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MORPHOLOGICAL DIFFERENTIATION AMONG POPULATIONS OF *QUERCUS ELLIPTICA* NÉE (FAGACEAE) ALONG AN ENVIRONMENTAL GRADIENT IN MEXICO AND CENTRAL AMERICA

DIFERENCIACIÓN MORFOLÓGICA ENTRE POBLACIONES DE *QUERCUS ELLIPTICA* NÉE (FAGACEAE) A LO LARGO DE UN GRADIENTE AMBIENTAL EN MÉXICO Y AMÉRICA CENTRAL

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Abstract

Background: Variation in leaf morphology is an important indicator of how plants respond to different environmental conditions. Leaf trait variation is associated with physiological responses of plants to gradients of humidity and temperature.
Objective: We analyzed the variation in the leaf morphological and functional traits of *Quercus elliptica* and its relationships with environmental and geographic variables across the distribution of this species to evaluate population differentiation using ecological niche models.
Study species: *Quercus elliptica* Née (Fagaceae).
Study sites and dates: Plants were collected in diverse forest types between 350 and 2,400 m in elevation in Mexico and Central America during 2016 and 2017.
Methods: We measured and analyzed the differentiation in morphological and functional traits of 4,017 leaves from 402 trees from 41 populations using univariate and multivariate analyses.
Results: The leaf length and thickness and specific leaf area (SLA) of *Q. elliptica* were significantly correlated with the seasonality of temperature, precipitation, elevation and aridity. We identified two divergent morphological groups: (1) populations distributed along the Pacific coast with broad and thin elliptical leaves with high SLA values and inhabited humid forests at more than 1,200 m elevation, and (2) populations located along the Gulf of Mexico coast, and in southern Mexico and Central America with thicker, narrower leaves and lower SLA values and inhabited seasonal tropical forests in less than 1,200 m in elevation.
Conclusions: Climate and geographic barriers and the ecological niche models supported the population differentiation of *Q. elliptica*.
Keywords: Ecological niche modeling, environmental gradients, leaf functional traits, leaf morphology, population differentiation, *Quercus*.

Resumen

Antecedentes: La variación morfológica foliar es un indicador de las respuestas de las plantas a diferentes condiciones ambientales. La variación foliar está asociada con respuestas fisiológicas de las plantas a gradientes de humedad y temperatura.
Objetivo: Analizamos la variación morfológica y funcional foliar de *Q. elíptica* en toda su distribución y sus relaciones con variables ambientales y geográficas para evaluar su diferenciación poblacional utilizando modelos de nicho ecológico.
Especie de estudio: *Quercus elliptica* Née (Fagaceae).
Sitio de estudio y fechas: Las plantas fueron colectadas en diversos tipos de bosques entre 350 y 2,400 m en altitud en México y América Central en 2016-2017.
Métodos: Medimos y analizamos la diferenciación morfológica y funcional de 4,017 hojas de 402 árboles de 41 poblaciones utilizando análisis univariados y multivariados.
Resultados: La longitud y el grosor de la hoja y el área foliar específica (AFE) de *Q. elliptica* se correlacionaron significativamente con la estacionalidad de la temperatura, precipitación, elevación y aridez. Identificamos dos diferentes grupos morfológicos: (1) poblaciones distribuidas a lo largo de la costa del Pacífico, con hojas elípticas anchas y delgadas, con altos valores de AFE que habitan en bosques húmedos a más de 1,200 m en altitud y (2) poblaciones en el Golfo de México, el sur de México y América Central con hojas gruesas y estrechas y bajos valores de SLA en bosques tropicales estacionales de menos de 1,200 m.
Conclusiones: Las barreras climáticas y geográficas y los modelos de nicho ecológico apoyan la diferenciación de poblaciones en *Q. elliptica*.
Palabras clave: Caracteres funcionales foliares, diferenciación entre poblaciones, gradientes ambientales, modelo de nicho ecológico, morfología foliar, *Quercus*.

The functional traits of plants explain their species response to changes in environmental gradients (Gouveia & Freitas *et al.* 2009, Sterck *et al.* 2011, Kichenin *et al.* 2013, Salgado-Negrete *et al.* 2013, Valladares *et al.* 2014), which can be used to predict the responses of communities to environmental change (Paine *et al.* 2011, Violle *et al.* 2012, Lohbeck *et al.* 2013).

Differences in phenotypic and physiological responses are associated with the geographical locations of populations at local or regional scales (Albert *et al.* 2010, Nicotra *et al.* 2011, Fajardo & Piper 2011). Leaves are organs that are exposed to different environmental factors, and it is reasonable to expect that their morphology and structure represent the responses of the plants to local conditions, such as water availability or light intensity, as well as intra- and interspecific interactions (Castro-Díez *et al.* 1997, Bruschi *et al.* 2003, Lambrecht & Dawson 2007, Cuevas-Reyes *et al.* 2018).

Rainfall deficit and seasonality are important determinants of the structure, composition and physiognomy of vegetation (Moles *et al.* 2014). Low precipitation rates promote changes in foliar traits that in turn reduce water loss and increase photosynthetic capacity, and thus high leaf densities impart dehydration tolerance (Niinemets 2001, McLean *et al.* 2014). Plants that inhabit seasonal forests have mechanisms that allow them to remain unharmed by extended periods of drought, reducing carbon absorption as a result of the strong control of stomatal conductance and canopy deciduousness (Rossatto *et al.* 2013). On the other hand, temperature also affects the energy balance of leaves as well as the metabolic rate of plants (Moles *et al.* 2014). High temperatures associated with high solar incidence promote an increase in leaf thickness and a low specific leaf area, which reduce damage to leaf tissue from the sun (Leigh *et al.* 2012, McLean *et al.* 2014). Specific leaf area is related to the photosynthetic efficiency of plants and is considered to be very important for the biogeochemical cycles of forests (Meier & Leuschner 2008). It is also related to changes in leaf density and thickness (Gouveia & Freitas 2009), which, in turn, are affected by both precipitation and temperature gradients.

Different ecological and evolutionary studies have suggested that temperature and precipitation are the main determinants of plant morphological features on a global scale (Moles *et al.* 2014). However, leaf phenotypic variability can also be explained by latitudinal and elevational gradients (Tang & Ohsawa 1999). Previous studies have documented the importance of geographic and environmental factors as regulators of plant structure and morphology and species colonization and establishment in different habitats (Bruschi *et al.* 2003, Díaz & Cabido 2001). In particular, the variation in foliar traits in oak species has been correlated with specific environmental factors such as temperature and precipitation at different spatial scales, suggesting plastic responses or adaptive genetic differentiation within and among populations (Balaguer *et al.* 2001, Uribe-Salas *et al.* 2008, Aguilar-Romero *et al.* 2016, Rodríguez-Gómez *et al.* 2018, Albarrán-Lara *et al.* 2019).

Oak species (Fagaceae, *Quercus*) occur in a wide variety of habitats ranging from temperate to tropical forests and in both humid and dry conditions along a wide geographical range in the Northern Hemisphere, which has promoted remarkable morphological variation. The high morphological diversity of oaks has been of great interest in taxonomic (Valencia-A 2004, Rodríguez-Rivera & Romero-Rangel 2007, Martínez-Cabrera *et al.* 2011) and ecological studies analyzing the patterns of variation in morphological traits in relation to environmental gradients (González-Rodríguez & Oyama 2005, Uribe-Salas *et al.* 2008).

In this study, we analyzed the leaf morphological variation in populations of *Quercus elliptica* Née (Fagaceae) to determine the degree of population differentiation across its geographic distribution in Mexico and Central America. *Quercus elliptica* occurs in very diverse habitat types from tropical deciduous forests at low altitudes to humid temperate forests at higher altitudes. Therefore, this red oak species represents an ideal system for testing the effects of environmental variables on morphological and functional traits along latitudinal and altitudinal gradients. We evaluated population differentiation using ecological niche analysis and projection with distribution models.

