Variation in leaf traits across a precipitation gradient in coastal sand dunes in Yucatan Peninsula

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ABSTRACT

Environmental filters play an important role in plant community assembly. Evaluating spatial variation in functional traits across environmental gradients may help determine the environmental filters that play a role in community assembly and how plant communities respond to prevailing environmental conditions. In this study, we evaluated spatial variation in leaf traits (size, thickness, specific area and dry matter content) of coastal sand dune plant communities across 16 sites along a precipitation gradient in the Yucatan Peninsula. We described community-wide trait variation in terms of dispersion and dominant values across the gradient in order to answer the following questions: Which environmental filters explain variation in leaf traits? What ecological strategies, in terms of leaf economics, do these environmental filters favour? Mean specific leaf area and dispersion in leaf thickness tended to be lower in drier sites, suggesting that plants invest more biomass per leaf (a conservative strategy) and become more succulent as aridity increases. Contrary to expectation, leaf size increased with proximity to the coastline and dry matter content was significantly greater in the wettest region. Therefore, variation in these leaf traits content cannot be explained by the precipitation gradient. We have shown that predictable variation in some functional leaf traits can be found, even at small scales within the same vegetation zone in coastal sand dunes. Our study supports the notion that variation in water availability can be an important driver of functional trait distribution in the plant communities of some arid environments.

1. Introduction

A major goal in community ecology is to understand what mechanisms determine local species composition in biotic communities (Vellend, 2010). Community assembly rules, or the generalized restriction on species coexistence first envisioned by Diamond (1975), suggest that environmental filtering is a key process to explain species composition in a given community. Environmental filtering refers to the survival and persistence of certain species in the community and the elimination of others in response to abiotic environmental constraints (e.g. Kraft et al., 2015). In this sense, the trait-based approach has provided great insight into the role of environmental filters in plant community assembly (McGuill et al., 2006). From a trait-centred perspective, we can envisage a community as a frequency distribution of trait values (Garnier et al., 2016; McGuill et al., 2006). In this sense, environmental filters can reduce the distribution range of functional

traits while increasing the frequency of traits that favour species permanence (e.g. Cornwell and Ackerly, 2009; de Bello et al., 2009; Lebrija-Trejos et al., 2010). For instance, evaluation of variation in functional traits across environmental gradients, where sharp changes have been observed over relatively short distances, has been particularly useful to infer the predominant assembly process (Garnier et al., 2016). Thus, in cases where environmental filtering is strong, increasing trait convergence is expected as environmental conditions become harsher (e.g. Cornwell and Ackerly, 2009; de Bello et al., 2009).

Functional traits of plant communities in harsh environments (e.g. alpine, desert, Mediterranean ecosystems, etc.) are expected to have relatively narrower distributions due to the strength of the prevailing environmental filters in these ecosystems (Ackerly, 2004; Mouillot et al., 2007). Coastal sand dunes are one example of harsh environments where functional diversity is severely constrained by environmental filters, such as salt spray and sand blast, as well as low nutrient

and water availability (Hesp, 1991; Maun, 1994, 2009). In particular, coastal sand dunes in the tropics are restricted to arid and semiarid regions (Maun, 2009). Low water availability in coastal sand dunes is not only the result of reduced or seasonally restricted rainfall, but also the soil salinity, which acts to limit water absorption in some plants species since salt increases the osmotic pressure of the water (Conti et al., 2017; Maun, 2009). Thus, low water availability has the potential to act as a strong environmental filter on plant communities, determining species composition and ecological strategies in plants (Delgado-Banquerizo et al., 2013; Nunes et al., 2017). Water scarcity has also been shown to affect the dispersion and dominant values of plant functional traits in other ecosystems (e.g. Nunes et al., 2017), usually favouring small, thick and dense leaves (low leaf size, low specific leaf area [SLA], high leaf dry matter content [LDMC] and leaf thickness) (Meng et al., 2015). Thus, with increasing aridity, plants with a more conservative strategy in terms of resource use, tend to be favoured (i.e., expensive-to-construct leaves that tolerate environmental stress and better conserve the acquired resources; Wright et al., 2004).

Coastal sand dunes are a good model with which to assess how assembly mechanisms vary across environmental gradients (Conti et al., 2017). Within their range of distribution, coastal sand dunes are exposed to variable water availability and other environmental stresses (Maun, 2009), which can lead to a variable combination of functional traits in plant communities. Moreover, coastal sand dunes exhibit a typical zonation of vegetation as a result of the sea-inland environmental gradient (salt spray, sand blast, solar radiation and high winds are progressively stronger with proximity to the sea). Across this gradient, plant communities (vegetation zones) become progressively more species-rich, as well as structurally (vegetation is taller and has two or more strata) and functionally more complex, with increasing distance from the sea (Conti et al., 2017; Maun, 2009). The zone closer to the coastline presents the harsher environment and is known as the pioneer zone. This zone is followed by the high beach and dune ridge zones, which are characterized by the presence of dune-building species and, finally, the transition zone to the forest, which presents the most benign environmental conditions (Maun, 2009). To our knowledge, few studies have assessed geographic variation in functional diversity within a given vegetation zone (mainly the foredune) along the coastline (Gallego-Fernández and Martínez, 2011; García-Mora et al., 1999; Mahdavi and Bergmeier, 2016). These studies have shown large-scale variation in plant functional groups along the coastline; however, it is unclear which specific traits are being favoured and by which environmental filters (Gallego-Fernández and Martínez, 2011; García-Mora et al., 1999; Mahdavi and Bergmeier, 2016). Overall, it seems that spatial variation in functional diversity within the same vegetation zone (i.e. along the coastline) is far less predictable than variation across vegetation zones (in the sea-inland gradient). Furthermore, most studies that have evaluated spatial variation in functional diversity in costal sand dunes have used a plant functional group approach (*a posteriori* categorization of functional groups based on variable criteria; Gallego-Fernández and Martínez, 2011; García-Mora et al., 1999, 2000; Mahdavi and Bergmeier, 2016). This approach has received some criticism since many relevant functional traits are continuous and thus, the supposed boundaries between functional groups are arbitrary and overlook within-group variation (Petchey et al., 2009). In contrast to the functional group approach, a trait-centred approach considers the continuous variation in functional traits (Petchey et al., 2009). The trait-centred approach may therefore be a more suitable approach for the detection of fine variation in functional traits and identification of associated environmental filters at smaller scales. To our knowledge, no previous study has evaluated small-scale variation in leaf traits within a specific vegetation zone using a trait-based approach in coastal sand dunes.

