Botanical Sciences 103 (1): 60-82. 2025
DOI: 10.17129/botsci.3526

Received: April 29, 2024, Accepted: September 1, 2024
On line first: October 18, 2024

Ecology / Ecología

THE EFFECTS OF ENVIRONMENTAL HETEROGENEITY ON THE MORPHOLOGICAL SIMILARITY OF TOOTHED-LEAFED RED OAK SPECIES (ACUTIFOLIAE; *QUERCUS*) IN MEXICO AND CENTRAL AMERICA

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Abstract

Background: In plants, environmental gradients can promote similar morphophysiological traits in species that inhabit areas with similar climatic conditions. Here, to evaluate possible causes of morphological similarity, we analyzed leaf morphological and functional variation in toothed-leaf oaks and its relationships with environmental and geographic variables.

Hypotheses: We expected that species with a greater degree of environmental overlap would exhibit similar leaf morphology, and those with a broader range of environmental tolerance would exhibit greater leaf morphological variation.

Studied species: Acutifoliae group (Fagaceae, *Quercus*)

Study sites and dates: Leaf samples were collected from adult trees distributed in diverse forest types between 495 and 2,566 meters above sea level (m asl) in Mexico and Guatemala.

Methods: We compared patterns of leaf variation in a total of 2,934 leaves from 640 individuals corresponding to 68 populations of ten oak species using univariate and multivariate analyses. We also characterized the environmental conditions where each of the species occurred using the available geographical records and bioclimatic variables.

Results: We found morphological overlap in leaf traits in oak species occurring in similar climatic environments. Additionally, oak species with a greater range of environmental distributions showed greater leaf shape morphological variation.

Conclusions: The environment influenced the generation of similar leaf morphologies among oak species despite geographical distance and phylogenetic relationships.

Keywords: Fagaceae, morphological variation, leaf similarity, environmental gradients, oaks.

Resumen

Antecedentes: En las plantas, los gradientes ambientales pueden promover rasgos morfofisiológicos similares entre especies que habitan áreas con condiciones climáticas similares. En este estudio analizamos la variación morfológica y funcional de las hojas de las especies de encinos rojos de hoja dentada y su relación con variables ambientales y geográficas para evaluar posibles causas de la similitud morfológica.

Hipótesis: Esperamos que las especies con mayor grado de solapamiento ambiental exhiban una morfología foliar similar, y que las especies con mayor tolerancia ambiental presenten mayor variación morfológica foliar.

Especies de estudio: Grupo Acutifoliae (Fagaceae, *Quercus*).

Sitio y años de estudio: Se colectaron muestras foliares de árboles adultos distribuidos en diversos tipos de bosques entre 495 y 2,566 metros sobre el nivel del mar (m snm) en México y Guatemala.

Métodos: Comparamos los patrones de variación foliar en un total de 2,934 hojas de 640 individuos correspondientes a 68 poblaciones de diez especies de encino utilizando análisis univariados y multivariados. Además, caracterizamos las condiciones ambientales donde se distribuye cada especie usando los registros geográficos disponibles y variables ambientales.

Resultados: Encontramos un solapamiento morfológico en los rasgos foliares en especies de encino que se distribuyen en ambientes similares. Además, las especies de encino con mayor rango de distribución ambiental mostraron mayor variación morfológica en la forma de las hojas.

Conclusiones: El ambiente influyó en la generación de morfologías foliares similares en especies de encino a pesar de la distancia geográfica y las relaciones filogenéticas.

Palabras clave: Fagaceae, variación morfológica, similitud foliar, gradientes ambientales.

Leaf morphology may develop different forms for a specific function (*i.e.*, light capture, water retention, or protection), depending on the environmental conditions in which the species occurs (Reich *et al.* 1997, 2007, Warren *et al.* 2005, Nicotra *et al.* 2011, Maya-García *et al.* 2020, Ramirez *et al.* 2020). There are patterns of interspecific similarity between leaf morphology and function in regions with similar climatic conditions, indicating a convergence in plant functioning at different geographic scales (Reich *et al.* 1997, Akram *et al.* 2020). Oaks (*Quercus*) are a useful biological group for understanding these dynamics since they inhabit a large number of biomes, present various growth forms, have a wide geographical distribution and exhibit extensive foliar polymorphism (Valencia-A 2004, González-Rodríguez & Oyama 2005, Cavender-Bares *et al.* 2015, Eaton *et al.* 2015, Hipp *et al.* 2020, Morales-Saldaña *et al.* 2022). There are cases where species distantly related share leaf morphological traits when they occupy the same niches in different physiographic regions (Cavender-Bares & Bazzaz 2004, Cavender-Bares *et al.* 2004).

Important advances have been made in understanding the functioning of oak species and their biogeographic history, physiology and phylogenetic relationships (González-Rodríguez & Oyama 2005, Eaton *et al.* 2015, Sork *et al.* 2016, Oyama *et al.* 2018, García de la Riva *et al.* 2019, Hipp *et al.* 2018, 2019, 2020). However, the taxonomic complexity between closely related species continues to present a challenge, especially in highly diverse areas such as Mexico and Central America (Valencia-A 2004, Valencia 2010, Albarrán-Lara *et al.* 2010, Valencia-Cuevas *et al.* 2015, McCauley *et al*. 2019, Maya-García *et al.* 2020, Morales-Saldaña *et al.* 2022). Mexico is one of the main centers of diversification of *Quercus* (Kremer & Hipp 2020, Hipp *et al.* 2020) due to the great relief heterogeneity, environments and soil types present in the country, which favors species diversification (Valencia-A 2004, Valencia 2010, Oyama *et al.* 2018, McCauley *et al*. 2019, Morales-Saldaña *et al.* 2022). In turn, this wide diversity of environments favors finding groups of species that share a large number of morphological traits, despite not being phylogenetically related (Trelease 1924, Tucker 1974, Nixon 1993, Romero-Rangel 2006, McCauley *et al*. 2019, Morales-Saldaña *et al.* 2022, De Luna-Bonilla *et al.* 2023). Early classification of *Quercus* species was based on leaf and fruit traits, suggesting that several groups could be products of morphological convergence (Trelease 1924, Nixon 1993). This provides the opportunity to understand the similarity of morphological traits between oak species (Alvarado-Cárdenas *et al*. 2013, Zhang *et al*. 2019).

The study of leaf morphology in plant populations allows us to identify the environmental factors that influence the processes of adaptation, diversification and convergence of species (Warren *et al.* 2005, Ashcroft *et al.* 2011). The study of functional traits via morphometric analysis allows the quantitative evaluation of morphological changes (Tovar-Sánchez & Oyama 2004, Viscosi *et al.* 2009, 2012, Viscosi 2015, Martínez-Cabrera *et al.* 2011, Liu *et al.* 2018, De Luna-Bonilla *et al.* 2023). In addition, the use of climate models, geographic information systems, and niche modeling allows us to evaluate the contribution of the environment to the patterns of foliar morphological variation (Kozak *et al.* 2008, Torres-Miranda *et al.* 2011). From a morpho-environmental perspective, when species with morphological similarity overlap in the environmental space, this could be indicative of convergence (or phylogenetic conservatism in closely related species); conversely, divergence can be interpreted as when closely related species occupy different areas in morpho-environmental space (Kozak *et al.* 2008, Akram *et al.* 2020). Analyses combining morpho-environmental data also allow us to understand the differential response of plants to climatic gradients, particularly in regions with a high degree of environmental heterogeneity (Kozak *et al.* 2008, Alberto *et al.* 2013, Maya-García *et al.* 2020).

Leaf variation patterns in oaks are the result of interactions among several factors, including introgressive hybridization, phenotypic plasticity, neutral differentiation and adaptation to environmental gradients (González-Rodríguez & Oyama 2005, Cannon & Petit 2019, Morales-Saldaña *et al.* 2022). Exposure to similar environmental factors can generate similar forms in some species, which, combined with great interspecific variation and the generation of hybrids with peculiar morphologies, can generate taxonomic ambiguity in some groups or species complexes (Tovar-Sánchez & Oyama 2004, Morales-Saldaña *et al*. 2022, De Luna-Bonilla *et al*. 2023). In this sense, within the most recognized taxonomic studies (Trelease 1924, Muller 1942, Nixon 1993), the Acutifolia group is considered one of the most diverse groups in the *Lobatae* section (Trelease 1924). This group is taxonomically defined mainly by the similarity of its leaves (*e.g.*, usually toothed-awned from the base, glabrescent and with long peduncles) and comprises approximately 10 species according to the most recent taxonomic studies (Romero-Rangel 2006, Valencia-A *et al*. 2015, 2016): *Q. acutifolia* Née, *Q. albocincta* Trel., *Q. canbyi* Trel., *Q. grahamii* Benth., *Q. meavei* Valencia, Sabas & Soto, *Q. paxtalensis* C.H.Mull., *Q. sartorii* Liebm., *Q. skinneri* Benth., *Q. uxoris* McVaugh, and *Q. xalapensis* Bonpl. These species share a large number of morphological characteristics, such as having mostly glabrous leaves with toothed-awned edges from the base of the blade and ovate, elliptical, lanceolate or obovate shapes (Figure 1) (Romero-Rangel 2006, Martínez-Cabrera *et al.* 2011, Valencia-A *et al.* 2015, Pérez-Pedraza *et al.* 2021). This group is distributed in the mountains of northern Mexico to Central America in the Sierra Madre Oriental (SMOr), Sierra Madre Occidental (SMOc), Trans-Mexican Volcanic Belt (TMVB), Sierra Madre del Sur (SMS), Soconusco (S), Highlands of Chiapas (HC), Volcanic Highlands of Guatemala (VHG) and Crystalline Highlands of Guatemala (CHG) (Figure 2) (Morrone *et al.* 2017); some of the species have a wide range of distributions and inhabit a large number of physiographic regions (*e.g.*, *Q. acutifolia*), while others have a restricted distribution (*e.g.*, *Q. meavei*) (Table S1) (Valencia-A 2004, Romero-Rangel 2006, Martínez-Cabrera *et al.* 2011, Pérez-Pedraza *et al.* 2021). We hypothesized that the leaf morphology of the Acutifoliae group is related to environmental factors and the greatest morphological overlap in leaf shape occurs in species that, despite being distantly related, live under similar climatic conditions.