Material and methods

Study species. *Quercus elliptica* Née is a red oak species widely distributed in Mexico ranging from southern Sinaloa to Nayarit, Jalisco, Guerrero, State of Mexico, Oaxaca, Veracruz and Chiapas, and into Central America (Figure 1). *Quercus elliptica* occurs under many types of environmental conditions in a wide elevational range between 500 and 3,100 m in canyons to plains and in pine-oak, oak, cloud and deciduous forests (Romero-Rangel *et al.* 2002, Valencia-A 2004). This tree reaches a height of up to 20 m with a trunk diameter of up to 60 cm. *Quercus elliptica* is a deciduous species with mature coriaceous leaves and elliptical-narrow or elliptical-wide shapes (Rodríguez-Rivera & Romero-Rangel 2007). The petiolate leaves have fasciculate trichomes with 5-7 rays and a short stipe, sometimes with crushed hairs, mainly near the primary veins (González-Villarreal 1986, Rodríguez-Rivera & Romero-Rangel 2007) and sometimes stellate trichomes on the middle vein.

Plant collection. A database of populations of *Q. elliptica* with geographical and environmental information was constructed using data from the National (MEXU) and

Bajío (IEB) herbariums. On the basis of this information, we selected 41 populations representing the entire geographical distribution of *Q. elliptica* ranging from Sinaloa and Veracruz (Mexico) to Central America (Honduras) (Table 1, Figure 1). Fifteen mature leaves of 10 different individuals that were without apparent leaf damage and exposed to sunlight were collected from each population, except in Tlatlauquitepec, Guerrero (only five individuals), and Esperanza, Honduras (seven individuals). Sampling was carried out during the rainy season (June-August) in 2016 and 2017. We selected leaves from the lower branches of each sampled tree, and the leaves were pressed for further morphological measurements.

Morphological and functional traits. In total, 4,017 leaves from 402 trees from 41 populations were measured considering 15 morphological and functional traits. Highly correlated morphological and functional traits were eliminated to avoid collinearity in subsequent analyses. After this procedure, four leaf morphological traits (*i.e.*, leaf length: L, leaf width: Wi, petiole length: PL and the leaf length / leaf width ratio: LWR) and three functional traits (*i.e.*, leaf thickness: T, leaf weight: We and specific leaf area: SLA) were selected (Table 2). These morphological traits were used because they represent standardized measurements of plant functional traits (Pérez-Harguindeguy *et al*. 2013), and were previously reported for different oak species (Kremer *et al*. 2002, Bruschi *et al*. 2003, Ponton *et al*. 2004, Tovar-Sánchez & Oyama 2004, González-Rodríguez & Oyama 2005, Albarrán-Lara *et al*. 2010, Martínez-Cabrera *et al*. 2011, Viscosi *et al*. 2012).

Environmental variables. To analyze the differences in environmental variables among the populations of *Q. elliptica*, we obtained climatic information for each record using data for 19 climatic variables with a 0.08° resolution available through the WorldClim database (Hijmans *et al*. 2005 www.worldclim.org). Highly correlated bioclimatic variables were eliminated to avoid collinearity in subsequent analyses. After this procedure, six variables were considered in the analysis (Table 2). In addition, values of an aridity index that considers evapotranspiration potential and solar radiation per unit area were obtained (Zomer *et al*. 2008, Trabucco & Zomer 2009). Finally, elevation, latitude and longitude were used as geographic variables.

Statistical data analysis. Pearson correlation analysis was performed to identify the relationships between leaf morphological and functional traits and environmental variables. To determine the differences in leaf morphological and functional traits among populations of *Q. elliptica*, we used an ANOVA for each variable, and a Tukey-Kramer test was conducted for *a posteriori* comparison using SAS (Stokes *et al*. 2000).

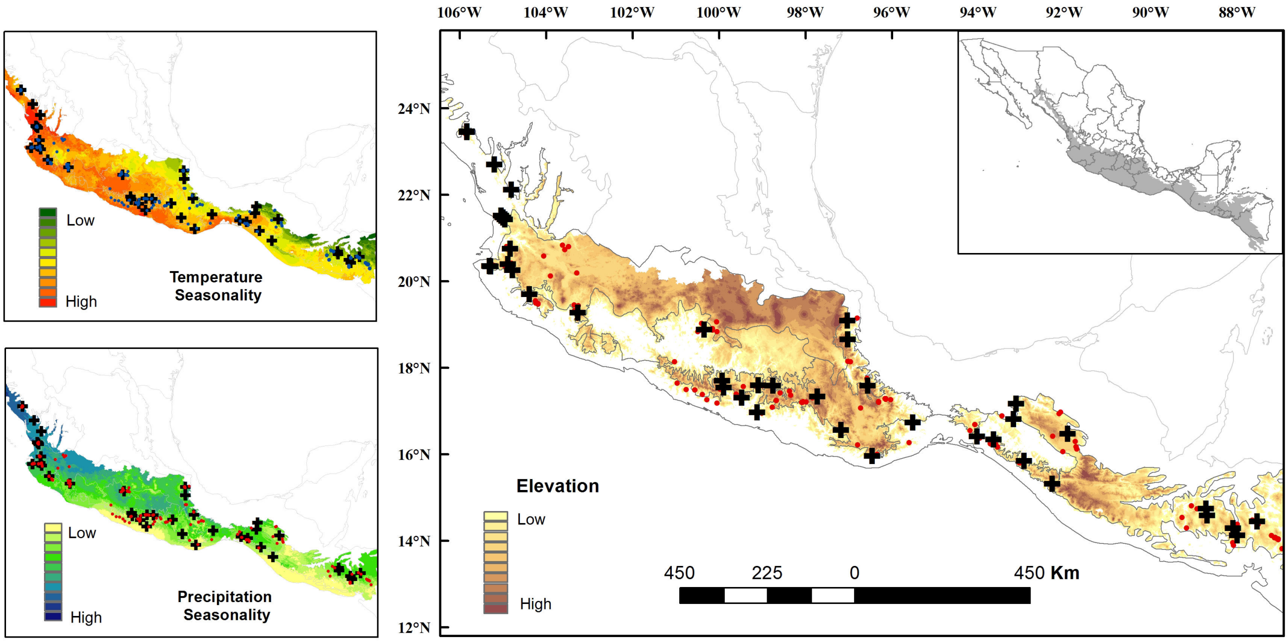

Figure 1. Geographic distribution of the 41 populations of *Quercus elliptica* collected for this study. Red circles represent the potential area of distribution of *Q. elliptica* according to herbarium records and collections. The black crosses represent the populations collected of *Q. elliptica*.

Table 1. Localities of *Quercus elliptica* along its distribution in Mexico and Central America. Vegetation types: pine oak forest (POF), oak forest (OF), oak pine *Juniperus* forest (OPJF), deciduous low forest (DLF), cloud forest (CF) and pine - oak tropical forest (POTF).