In this study, we evaluated spatial variation in leaf functional traits (size, thickness, SLA and LDMC) across an environmental gradient in the northernmost region of the Yucatan Peninsula. Environmental variation in this area is mainly driven by variables related to aridity. While temperature steadily increases from west to east, the lowest and highest rainfall values have been recorded in the central and eastern regions respectively, with intermediate values found in the west region. Since this area presents a predominantly flat relief and homogenous soil characteristics (Duch, 1988), other environmental variables exhibit only minor variation along this gradient. The study area therefore represents an excellent model system with which to assess the effect of precipitation and temperature on the functional diversity of leaf traits. For this study, we selected plant communities of the pioneer zone and evaluated variation in leaf traits indicative of water stress (leaf size, leaf thickness) and also of the particular ecological strategy within the leaf economic spectrum (SLA and LDMC). Plants with larger SLA and lower LDMC usually have a strategy of greater resource acquisition (i.e. plants with cheap-to-construct leaves that maximize resource capture; Wright et al., 2004), while plants with the opposite pattern (i.e. lower SLA and higher LDMC) typically have a more conservative strategy (Wright et al., 2004). Thus, in this study we describe community-wide variation in leaf functional traits across an environmental gradient in order to answer the following specific questions: Which environmental filters explain leaf trait variation in coastal sand dune plant communities? What are the plant functional strategies (acquisitive vs. conservative) being favoured by environmental filters in these communities? We predicted significant covariation between environmental variables related to precipitation and temperature and functional leaf traits related to water stress. In sites with harsher conditions (less rainfall and higher temperature), we expect less dispersion in all functional traits compared to sites with more favourable environmental conditions. We also expect variation in terms of the dominant trait value; i.e., in drier sites, we expect a higher frequency of plants with smaller, more succulent leaves as well as low SLA and high LDMC (i.e. a conservative strategy), while the opposite is expected in sites with higher precipitation.

2. Materials and methods

2.1. Study area

The study area was located in the coastal sand dunes of the Yucatan Peninsula (Fig. 1). These dunes are distinctive in the region of the Gulf of Mexico and the Caribbean due to their relatively recent origin (emergence during the early Tertiary) and high number (4–6%) of plant endemisms (Espejel, 1987; Moreno-Casasola and Espejel, 1986). Coastal sand dunes are distributed along the entire coast of Yucatan; the vegetation type extends over *ca.* 320 km but is interrupted in a few areas by mangrove and coastal lagoons (Espejel, 1987). Thus, this study encompasses the full distribution of the sand dune ecosystem along the northern coast of the Peninsula. Plant communities in the coastal sand dunes of Yucatan are dominated by herbaceous plants and, to a lesser extent, by short shrub species. Seventy-five plant species have been reported in the study area (Parra-Tabla et al., 2018). Of these, some representative species are: *Ambrosia hispida* (Asteraceae), *Croton punctatus* (Euphorbiaceae), *Euphorbia mesembrianthemifolia* (Euphorbiaceae), *Scaevola plumeri* (Goodeniaceae), *Sesuvium portulacastrum* (Aizoaceae), *Cakile edentula* (Brassicaceae), *Ipomoea pes-caprae* (Convolvulaceae) and *Suriana maritima* (Surianaceae) (Espejel, 1987; Parra-Tabla et al., 2018).

Across the whole region, the climate is tropical with summer rains, mean temperature is 26 °C and mean annual precipitation is 700 mm (Orellana et al., 2009). The soil is sandy and slightly variable along the coast (Duch, 1988). However, in the northernmost part of the Peninsula, along the coast of Yucatan, the climate varies from west to the east in terms of precipitation (Orellana et al., 2009; White and Hood, 2004). The central part of this area has the lowest precipitation (mean annual rainfall: 588 mm), while the eastern part receives the most rain (700 mm) and the western part is intermediate, with a mean annual
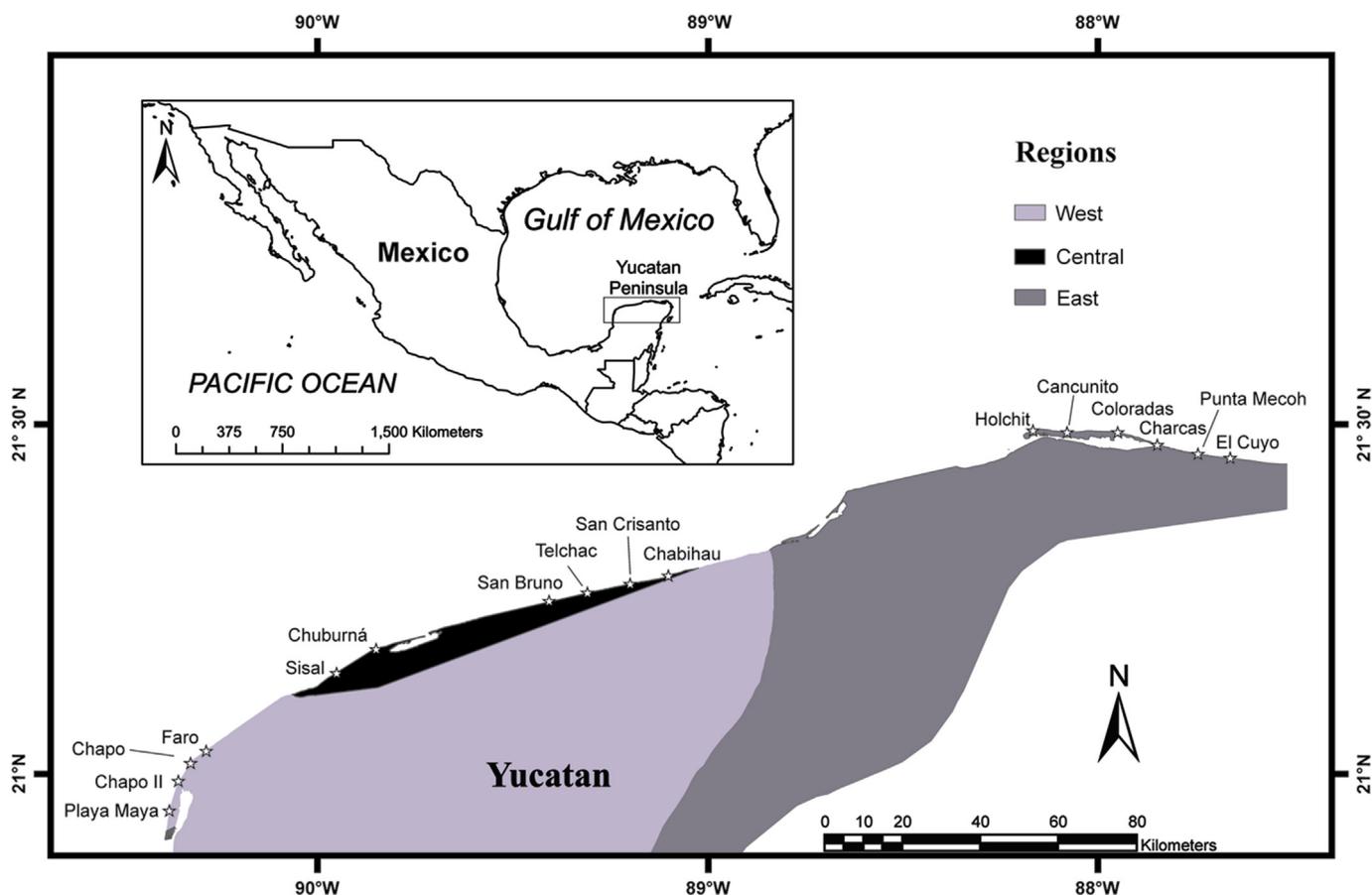
Fig. 1. Map of the study area. Different colours show the three dominant bioclimatic regions in the coast of Yucatan peninsula: West (semidry and warm), Central (dry and warm) and East (very warm and sub-humid). Sampled communities are indicated with a star. The top-left square shows the position of the study area in the country (Mexico). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

