

Morphometric analysis provides evidence for two traditionally defined species of the *Tillandsia erubescens* complex (Bromeliaceae)

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Background and aims – A linear morphometric analysis of three taxa of the *Tillandsia erubescens* complex, composed of *T. erubescens* var. *arroyoensis*, *T. erubescens* var. *erubescens*, and *T. erubescens* var. *patentibracteata*, is presented to evaluate their circumscription. Additionally, their taxonomic rank as varieties or species is discussed considering the obtained results. Geographic distribution, the influence of climate, elevation, and geographic distance on morphological differences between the taxonomic entities is explored.

Material and methods – Of a total of 110 herbarium specimens reviewed, 44 were measured. These were previously identified as *T. erubescens* var. *arroyoensis*, *T. erubescens* var. *erubescens*, or *T. erubescens* var. *patentibracteata*. Factor and cluster analyses were performed using 16 quantitative morphological characters. The resulting groups were considered as taxonomic entities supported by morphometric characters, and species distributions were plotted against Mexican biogeographic provinces. A single Mantel test was performed to evaluate the correlation between morphology and climatic variables, elevation, and geographic distance.

Key results – The specimens referred to as *T. erubescens* var. *arroyoensis* were separated morphometrically from the other two varieties. The most important characters to differentiate *T. erubescens* var. *arroyoensis* from *T. erubescens* var. *erubescens* were total size, width and length of the leaf sheath and leaf blade, and the number of flowers. The non-overlapping geographical distribution of *T. erubescens* var. *arroyoensis* and *T. erubescens* var. *erubescens* supports their recognition as independent taxonomic entities. Our study did not support the separation between *T. erubescens* var. *erubescens* and *T. erubescens* var. *patentibracteata*, which is also reflected by their overlapping geographic distributions. Both precipitation and geographic distance were correlated with the morphological differences among the species.

Conclusion – Our morphometric and geographical distribution study supports the recognition of *T. arroyoensis* and *T. erubescens* as different species, while no evidence was found to maintain *T. erubescens* var. *erubescens* and *T. erubescens* var. *patentibracteata* as different taxonomic entities. We provide a set of morphological characters that can be used to distinguish between *T. arroyoensis* and *T. erubescens*, including the leaf sheath and leaf blade width, and the number of flowers. Morphological characters agree with the geographic distribution of the studied taxa.

Keywords – Geographic distribution; linear morphometry; species delimitation; *Tillandsia*.

INTRODUCTION

Species are the fundamental unit of biological classification; thus, carefully determining their identification, delimitation, and description is crucial in studies of systematic, evolutionary biology, biogeography, ecology, population genetics, and conservation biology (de Queiroz 2007; Freudenstein et al. 2017; Pinheiro et al. 2018).

Since the beginning of taxonomy, species recognition has been based on distinctive morphological traits (Castillo-Batista et al. 2017) but recently other approaches for species recognition have been proposed, such as population genetics, phylogenetics, and morphometry, among others. Morphometric analysis, whether linear or geometric, has proved to be a useful tool to clarify several problems that are difficult to solve with traditional taxonomy (Castillo-Batista et al. 2017; De Luna 2020). This is shown by works on plant families with groups of species whose limits are difficult to establish, such as Amaryllidaceae (Gage & Wilkin 2008), Brunelliaceae (Orozco 1991), Brassicaceae (Marhold 1996), Compositae (Hodálová & Marhold 1998), Dipsacaceae (Caputo et al. 1996), Lamiaceae (Otieno et al. 2006), Leguminosae (de la Estrella et al. 2009; Egan 2015; Fritsch et al. 2009; Mascarenhas et al. 2014), Orchidaceae (Ponsie et al. 2009; Pedersen 2010; Menini Nieto et al. 2019), Solanaceae (Castillo-Batista et al. 2017), and Bromeliaceae (Costa et al. 2009; Chew-Taracena 2010; Faria et al. 2010; Pinzón et al. 2011; Castello & Galetto 2013; García-Cruz 2015; Guarçoni & Costa 2017; Neves et al. 2018; González-Rocha et al. 2018; Uribbe et al. 2020).

The *Tillandsia erubescens* Schldl. complex (Tillandsioideae, Bromeliaceae) currently includes eight morphologically similar species, some of them difficult to identify (Granados Mendoza et al. 2016). These species are endemic to Mexico and are distributed in temperate high mountain forests in a range of 1150–3200 m a.s.l., from the north to the south of Mexico (Granados Mendoza 2008).