In this study, we used the Acutifoliae group to determine whether morphological similarity between species may be an indicator of environmental selective pressures (Alvarado-Cárdenas *et al.* 2013, Zhang *et al.* 2019), although they do not form a monophyletic group (Hipp *et al.* 2018, 2020). Therefore, considering that environmental conditions play an important role in the morphological variation of species, we expected that 1) species with a greater degree of environmental overlap would exhibit similar leaf morphology, regardless of geographical isolation, and 2) species with a greater range of environmental tolerance would exhibit greater leaf morphological variation than species with a lower range. This is a result of the increased environmental pressures to which widely distributed species are exposed. This study contributes to the understanding of leaf morphological similarity in species distributed at sites with a high degree of environmental heterogeneity, which will be useful in the taxonomic clarification of complex groups such as oaks.

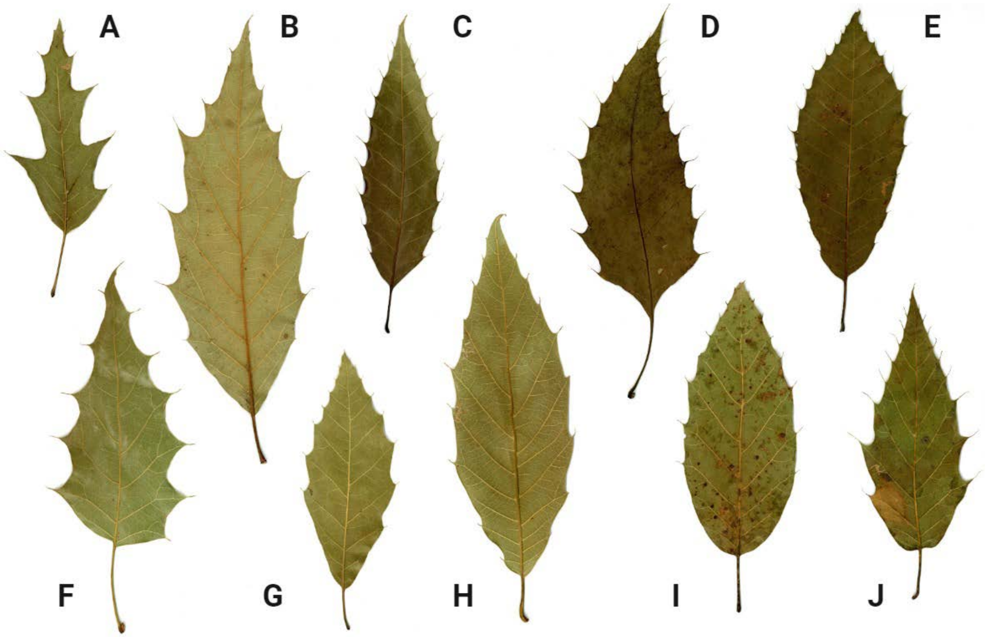

Figure 1. Typical leaf shape of species in the Acutifoliae group (section *Lobatae*). A) *Quercus canbyi*, B) *Q. acutifolia*, C) *Q. paxtalensis*, D) *Q. skinneri*, E) *Q. meavei*, F) *Q. albocincta*, G) *Q. grahamii*, H) *Q. uxoris*, I) *Q. xalapensis* and J) *Q. sartorii*.

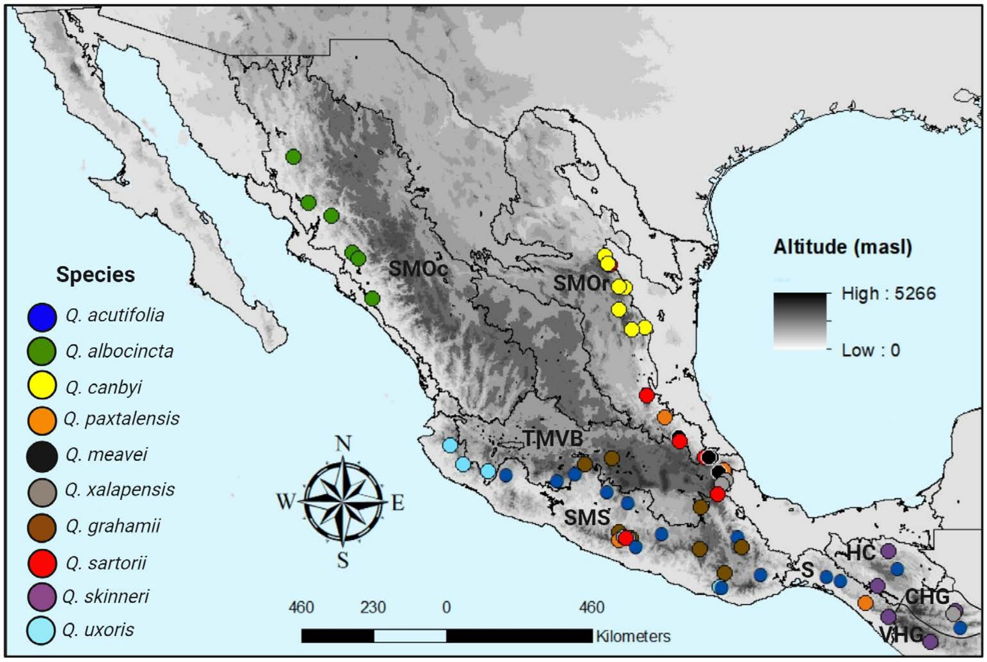

Figure 2. Sample collection of 10 species in the Acutifoliae group within Mexico and Guatemala. Sierra Madre Oriental (SMOr), Sierra Madre Occidental (SMOc), Trans-Mexican Volcanic Belt (TMVB), Sierra Madre del Sur (SMS), Soconusco (S), Highlands of Chiapas (HC), Volcanic Highlands of Guatemala (VHG) and Crystalline Highlands of Guatemala (CHG).

Materials and methods

Sample collection. A total of 640 individuals (approximately 5 leaves per individual for a total of 2934 leaves) distributed in 68 localities of the 10 species were collected (Figure 2, Table S1). The number of localities per species differed because some species have wider geographical distributions than others. At each locality, we randomly collected five samples of mature leaves from adult tree. Sampled trees were separated by at least 40 m to avoid sampling genetically related individuals. The samples were dried in an oven until they were scanned to generate digital images. Additionally, databases of georeferenced collections of the National (MEXU) and Bajío (IEB) herbariums were used (Thiers 2024), as well as records from the scientific literature (Romero-Rangel 2006, Martínez-Cabrera *et al.* 2011, Valencia-A *et al.* 2015, 2016, Romero *et al.* 2000). This database contained a total of 1162 collection records of the 10 species studied (*Q. acutifolia* = 378 records*, Q. albocincta* = 39*, Q. canbyi* = 56*, Q. grahamii* = 178*, Q. meavei* = 30, *Q. paxtalensis* = 72*, Q. sartorii* = 145, *Q. skinneri* = 110*, Q. uxoris* = 41, and *Q. xalapensis* = 113) (Figure S1).

Morphological analysis. To assess morphological variation within the Acutifoliae group, we first constructed two morphological databases based on geometric morphometry (GM) and linear measurements (LM) (Viscosi *et al.* 2009, 2012, An *et al.* 2017, Albarrán-Lara *et al.* 2019). The GM consisted of scanned images with an Epson Work Force DS-60000 scanner at a resolution of 800 dpi and included a scale. Subsequently, three reference images were drawn on the digitized leaves in a comb-like pattern (Figure S2) using the Makefan6 software of the IMP8 package, with the apex and base of the leaves used as homologous marks (Rohlf & Slice 1990, Toro-Ibacache *et al.* 2010). The first consisted of a straight comb that divided the blade of the leaves into 12 equal sections, starting at the base of the blade and ending at the apex. The remaining two images consisted of a straight comb that divided the first third of the leaf blade into seven equal sections and a circular comb with 18 rays that were located on the main vein in the last third of the leaf blade; this was performed to capture the changes in the apex and base of the leaves (Figure S2). Then, the obtained reference images were used as the basis for the location of 38 position marks (pseudolandmarks) in all samples (Figure S2) using TPSdig software in the IMP8 package (Integrated Morphometry Package) (Rohlf 2005, Toro-Ibacache *et al.* 2010). Finally, to minimize the differences between the reference configurations (Toro-Ibacache *et al.* 2010), a generalized overlap by least squares fit (procrustes) was performed (Rohlf & Slice 1990, Toro-Ibacache *et al.* 2010) using Coordgene6 software in the IMP8 series.