precipitation of 665 mm (data from www.worldclim.org). There is also moderate variation in temperature across this area, which increases from the east (25.32 °C) toward the west (26.21 °C), with intermediate values in the central part (25.65 °C) (data from www.worldclim.org). Since each geographic region (east, central and west) presents a different climate (following Koppen's classification, west: $BS_1(h')w(i')gw$, centre: $BSo(h')w(x')$, east: $Ax'(w_1)$ (i') gw), as well as a different biogeographic influence in terms of the vegetation (western region is mainly influenced by vegetation from the Gulf of Mexico while the eastern region is influenced by the Caribbean; Espejel, 1987; Moreno-Casasola and Espejel, 1986), some authors have suggested that these regions represent three well differentiated bioclimatic regions (Martínez-Natarén et al., 2014; Orellana et al., 2009). The pioneer zone vegetation is the most species-rich in the western region (37 species) with no apparent differences (in terms of species richness) between the central and eastern regions (26 and 25 species, respectively) (Parra-Tabla et al., 2018). Some authors have also suggested that the important intraregional environmental variation in this area is not discrete but rather continuous (i.e. an environmental gradient; White and Hood, 2004).

2.2. Vegetation and leaf sampling

Sixteen study sites were selected along 205 km of coastline in the northernmost part of the Yucatan peninsula. We selected only sites with low human disturbance that presented similar conservation status. Four sites were located in the western region, six in the centre and six in the eastern region (Fig. 1). Minimum and maximum distances between sites were 4 and 106 km, respectively (average: 18.5 km). Species identity

and abundance were surveyed at each site using the line intercept method (Canfield, 1941) from January to March 2016, in which two 100 m linear transects were established parallel to the coastline and 50 m apart. Within each of these two main transects, ten 10 m subtransects were established transversally and alternated every 10 m, one on each side on the main transect. In total, 20 sub-transects were established at each site for total sampled area of 200 m in length. Sampling sufficiency was > 77% on average across sites (range: 77–93%), when compared to the species richness predicted by the Chao-2 nonparametric estimator, which is highly reliable and not sensitive to patchiness when grain size is constant (Hortal et al., 2006), as was the case in this study. Species turnover among the 16 plant communities ranged from 0.05 to 0.7 (Simpson's pairwise dissimilarity index; see Appendix A in online supplementary material for a complete species dissimilarity matrix).

From this vegetation survey, we identified the 33 most abundant plant species that represent, in terms of abundance, more than 90% of all species in the study area (See Appendix B in online supplementary material). Following standardized protocols (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013), five true leaves (i.e. non-cotyledonary leaves) from at least five individuals per species per site were collected (1–4 sites per plant species were collected). Only adult plants growing in unshaded locations were selected and fully expanded leaves with no evident signs of pathogens or herbivory, were collected. Leaves were placed in plastic bags with wet paper inside, stored in a cooler with ice and transported to the laboratory. All leaves were processed within two days of collection.

2.3. Functional traits

In the laboratory, leaf size, thickness, SLA and LDMC were determined following the methods outlined in Cornelissen et al. (2003). Leaf size was measured as the one-sided leaf area of fresh leaves (in cm^2) using a leaf-area meter (LI-COR, LI300-A). Leaf thickness was measured in fresh leaves at the equatorial zone avoiding the main rib with a digital caliper ($\pm$ 0.1 mm). To measure SLA, one-sided leaf lamina of leaves was measured, and the same leaves were then oven dried at 60 °C for 72 h and weighed. SLA was calculated as leaf area divided by leaf dry mass and expressed in cm^2 g^{-1}. To obtain LDMC, each fresh, water-saturated leaf was weighed and divided by its oven-dry mass (as obtained for SLA) and expressed in g g^{-1}.

Leaf size is negatively related to major environmental stressors such as heat, cold, drought and high solar radiation (Cornelissen et al., 2003), while leaf thickness is positively associated with aridity and water storage (Arellano-Rivas et al., 2018). SLA has a positive relationship with relative growth rate; plant species with low SLA typically have a long lifespan and high investment in defences (Dwyer et al., 2014). In contrast, LDMC usually has a negative relationship with relative growth rate and a positive association with lifespan (Cornelissen et al., 2003). Plants with high LDMC allocate more to durable tissues and present greater resistance to physical hazards (Cornelissen et al., 2003). SLA and LDMC typically present a negative and positive association, respectively, with environmental aridity (Meng et al., 2015).

Most of the pairwise correlations among leaf traits were not significant (t_{31} = 0.53–2.0, $P \geq 0.05$, $\mid$ r $\mid$ = 0.9–0.33), apart from that between SLA and leaf thickness, which was relatively low (t_{31} = 3.1, $P < 0.01$, r = 0.43).