This complex is a monophyletic group divided into two lineages. The first lineage is made up of five nominal species with purple corollas: 1) *Tillandsia andrieuxii* (Mez) L.B.Sm., 2) *T. macdougallii* L.B.Sm., 3) *T. oaxacana* L.B.Sm., 4) *T. tecolometl* Granados, Flores-Cruz & Salazar, and 5) *T. pseudooaxacana* Ehlers. The second lineage contains three nominal species with green corollas: 1) *T. arroyoensis* (W.Weber & Ehlers) Espejo & López-Ferrari, 2) *T. erubescens*, and 3) *T. quaquaflorescens* Matuda (Granados Mendoza 2008). Although efforts have been made to delimit the species with purple corollas (Granados Mendoza et al. 2016), no formal species delimitation methods have been applied to the species with green corollas.

Within the green corollas group, *T. quaquaflorescens* can easily be distinguished from the other two species by its deep violet and broadly ovate leaf sheaths, glaucous-greenish leaf blades, bright red scape bracts, and horizontally curved inflorescence. This species is restricted to the humid oak forest in the northern portion of the Sierra Madre del Sur (SMS), at elevations ranging from 700 to 3100 m (INEGI 2021).

However, morphological criteria used to separate *T. erubescens* from *T. arroyoensis* have been rather ambiguous (Weber 1983), presumably inconsistent (Granados Mendoza 2008), or not explicitly stated (Espejo-Serna et al. 2004). *Tillandsia erubescens* was first described by Schlechtendal in 1845. After this, two varieties were proposed by Weber (1983); namely, *T. erubescens* var. *arroyoensis* W.Weber & Ehlers and *T. erubescens* var. *patentibracteata* W.Weber & Ehlers. According to these authors, *T. erubescens* var. *arroyoensis* differs from the type variety in that all its structures are narrower, while *T. erubescens* var. *patentibracteata* shows a longer inflorescence with divergent bracts. Later, Espejo-Serna et al. (2004) changed the taxonomic rank of *T. erubescens* var. *arroyoensis* to the species rank (*T. arroyoensis*), and synonymized *T. erubescens* var. *patentibracteata* with *T. erubescens*, albeit without stating the specific criteria supporting their decision.

According to Gardner (1986) and Granados Mendoza (2008), the three taxa share the presence of leaf blades densely covered by cinereous winged trichomes, simple and pendulous inflorescences, pink floral bracts, green petals, and green filaments and styles (exposed portion). Granados Mendoza (2008) suggested that *T. erubescens* var. *erubescens* differs from *T. erubescens* var. *arroyoensis* in its solitary growth or in colonies of up to four individuals (vs colonies of 25 to 40 individuals), threefold larger rosettes, ecarinate (vs carinate) and acute (vs rounded) sepals. However, a revision of herbarium and recently collected living specimens showed that the morphological features proposed by Granados Mendoza (2008) to differentiate *T. erubescens* var. *erubescens* from *T. erubescens* var. *arroyoensis* could be insufficient, since several individuals present overlapping characters (A. Martínez-García pers. obs.).

It has been reported that *T. erubescens* var. *erubescens* has a wide distribution, being located in pine oak forests and xerophilous scrub in the main mountain ranges of Mexico. That is, the Sierra Madre Occidental (SMOc), the Trans-Mexican Volcanic Belt (TMVB), the Sierra Madre del Sur (SMS), and the southern part of the Sierra Madre Oriental (SMOr) (Granados Mendoza 2008), at elevations from 1100 to 2900 m, at an average temperature of 17°C in a temperate subhumid climate (INEGI 2021). On another hand, *T. erubescens* var. *patentibracteata* is only documented in the central part of the SMOc (Weber 1983) in oak forests with climatic conditions similar to those recorded for *T. erubescens* var. *erubescens*. *Tillandsia erubescens* var. *arroyoensis* has been reported in pine oak forests only in the northern part of the SMOr (Granados Mendoza 2008) at elevations ranging from 1500 to 2900 m and an average temperature of 17°C in a temperate subhumid climate (INEGI 2021). Since *T. erubescens* var. *erubescens* and *T. erubescens* var. *arroyoensis* have not been documented in sympatry, their distribution could be determined by the presence of biogeographic barriers; however, this aspect has not been formally studied.

The aims of the present study were: 1) to test if the three taxa proposed by Schlechtendal (1845) and Weber (1983) (i.e. *T. erubescens* var. *erubescens*, *T. erubescens* var. *patentibracteata*, and *T. erubescens* var. *arroyoensis*) belong to separate taxonomic entities through linear morphometric

Table 1 – Measured quantitative morphological characters, abbreviations, and descriptions.