The database of linear measurements (LM) included a total of 10 foliar morphological attributes that are related to the response of oaks to environmental conditions (Tables 1 and 2). Discontinuous variables such as the number of teeth were transformed using the formula $x = (y)\ 0.5^{+0.5}$ (where x corresponds to the transformed variable and y to the original variable). Similarly, percentage values of traits such as the ratio of the length and width of the leaves (LL/LW) and the relationship between the width of the apex and the base (LS) were transformed following the formula $x = \text{arcsen}^{(y)\,0.5}$ (where x corresponds to the transformed variable and y to the original variable). Variable transformations were performed following Zar (1999).

Table 1. Morphological attributes, bioclimatic, and geographic variables used in the statistical analyses.

Abbreviation	Variable name	Units
	Morphological attributes (LM)	
LA	Leaf area	mm^3
AA	Angle formed by the first third of the leaf with respect to the apex	°
AB	Angle formed by the first third of the leaf blade with respect to the base	°
LL	Maximum leaf length	mm
W1	Width at 1/4 of the leaf (Base)	mm
WL	Maximum leaf width	mm
W3	Width at 3/4 of the leaf blade (Apex)	mm
NT	Number of teeth	unit
LL/LW	Leaf shape (leaf length/ maximum leaf width)	%
LS	Leaf shape (the ratio of the width at 3/4 of the leaf over the width at 1/4)	%
	Bioclimatic variables	
Bio 4	Temperature Seasonality (standard deviation ×100)	%
Bio 5	Max Temperature of Warmest Month	° c
Bio 7	Temperature Annual Range (Bio 5-Bio 6)	° c
Bio 9	Mean Temperature of Driest Quarter	° c
Bio 12	Annual Precipitation	mm
Bio 17	Precipitation of Driest Quarter	mm
AI	Aridity index	
	Geographic variables	
Longitude	-	°
Latitude	-	°
Altitude	meters above sea level	m

Table 2. The mean and standard error of morphological (LM data), environmental variables, and altitude corresponding to Acutifoliae group (units according to Table 1). The standard error is shown in parentheses and below the mean value.

Species	***LA***	***AA***	***AB***	***LL***	***W1***	***WL***	***W3***	***NT***	***LL/LW***	***LS***
Q. acutifolia	46.8	40.8	82.0	13.4	3.4	4.5	2.0	0.9	3.1	2.1
	(3.6)	(2.8)	(1.6)	(0.4)	(0.1)	(0.2)	(0.2)	(0.1)	(0.1)	(0.2)
Q. albocincta	35.3	30.1	101.3	11.7	3.9	3.3	0.9	1.5	3.3	4.2
	(4.1)	(2.7)	(1.6)	(0.4)	(0.1)	(0.3)	(0.2)	(0.2)	(0.1)	(0.2)
Q. canbyi	14.5	41.4	78.7	7.8	1.9	2.1	0.9	1.4	3.6	2.1
	(4.0)	(2.8)	(2.1)	(0.5)	(0.1)	(0.3)	(0.2)	(0.2)	(0.1)	(0.3)
Q. grahamii	26.4	36.6	85.4	11.6	2.6	3.3	1.5	1.6	3.5	2.0
	(4.1)	(3.0)	(2.2)	(0.4)	(0.1)	(0.3)	(0.2)	(0.2)	(0.1)	(0.3)
Q. meavei	32.1	42.3	80.3	11.1	2.6	3.7	1.7	1.7	3.1	1.7
	(3.9)	(3.0)	(2.5)	(0.4)	(0.1)	(0.3)	(0.2)	(0.2)	(0.1)	(0.3)
Q. paxtalensis	39.5	37.5	65.4	13.1	2.5	3.8	1.6	1.6	3.3	1.6
	(3.1)	(2.6)	(3.2)	(0.5)	(0.1)	(0.2)	(0.2)	(0.1)	(0.1)	(0.3)
Q. sartorii	32.9	46.5	84.2	10.6	2.8	3.7	1.8	1.6	3.0	1.7
	(3.2)	(2.6)	(3.7)	(0.5)	(0.1)	(0.2)	(0.2)	(0.1)	(0.1)	(0.3)
Q. skinneri	45.0	43.8	73.7	13.2	3.1	4.4	2.0	1.7	3.0	1.7
	(3.5)	(2.4)	(3.8)	(0.4)	(0.2)	(0.2)	(0.2)	(0.1)	(0.1)	(0.3)
Q. uxoris	71.4	50.2	77.2	16.1	3.9	5.7	2.9	1.7	2.8	1.5
	(3.8)	(2.4)	(3.7)	(0.5)	(0.2)	(0.2)	(0.2)	(0.1)	(0.1)	(0.3)
Q. xalapensis	43.4	47.2	73.8	12.6	2.9	4.4	2.1	1.6	2.9	1.5
	(3.8)	(2.3)	(3.7)	(0.6)	(0.2)	(0.3)	(0.2)	(0.1)	(0.1)	(0.3)

Species	***bio4***	***bio5***	***bio7***	***bio9***	***bio12***	***bio17***	***AI***	***Altitude***
Q. acutifolia	145.8	29.3	19.2	18.9	1298.0	44.5	7196.2	1493.5
	(8.5)	(0.6)	(0.6)	(0.5)	(140.3)	(12.1)	(673.5)	(122.1)
Q. albocincta	419.6	33.9	27.4	20.7	936.5	32.2	4318.3	854.8
	(22.4)	(0.8)	(0.9)	(0.5)	(142.2)	(12.1)	(677.0)	(131.4)
Q. canbyi	338.7	28.9	23.8	13.8	549.4	37.6	2933.1	1375.1
	(26.2)	(0.7)	(0.9)	(0.5)	(142.3)	(12.0)	(685.1)	(127.4)

Species	***bio4***	***bio5***	***bio7***	***bio9***	***bio12***	***bio17***	***AI***	***Altitude***
Q. grahamii	152.9 (30.3)	26.0 (0.8)	19.7 (1.1)	15.0 (0.5)	1017.3 (141.0)	30.7 (10.3)	5689.0 (645.3)	2080.8 (130.2)
Q. meavei	191.2 (33.5)	23.5 (0.8)	18.0 (1.2)	13.7 (0.5)	1433.1 (141.6)	117.5 (10.2)	9634.2 (645.7)	1879.7 (130.8)
Q. paxtalensis	181.3 (34.1)	27.1 (0.9)	18.9 (1.2)	16.5 (0.6)	1677.7 (142.3)	70.3 (10.2)	9198.3 (655.5)	1684.1 (141.7)
Q. sartorii	230.8 (38.7)	26.4 (0.9)	19.0 (1.3)	15.3 (0.6)	1336.6 (126.6)	81.0 (6.5)	7953.8 (619.1)	1618.0 (148.7)
Q. skinneri	127.8 (38.6)	29.5 (1.0)	19.4 (1.3)	19.4 (0.7)	2146.4 (133.7)	143.8 (6.5)	11587.8 (675.5)	1608.6 (137.4)
Q. uxoris	161.1 (40.0)	28.2 (1.0)	20.7 (1.3)	17.0 (0.7)	1245.0 (138.5)	24.0 (6.3)	7413.1 (705.0)	1729.6 (138.9)
Q. xalapensis	169.0 (38.6)	28.7 (1.0)	19.2 (1.3)	17.8 (0.8)	2006.8 (141.5)	179.3 (6.2)	12590.6 (699.1)	1722.0 (137.8)

Subsequently, we performed two canonical discriminant analysis (CDA) using both GM and LM databases, respectively, to visualize patterns of morphological variation in the species in the Acutifoliae group and evaluate the morphological correspondence of individuals within their original species descriptions (Pérez-Pedraza *et al.* 2021). In this analysis, we considered a tolerance value of 0.001 for the variation in the normal sample and a significance value of $p < 0.05$ (Tovar-Sánchez & Oyama 2004, Pérez-Pedraza *et al.* 2021). Additionally, to evaluate the precision of the results obtained in the CDA, cross-validation (Viscosi *et al.* 2009, Viscosi & Cardini 2011) was performed between the species in the Acutifoliae group. Similarly, to identify the species with greater morphological variation, the Mahalanobis distance of the individual values to their respective centroid was calculated, and the mean, standard deviation (*sd*), variance, and maximum and minimum values (Table S2) were obtained using IBM SPSS v19.0 statistical software (Pardo & Ruiz 2002). Multivariate analysis of variance based on distances and permutations (PERMANOVA) was also carried out to determine whether there was a significant difference in shape patterns and measured characteristics. For this purpose, we used the *adonis* command in the vegan v. 2.4 package (Oksanen *et al.* 2022). Finally, we calculated the degree of morphological overlap among the species (considering 95 % of the data distribution) with the *maxLikOverlap* command in the Siber v. 2.1.6 package (Jackson *et al.* 2011).