Population	State / Country	Code	Latitude	Longitude	Vegetation	Elevation (m)
Tecalitlán	Jalisco	J7	19.27	-103.27	POF	2002
Los Mazos	Jalisco	J6	19.70	-104.39	POF	1362
Maple	Jalisco	J5	20.26	-104.78	POF	1283
Talpa	Jalisco	J2	20.40	-104.88	OF	1415
Juquila	Oaxaca	O4	16.54	-97.18	OPJF	1752
Loxicha	Oaxaca	O5	15.96	-96.45	DLF	1115
Yolox	Oaxaca	O1	17.59	-96.55	OF	1849
Numi	Oaxaca	O2	17.33	-96.72	POF	2192
Chilapa	Guerrero	G2	17.60	-99.09	POF	2058
Tlatlauquitepec	Guerrero	G3	17.58	-98.75	POF	1911
Aobispo	Guerrero	G5	17.31	-99.47	DLF	1041
Ayutla	Guerrero	G6	16.97	-99.12	DLF	365
Carrizal	Guerrero	G4	17.54	-99.89	POF	2058
Tlacotepec	Guerrero	G1	17.70	-99.93	OF	1913
Loberas	Sinaloa	S1	23.47	-105.83	POF	1719
Potrerillos	Sinaloa	S2	23.45	-105.83	POF	1326
Huajicori	Nayarit	N1	22.70	-105.20	POF	1430
Nayar	Nayarit	N2	22.12	-104.80	POF	1269
Cuarenteno	Nayarit	N4	21.47	-105.00	POF	1624
San Blas	Nayarit	N3	21.52	-105.04	DLF	1109
Xalisco	Nayarit	N5	21.43	-104.95	OF	1401
Tuito	Jalisco	J3	20.35	-105.31	DLF	771
Provincia	Jalisco	J4	20.34	-105.28	DLF	1221
Sebastián	Jalisco	J1	20.75	-104.83	POF	1587
Lachiguirri	Oaxaca	O3	16.73	-95.52	OF	1330
Sinai	Chiapas	CH3	16.47	-91.93	CF	1911
Motozintla	Chiapas	CH7	15.31	-92.28	CF	1768
Ocozocuautla	Chiapas	CH1	17.17	-93.12	OF	1925
Antenas	Chiapas	CH4	16.41	-94.02	DLF	821
Josefa Ortiz	Chiapas	CH5	16.34	-93.64	DLF	953
Tuxtla	Chiapas	CH2	16.81	-93.18	DLF	896
Triunfo	Chiapas	CH6	15.85	-92.94	DLF	744
Zongolica 1	Veracruz	V2	18.66	-97.02	CF	1545
Zongolica 2	Veracruz	V3	18.65	-97.02	CF	1401
Coscomatepec	Veracruz	V1	19.09	-97.02	DLF	1527
Nanchititla	Estado de México	M1	18.88	-100.34	POF	2016
Purulha	Honduras	HO5	14.12	-88.70	POTF	1487
Celaque	Honduras	HO2	14.58	-88.70	POTF	2392
Marcalá	Honduras	HO1	14.74	-88.72	POTF	1110
Esperanza	Honduras	HO4	14.29	-88.10	POTF	1839
Achiote	Honduras	HO3	14.44	-87.54	POTF	1560

Table 2. Leaf morphological and functional traits of *Quercus elliptica* and geographic variables without collinearity included in this study.

Traits	**Description**
Morphological traits	
L	Leaf length
Wi	Leaf width
PL	Petiole length
LWR	Leaf length/leaf width ratio
Functional traits	
We	Leaf weight
T	Leaf thickness
SLA	Specific leaf area
Bioclimatic variables	
BIO1	Annual mean temperature
BIO4	Temperature seasonality (standard derivation*100)
BIO11	Mean temperature of the coldest quarter
BIO12	Annual precipitation
BIO15	Precipitation seasonality
BIO17	Precipitation of the driest quarter
Latitude	
Longitude	
Elevation	
Aridity	

A discriminant function analysis (DFA) was performed using the morphological traits measured in the 4,017 leaves to determine the differences among populations and identify the most important morphological variables distinguishing groups or populations. Both the population centroids and the percentage of correct allocation among populations were considered in the analysis.

Redundancy analysis (RDA) was performed considering two sets of environmental data: one set that includes the eight bioclimatic variables without high collinearity and another containing three geographical variables (elevation, longitude and latitude). To evaluate the contributions of geography and climate to leaf morphological variation, the following models were constructed: a) a complete model that included both the climatic and geographical variables (full redundancy analysis (FRDA): space + climate); b) a partial model that considered the climatic variables as controls of geographical effects (PRDA1: climate | space); and c) a partial model that considered geographical variables as controls of climatic effects (PRDA2: space | climate). We calculated the joint contributions of climate and geography. In this way, the RDA allowed us to identify those variables that have the most importance (climate or geography) in the variation in *Q. elliptica*.

We used a generalized linear model (GLM) to evaluate the effects of the climatic variables on the leaf traits (response variables). The GLM was used to predict the probability of occurrence of *Q. elliptica* throughout its distribution. We identified the contribution of each of the variables and their levels of significance ($P < 0.05$) as well as the confidence interval for each of the variables. All statistical analyses were performed with SPSS v.23 (IBM Corp 2015) and a statistical environment R (R Core Team 2014).

Ecological niche modeling. Considering the occurrences of the 41 populations of *Q. elliptica*, we predicted the distribution of this species based on the different morphological groups previously identified in the statistical analyses. For the modeling process, the WorldClim layers were used to cut the mask defined by the biogeographic provinces in which species is distributed (Sierra Madre Occidental, Sierra Madre del Sur, Sierra Madre de Oaxaca, the Trans-Mexican Volcanic Belt, the Coastal Plain of the Pacific and Serranías Transístmicas). According to Pearson *et al*. (2007), we chose 10 randomized subsets containing 60 % of the records to model the whole distribution of *Q. elliptica* (*i.e.*, 25 records) and each morphological group separately (*i.e.*, 12 records for the Pacific group and 13 records for the Gulf of Mexico group) using MaxEnt software (Phillips & Dudik 2008) with the default convergence threshold and a maximum number of iterations of 1,000 for each of the 10 replicates. Each map obtained for each replicate with MaxEnt was binarized according to the following procedure: we extracted the probability of each model obtained with 50 % of the records that were not used in the generation of the model to set the probability thresholds, ensuring not to omit the values for the records used to generate the model.

To test the concordance between the models obtained for *Q. elliptica* and the sampled records, we used the kappa index proposed by Cohen (1960) and the area under the curve (AUC) value (< 0.7 indicating low representation in the models and ≥ 0.9 indicating the best models) following Pearce & Ferrier (2000) and Wollan *et al.* (2008). We also conducted a jackknife test in MaxEnt that stresses the importance of each variable in the model construction; variables with high values indicated a greater contribution to the model and a higher influence on AUC values than those with lower values (Wollan *et al.* 2008).

Results

Some leaf morphological variables were correlated with some environmental variables (Table 3). Leaf length (L) was negatively correlated with elevation (r = -0.379, P < 0.01) and positively correlated with temperature seasonality (r = 0.526, P < 0.01). A significant positive relationship was observed between leaf thickness (T) and precipitation seasonality (r = 0.478, P < 0.01), and a significant negative relationship was observed between specific leaf area (SLA) and precipitation seasonality (r = -0.527, P < 0.01). Similarly, a significant positive relationship was observed between SLA and precipitation of the driest quarter (r = 0.509, P < 0.01) and the aridity index (r = 0.391, P < 0.05), and a negative relationship was observed between leaf weight (We) and the aridity index (r = -0.323, P < 0.05) (Table 3; Figure 2).

The ANOVA tests showed differences in all leaf morphological and functional traits among the populations (Table 4). Leaf width, leaf length/width ratio, leaf thickness, leaf weight and specific leaf area differed among the populations, showing the separation of two groups: the Pacific and Gulf of Mexico populations (Table 5). The separation between these two groups was not evident for the other morphological traits.

The discriminant function analysis (DFA) identified two main groups: populations distributed along the Pacific coast in tropical deciduous or subdeciduous forests (hereafter the Pacific group) and populations distributed along the Gulf of Mexico and in southern Mexico and Central America occurring in temperate, mixed and cloud forests and tropical humid or subhumid forests (hereafter the Gulf of Mexico group) (Figure 3). The first axis of the discriminant function (DF1) explained 49.7 % of the variation in the 4,017 leaves analyzed. Leaf thickness was the most important plant trait for DF1 (r = 0.541, P < 0.01). Finally, it is important to mention that the leaf shape ratio (length/width) is a variable that varies considerably depending on precipitation. Leaves that were longer than wider were found in the Pacific group populations, and they were also thicker with lower specific leaf area values, while the leaves of the populations of the Gulf of Mexico group had a smaller leaf length/leaf width ratio, lower thickness and higher specific leaf area values.