	Morphological character	Abbreviation	Description
1	Plant total size	TS	Measured from the base of the rosette to the apex of the inflorescence
2	Rosette width	WR	Measured from the widest part from one extreme to the other of the rosette leaves
3	Leaf sheath width	WS	Measured at the widest part of the leaf sheaths
4	Leaf sheath length	LS	Measured from the base of the leaf sheath to the apex
5	Leaf blade width	WLB	Measured at the widest part of the blade
6	Leaf blade length	LLB	Measured from the base of the leaf blade to the apex
7	Peduncle length	LPII	Measured from the base of the peduncle to the apex of the inflorescence
8	Inflorescence length excluding the peduncle	LI	Measured from the base to the apex of the inflorescence
9	Inflorescence width	WI	Measured at the widest part of the inflorescence
10	Number of flowers per inflorescence	NF	Number of flowers present in the inflorescence
11	Floral bract width	WFB	Measured at the widest part of the flower bract
12	Floral bract length	LFB	Measured from the base of the peduncle to the apex of the floral bract
13	Total size/leaf blade length	TS/LLB	Ratio of the plant total size and the leaf blade length
14	Total size/inflorescence length	TS/LI	Ratio of the plant total size and the inflorescence length
15	Inflorescence length/leaf blade length	LI/LLB	Ratio of the inflorescence length and the leaf blade length
16	Leaf blade length/leaf sheath length	LLB/LS	Ratio of the leaf blade length and the leaf sheaths length

analyses of both vegetative and reproductive characters; 2) to evaluate which taxonomic rank better reflects the morphological distance of the resulting taxonomic entities; 3) to address the geographic distribution patterns of the taxonomic entities recognized herein; and 4) to analyze the relationship among geographic distance, climatic variables, and elevation with morphological variables.

MATERIAL AND METHODS

Plant material and data collection

A total of 110 specimens were studied, including new collections from the field, and type and regular herbarium specimens housed at the herbaria CHAP, CHAPA, ENCB, HAL, HGOM, JES, MEXU, UAMIZ, and WU (herbarium acronyms following Thiers continuously updated), which were previously named in herbaria as one of the following a priori taxa: *T. arroyoensis*, *T. erubescens* var. *arroyoensis*, *T. erubescens*, and *T. erubescens* var. *patentibracteata*, and were preliminary identified as such. Of the 110 specimens studied, only 44 were used in the multivariate analyses because they had complete and appropriate structures that could be measured. In some cases, floral characters (such as sepals, petals, and filaments) were not present and could therefore not be measured, and in many cases the samples only had fruits. In other cases, it was not possible to obtain permission to remove floral structures for rehydration and measurement. In the end, measurements were taken from 21 specimens corresponding to *T. erubescens* var. *arroyoensis*, 21 to *T. erubescens* var. *erubescens*, and two belonging to *T. erubescens* var. *patentibracteata* (which are the only existing records for this taxon) (supplementary file 1). Each specimen was treated as an individual taxonomic unit (OTU),

conserving the previous identifications (as variety or species) as a reference.

Measurements were taken directly from dry specimens; large structures such as leaves and inflorescences were measured with a ruler, and smaller structures such as floral bracts were measured with a precision digital calliper (0.1 mm, Weston). Additional measurements were recorded from photographs taken by the first author with a CANON Powershot G10 camera and including a scale. In the case of the nomenclatural types, data were obtained from high resolution scans that included a scale available from the herbaria websites. All images were processed with TpsDig2 software (Rohlf 2018).

Linear morphometric analysis

Sixteen quantitative morphological characters were measured, six vegetative and six reproductive, as well as four proportions between two of the characters. An explanation of how these measurements were taken is provided in table 1. Due to the wide ranges of values, the data were standardized with the function $(\log + 1)$. Subsequently, a factor analysis (FA) was performed to reduce the dimensionality of the data. In order to find potential patterns of similarity between the OTUs and the consequent formation of groups (McGarigal et al. 2000), a cluster analysis (CA) was conducted based on a Euclidean distance matrix constructed with the selected variables from the FA. If the cophenetic value is close to 1, it is assumed that the clustering results give a good representation of the original distances.

To determine if there were statistically significant differences between the retrieved groups (taxa), a discriminant function analysis (DFA) was implemented. The morphological characters were used as discriminating

variables and the grouping variable was the species. To measure the similarities or differences between the groups (species), Wilks' lambda (λ) was used, which is easy to interpret because its values vary from 1 to 0, where 1 means total similarity and 0 total difference. All the aforementioned analyses were performed using the software STATISTICA v.7.0 (StatSoft Inc. 2004).