Environmental and geographical variation. A CDA was performed to detect similarities between the environmental conditions to which the species in the Acutifoliae group were exposed and calculate the degree of overlap between them. We collected 19 bioclimatic variables of WorldClim 2 (Fick & Hijmans 2017) using the *extract multiple values to points* function in ArcMap 10.5 software (Desktop 2011) and a database of the records of geographic coordinates of each species (1,162 records). We filtered the 19 bioclimatic variables by principal component analysis (PCA) using the *princomp* function in the R v. 4.1.0 software (R Core Team 2020) (Figure S3A). From this analysis, we selected the most explanatory variables of the first two components and then performed correlation analyses using the *corrplot* function in the corrplot v. 0.94 package (Wei & Simko 2021) to detect collinearity (correlation greater than 90 %) (Figure S3B). It is known that collinearity reduces the ability to interpret the individual contribution of each of the variables when performing multivariate statistical analyses (Phillips & Schapire 2004). Therefore, under these criteria, we retained six bioclimatic variables: Bio 4, Bio 5, Bio 7, Bio 9, Bio 12, and Bio 17 (Table 1 and Table 2) (Fick & Hijmans 2017). We also included the aridity index (AI) (Zomer *et al.* 2022) (Tables 1 and 2) since it has been useful for detecting foliar morphological responses to humidity gradients (Reich *et al.* 1997, García de la Riva *et al.* 2019, Akram *et al.* 2020, Maya-García *et al.* 2020, Pérez-Pedraza *et al.* 2021). Subsequently, to verify that there was a significant difference between the patterns found in the CDA, we performed a PERMANOVA based on the scores of the first two factors. Like the morphological data, the environmental overlap was calculated from the ellipses obtained in the CDA. Finally, to identify homologous units between the morphological and climatic data, we calculated the Mahalanobis squared distance to the centroid of each species to search for direct relationships between the two databases.

The response of morphological characteristics to environmental variation. We calculated the climatic variation of the species in the Acutifoliae group across Euclidean distances using the bioclimatic variables previously selected for each of the species with the *dist* command in the R v. 3.6.2 software (R Core Team 2020), and matrix mapping was performed with the *MRM* command in the ecodist v. 2.0.9 package (Goslee & Urban 2007). From these values, we performed a regression against morphological overlap to test whether there was a significant effect between environmental and leaf shape similarity. Subsequently, to determine whether the species with greater morphological variation corresponded to those with greater environmental variation, linear regressions were carried out based on the Mahalanobis distances obtained from morphological (GM and LM) and environmental data. The package used to perform the regressions was ecodist v. 2.0.9 (Goslee & Urban 2007) using the *MRM* command with 5,000 permutations. On the other hand, the latitude, longitude and altitude of the georeferenced records for each species were used in a regression analysis to determine the relationships between these variables and the LM characteristics. Finally, a redundancy analysis (RDA) was carried out using the *rda* command in the vegan v. 2.4 package (Oksanen *et al.* 2022) to comprehensively visualize the relationship between leaf morphology and the environment of Acutifoliae species.

Results

Patterns of morphological variation. The canonical discriminant analysis (CDA) generated from the GM data explained 60.9 % of the variance for the species in the Acutifoliae group (Figure 3A, Table S3). *Quercus albocincta* and *Q. canbyi* were segregated from the remaining species (Figure 3A, Table S3). *Quercus paxtalensis*, *Q. sartorii* and *Q. skinneri* were the species with the lowest certainty of assignment (Table 3), but they were grouped together with the remaining species (*Q. xalapensis*, *Q. acutifolia*, *Q. uxoris*, *Q. meavei* and *Q. grahamii*), forming a predominant group with similar leaf morphologies (Figure 3A). Within this main group, however, two subgroups were formed, corresponding to the species that inhabit the Sierra Madre Oriental (SMOr) and the species that inhabit the Sierra Madre Occidental (SMOc), part of the Trans-Mexican Volcanic Belt (TMVB), Sierra Madre del Sur (SMS) and the mountains of Chiapas and Guatemala (S, HC, CHG and VHG) (close to the Pacific slope) (Figure 3B), except in the case of *Q. grahamii*, which was grouped with the species of SMOr. In addition, to facilitate the visualization of these subgroups and determine the typical leaf morphology of each species, the centroid of each subgroup was plotted (Figure 3B). In total, four groups were identified: The first and second groups were composed of *Q. albocincta* (with lanceolate leaves with very broad bases) and *Q. canbyi* (with predominant elliptical leaves), respectively; the third group included *Q. grahamii*, *Q. meavei*, *Q. paxtalensis*, *Q. sartorii* and *Q. xalapensis,* which presented elliptic, obovate and oblanceolate leaves; and the fourth group consisted of *Q. acutifolia*, *Q. skinneri* and *Q. uxoris*, which had lanceolate leaves (Figure 3B).

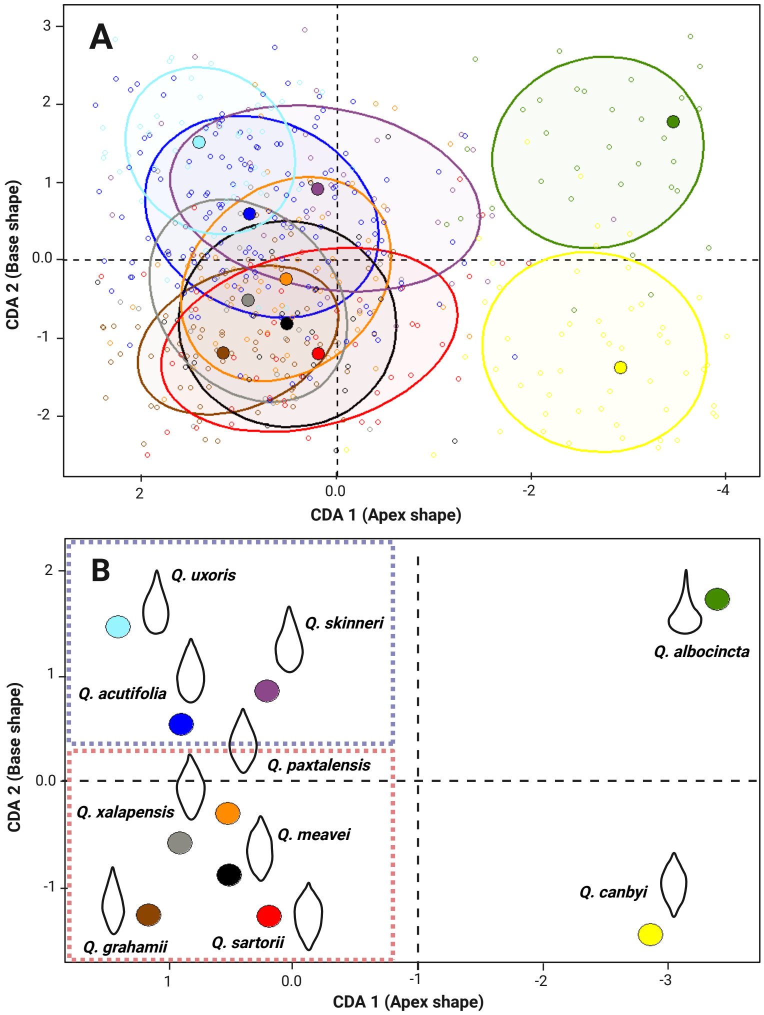

Figure 3. Canonical discriminant analysis (CDA) using geometric morphometric data (GM). **A)** CDA results showing ellipses calculated with 64 % of the data (colors according to Figure 2). **B)** Typical shape of each species in the Acutifoliae group. The dotted boxes indicate the subgroups of species sharing similar morphologies and inhabit physiographic regions near the Pacific slope (blue box) and the Gulf of Mexico slope (red box).

On the other hand, the patterns observed in the CDA using the LM data were similar to those obtained with the GM data (Tables 3, S3, Figure S4). The species that presented the greatest differences were *Q. albocincta* and *Q. canbyi*, although *Q. acutifolia* was also differentiated within the main group of species with similar morphologies. The rest of the species presented a greater morphological overlap compared to what was obtained with the GM data, which makes it difficult to differentiate the subgroups of species that inhabit regions along the Gulf of Mexico with respect to those distributed in the Pacific Ocean. This is supported by the results of the CDA cross-validation, since there was less certainty in the assignment of individual values to the species compared to what was obtained with the GM data (Table 3). In this way, *Q. acutifolia*, *Q. meavei* and *Q. skinneri* obtained the lowest values of assignment certainty when using the LM data. It should be noted that *Q. skinneri* was the species that obtained the highest values of morphological overlap and low values of certainty of assignment with both databases. Only *Q. skinneri* showed considerable morphological overlap with both databases. Furthermore, a greater resolving power was obtained when using the LM data (69 % of the variation explained) (Table 3). This can be explained by the greater differentiation of *Q. acutifolia*, which differs from the other species in terms of the number of teeth, being the only species in the group with entire edges or a low number of teeth on the margin.