The first two axes of the full redundancy analysis (FRDA), which included geographic and environmental variables, explained a significant proportion of the leaf variation (51.32 %) (F = 4.7, P < 0.001) (Figure 4). According to the redundancy analysis (RDA), climate explained 21.58 % of the variation, geography explained 21.17 %, and the interaction between climate and space explained only 8.57 %. In both, partial RDA1 (climate as a control of geography) and RDA2 (space as a control of

Table 3. Relationships between leaf morphological and functional traits of *Quercus elliptica* with environmental variables.

Character	BIO1	BIO4	BIO11	BIO12	BIO15	BIO17	Latitude	Longitude	Elevation	Aridity
Morphological traits										
L		0.526**	0.045						-0.379**	-0.095
Wi		0.431**		-0.012			0.023			0.100
PL	0.340*					-0.331*	0.061	-0.071	-0.358*	
LWR	0.348*	0.109	0.310*	-0.143	0.582**	-0.464**		-0.409**		
LL/PLR								-0.102	0.002	
Functional traits										
We		0.394**	0.161		0.518**	-0.416**	0.353*	-0.431**	-0.210	-0.323*
T			-0.108		0.478**		0.481**	-0.593**	-0.041	
SLA		0.141	-0.284		-0.527**	0.509		0.432**	-0.075	0.391**

* The correlation is significant at P < 0.05

** The correlation is significant at P < 0.01

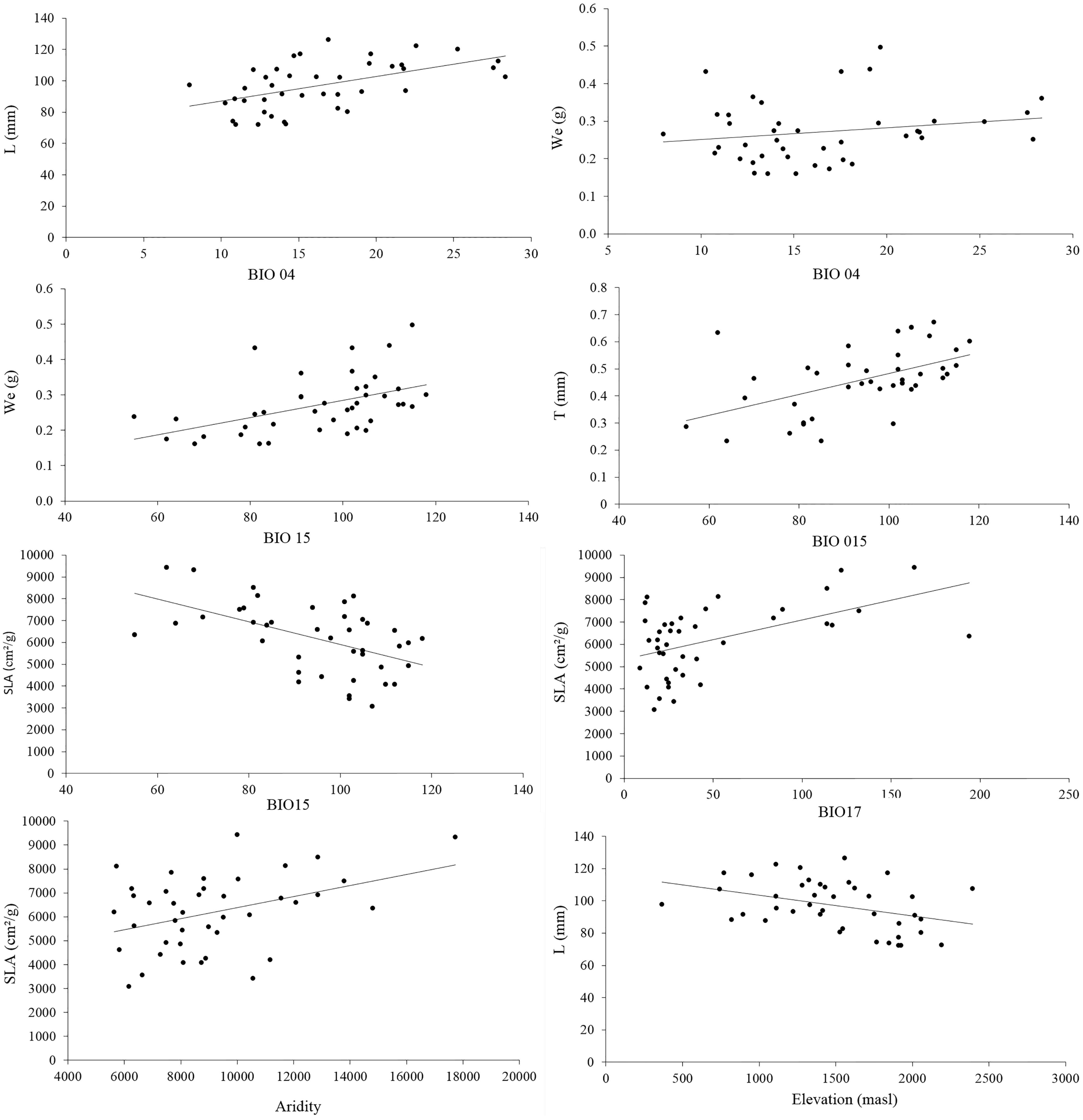

Figure 2. Examples of significant Pearson correlation analyses (at $P < 0.01$) between leaf morphological and functional traits and bioclimatic and geographic variables and the aridity index.

climate) were both significant only for their first axes (F =10.9, $P < 0.002$ and F =12.3, $P < 0.001$, respectively). On the first axis of the FRDA, the seasonality of temperature (F = 7.0, $P < 0.001$) and latitude (F = 9.5, $P < 0.001$) were the main variables explaining the leaf variation, and these two variables were the most important variables according to RDA1 (F = 10.021, $P < 0.001$) and RDA2 (F = 9.469, $P < 0.001$), respectively. For the second axis, the principal variables were seasonality of precipitation (F = 5.9, $P < 0.003$), aridity (F = 5.1, $P < 0.006$) and elevation (F = 3.5, $P < 0.015$). The most important morphological variables were specific leaf area and leaf width for the first axis and the lengths of both the lamina and petiole for the second axis.

Table 4. Differences in leaf morphological and functional traits among the populations of *Q. elliptica*. Different letters indicate significant differences in mean values according to Tukey-Kramer test ($P < 0.05$). Names of populations as indicated in Table 1 and names of leaf traits as in Table 2.