Geographic distribution and climatic variables

Distribution records from 274 accessions corresponding to the three studied varieties were obtained from the Global Biodiversity Information Facility (GBIF 2020) and Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO 2020) databases, as well as from the collection locality named on the herbarium label. Those records without coordinates were manually georeferenced with the online version of Google Earth (Google Earth 2020). Once the result of the morphometric analysis was obtained, the information about the distribution documented in the online databases was compared to the distribution registered on the herbarium labels. Finally, the distribution projections were built from the taxonomic entities resulting from the morphometric analysis based on a comprehensive and well curated geographic database. The species distribution map was generated with QGIS v.3.4 (QGIS Development Team 2020), projecting the coordinates of each record on a layer of the biogeographic provinces of Mexico (Morrone et al. 2017).

Additionally, we explored if, 1) climatic variables 2) elevation, and 3) geographic distance have an influence on morphological differences among taxonomic entities. For the above, we constructed a data matrix including the coordinates of the 44 localities, which corresponds to each of the measured specimens. Moreover, we used DIVA-GIS v.7.5.0 (DIVA-GIS Development Team 2021) to extract the values of the climatic variables of each site (temperature, precipitation) available in the WorldClim database (Fick & Hijmans 2017) at 30 arc-seconds resolution. Whenever available, elevation data were taken from the labels of the herbarium specimens and when not, it was taken by georeferencing the locality through Google Earth (Google Earth 2020). We performed a series of single Mantel tests using the R package vegan v.2.5-7 (Oksanen et al. 2020; R Core Team 2020) with significance determined using 9999 permutations, testing the correlation between various dissimilarity matrices: 1) climatic variables temperature and precipitation (Euclidean distance), 2) elevation (Euclidean distance), 3) geographic distance (Haversine distance), and 4) resultant scores from the morphological FA analysis (Euclidean distance).

RESULTS

Groups recovered by linear morphometrics and taxonomic rank

Of the 16 characters analyzed in the FA, there were 13 characters that contributed the most to the differentiation of the groups: total size of the plant (TS), width of the rosette (WR), all characters of the leaf sheath and blade (WS, LS,

Table 2 – Loading of the first two axes of a factor analysis (FA) on morphological variables. Character abbreviations are explained in table 1.

Character	Factor 1	Factor 2
TS	-0.908132	-0.162762
WR	-0.595346	-0.077055
WS	-0.918033	-0.030565
LS	-0.891410	0.190433
WLB	-0.912838	-0.018520
LLB	-0.875408	0.337116
LPII	-0.896598	-0.108666
LI	-0.794538	-0.507749
WI	-0.886761	-0.062671
NF	-0.924131	-0.015523
WFB	-0.781391	-0.245557
LBF	-0.811939	-0.206104
TS/LLB	0.117024	0.814031
TS/LI	0.469781	-0.466751
LI/LLB	-0.265396	0.932809
LLB/LS	-0.652465	0.509153
Variance explained	9.492041	2.570053

WLB, LLB), all characters of the inflorescence (LPII, WI, LI, WFB, LFB), number of flowers (NF), and the ratio between the total size of the inflorescence and the length of the leaf blade (TS/LLB) (table 2, fig. 1). According to the morphometric analysis, two different groups that can be associated with two taxonomic entities were recognized: *T. erubescens* (including *T. erubescens* var. *erubescens* and *T. erubescens* var. *patentibracteata*) and *T. arroyoensis*. The FA showed that factors 1 and 2 together explain 76.56% of the variation of the group (F1: 60.10%, eigenvalue 9.6167; F2: 16.46%, eigenvalue 2.6341). The scatter diagram (fig. 2) also reveals the existence of two groups; the first one includes specimens a priori determined as *T. erubescens* var. *arroyoensis*, and the second includes specimens identified a priori as *T. erubescens* var. *erubescens* and *T. erubescens* var. *patentibracteata*. Although the two specimens of *T. erubescens* var. *patentibracteata* are closely positioned in the morphospace, they are imbedded within the *T. erubescens* var. *erubescens* specimen morphospace. The dendrogram derived from CA confirms the two main groups as well (fig. 3), with *T. erubescens* var. *patentibracteata* and *T. erubescens* var. *erubescens* in the same clade, and *T. erubescens* var. *arroyoensis* in a separate clade. The high value of the cophenetic correlation of this analysis (0.820) shows that the resolution of the CA (i.e. dendrogram) faithfully represents the structure of the original dataset. Values close to 1 (as in this cluster analysis) means a good representation of the original distances.