Table 3. Results of the cross-validation test of the canonical discriminants analysis of morphological attributes, shapes, and environmental data. We also show the percentage of individuals within their original species descriptions.

Species	***Q. acutifolia***	***Q. canbyi***	***Q. albocincta***	***Q. paxtalensis***	***Q. meavei***	***Q. xalapensis***	***Q. grahamii***	***Q. sartorii***	***Q. skinneri***	***Q. uxoris***	***% Total***
GM data (82.4 % of the original cases grouped correctly)											
Q. acutifolia	79.3	0.0	0.7	4.7	0.0	0.0	6.7	2.7	1.3	4.7	100
Q. canbyi	1.4	92.9	1.4	1.4	0.0	1.4	0.0	0.0	1.4	0.0	100
Q. albocincta	0.0	1.9	98.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100
Q. paxtalensis	12.1	0.0	0.0	74.1	3.4	0.0	5.2	3.4	1.7	0.0	100
Q. meavei	3.8	0.0	0.0	7.7	76.9	0.0	7.7	0.0	0.0	3.8	100
Q. xalapensis	14.8	0.0	0.0	0.0	0.0	77.8	0.0	7.4	0.0	0.0	100
Q. grahamii	9.0	0.0	0.0	1.3	1.3	0.0	87.2	1.3	0.0	0.0	100
Q. sartorii	4.1	2.0	0.0	2.0	2.0	0.0	16.3	73.5	0.0	0.0	100
Q. skinneri	9.8	0.0	0.0	4.9	0.0	0.0	2.4	2.4	73.2	7.3	100
Q. uxoris	7.8	0.0	0.0	3.9	0.0	0.0	0.0	2.0	2.0	84.3	100
LM data (68.5 % of the original cases grouped correctly)											
Q. acutifolia	59.3	0.0	5.3	9.3	0.0	4.0	10.0	6.0	3.3	2.7	100
Q. canbyi	1.4	90.0	0.0	0.0	0.0	0.0	0.0	8.6	0.0	0.0	100
Q. albocincta	1.9	0.0	90.6	0.0	0.0	0.0	7.5	0.0	0.0	0.0	100
Q. paxtalensis	5.2	0.0	0.0	62.1	0.0	6.9	1.7	10.3	8.6	5.2	100
Q. meavei	0.0	0.0	0.0	0.0	53.8	0.0	3.8	30.8	7.7	3.8	100
Q. xalapensis	0.0	0.0	0.0	0.0	0.0	74.1	7.4	14.8	0.0	3.7	100
Q. grahamii	3.8	0.0	1.3	2.6	1.3	2.6	61.5	21.8	3.8	1.3	100
Q. sartorii	2.0	2.0	0.0	2.0	2.0	6.1	4.1	73.5	0.0	8.2	100
Q. skinneri	4.9	0.0	0.0	4.9	0.0	7.3	2.4	14.6	51.2	14.6	100
Q. uxoris	7.8	0.0	0.0	3.9	0.0	0.0	0.0	2.0	2.0	84.3	100
Environmental data (63.5 % of the original cases grouped correctly)											
Q. acutifolia	64.8	0.0	0.0	1.3	1.6	2.4	15.3	3.7	8.5	2.4	100
Q. canbyi	0.0	96.4	0.0	0.0	0.0	1.8	0.0	1.8	0.0	0.0	100
Q. albocincta	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100
Q. paxtalensis	12.5	1.4	0.0	4.2	8.3	2.8	4.2	44.4	19.4	2.8	100
Q. meavei	0.0	0.0	0.0	0.0	80.0	0.0	0.0	20.0	0.0	0.0	100
Q. xalapensis	3.5	11.5	0.0	0.0	1.8	18.6	0.0	54.9	8.8	0.9	100
Q. grahamii	6.7	0.0	0.0	0.0	0.0	0.0	84.8	1.1	0.0	7.3	100
Q. sartorii	0.7	10.3	0.0	0.7	9.7	14.5	1.4	62.8	0.0	0.0	100
Q. skinneri	26.4	0.0	0.0	3.6	0.0	0.0	0.0	1.8	68.2	0.0	100
Q. uxoris	4.9	0.0	0.0	2.4	0.0	0.0	7.3	0.0	0.0	85.4	100

Similarly, the results of the PERMANOVA revealed a significant difference between *Q. albocincta* and *Q. canbyi* for most of the species in the group (Table 4). However, there were several exceptions; for example, *Q. canbyi* did not differ significantly from *Q. sartorii* or *Q. skinneri* when using GM data, while with LM data, *Q. grahamii* and *Q. uxoris* were not significantly different. On the other hand, despite being the most differentiated species, *Q. albocincta* did not differ significantly from *Q. meavei* or *Q. skinneri* according to the LM data (Table 4). In the remaining species, no clear pattern of differentiation was observed with the PERMANOVA of either database (Table 4). The results of morphological overlap analyses showed that there was greater morphological overlap when using LM data than when using GM data. Thus, when using GM data, the species that overlapped to a greater extent were *Q. paxtalensis* (81.2 %) and *Q. xalapensis* (71 %) with *Q. meavei* (Table 5). Similarly, the overlap between *Q. skinneri* (69.7 %) and *Q. uxoris* (69 %) with *Q. acutifolia* was considerable. On the other hand, according to the LM data, the species with the greatest morphological overlap were *Q. paxtalensis* with *Q.* meavei (71.9 %) and *Q. sartorii* with *Q. grahamii* (79.1 %) (Table 5).

Climatic patterns. The results of the environmental characterization showed that in the CDA (80.9 % of the variance explained) (Table 3 and Table S3), the species were segregated into three main groups: a predominant group with most of the species (*Q. acutifolia*, *Q. grahamii*, *Q. uxoris*, *Q. skinneri*, *Q. xalapensis*, *Q. paxtalensis* and *Q. sartorii*) and two small groups that corresponded to the most morphologically differentiated species, *Q. albocincta* and *Q. canbyi* (Figure 4). In the case of the main group, the maximum temperature of the warmest month (Bio 5), the annual precipitation (Bio 12), and the aridity index (AI) played fundamental roles in its grouping because the species that shaped this group inhabit the mountains of central-southern Mexico and part of Central America, where mountain ranges maintain temperate climates and promote greater rainfall compared to northern Mexico. On the other hand, *Q. albocincta* and *Q. canbyi* were separated from the main group by factors such as isothermality (Bio 4), the annual temperature range (Bio 7), and the mean temperature of the driest quarter (Bio 9); this suggested that the temperature gradient is a determinant in segregating these two species. In this context, *Q. albocincta* clearly differed from the rest of the members of the Acutifoliae group due to higher isothermality and temperatures, while in the case of *Q. canbyi*, the separation was less evident compared to morphological characteristics (Figure 4).

Table 4. Multivariate analysis of variance based on distances and permutations (PERMANOVA) of the morphological attributes, shapes, and environmental data performed with 1000 permutations. *F* value/ *P* value * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001.

Species	***Q. acutifolia***	***Q. canbyi***	***Q. albocincta***	***Q. paxtalensis***	***Q. meavei***	***Q. xalapensis***	***Q. grahamii***	***Q. sartorii***	***Q. skinneri***	***Q. uxoris***
GM data										
Q. acutifolia	-	15.9	2.7	1.5	0.0	0.1	0.8	1.0	0.0	1.5
Q. canbyi	***	-	5.3	7.4	4.0	3.7	7.0	0.0	0.4	12.7
Q. albocincta	ns	*	-	8.5	41.5	40.6	2.6	16.1	6.6	4.4
Q. paxtalensis	ns	*	**	-	0.0	1.7	0.0	0.9	1.7	2.8
Q. meavei	ns	ns	***	ns	-	0.9	0.1	0.6	0.7	0.0
Q. xalapensis	ns	ns	***	ns	ns	-	2.3	2.2	1.0	0.0
Q. grahamii	ns	**	ns	ns	ns	ns	-	0.4	4.3	0.0