Populations	**L**	**Wi**	**PL**	**We**	**T**	**LWR**	**LL/LWR**	**SLA**
	$F = 58.6$	47.8	40.4	19.7	105.78	11.5	36.31	42.43
	$\boldsymbol{P < 0.0000}$	**0.0001**	**0.0001**	**0.0001**	**0.0000**	**0.0001**	**0.0001**	**0.0001**
S1	102.7 ± 1.9^{a}	37.6 ± 0.7^{a}	5.8 ± 0.2^{a}	0.5 ± 0.01^{a}	0.4 ±0.006^{a}	2.8 ± 0.1^{a}	19.1 ± 0.8^{a}	6095.8 ± 23^{a}
S2	110.8 ± 1.9^{b}	37.0 ± 0.7^{a}	4.6 ± 0.1^{b}	0.7 ± 0.03^{b}	0.3 ± 0.006^{a}	3.0 ± 0.1^{a}	26.4 ± 0.8^{b}	6,768.6 ± 220.1^{b}
N1	108.5 ± 2.1^{b}	40.5 ± 0.8^{b}	6.1 ± 0.2^{a}	0.4 ± 0.03^{a}	0.3 ± 0.001^{a}	2.7 ± 0.1^{a}	19.1 ± 0.9^{a}	6,025.9 ± 258.1^{a}
N2	121.5 ± 1.9^{c}	38.0 ± 0.7^{a}	4.3 ± 0.2^{b}	0.7 ± 0.03^{b}	0.3 ± 0.006^{a}	3.3 ± 0.1^{b}	30.2 ± 0.8^{c}	6,294.5 ± 230.8^{c}
N3	122.6 ± 1.9^{c}	37.8 ± 0.7^{a}	4.3 ± 0.2^{b}	0.6 ± 0.03^{b}	0.3 ± 0.006^{a}	3.7 ± 0.1^{c}	30.3 ± 0.8^{c}	6,800.10 ± 230.8^{b}
N4	107.9 ± 1.9^{b}	35.1 ± 0.7^{c}	5.5 ± 0.2^{a}	0.5 ± 0.03^{a}	0.3 ± 0.006^{a}	3.1 ±0.1^{a}	20.9 ± 0.8^{a}	7,154.2 ± 230.8^{b}
N5	110.3 ± 1.9^{b}	31.8 ± 0.7^{d}	4.9 ± 0.1^{b}	0.5 ± 0.03^{a}	0.3 ± 0.006^{a}	3.9 ± 0.1^{c}	24.0 ± 0.8^{b}	6,175.9 ± 230.8^{c}
J1	111.4 ± 1.9^{b}	33.6 ± 0.7^{d}	4.4 ± 0.2^{b}	0.5 ± 0.3^{a}	0.3 ± 0.006^{a}	3.4 ± 0.1^{b}	26.4 ± 0.8^{e}	5,965.3 ± 230.8^{c}
J2	93.9 ± 1.9^{d}	36.4 ± 0.7^{c}	4.2 ± 0.2^{b}	0.4 ± 0.03^{a}	0.2 ± 0.001^{b}	2.6 ± 0.1^{a}	23.2 ± 0.8^{b}	6,450.2 ± 230.8^{c}
J3	117.3 ± 1.9^{c}	36.3 ± 0.7^{c}	4.9 ± 0.2^{b}	0.6 ± 0.03^{b}	0.3 ± 0.006^{a}	3.3 ± 0.1^{b}	24.9 ± 0.8^{b}	6,279.5 ±230.8^{c}
J4	93.8 ± 1.87^{d}	36.0 ± 0.7^{c}	7.1 ± 0.2^{c}	0.7 ± 0.03^{c}	0.4 ± 0.006^{a}	2.8 ± 0.1^{a}	15.4 ± 0.8^{d}	4,822.5 ± 220.1^{d}
J5	109.5 ± 2.2^{b}	41.2 ± 0.8^{b}	4.0 ± 0.2^{b}	0.6 ± 0.02^{b}	0.2 ± 0.007^{b}	2.7 ± 0.1^{a}	27.8 ± 0.8^{e}	6,743.2 ± 258.2^{b}
J6	103.2 ± 1.9^{a}	36.3 ± 0.7^{c}	3.7 ± 0.2^{d}	0.4 ± 0.03^{a}	0.2 ± 0.006^{b}	2.9 ± 0.1^{b}	28.7 ± 0.7^{e}	6,973.9 ± 230.8^{b}
J7	102.3 ± 1.9^{a}	35.6 ± 0.7^{c}	4.6 ± 0.1^{b}	0.4 ± 0.02^{a}	0.1 ± 0.006^{c}	3.0 ± 0.1^{b}	24.0 ± 0.7^{b}	7,212.0 ± 230.8^{b}
V1	80.5 ± 1.9^{e}	29.7 ± 0.7^{d}	2.2 ± 0.1^{e}	0.3 ± 0.02^{d}	0.1 ± 0.006^{c}	2.7 ± 0.1^{a}	39.7± 0.7^{f}	7,702.3 ± 230.8^{e}
M1	91.0 ± 1.9^{d}	26.5 ± 0.7^{e}	4.1 ± 0.1^{b}	0.4 ± 0.2^{a}	0.2 ± 0.006^{b}	3.6 ± 0.1^{c}	25.4 ± 0.7^{b}	6,186.2 ± 23^{c}
V2	82.7 ± 1.9^{e}	31.0 ± 0.7^{d}	3.4 ± 0.1^{d}	0.3 ± 0.02^{d}	0.2 ± 0.006^{b}	2.7 ± 0.1^{a}	25.7 ± 0.7^{b}	7,118.1 ±230.8^{b}
V3	91.4 ± 1.9^{d}	33.9 ± 0.7^{d}	3.3 ± 0.1^{d}	0.3 ± 0.02^{d}	0.2 ± 0.006^{b}	2.7 ± 0.1^{a}	29.1 ± 0.7^{d}	8,960.7 ± 230.8^{f}
G1	85.8 ± 1.9^{f}	31.7 ± 0.7^{d}	4.0 ± 0.1^{b}	0.6 ± 0.2^{b}	0.4 ± 0.006^{a}	3.1 ± 0.1^{a}	25.6 ± 0.7^{e}	3,476.7 ±230.8^{g}
G2	80.2 ± 2.1^{e}	30.0 ± 0.8^{d}	4.1 ±0.2^{b}	0.5 ± 0.03^{a}	0.4 ± 0.006^{b}	3.0 ± 0.1^{a}	20.9 ± 0.8^{a}	3,650.8 ± 243.3^{g}
O1	73.8 ± 2.0^{g}	32.1 ± 0.7^{d}	3.7 ±0.1^{d}	0.3 ±0.03^{d}	0.3 ± 0.006^{a}	2.3 ± 0.11^{d}	20.4 ± 0.7^{a}	6,283.9 ± 230.8^{c}
G3	77.3 ± 2.19^{g}	24.5 ± 0.8^{f}	4.8 ± 0.2^{b}	0.5 ± 0.02^{a}	0.3 ± 0.007^{a}	3.6 ± 0.1^{c}	17.3 ± 0.8^{d}	3,132.1 ± 258.1^{g}
G4	88.6 ± 2.0^{d}	27.7 ±0.8^{e}	5.0 ± 0.2^{b}	0.5 ± 0.03^{a}	0.3 ± 0.007^{a}	3.3 ± 0.1^{a}	19.9 ± 0.8^{a}	4,384.1 ± 258.1^{d}
O2	72.7 ± 1.9^{g}	34.2 ± 0.7^{d}	3.9 ± 0.1^{d}	0.4 ± 0.03^{a}	0.3 ± 0.006^{a}	2.2 ± 0.1^{d}	18.6 ± 0.8^{a}	4,781.3± 230.8^{d}
G5	87.5 ± 2.0^{d}	28.8 ± 0.7^{e}	4.4 ± 0.1^{b}	0.5 ± 0.02^{a}	0.3 ± 0.006^{a}	3.3 ± 0.1^{a}	22.1 ± 0.8^{b}	4,288.6 ± 230.8^{d}
C1	72.3 ± 1.9^{g}	30.7 ±0.74^{d}	4.6 ± 0.1^{b}	0.3 ± 0.02^{d}	0.2 ± 0.006^{b}	2.4 ± 0.1^{d}	16.2 ± 0.^{d}	6,434.6 ± 230.8^{c}
G6	97.6 ± 1.9^{a}	32.7 ± 0.7^{d}	5.1 ±0.1^{b}	0.5 ± 0.03^{a}	0.3 ± 0.006^{a}	3.1 ± 0.1^{a}	22.2 ± 0.8^{b}	5,154.2 ± 220.0^{b}
C2	91.6 ± 2.1^{d}	35.4 ±0.8^{c}	4.9 ±0.2^{b}	0.4 ± 0.03^{a}	0.2 ± 0.006^{b}	2.6 ± 0.1^{d}	18.8 ± 0.8^{a}	6,768.3 ± 243.3^{c}
O3	97.3 ± 1.9^{a}	35.4 ± 0.7^{c}	4.6 ± 0.1^{b}	0.4 ± 0.03^{a}	0.2 ± 0.006^{b}	2.8 ± 0.1^{a}	20.0 ± 0.8^{a}	7,821.0 ± 230.8^{c}
O4	91.9 ± 1.9^{d}	26.7 ± 0.7^{e}	4.0 ± 0.1^{d}	0.5 ± 0.03^{a}	0.3 ± 0.006^{a}	3.6 ± 0.1^{c}	25.9 ± 0.8^{e}	4,875.3 ± 230.8^{d}
C3	72.2 ± 1.9^{g}	27.2 ± 0.7^{e}	3.3 ±0.1^{d}	0.2 ±0.02^{d}	0.2 ± 0.006^{b}	2.7 ± 0.1^{a}	22.8 ± 0.8^{b}	7,169.1± 230.8^{c}
C4	88.2 ± 1.9^{d}	32.6 ±0.7^{d}	6.9 ± 0.1^{c}	0.3 ± 0.03^{d}	0.2 ± 0.006^{b}	2.7 ± 0.1^{a}	13.7 ± 0.8^{f}	8,292.0 ± 230.8^{e}
C5	116.1 ± 1.9^{c}	38.5 ± 0.7^{b}	5.3 ±0.1^{b}	0.4 ± 0.03^{a}	0.2 ± 0.006^{b}	3.0 ± 0.1^{a}	22.4 ± 0.8^{b}	8,963.2 ±230.8^{f}
O5	95.4 ± 2.1^{a}	28.2 ± 0.8^{e}	5.5 ± 0.2^{b}	0.5 ± 0.03^{a}	0.3 ± 0.006 ^{a}	3.5 ± 0.1^{c}	18.4 ± 0.8^{a}	4,461.8 ± 243.3^{d}
C6	108.9 ± 1.9^{b}	37.8 ±0.7^{b}	5.5 ± 0.1^{b}	0.5 ± 0.03^{a}	0.2 ±0.001^{b}	2.9 ± 0.1^{a}	20.4 ± 0.8^{a}	6,952.2 ± 230.8^{c}
C7	74.5 ± 1.9^{g}	26.9 ± 0.7^{e}	3.8 ± 0.1^{d}	0.2 ± 0.03^{d}	0.2 ± 0.004^{b}	2.8 ± 0.1^{a}	20.7 ± 0.8^{s}	7,381.7±230.8^{e}
H1	102.9 ± 1.9^{a}	40.0 ± 0.7^{b}	5.4 ± 0.1^{b}	0.5 ± 0.03^{a}	0.2 ± 0.006^{b}	2.6 ± 0.1^{d}	20.5 ± 0.8^{a}	7,261.0 ±230.8^{e}
H2	107.5 ± 1.9^{b}	41.8 ±0.7^{b}	4.9 ± 0.1^{b}	0.4 ± 0.03^{a}	0.2 ± 0.002^{b}	2.6 ± 0.1^{d}	24.3 ± 0.8^{b}	9,794.1 ± 230.8^{f}
H3	126.4 ± 1.9^{h}	48.9 ± 0.8^{f}	4.6 ± 0.1^{b}	0.6 ± 0.03^{b}	0.2 ± 0.003^{b}	2.6 ± 0.1^{d}	28.5 ± 0.8^{e}	8,488.0 ± 233.1^{d}
H4	117.3 ± 1.9^{c}	43.2 ± 0.1^{b}	5.1 ± 0.1^{b}	0.5 ±0.02^{a}	0.2 ± 0.006^{b}	2.7 ± 0.1^{d}	24.3 ± 0.8^{b}	8,393.4 ± 230.8^{d}
H5	102.3 ± 1.9^{a}	39.9 ± 0.7^{b}	4.7 ± 0.1^{b}	0.5 ± 0.03^{a}	0.2 ± 0.002^{b}	2.6 ± 0.1^{d}	24.2 ± 0.8^{b}	7,130.8 ± 230.8^{e}