2.4. Climatic and spatial data

Nineteen bioclimatic variables were obtained from the worldclim bioclimatic database (www.worldclim.org) for each study site. These bioclimatic variables were: annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature annual range, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation seasonality, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter and precipitation of the coldest quarter. All of these variables were based on precipitation and temperature values recorded across the year and have been shown to be relevant to the ecological modelling and distribution of several taxa (O'Donell and Ignizio, 2012). We therefore evaluated their influence on leaf functional trait variation across the sand dune plant communities studied. The bioclimatic variables have a resolution of 1 km, which was considered suitable for the scale of our study (the study area is *ca.* 300 km with an average distance between sites of 18.5 km). More extensive detail regarding bioclimatic data collection and/or variable calculation is available in O'Donell and Ignizio (2012).

Some other important environmental filters (sand blast and salt spray) may also vary in intensity along the sea-inland gradient (Maun, 2009). We therefore controlled for this source of variation by calculating the distance from the central part of each individual site to the coastline using the most recent digital cartography available in Google Earth Pro (November 2015) and including this distance as a covariate in the statistical analyses (see the *Functional metrics and statistical analyses* subsection).

2.5. Functional metrics and statistical analyses

Community weighted mean (CWM) and weighted coefficient of variation (WCV) per functional trait per species were calculated as metrics of functional dominance and functional dispersion or diversity, respectively. CWM measures the dominant functional trait value in each site and reflects the main functional strategy favoured by environmental filters. It is related to the mass ratio hypothesis, which states that functional traits of dominant species determine ecosystem processes (Grime, 1998), and was calculated as the mean of each functional trait weighted by species' relative abundance. That is, if the mean value of a given trait for all plant species in the community increases, the value of CWM for that trait also increases (Pla et al., 2012). WCV was used as a univariate measure of functional diversity per site and was calculated as the weighted standard deviation divided by the weighted mean. As with the CWM, species' abundance was used as a weighting factor with which to calculate WCV. This measure of dispersion is useful to compare variability of traits measured at different scales since it is unit-free and represents the dispersion of a given trait value relative to the mean. Unweighted versions of these two metrics: Community mean (CM) and coefficient of variation (CV), were also calculated with the aim of separating the effects of species turnover (change in unweighted metrics) and abundance (change in weighted metrics) on the metrics (Munguía-Rosas et al., 2014). As carried out by several other authors, we assumed that intraspecific variability in leaf trait was far lower than interspecific variation and therefore used mean trait values to calculate the metrics (Cornelissen et al., 2003; Garnier et al., 2016 and references therein). We selected single-trait indices over multi-trait indices since the former are more effective in terms of linking function with environmental filters.

All metrics were compared among regions with one-way ANOVAs and *post hoc* Tukey tests. Since the bioclimatic variables obtained from worldclim are correlated, we first conducted a principal component analysis (PCA) to reduce the dimensionality of the data set. We then used the loadings to predict an orthogonal combination of bioclimatic variables (principal components) for each site. The first two components (PC1 & PC2, explained variance = 92%, see the *Results* section) and distance to the coastline were used as predictors of CWM, WCV, CM and CV per functional trait in multiple linear regression models (one model per functional trait and metric: 16 models in total). The variance inflation factor was lower than 1.4 for all predictors in all the regression models.

In order to discard potential spatial autocorrelation, Mantel's tests were used to assess correlation between geographic distance and Euclidean distance for each functional trait per metric. All of the analyses were run in R software version 3.4.2 (R Core Team, 2017).

3. Results

3.1. Variation among bioclimatic regions

The community weighted mean of LDMC differed statistically among bioclimatic regions; specifically, plants in the eastern region had 13% more LDMC than those in the central region (Table 1). No difference was detected between eastern and western regions or between western and central regions (Table 1). The bioclimatic regions did not significantly explain variation in CWM of leaf size, leaf thickness and SLA (Table 1). No difference among bioclimatic regions was found for the CM of any leaf trait considered in the analyses (Table 1). The WCV of leaf thickness was significantly lower (54%) in the central region, relative to the western and eastern regions; however, western and eastern regions did not differ statistically (Table 1). The WCV of leaf size, SLA and LDMC did not differ statistically among regions. The CV for all leaf traits considered in the analyses did not differ significantly among bioclimatic regions (Table 1).

Table 1
Mean values (± 1 SE) of functional leaf traits (Traits) of plant species from 16 sites located in three different bioclimatic regions (Region) along the coastline of Yucatan Peninsula: West, Centre and East. Community weighted (CWM) and unweighted means (CM) as well as weighted (WCV) and unweighted coefficients of variation (CV) per trait were calculated. Different superscript letters indicate statistically significant differences between means. The statistics shown in the last column are F values with 1 and 13 degrees of freedom.

Metric	Trait	Region			Statistics
		West	Centre	East	
CWM	Leaf Size (cm^2)	14.55 ± 1.86	12.27 ± 1.33	11.77 ± 2.31	0.57
	Leaf Thickness (mm)	0.93 ± 0.07	1.01 ± 0.14	0.77 ± 0.11	0.98
	SLA (cm^2 g^{-1})	96.06 ± 2.61	90.79 ± 3.04	90.08 ± 1.24	2.98
	LDMC (g g^{-1})	0.24 ± 0.02 [ab]	0.22 ± 0.01 [a]	0.25 ± 0.01 [b]	3.76 *
CM	Leaf Size (cm^2)	18.81 ± 2.86	18.17 ± 2.16	14.28 ± 2.24	1.11
	Leaf Thickness (mm)	0.83 ± 0.06	0.76 ± 0.07	0.88 ± 0.09	0.53
	SLA (cm^2 g^{-1})	98.88 ± 1.54	96.46 ± 1.87	97.48 ± 2.71	0.25
	LDMC (g g^{-1})	0.28 ± 0.02	0.27 ± 0.01	0.26 ± 0.02	0.11
WCV	Leaf Size	1.41 ± 0.06	1.25 ± 0.11	1.35 ± 0.15	0.39
	Leaf Thickness	0.97 ± 0.06 [a]	0.54 ± 0.05 [b]	0.97 ± 0.09 [a]	10.47**
	SLA	0.33 ± 0.02	0.28 ± 0.04	0.28 ± 0.03	0.63
	LDMC	0.47 ± 0.09	0.41 ± 0.05	0.34 ± 0.05	0.94
CV	Leaf Size	1.51 ± 0.02	1.49 ± 0.11	1.54 ± 0.13	0.1
	Leaf Thickness	1.07 ± 0.06	0.89 ± 0.06	0.94 ± 0.08	1.51
	SLA	0.37 ± 0.01	0.35 ± 0.01	0.37 ± 0.01	1.06
	LDMC	0.53 ± 0.04	0.53 ± 0.02	0.50 ± 0.05	0.19

SLA = Specific leaf area, LDMC = Leaf dry matter content.
*$P < 0.05$; **$P < 0.01$.