Species	***Q. acutifolia***	***Q. canbyi***	***Q. albocincta***	***Q. paxtalensis***	***Q. meavei***	***Q. xalapensis***	***Q. grahamii***	***Q. sartorii***	***Q. skinneri***	***Q. uxoriS***
Q. sartorii	ns	ns	***	ns	ns	ns	ns	-	0.1	4.9
Q. skinneri	ns	ns	**	ns	ns	ns	*	ns	-	0.4
Q. uxoris	ns	***	*	ns	ns	ns	ns	*	ns	-
LM data										
Q. acutifolia	-	23.7	2.5	0.7	1.9	0.2	15.8	13.6	5.9	23.7
Q. canbyi	***	-	0.0	2.0	0.00	0.8	0.0	0.2	0.0	4.8
Q. albocincta	ns	ns	-	0.4	0.9	11.7	0.1	0.0	2.4	1.4
Q. paxtalensis	ns	ns	ns	-	0.0	0.0	0.1	0.1	0.00	0.5
Q. meavei	ns	ns	ns	ns	-	0.1	0.1	1.2	1.4	0.4
Q. xalapensis	ns	ns	***	ns	ns	-	0.9	0.0	0.3	0.4
Q. grahamii	***	ns	ns	ns	ns	ns	-	1.0	1.8	0.2
Q. sartorii	**	ns	ns	ns	ns	ns	ns	-	0.9	0.0
Q. skinneri	*	ns	ns	ns	ns	ns	ns	ns	-	0.9
Q. uxoris	***	*	ns	ns	ns	ns	ns	ns	ns	-
Environmental data										
Q. acutifolia	-	93.9	39.7	9.9	40.3	3.7	4.7	4.8	14.5	5.1
Q. canbyi	***	-	8.1	6.7	68.0	8.3	4.4	21.0	6.35	1.0
Q. albocincta	***	**	-	9.6	0.0	18.1	10.1	41.9	2.3	5.6
Q. paxtalensis	***	*	**	-	9.4	0.6	10.2	15.3	0.2	1.1
Q. meavei	***	***	ns	**	-	26.3	0.2	4.6	54.3	2.1
Q. xalapensis	ns	**	***	ns	***	-	1.4	18.1	0.8	13.1
Q. grahamii	*	*	**	**	ns	ns	-	26.7	0.0	27.6
Q. sartorii	*	***	***	***	*	***	***	-	7.4	99.2
Q. skinneri	***	**	ns	ns	***	ns	ns	**	-	0.8
Q. uxoris	*	ns	*	ns	ns	***	***	***	ns	-

In addition, the environmental distance results (Table 5) confirmed the separation of the species from northern Mexico from the other species. In this context, *Q. albocincta* and *Q. canbyi* presented the greatest environmental distance with respect to the rest of the species in the Acutifolia group, followed by *Q. acutifolia.* The main species group had low environmental distance values. Thus, the species with the greatest climatic similarity were *Q. paxtalensis* with *Q. sartorii*, *Q. acutifolia* with *Q. uxoris* and *Q. skinneri* with *Q. xalapensis.* This was corroborated by the PERMANOVA, which supported this significant difference in the species from northern Mexico (with some exceptions, such as *Q. uxoris* species with *Q. canbyi* and *Q. meavei* and *Q. skinneri* with *Q. albocincta*). A noteworthy result of this analysis was the evident differentiation of *Q. sartorii*, although in previous analyses, this pattern was not detected (Table 5).

Table 5. Morphological and environmental overlap of the species in the Acutifolia group. A) Percentage of morphological overlap between species-pair calculated from ellipses with 95 % of the distribution. B) Percentage of niche overlap between species-pair and environmental Euclidean distances.

Species	***Q. acutifolia***	***Q. canbyi***	***Q. albocincta***	***Q. paxtalensis***	***Q. meavei***	***Q. xalapensis***	***Q. grahamii***	***Q. sartorii***	***Q. skinneri***	***Q. uxoris***
A) GM data overlap\ LM data overlap										
Q. acutifolia	-	13.44	29.51	40.01	36.64	31.16	28.20	29.54	40.40	35.03
Q. canbyi	2.17	-	12.76	16.51	26.18	11.89	31.18	29.11	16.45	5.29
Q. albocincta	4.97	7.18	-	8.23	7.64	6.64	12.56	11.09	8.04	4.76
Q. paxtalensis	47.25	3.72	3.94	-	71.91	58.99	53.57	58.35	66.29	45.47
Q. meavei	47.47	5.25	4.76	81.24	-	56.33	59.41	66.00	66.95	42.05
Q. xalapensis	48.15	2.47	1.46	64.99	71.00	-	44.15	53.90	56.17	43.92
Q. grahamii	39.95	0.37	1.68	64.35	62.18	57.24	-	79.17	45.07	23.86
Q. sartorii	34.41	16.25	5.07	55.45	64.81	58.48	50.04	-	51.72	27.80
Q. skinneri	69.76	10.88	10.68	43.89	46.68	44.12	33.51	42.56	-	65.88
Q. uxoris	69.04	0.00	0.18	28.83	28.59	37.72	29.15	20.71	48.66	-
B) Environmental data overlap \ Environmental Euclidean distances										
Q. acutifolia	-	3.97	4.62	1.75	3.49	3.44	2.2	2.17	2.94	1.14
Q. canbyi	0.00	-	3.84	4.18	4.56	5.89	3	3.36	5.98	3.29
Q. albocincta	0.00	0.00	-	5.45	6.78	6.31	5.41	5.27	6.02	4.58
Q. paxtalensis	51.03	15.74	0.00	-	2.06	2.54	2.11	1.14	2.45	1.59
Q. meavei	9.23	0.00	0.00	11.47	-	3.23	2.58	1.63	3.74	3.08
Q. xalapensis	34.29	24.14	0.00	69.84	13.55	-	4.4	3.13	1.16	3.76
Q. grahamii	43.87	0.00	0.00	38.29	22.92	45.34	-	1.62	4.33	1.42
Q. sartorii	15.29	14.01	0.00	40.06	23.64	50.87	30.81	-	3.32	1.73
Q. skinneri	54.82	0.00	0.00	35.45	0.63	21.00	23.87	5.48	-	3.45
Q. uxoris	44.74	0.00	0.00	26.78	5.65	27.06	40.34	10.38	38.33	-

Morphology-environment relationship. Since the patterns of morphological variation followed the same patterns as the environmental characterization of the species, a relationship was found between these two databases. In this sense, the RDA suggested that the species that inhabit areas with relatively high precipitation rates (*Q. uxoris*, *Q. skinneri*, *Q. xalapensis*, *Q. paxtalensis* and *Q. meavei*) presented large leaves with considerable leaf areas (LL, W2 and LA) (Figure 5). The number of teeth (NT) had great importance in the description of *Q. acutifolia* (Figure 5). This is because this species is quite unique in this characteristic, being able to have populations with numerous teeth and others with the absence of them. On the other hand, *Q. albocincta* had leaves with wide bases (AB) and an acute apex of the leaves (AA), which agrees with the leaf shape analysis (Figure 5). Finally, it can be seen in the RDA that *Q. canbyi* remained close to the species inhabiting humid areas because it shared characteristics that responded positively to precipitation in the driest quarter (Bio 17) (Figure 5).

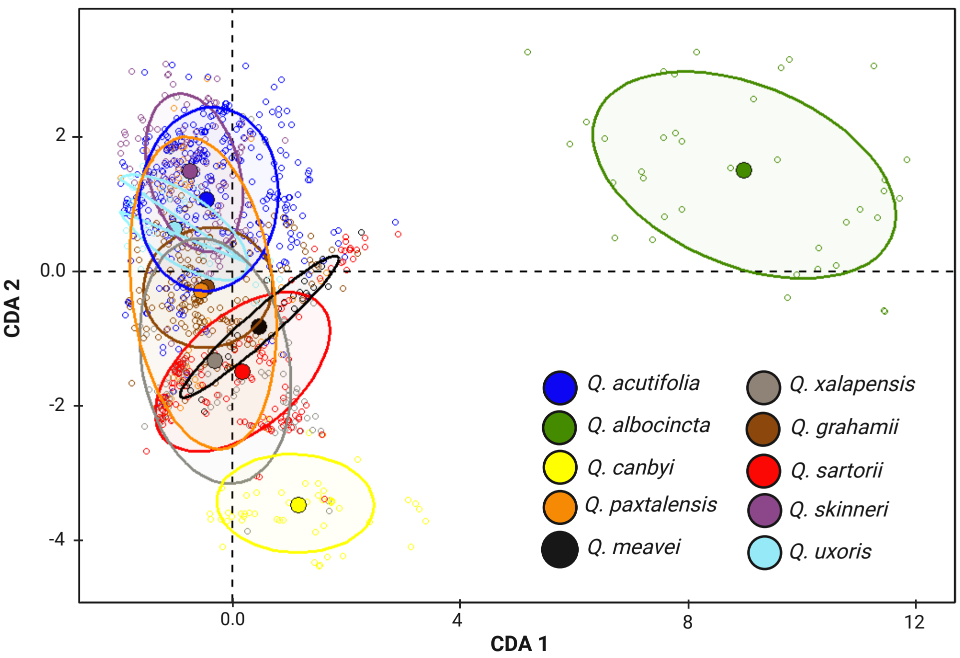

Figure 4. CDA results using environmental variables and ellipses calculated with 64 % of the data.

