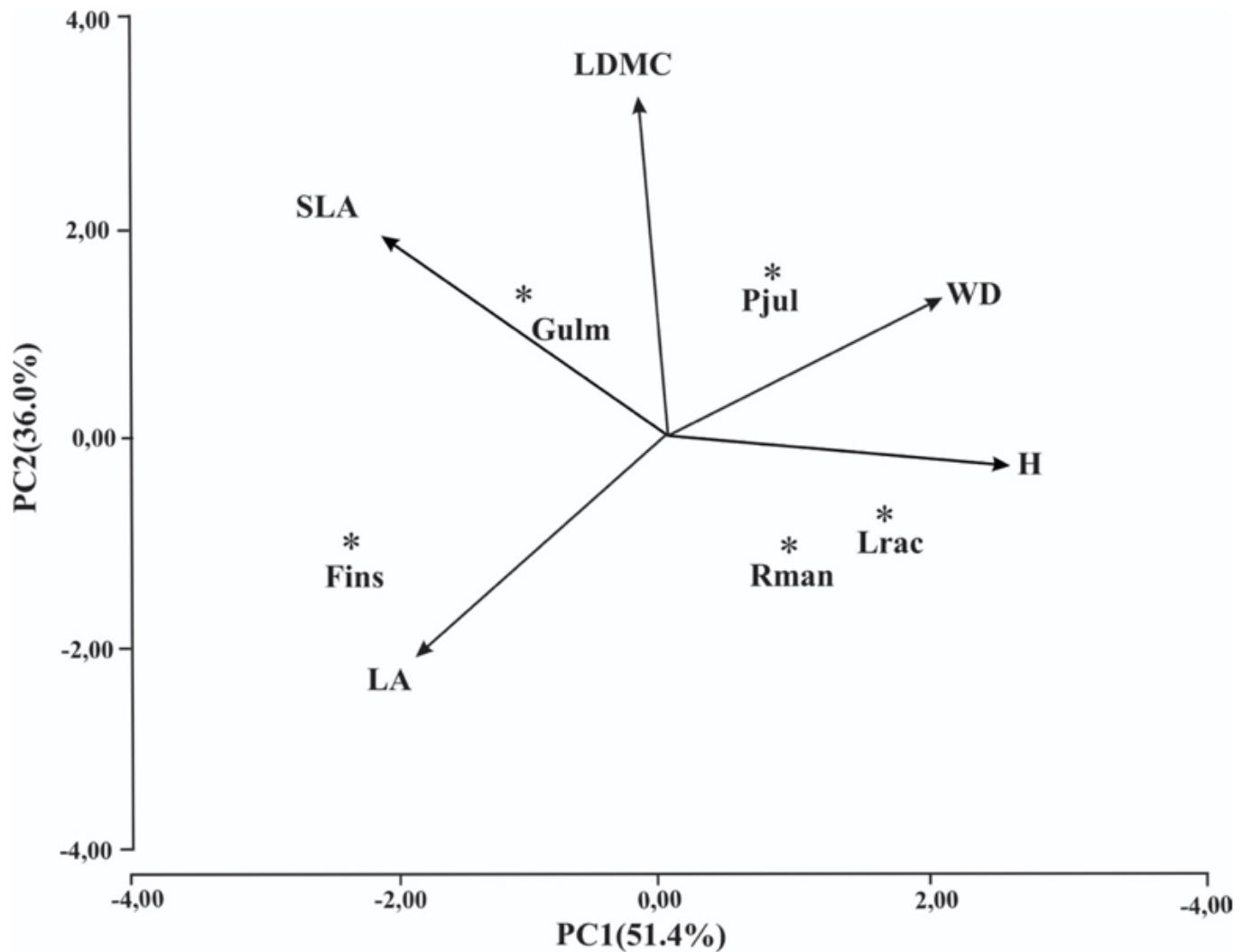


Figure 2

Principal Component Analysis of the species (Fins: *Ficus insipida*; Gulm: *Guazuma ulmifolia*; Lrac: *Laguncularia racemosa*; Pjul: *Prosopis juliflora*; Rman: *Rizhophora mangle*) according to functional trait (LA: leaf area; SLA: specific leaf area; LDMC: leaf dry-matter content; H: tree height; WD: wood density). The direction and size of vectors represents the functional trait weight considered in this study.

Figure 3

Redundancy Analysis of the functional traits CWM in response to interstitial water variables. H: tree height; LA: leaf area; LDMC: leaf dry matter content; SLA: specific leaf area; WD: wood density; pH_D: pH on dry season; pH_W: pH on wet season; Sal_D: salinity on dry season.