3.2. Variation in the environmental gradient

According to the PCA, the first two principal components combined explained 92% of variance in the 19 environmental variables. PC1 explained 60% and PC2 32% of environmental variability. Minimum temperature of the coldest month (loading = 0.31) and precipitation seasonality (loading = 0.30) had the greatest positive loadings on PC1, while precipitation in the wettest month (loading = − 0.47) and quarter (loading = − 0.47) had the strongest and negative influence on PC2. Owing to the negative values of loadings, high values in PC2 indicate low precipitation during the wettest period of the year. While the bioclimatic regions were clearly different groups in the PC1 and PC2 axes, there was also important intraregional variation, particularly in the central region (Fig. 2).

According to the regression models, distance to the coastline and PC2 were reliable predictors of CWM of leaf size and SLA, respectively (Table 2, Fig. 3). The effect of PC2 on CWM of SLA was positive (Fig. 3 A) and the effect of distance to the coastline on CWM of leaf size was negative (Fig. 3 B). PC1, PC2 and distance to the coastline had no effect on the CWM values of other functional traits (Table 2). Distance to the coastline was also a reliable predictor of CM for leaf size, and the
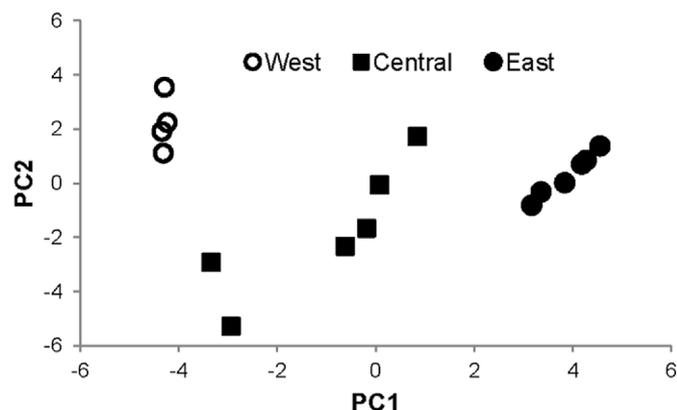

Fig. 2. Scatter plot showing the position of the 16 sampled communities in two axes of environmental principal components (PCI & PC2) obtained from 19 bioclimatic variables with a principal component analysis. The symbols show the bioclimatic region to which each community belongs.

relationship between these two variables was also negative (Table 2, Fig. 3C). PC1, PC2 and distance to the coastline had no effect on the CM values of other functional traits considered in the analysis (Table 2). No explanatory variable included in the regression models (PC1, PC2, distance to the coast line) predicted variation in the WCV or CV of any of the leaf functional traits (Table 2).

Pairwise Euclidean distance between plant communities was not significantly correlated with geographic distance between sites for any of the leaf functional traits (r = - 0.11– 0.15, $P > 0.05$ in all cases).

4. Discussion

Our results suggest that there is a predictable pattern in SLA variation across a precipitation gradient in the pioneer zone of coastal sand dunes in the study area. The negative association between SLA and precipitation suggests that, as expected, plants with a more conservative strategy are favoured under relatively drier conditions. In addition, as predicted, dispersion in leaf thickness was lower in the driest region. We also detected spatial variation in leaf size and dry matter content; however, variation in these traits was not related to precipitation.

According to the results, some environmental variables explained the variation in the dominant trait values of SLA and LDMC, but did not affect the dispersion of these traits (CV); i.e, the range of variation in SLA and LDMC was unaffected by environmental filters, while its frequency was affected. The fact that significant effects were only found in abundance weighted but not unweighted metrics suggests that these effects are mediated more by changes in species abundance than in species turnover. We suggest that the moderate variation in the strength of environmental filters seen in the study area was insufficient to completely exclude species or groups of species with particular trait values (Hesp, 1991; Garnier et al., 2016). The dominant trait value of SLA was positively related to PC2; however, in this component, precipitation in the wettest month/quarter had strong and negative loadings, signifying that high values in PC2 actually indicate low precipitation. Covariation between SLA and PC2 therefore suggests that the mean value of SLA decrease with low precipitation levels. This pattern of covariation supports our prediction and those of previous studies in different ecosystems (e.g. Dwyer et al., 2014; Meng et al., 2015; Poorter et al., 2009). A relatively lower SLA in drier sites suggest that a greater

Table 2

Results of multiple regression models to assess the effects of two principal components (PC1 & PC2) obtained from 19 climatic variables, as well as distance to the coastline (m), on some leaf traits (Trait) of sand dune plant communities. Community weighted (CWM) and unweighted means (CM) as well as weighted (WCV) and unweighted coefficients of variation (CV) per functional trait were calculated. Data are model coefficients (± 1 SE). Full model statics (F values with 3 and 12 degrees of freedom) are also shown.

Response		Explanatory variables			
Metric	Trait	PC1	PC2	Distance to coastline	Full model statistics
CWM	Leaf Size	-0.49 ± 0.33	0.71 ± 0.49	$-0.06 \pm 0.03*$	1.83
	Leaf thickness	-0.03 ± 0.02	-0.04 ± 0.03	$-4.41e^{-5} \pm -2.45e^{-4}$	1.35
	SLA	0.77 ± 0.42	$1.41 \pm 0.62*$	0.02 ± 0.04	3.35*
	LDMC	0.01 ± 0.02	0.03 ± 0.03	$-1.48e^{-5} \pm -2.47e^{-5}$	0.78
CM	Leaf Size	-1.03 ± 0.31	0.74 ± 0.46	$-0.01 \pm 0.01e^{-2}**$	6.28**
	Leaf thickness	0.01 ± 0.01	0.01 ± 0.02	$1.73e^{-5} \pm 1.82e^{-4}$	0.17
	SLA	0.03 ± 0.44	-0.17 ± 0.65	$0.03e^{-1} \pm 0.04e^{-1}$	0.18
	LDMC	$1.44e^{-3} \pm 3.72e^{-3}$	$1.33e^{-3} \pm 5.48e^{-3}$	$4.43e^{-6} \pm 4.03e^{-5}$	0.11
WCV	Leaf Size	-0.02 ± 0.02	0.05 ± 0.03	$0.04e^{-4} \pm 0.02e^{-2}$	1.79
	Leaf thickness	$8.71e^{-3} \pm 23.33e^{-3}$	0.04 ± 0.03	$2.03e^{-5} \pm 2.52e^{-5}$	0.54
	SLA	-0.08 ± -0.06	0.01 ± 0.01	$1.52e^{-5} \pm 7.26e^{-5}$	0.59
	LDMC	-0.02 ± -0.02	0.09 ± 0.16	0.01 ± 0.01	1.13
CV	Leaf Size	-0.06 ± 0.18	0.05 ± 0.03	$3.72e^{-4} \pm 2.03e^{-4}$	1.79
	Leaf thickness	-0.01 ± 0.01	0.02 ± 0.02	$0.98e^{-4} \pm 1.51e^{-4}$	0.79
	SLA	-0.01 ± 0.03	0.02 ± 0.04	$3.74e^{-5} \pm 2.93e^{-5}$	0.56
	LDMC	-0.05 ± 0.07	0.05 ± 0.11	$4.11e^{-5} \pm 8.15e^{-5}$	0.25