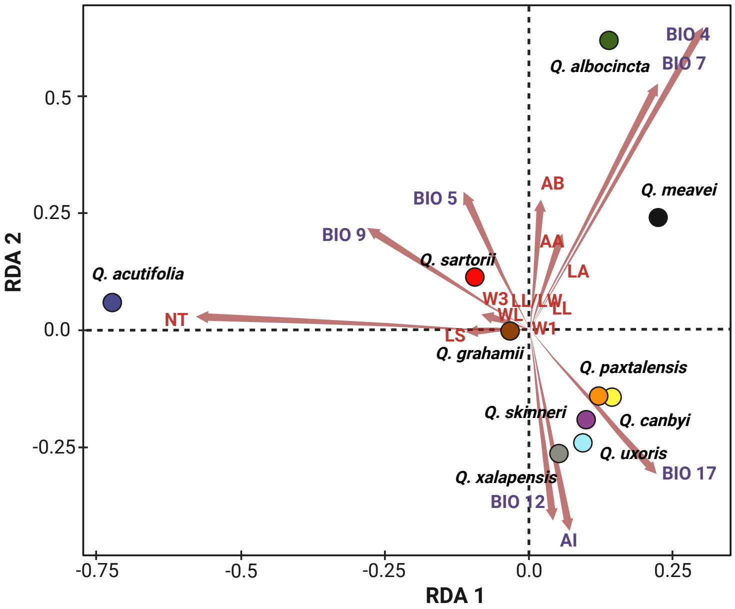

Figure 5. RDA analysis of the morphological attributes (LM) (in red color) and their relationship with the environmental variables (in purple). Color by species in the Acutifoliae group according to Figure 2.

The morpho-environmental analysis revealed significant correlations between the number of teeth (NT) and the aridity index (AI) ($r^2 = 0.251$, $P = 0.045$); this pattern was much more appreciable when NT values lower than 1.4 were omitted (these values correspond to populations of *Q. acutifolia* where entire edges predominate) ($r^2 = 0.336$, $P = 1.362e^{-6}$) (Figure 6A). Another significant relationship was between leaf area (LA) and annual precipitation (Bio 12) ($r^2 = 0.085$, $P = 0.0175$) (Figure 6B). The width and length of the leaves (WL and LL) also had significant correlations with temperature seasonality (Bio 4) ($r^2 = 0.206$, $P = 1.294\ e^{-4}$ and $r^2 = 0.182$, $P = 3.539\ e^{-4}$, respectively)

(Figure 6C). Finally, the width of the base of the leaves (W1) was correlated with the mean temperature of the driest quarter (Bio 9) ($r^2 = 0.222$, $P = 6.379$ e^{-05}) (Figure 6D). Among the geographical variables studied, only latitude had a significant correlation with LL, WL, LA and AB (Figure S5).

Finally, the morphological overlap of the species in the Acutifoliae group showed a significant relationship with the environmental similarity of their habitats (GM data: $r^2 = 0.422$, $P = 0.011$ and LM data: $r^2 = 0.417$, $P = 0.004$). In this context, the species with the greatest morphological overlap corresponded to species that lived in areas with high environmental similarity (Figure 7A, B). Similarly, the species that inhabited areas with greater environmental variation also presented the most foliar morphological variation ($r^2 = 0.944$, $P = 2.595$ e^{-6}) (Figure 7C). Thus, the species that presented greater foliar morphological variation were *Q. albocincta, Q. canbyi* and *Q. skinneri* (Figure 7C). In contrast, the species with the lowest degree of morphological variation were *Q. meavei, Q. sartorii* and *Q. xalapensis* (Figure 7C). However, when using LM data, the same relationship between morphological variation and environmental variation was not found ($r^2 = 0.076$, $P = 0.439$) (Figure 7D).

Discussion

Environmental factors such as temperature, water availability, light intensity, and intra- and interspecific interactions can drive the patterns of morphological variation in plant species at different spatial scales (Díaz & Cabido 2001, Bruschi *et al*. 2003, Nicotra *et al*. 2011, Moles *et al.* 2014, López-Caamal *et al*. 2017, McCauley *et al*. 2019, Maya-García *et al*. 2020, Sánchez-Acevedo *et al*. 2022). In general, plant species with wide geographic distributions usually show greater morphological variation within and between populations (Jones *et al.* 2009, Mclean *et al.* 2014). It is also known that the plant species that inhabit areas with abundant rainfall, such as cloud forests, usually have larger

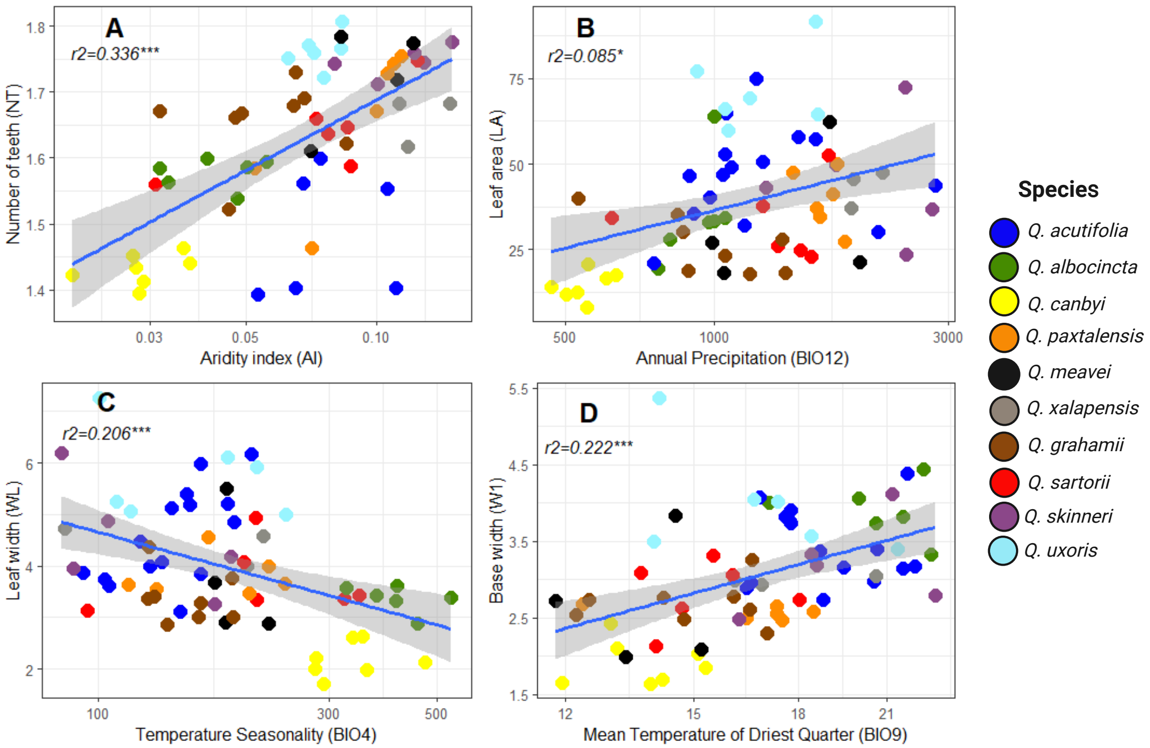

Figure 6. Linear regressions between some prominent morphological characters and environmental variables (colors according to Figure 2). r^2 value/ P value * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001. A) Linear regression between the number of teeth (NT) and aridity index (AI) (excluding values below 1.4 for NT). B) Regression between leaf area (LA) and the annual precipitation (Bio 12). C) Regression between maximum leaf width (WL) and temperature seasonality (Bio 4). D) Regression between the width at 1/4 of the leaf (W1) and the mean temperature of driest quarter (Bio 9).

leaves and larger leaf areas, which are related to water availability and light incidence (Klich 2000, Leigh *et al.* 2012, Mclean *et al.* 2014, Valladares *et al.* 2014). In the case of Acutifoliae group, annual precipitation and the aridity index influenced the generation of similar morphotypes (*i.e.*, large leaves with large leaf areas) among several oak species (*Q. acutifolia*, *Q. uxoris*, *Q. skinneri*, *Q. grahamii*, *Q. meavei*, *Q. xalapensis*, *Q. paxtalensis* and *Q. sartorii*); these oak species are not closely related phylogenetically (Hipp *et al.* 2018, 2020).

We found a notable pattern of morphological differentiation between the species of this predominant group that inhabit regions close to the Pacific slope (part of TMVB, SMS, and the mountains of Chiapas and Guatemala (S, HC, CHG and VHG)) and those of the Gulf of Mexico (mainly SMOr). It is known that the slope of the Gulf of Mexico has greater humidity and precipitation than the Pacific slope (Martínez-Cabrera *et al.* 2011, Maya-García *et al.* 2020). In turn, the oak species that inhabit each of these slopes showed morphological similarity, presumably due to occupying similar habitats (Moles *et al.* 2014, Maya-García *et al.* 2020). An exceptional case was *Q. grahamii* (a species that inhabits TMVB and SMS), which, due to their great morphological similarity, was grouped with *Q. sartorii*, *Q. meavei* and *Q. xalapensis* (species mainly distributed in SMOr), despite remaining geographically isolated. This suggested the strong influence of environmental factors on the generation of similar morphologies, despite the large geographical distance.