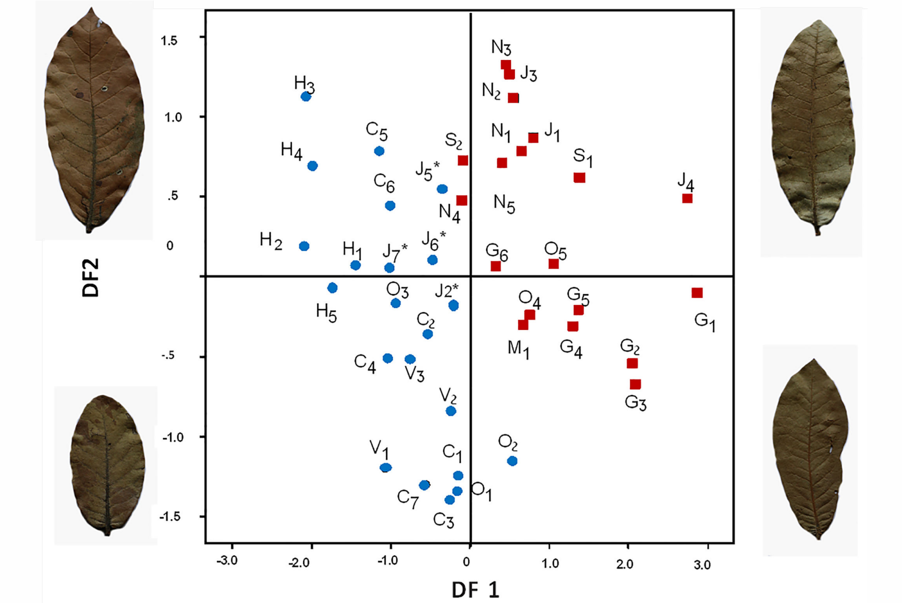

Figure 3. Discriminant function analysis scattergram of leaf traits. Two main groups were identified: the Pacific group (red squares) and the Gulf of Mexico group (blue circles). Letters with numbers codes represent the populations studied.

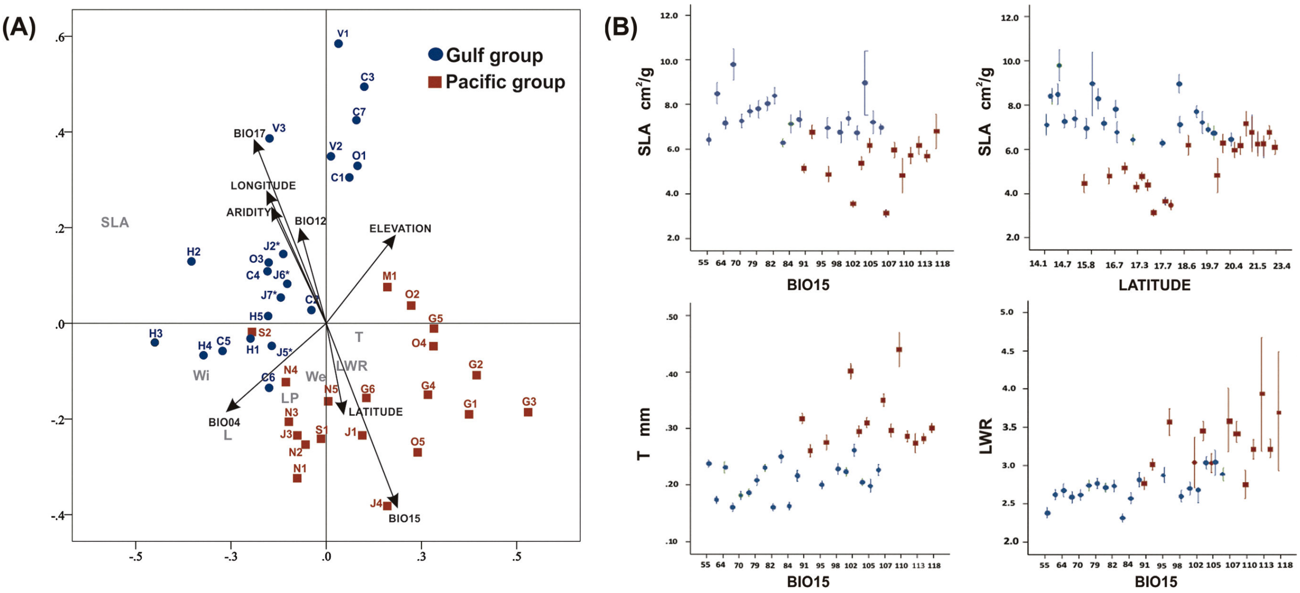

Figure 4. Full redundancy analysis (RDA) on morphological, bioclimatic and geographical variables produced two main groups: the Pacific group (red squares) and the Gulf of Mexico group (blue circles) Letters with code numbers represent the populations studied. (A). Graphs of the most important morphological and environmental variables that differentiated populations identified by RDA (B).