SLA = Specific leaf area, LDMC = Leaf dry matter content.
*$P < 0.05$; **$P < 0.05$.

number of plants in these sites invest more biomass per leaf, which is very important in terms of maintaining leaf function under unfavourable conditions (i.e. low precipitation; Fonseca et al., 2000; Shipley et al., 2005; Wright and Westoby, 2000). A representative example of this ecological phenomenon in our study area is *Pithecellobium keyense*, which has an SLA far lower than the mean ($76.6 \, cm^2 \, g^{-1}$, community unweighted mean SLA = $103.9 \pm 6.4 \, cm^2 \, g^{-1}$) and is abundant in the driest sites, while being absent in the wettest. On the other hand, the herbaceous plant *Flaveria linearis* had an SLA far above the mean ($135.8 \, cm^2 \, g^{-1}$) and was abundant in sites with the highest precipitation but absent in the driest sites. This pattern of spatial variation in SLA is not influenced by spatial autocorrelation, as suggested by the Mantel's test.

Variation in the dominant value of LDMC was also observed. Surprisingly, leaves with significantly greater LDMC were found in the eastern bioclimatic region, which is also the rainiest site. Typically, drier conditions are related to higher LDMC (Cornelissen et al., 2003; Meng et al., 2015); however, the contrary was found in this study. We ruled out the possibility that the observed pattern was due to the greater precipitation found in this region and this notion is also supported by the fact that LDMC was not explained by PC2 (which was strongly influenced by precipitation). Thus, we suggest that other environmental variables could explain the greater LDMC of leaves in the eastern region. Plants with high LDMC allocate more resources to durable tissues and thus have greater resistance to physical hazards (Cornelissen et al., 2003). We suggest that high wind speeds could also play an important role as an environmental filter on LDMC in the eastern bioclimatic region. Although no frequently invoked, winds may act as a strong environmental filter; specifically, leaves may suffer severe damage during high winds (Vogel, 2009). Every year in the Caribbean, several storms hit the Yucatan peninsula and the northeastern region is often the site of landfall. For instance, in the last 105 years, 38 of 56 (68%) hurricanes that hit the Yucatan Peninsula made landfall in this region (Boose et al., 2003). As examples, *Metopim brownei* and *Gossypium hirsutum* are both far more abundant in the eastern region (more than ten times more frequent than in the other two regions) and have some of the highest dry matter content values relative to those of other members of the community ($0.69 \, g \, g^{-1}$ and $0.58 \, g \, g^{-1}$, respectively; mean community value = $0.31 \pm 0.03 \, g \, g^{-1}$).

Dispersion in leaf thickness was significantly lower in the driest region, which agrees with our prediction and the findings of previous studies (e.g. Meng et al., 2015). Since only the abundance-weighted metric was significant, we suggest that the detected effect is more influenced by changes in abundance than in species turnover. It is likely that species with thinner leaves are filtered or less abundant in the central region and, as a result, dispersion in leaf thickness is smaller in this region. For example, *Ernodea littoralis*, a species with some of the most succulent leaves in the study area (thickness = 1.8 mm; mean community value = 0.69 ± 0.13 mm) is far more abundant in central (64% of total sampled individual) than in western and eastern regions.

Despite comprising a narrow vegetation belt (Maun, 2009), the pioneer zone in the study area showed variable leaf size from the sea toward the continent. Mean leaf size (weighted and unweighted) decreased with increasing distance to the coastline. This result was unexpected, since plants closer to the sea are more exposed to environmental filters such as wind, salt spray and sand burial, which would be expected to favour smaller leaves (Maun and Perumal, 1999; Maun, 2009). Certainly, stressful conditions can also have a negative impact on leaf size (Cornelissen et al., 2003); however, how stressful an environmental variable is depends on the plant species. Plants in the coastal sand dunes are well adapted to the prevailing environmental conditions as a result of the strong environmental filters (Hesp, 1991). The prevailing environmental conditions closer to the sea may no longer be stressful for sand dune plants. Sand burial can also play a prominent role in the zonation of sand coastal dunes, which implies that sand burial becomes greater with increased proximity to the coastline (Maun and Perumal, 1999). In some plant species characteristic of sand dunes, sand burial positively influences leaf traits such as chlorophyll content, net CO_2 uptake and size (Martínez and Moreno-Casasola, 1996; Maun, 1997). This suggests that sand burial may in fact be beneficial for sand dune plants. Greater sand burial is likely to prevail closer to the sea and plant species with big leaves are favoured in this habitat as a result (e.g. *Ipomea pes-caprae*: leaf size = $36.88 \, cm^2$ and *Scaevola plumeiri*, leaf size = $21 \, cm^2$). We recognize that this aspect requires further evaluation and therefore recommend further studies to evaluate variation in functional traits along the sea-inland axis within a single vegetation zone.