The influence of the environment is much clearer in the case of the species from northern Mexico (*Q. canbyi* and *Q. albocincta*). These species, despite being geographically isolated (*Q. canbyi* inhabits SMOr, and *Q. albocincta* inhabits SMOc), share characteristics such as low LA and acute apex. In turn, these characteristics were related to environmental factors such as temperature seasonality, temperature annual range and precipitation in the driest

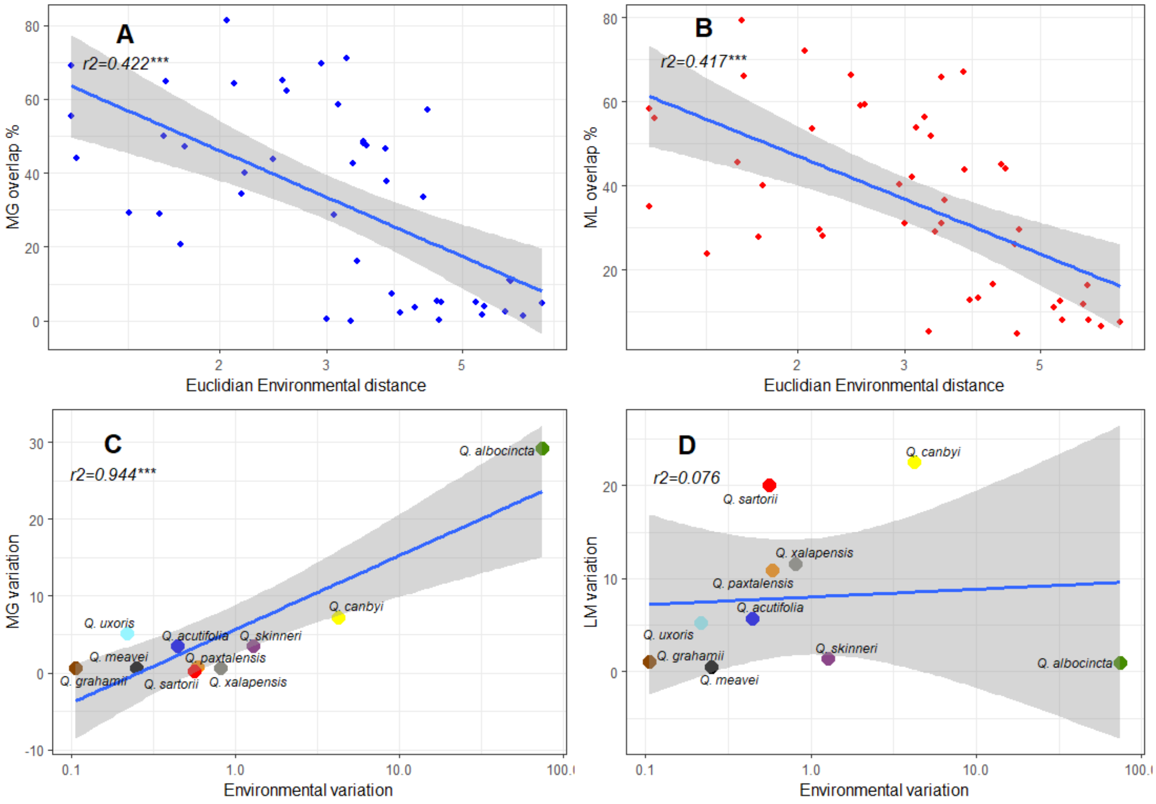

Figure 7. Correlation between the degree of morphological overlap with the Euclidean environmental distances. A) and B) using the geometric morphometric (GM) data and linear morphological data (LM), respectively). C) Correlation between Mahalanobis distances for the geometric morphometric data (GM) and the bioclimatic variables. D) Correlation between the Mahalanobis distances for linear morphological data (LM) and the environmental data. Figures C and D follow the color pattern according to Figure 2. r^2 value / *P* value * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001

quarter. Higher temperatures and lower precipitation were important filters for separating the species from northern Mexico (*Q. albocincta* and *Q. canbyi*) from the rest of the species in the Acutifoliae group. However, in contrast to *Q. canbyi*, which has acute or attenuated bases, *Q. albocincta* has very wide leaf bases (mostly obtuse or truncated).

Latitude was the only geographical variable that presented a significant relationship with several LM characteristics. It is known that latitude has a very important effect on leaf morphology on a global scale since it increases the isothermality of the regions closest to the poles (Givnish 1987, Edwards *et al.* 2016). In this sense, characteristics such as LL, WL, and LA were negatively related to latitude, while AB was positively related. As we observed earlier, these characteristics are related to the species inhabiting areas with high levels of humidity; therefore, this negative influence of latitude corresponds to the moisture gradient present in Mexico (drier zones occur mainly in the northern part of the country). Although the presence of toothed leaves is related to high latitudes (*i.e.*, as latitude increases, the presence of toothed or lobed species increases) (Peppe *et al.* 2011, Edwards *et al.* 2016), our results did not follow this pattern. However, NT responded positively to AI, suggesting that oak species with toothed leaves, at least in Mexico, are mostly present in regions and biomes with high humidity levels. Leaves with toothed-awned margins facilitate water transport and support the leaf blade between secondary veins, which favors hydraulic conductance (Edwards *et al*. 2016).

On the other hand, the influence of introgressive hybridization on the generation of new morphotypes should not be completely ruled out since hybridization seems to be common among several species in the Acutifoliae group with geographical proximity (Pérez-Pedraza *et al*. 2021). We can consider that at least some of the species in the Acutifoliae group are involved in genetic exchange networks that could form a syngameon (Grant 1989, Cannon & Petit 2019, Buck & Flores-Rentería 2022). It is thought that within the syngameons, some of the species that comprise them function as genetic links between geographically isolated species; these species generally have a wide distribution and a wide range of environmental tolerances (this could be the case for *Q. acutifolia*), which helps them remain in contact with the rest of the species and present the highest rates of genetic exchange (Cannon & Lerdau 2019, Cannon & Petit 2019, Cronk & Suarez-Gonzalez 2018, Levi *et al.* 2019). This property of syngameons could favor morphological similarity between species that do not overlap in distribution, since the gene flow facilitated by the main syngameon species and equivalent selection pressures would generate morphological similarity despite geographical isolation (Cannon & Lerdau 2019, Cannon & Petit 2019, Levi *et al.* 2019, Buck & Flores-Rentería 2022).

In conclusion, we found a positive and significant relationship between the degree of morphological overlap between the oak species in the Acutifoliae group and the environmental similarity of their habitats. The species with the greatest morphological overlap were those that inhabited sympatric areas or had adjacent distributions, as was the case for *Q. sartorii*, *Q. paxtalensis* and *Q. xalapensis*. Similarly, we found evidence suggesting that the species that presented greater morphological variation corresponded to the species with the greatest range of environmental tolerance. The species from northern Mexico (*Q. albocincta* and *Q. canbyi*), which are present at higher latitudes where seasonality and the annual temperature range are high, presented greater foliar morphological variation than temperate-zone species. There are other factors that have not been addressed in this study that could add significantly to the search for the mechanisms of morphological similarity. Leaf micromorphological characteristics (*e.g.*, trichomes, stomata and waxes), vascular system anatomy or soil traits could also help sustain morphological similarity in response to the environment (López-Caamal *et al.* 2017, McCauley *et al.* 2019, Sánchez-Acevedo *et al*. 2022, Arenas-Navarro *et al.* 2023). In addition, the use of floral and fruit characters, as well as the phenology of the fruiting habit, can be highly informative for the taxonomic delimitation of oak species. Future studies on hybridization and introgression events will be useful to evaluate the morphological response of these newly hybridized individuals to the environmental conditions to which the different species of this group of oaks are exposed (Cannon & Lerdau 2019, Cannon & Petit 2019, Levi *et al*. 2019, Buck & Flores-Rentería 2022). Information on genetic exchange networks between multiple species of *Quercus* in Mexico will expand the understanding of the value of these interactions. Thus, all these considerations will help us to understand how the morphology of oaks responds to climate change, as well as the mechanisms that generate morphological similarity among the oak species that exist today.

Supplementary material

Supplemental data for this article can be accessed here: https://doi.org/10.17129/botsci.3526

Acknowledgements

We thank R. Aguilar-Romero, J. Contreras-León, D.E. Castillejos-Lemus, J. Piña-Torres, F. Hernández-Najarro, F.S. Maradiaga-Ceceña, and J. Llanderal-Mendoza for field and laboratory support. This paper constitutes a partial fulfillment of the doctoral thesis of Alberto Esteban Pérez-Pedraza at the Posgrado en Ciencias Biológicas, UNAM. We also thank to Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCYT).

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Associate editor: Eduardo Ruiz Sánchez

Author contributions: AEPP: Field work, attribute measurement and statistical analysis. MOZ: Writing and statistical analysis. SVA: Taxonomic determination and database evaluation. KO: Conceptualization and design of the project, writing and statistical analysis.

Supporting agencies: Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCYT, grant 717844 to AP-P) and Dirección General de Asuntos del Personal Académico, Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (DGAPA-PAPIIT), UNAM (grants IV 201016 and IA208218).

Conflict of interest: The authors declare that there is no conflict of interest, financial or personal, in the information, presentation of data and results of this article.