The generalized linear model (GLM) showed differences in some morphological traits between the two identified groups (Group 1: the Pacific group populations; Group 2: the Gulf of Mexico group) (Table 5). Leaves in the Pacific group were thicker, heavier with a lower specific leaf area. Leaves in the Gulf of Mexico group were wider and with a lower leaf length - leaf width ratio (Table 5).

The GLM analysis of the environmental variables also indicated significant differences among the populations of the two groups identified in the DFA. Populations of the

Pacific group experienced a higher seasonality precipitation and the Gulf of Mexico group showed higher annual precipitation.

Table 5. Comparison of means and standard error (SE) of the morphological and functional traits between populations of the Pacific group (Group 1) and the Gulf of Mexico group (Group 2). Significant differences at $P < 0.05$ in bold. Names of leaf traits as indicated in Table 2.

Trait	Group	Mean	SE	*F*	*P*
L	1	98.76	14.67	0.363	0.551
	2	95.89	15.83		
Wi	1	32.66	4.70	4.27	**0.04**
	2	35.97	5.50		
LP	1	4.87	0.81	2.43	0.127
	2	4.42	1.02		
LWR	1	3.04	0.34	20.74	**0.000**
	2	2.66	0.16		
LL/LPR	1	20.66	3.88	1.76	0.191
	2	22.51	4.97		
We	1	0.53	0.08	21.21	**0.000**
	2	0.39	0.11		
T	1	0.33	0.07	29.86	**0.000**
	2	0.22	0.06		
SLA	1	4,977.27	114.58	52.22	**0.000**
	2	7,328.94	936.63		

We obtained the best environmental niche models (ENMs) for the Pacific and Gulf of Mexico groups considering the highest values obtained for the kappa index of each replicate subset (Figure 5). The ENMs with the lowest kappa values were obtained for *Q. elliptica* (all populations) and the Pacific group populations (the kappa values for the best models were 0.61 and 0.611, respectively), while the highest values were obtained for the Gulf of Mexico group when the Jalisco populations were not considered (the kappa value for the best model was 0.706) (Table 6). The most important variables in the ENM for *Q. elliptica* (all populations) were elevation, aridity, mean annual temperature and annual rainfall; the most important variables in the ENM for the Pacific group were mean annual temperature, seasonality and elevation; and the most important variables in the ENM for Gulf of Mexico group were rainfall in the driest quarter and rainfall seasonality (Table 6). The ENMs for the Gulf of Mexico and Pacific groups significantly overlap in the western and central regions of the Trans-Mexican Volcanic Belt and western of the Sierra Madre del Sur.

Discussion

In this study, the relative importance of two sets of driving variables (*i.e.,* environmental and geographical) on the morphology and function of leaves was analyzed. It was demonstrated that precipitation and its seasonality are environmental factors that are associated with morphological variation in *Q. elliptica*, an oak species that occurs in different types of forests. Tropical forests differ in their seasonality in terms of the length of the dry and wet seasons, which can affect the morphological and functional variation in plants, promoting changes in the hydraulic structure of leaves (*i.e.,* leaf thickness and specific leaf area) in response to water stress and affecting phenological patterns and the content of secondary metabolites used in plant structure or defense (Ackerly 2004, Moles *et al.* 2014).

Variation in morphological and functional traits along environmental gradients. It has been documented that the leaf morphological variability of species along elevational gradients is related to environmental factors (Velázquez-Rosas *et al.* 2002). Uribe-Salas *et al.* (2008) identified a strong relationship between morphological features and environmental factors (mainly temperature). Leaf morphology and structure can be affected by microclimatic conditions such as temperature, solar incidence and humidity. In some cases, leaves that are exposed to the sun have a smaller foliar area and are thicker and more lobed than those that grow in shaded conditions (*e.g.,* basal strata of the canopy) (Mitchell *et al.* 1999, Klich 2000, Bruschi *et al.* 2003, Valladares *et al.* 2014). Leaves in different strata of the tree absorb, intercept and reflect light differently, which also influences leaf physiological processes (Ellsworth & Reich 1993).

We identified that the longest leaves with the highest leaf areas were not necessarily located in areas with high precipitation, as reported in some studies (Gouveia & Freitas 2009, Ramírez-Valiente *et al.* 2015). Meier & Leuschner (2008) showed that the leaf surface area decreased when precipitation increased, but in their conclusions, they mentioned that this may be because leaf size in *Fagus sylvatica* can respond more to changes in temperature than to changes in precipitation. According to the RDA, leaf length was found to be related to the seasonality of temperature, which may explain why the temperature could influence the variation in populations, although to a lesser extent. Additionally, leaf area decreases when the incidence of light increases (Niinemets 2001). Furthermore, the leaf support (petiole length) angle is an important feature that responds to the incidence of light reaching different canopy trees; a smaller petiole will result in more overlap of the leaves and a lower uptake of light (González-Rodríguez *et al.* 2004). It is also observed that

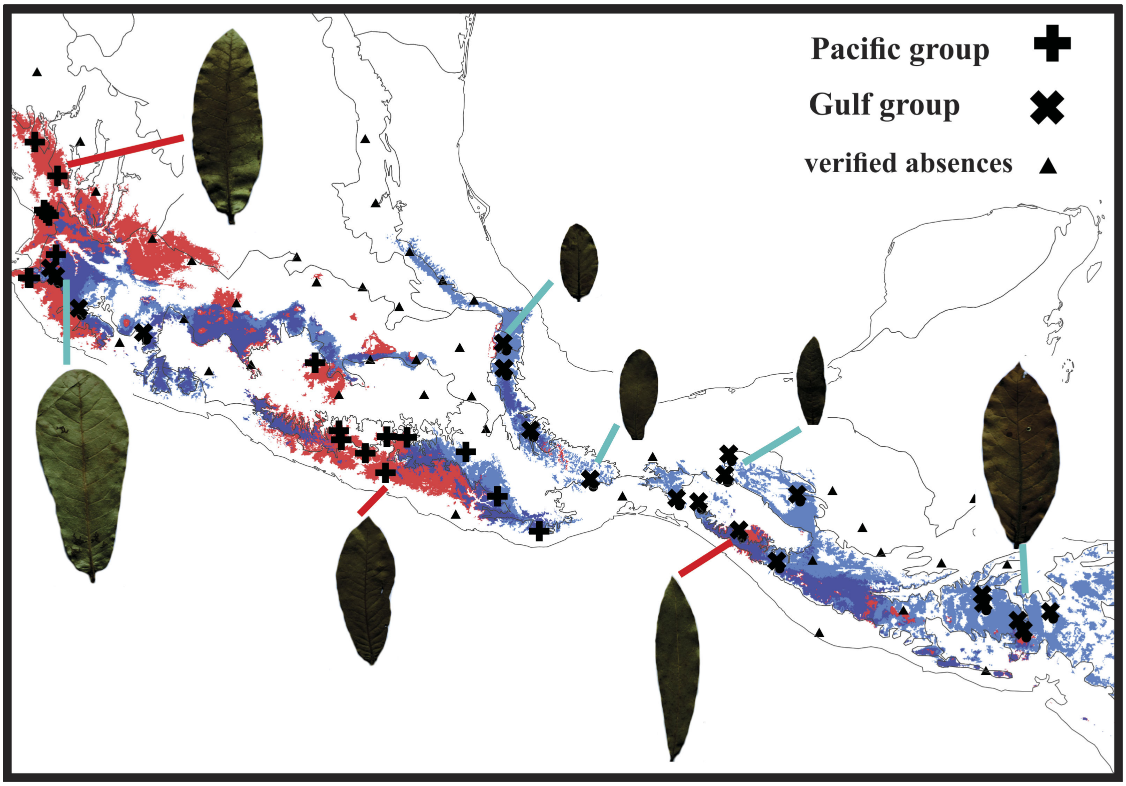

Figure 5. Niche modeled distribution of the two groups of populations identified in this study: The Pacific group (+) and the Gulf of Mexico group (x). Verified absences indicated by triangles.