While climatic regions are to some extent differentiated in the axes of environmental variables used in PCA analysis, there is some important within-region variation (see Fig. 2). Moreover, some
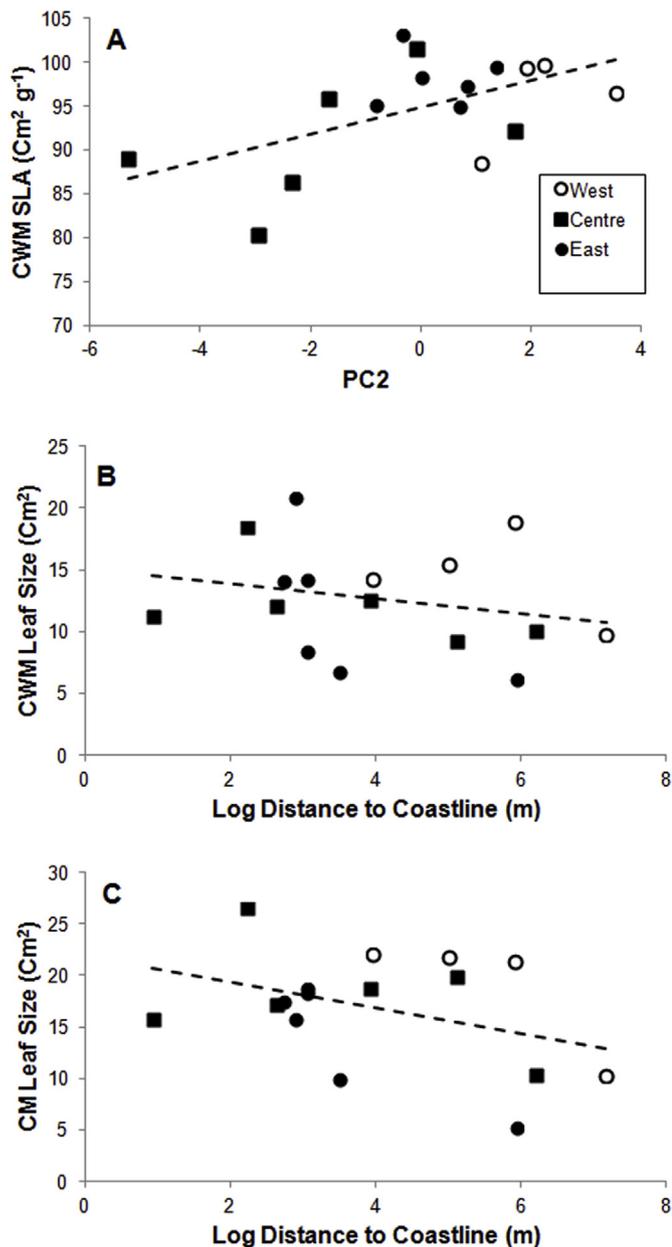
Fig. 3. Association between a principal component of a set of 19 environmental variables (PC2) and community weighted mean (CWM) of specific leaf area (SLA) (A), between distance to the coastline (log scale) and CWM of leaf size (B) and between distance to the coastline and unweighted community mean (CM) of leaf size (C). Different symbols in the scatter plot represent the climatic region (West, Centre and East) to which each plant community belongs. The regression lines were drawn considering the full data set. Slopes differed statistically from zero.

environmental filters that are important to coastal sand dune vegetation are unrelated to these climatic regions. For example, variation in distance to the coastline is greater within than between regions (See Fig. 3B and C) and it is recognized that distance to the coastline is negatively correlated to salt spray and sand blast (Maun, 2009). These facts may also partially explain why trait metrics affected by the climatic region factor (CWM of LDMC and WCV of leaf thickness) differ from those affected by continuous environmental variables in the precipitation gradient (CWM of LSA and CWM & CM of leaf size). It seems that traits and metrics affected by the climatic region factor are more sensitive to coarse-grained environmental variation while those affected by continuous environmental variables in the gradient are more

sensitive to fine-grained environmental variation and/or variation unrelated to the climatic regions (i.e. distance to coastline).

In conclusion, our results suggest that relatively low variation in precipitation patterns may play an important role as an environmental filter in coastal sand dune plant communities. A predictable variation pattern was found in SLA and, therefore, also in the ecological strategy of plants. Plant communities in the driest region also had lower diversity in leaf thickness. Specifically, drier sites in the Yucatan are dominated by plants with more succulent leaves that allocate relatively more biomass to durable tissue (conservative strategy). Variation in LDMC and leaf size was also observed but this seems to be unrelated to the precipitation gradient. While contradicting our initial predictions (i.e. higher LDMC and smaller leaf size under more benign environmental conditions), variation in the leaf size of sand dune plants may reflect the influence of other unmeasured environmental filters characteristic of this ecosystem (i.e. high winds and sand blast). Further experimental research is required to determine whether biotic and dispersal filters, in addition to abiotic environmental filters, can explain to some extent the observed variation patterns in the functional trait distribution of the studied coastal sand dunes.

Author's contributions

MAM-R, GA-G, DA and VP-T designed the study; DA collected data; MAM-R analysed data, MAM-R, DA, GA-G and VP-T wrote the manuscript and approved the current version.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaridenv.2018.12.001.

References

O´Donell, M.S., Ignizio, D.A., 2012. Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States. USGS, Virginia.

Ackerly, D.D., 2004. Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California chaparral. Am. Nat. 163, 654–671.

Arellano-Rivas, A., De-Nova, A., Munguía-Rosas, M.A., 2018. Patch isolation and shape predict plant functional diversity in a naturally fragmented forest. J. Plant Ecol. 11, 136–146.

Boose, E.R., Foster, D.R., Plotkin, A.B., Hall, B., 2003. Geographical and historical variation in hurricanes across the Yucatán Península. In: Gómez-Pompa, A., Allen, M.F., Fedik, S.L., Jimenez-Osorio, J.J. (Eds.), The Low Land Maya Area: Three Millennia at the Human-wildland Interface. The Haworth Press Inc., N.Y., USA, pp. 495–516.

Canfield, R.H., 1941. Application of the line interception method in sampling range vegetation. J. For. 38, 388–394.

Conti, L., de Bello, F., Lepš, J., Rosario-Acosta, A.T., Carboni, M., 2017. Environmental gradients and micro-heterogeneity shape fine-scale plant community assembly on coastal sand dunes. J. Veg. Sci. 28, 762–773.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heiden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51, 335–380.

Cornwell, W.K., Ackerly, D.D., 2009. Community assembly and shifts in plant trait distribution across an environmental gradient in coastal California. Ecol. Mongr. 79, 109–126.

de Bello, F., Thuiller, W., Lepš, J., Choler, P., Clément, J.-C., Macek, P., Sebastià, M.T., Lavorel, S., 2009. Partitioning of functional diversity reveals the scale and the extent of trait convergence and divergence. J. Veg. Sci. 20, 475–486.

Delgado-Banquerizo, M., Maestre, F.T., Gallardo, A., Quero, J.L., Ochoa, V., García-Gómez, M., Escolar, C., Gracía-Palacios, P., Berdugo, M., Valencia, E., Gonzalo, B.,

Noumi, Z., Derak, M., Wallenstein, M.D., 2013. Aridity modulates N availability in arid and semiarid mediterranean grasslands. PLoS One 8, e59807.

Diamond, J.M., 1975. Assembly of species communities. In: Diamond, J.M., Cody, M.L. (Eds.), Ecology and Evolution of Communities. Harvard University Press, Boston, pp. 342–344.