Table 6. AUC proportion and kappa concordance index values and the major variables identified after a jacknife test for *Q. elliptica*, Pacific and Gulf of Mexico groups validation models. In bold the highest AUC and kappa index values.

	Q. elliptica			**Pacific group**			**Gulf of Mexico group**		
Rep	AUC	kappa	jacknife	AUC	kappa	jacknife	AUC	kappa	jacknife
1	0.931	0.585	ele,BIO01	0.942	0.564	BIO15,BIO17	0.913	0.357	BIO04,BIO01
2	0.939	0.585	ele,BIO01,BIO11,BIO12	**0.971**	0.610	BIO15,BIO17	0.93	0.255	BIO04,BIO01,ele
3	0.936	0.561	ele,BIO01,BIO11,BIO12	0.908	0.470	BIO15,BIO17	0.866	0.456	BIO04,BIO01
4	0.933	0.512	ele,BIO01,BIO11,aridity	0.926	0.518	BIO15,BIO17	0.876	0.506	BIO04,BIO01
5	0.929	0.488	ele,aridity,BIO12	0.939	0.469	BIO15,BIO17	0.923	0.456	BIO04,BIO01
6	0.944	0.488	ele,aridity,BIO12,BIO01	0.957	**0.611**	BIO15,BIO17	**0.934**	0.356	BIO04,BIO01,BIO11,ele
7	0.943	0.39	ele,BIO01,BIO11,aridity	0.921	0.470	BIO15,BIO17	0.925	**0.706**	BIO01,BIO04,ele
8	0.925	0.512	ele,BIO15,BIO12	0.926	0.423	BIO15,BIO17	0.909	0.357	BIO04,BIO01
9	0.939	0.537	ele,ari,BIO01,BIO11BIO,12	0.903	0.375	BIO15,BIO17	0.928	0.606	BIO04,BIO01
10	**0.948**	**0.610**	ele,ari,BIO01,BIO11,BIO12	0.934	0.470	BIO15,BIO17	0.929	**0.706**	01,04,11,ele

there is a relationship between the morphological variables of specific leaf area (SLA) and the leaf length-width ratio (LWR) associated with geographical factors, such as latitude, longitude, altitude and precipitation-dependent variables (*i.e.,* BIO12 and BIO17). We observed that both the SLA and the precipitation levels decline as latitude increases, as mentioned by Rico-Gray & Palacios-Ríos (1996).

It is important to mention that the leaf shape ratio (leaf length/leaf width) varies considerably depending on precipitation. Leaves that are longer than wider were found in the Pacific group, and they had great thickness and lower values of SLA, while the populations of the Gulf of Mexico group had leaves with a smaller leaf length/width ratio, higher SLA values and lower thickness.

Low SLA values were found in plants at localities with a low rainfall and marked seasonality between the dry and rainy seasons. These plants can reduce the excessive loss of water by evaporation and make water use more efficient, generating an important mechanism to address the scarcity of water resources (Ogaya & Peñuelas 2003, Wright *et al.* 2004, Aranda *et al.* 2014, McLean *et al.* 2014). Our results agree with several studies that mention that a decrease in SLA also implies changes in other traits, such as an increase in leaf thickness, because the latter implies a higher density of both palisade and spongy parenchyma (Aranda *et al.* 2014). Additionally, Rossatto *et al.* (2013) argued that leaves that grow in closed forests (such as those in the Gulf of Mexico group) have greater SLA values as an adjustment to take advantage of patches of light (Valladares & Niinemets 2008), while leaves in open sites with high incidence, such as those in the Pacific group have lower SLA values.

Population differentiation. Ecological speciation is common in diverse groups of plants (Rundle & Nosil 2005). In *Q. elliptica*, we detected leaf morphological differentiation among populations. We suggest that environmental factors can contribute to morphological divergence in key adaptive traits such as thickness, length and SLA, which also allows us to recognize at least two geographically separated and environmentally distinct groups: the Pacific and Gulf of Mexico groups.

Populations of *Q. elliptica* distributed along the Pacific coast occurred in seasonal deciduous, mixed and oak forests at elevations less than 1,200 m; morphologically, these populations had large but narrowly elliptical and thick leaves and with lower SLA values. In contrast, populations of the Gulf of Mexico group were characterized by inhabiting humid climates with little seasonality at elevations higher than 1,200 m (oak, temperate and tropical mixed, and cloud forests); morphologically, these populations had small and less thick broadly elliptical leaves with high SLA values.

According to the RDA, both latitude and longitude were almost as important as the environmental conditions in terms of the variation in *Q. elliptica*. Pearse & Hipp (2012) identified that variation in defense against herbivory in oaks corresponds to latitudinal gradients; however, this gradient is driven predominantly by climatic differences across latitudes. Frenne *et al.* (2013) argued that variations in multiple environmental factors with latitude or longitude can be complex since variation patterns can hide factors that can differ across a geographical gradient.

The ecological niche modeling procedure allowed us to model the whole distribution of *Q. elliptica* and the morphological groups identified according to other statistical analysis. The obtained model showed the overprediction of the area of distribution of the species due to the wide range of environmental conditions in which the species occurs, extending the potential area of distribution. The geographical filtering and correction of sampling biases allow the improvement of the results obtained by ENMs (Boria *et al.* 2014, Galante *et al.* 2018) in comparison to the use of large databases with geographical biases, which can increase the environmental complexity of the obtained models. In this study, we decided to use only those locations where at least 10 individuals were collected as a geographical filter to remove the sampling bias instead of using all occurrences recorded in global databases. In addition, to reduce the environmental complexity associated with a species of wide geographical and ecological distribution such as *Q. elliptica*, it was decided to independently model the distributions of the two morphologically groups; this allowed the overadjustment of the distribution of the species, improving the resulting ENM in a similar manner to the proposal of Shcheglovitova & Anderson (2013) and Galante *et al.* (2018).

The differences in the niches of these two groups were also important, although there is an overlap between the two groups in the western parts of the Trans-Mexican Volcanic Belt and the Sierra Madre del Sur. The most important variables in the generation of the models were the climatic factors that determine the differentiation of populations between the Pacific and the Gulf of Mexico coasts. Biogeographical studies have recognized the differentiation of various organisms between these two regions (Espinosa-Organista *et al.* 2006, 2008, Escalante *et al.* 2013, Halffter & Morrone 2017).

More experimental studies are needed to show that morphological divergence in plants represents the local adaptation of populations in response to diverse selective pressures (Leimu & Fischer 2008, Frenne *et al.* 2013). For example, studies on the physiological responses of the germinative capacity of acorns or the growth rate of seedlings in common garden experiments under different controlled conditions are needed, as suggested by Weltzin & McPherson (2000) and Aguilar *et al.* (2017).

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