Duch, G.J., 1988. La Conformación Territorial del Estado de Yucatán: los Componentes del Medio Físico. Universidad Autónoma Chapingo, México.

Dwyer, J.M., Hobbs, R.J., Mayfield, M.M., 2014. Specific leaf area response to environmental gradients through space and time. Ecology 95, 399–410.

Espejel, I., 1987. Phytogeographic relationships of the Yucatan peninsula. J. Biogeogr. 14, 499–519.

Fonseca, C.R., Overton, J.M., Collins, V., Westoby, M., 2000. Shifts in trait combinations along rainfall and phosphorous gradients. J. Ecol. 88, 964–977.

Gallego-Fernández, J.B., Martínez, M.L., 2011. Environmental filtering and functional types on mexican foredunes along the Gulf of Mexico. Ecoscience 18, 52–62.

García-Mora, M.R., Gallego-Fernández, J.B., García-Novo, F., 1999. Plant functional types in coastal foredunes in relation to environmental stress and disturbance. J. Veg. Sci. 10, 27–34.

García-Mora, M.R., Gallego-Fernández, J.B., García-Novo, F., 2000. Plant diversity as a suitable tool for coastal dune vulnerability assessment. J. Coastal Res. 16, 990–995.

Garnier, E., Navas, M.-L., Grigulis, K., 2016. Plant Functional Ecology. Oxford University Press, U.K.

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–910.

Hesp, P.A., 1991. Ecological processes and plant adaptation on coastal dunes. J. Arid Environ. 21, 165–191.

Hortal, J., Borges, P.A.V., Gaspar, C., 2006. Evaluating the performance of species richness stimulators: sensivity and sample grain size. J. Anim. Ecol. 75, 274–287.

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. Funct. Ecol. 29, 592–599.

Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bonger, F., Poorter, L., 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. Ecology 91, 386–398.

Mahdavi, P., Bergmeier, E., 2016. Plant functional traits and diversity in sand dune ecosystems across different biogeographic regions. Acta Oecol. 74, 37–45.

Martínez, M.L., Moreno-Casasona, P., 1996. Effect of burial by sand on seedling growth and survival of six tropical sand dune species from the Gulf of Mexico. J. Coastal Res. 12, 406–419.

Martínez-Natarén, D., Parra-Tabla, V., Ferrer-Ortega, M., Calvo-Irabién, L.M., 2014. Genetic diversity and genetic structure in Mexican oregano (Lipia graveolens H.B.K.) and its relationship with chemical composition of the essential oil. Plant Syst. Evol. 300, 535–547.

Maun, M.A., 1994. Adaptation enhancing survival and establishment of seedling on coastal dune system. Vegetation 111, 59–70.

Maun, M.A., 1997. Adaptations of plants to burial in coastal sand dunes. Can. J. Bot. 76, 713–738.

Maun, M.A., 2009. The Biology of Coastal Sand Dunes. Oxford University Press, U.K.

Maun, M.A., Perumal, J., 1999. Zonation of vegetation on lacustrine coastal dune: effect of burial by sand. Ecol. Lett. 2, 14–18.

McGuill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185.

Meng, T.T., Wang, H., Harrison, S.P., Prentice, I.C., Ni, J., Wang, G., 2015. Response of leaf traits to climatic gradients: adaptive variation vs. composition shifts. Biogeosciences 12, 5339–5352.

Moreno-Casasola, P., Espejel, I., 1986. Classification and ordination of coastal dune vegetation along the Gulf and Caribbean Sea of Mexico. Vegetatio 66, 147–182.

Mouillot, D., Mason, N.H.W., Wilson, J.B., 2007. Is the abundance of species determined by their functional traits? a new method with a test using plant communities. Oecologia 152, 729–737.

Munguía-Rosas, M.A., Jurado-Dzib, S.G., Mezeta-Cob, C.R., Montiel, S., Rojas, A., Pech-Canché, J.M., 2014. Continuous forest has grater taxonomic, functional and phylogenetic plant diversity than an adjacent naturally fragmented forest. J. Trop. Ecol. 30, 323–333.

Nunes, A., Köbel, M., Pinho, P., Matos, P., de Bello, F., Correia, O., Branquinho, C., 2017. Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands. Agric. For. Metorol. 239, 176–184.

Orellana, R., Espadas, C., Conde, C., Gay, C., 2009. Atlas: Escenarios de Cambio Climático en la Península de Yucatán. Centro de Investigación Científica de Yucatán, Mexico.

Parra-Tabla, V., Albor-Pinto, C., Tun-Garrido, J., Agulo, D., Barajas, C., Silveira, R., Ortíz-Díaz, J.J., Arceo-Gómez, G., 2018. Spatial patterns of species diversity in sand dune plant communities in Yucatan, Mexico: the importance of invasive species in the species dominance patterns. Plant. Ecol. Divers. 11, 157–172. https://doi.org/10.1080/17550874.2018.1455232.

Pérez-Harguindeguy, N., Díaz, S., Granier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, J.E., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., De Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., vander Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardized measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167–234.

Petchey, O.L., O'Gorman, E.J., Flynn, D.F.B., 2009. A functional guide to functional diversity measures. In: Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C. (Eds.), Biodiversity, Ecosystem Functioning and Human Wellbeing: an Ecological and Economic Perspective. Oxford University Press, U.K., pp. 49–59.

Pla, L., Casanoves, F., Di Rienzo, J., 2012. Quantifying Functional Biodiversity. Springer, NY.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of variation leaf mass per area (LMA): a meta-analysis. New Phytol. 182, 565–588.

R Development Core Team, 2017. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Viena.

Shipley, B., Vile, D., Granier, E., Wright, I.J., Poorter, H., 2005. Functional linkage between leaf traits and net photosynthetic rate: reconciling empiric and mechanistic models. Funct. Ecol. 19, 602–615.

Vellend, M., 2010. Conceptual synthesis in community ecology. Q. Rev. Biol. 85, 183–206.

Vogel, S., 2009. Leaves in the lowest and highest winds: temperature, force and shape. New Phytol. 183, 13–26.

White, D.A., Hood, C.S., 2004. Vegetation patterns and environmental gradients in tropical dry forest of the northern Yucatan Peninsula. J. Veg. Sci. 15, 151–160.

Wright, I.J., Westoby, M., 2000. Cross species relationships between relative growth rate, nitrogen production and root vs. leaf function in 28 Australian woody species. Funct. Ecol. 14, 97–107.

Wright1, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier1, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economic spectrum. Nature 428, 821–827.