The DFA showed that the two groups (hereafter assumed to be species) are significantly different ($F_{13,30} = 32.128$, $p < 0.0000$, Wilks' lambda = 0.06701, eigenvalue = 13.92204, Canonical R = 0.965911, $\chi^2 = 95.95079$). In 100% of the

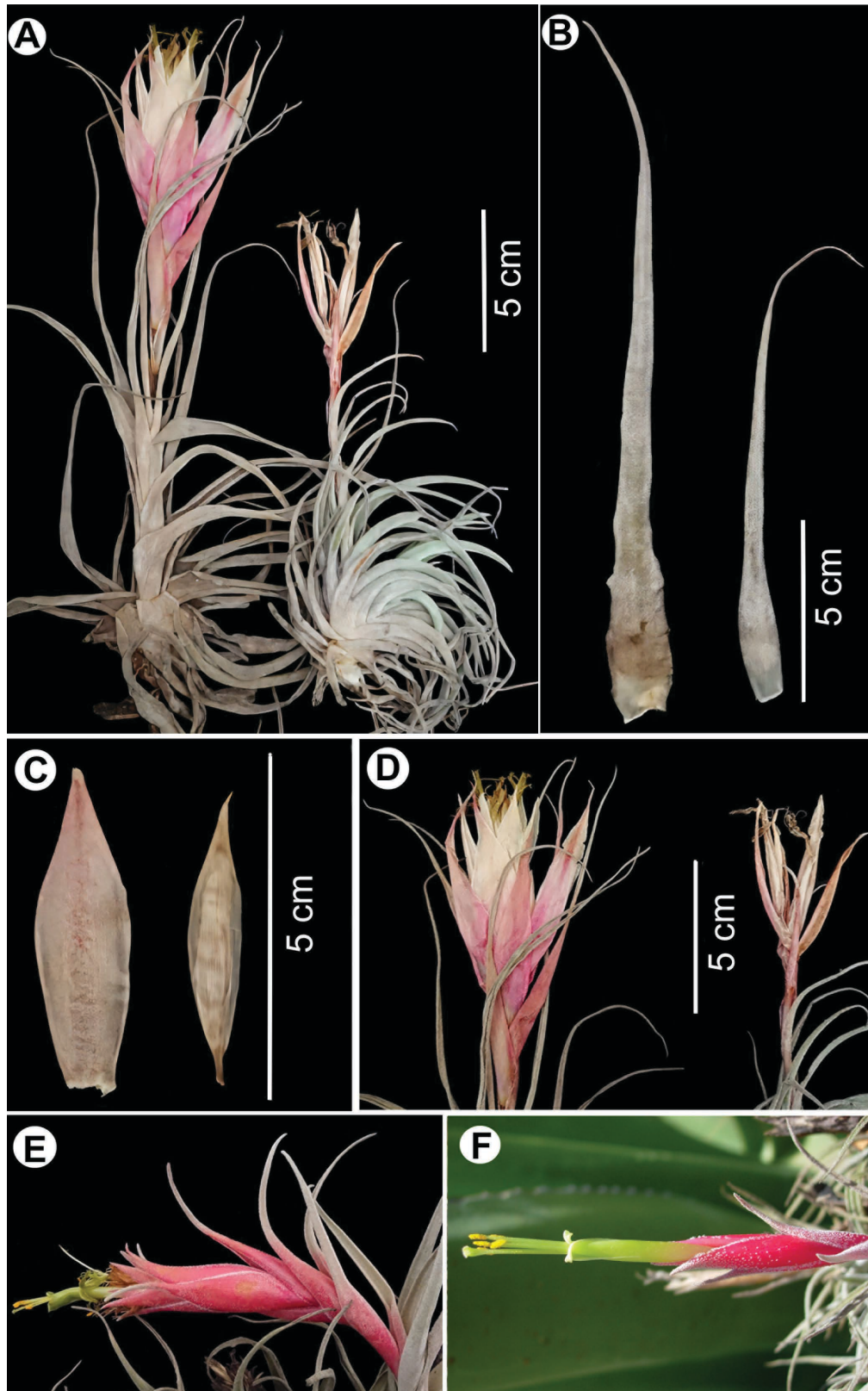


Figure 1 – Significant characters that differentiate *T. erubescens* (A–D, on the right) from *T. arroyoensis* (A–D, on the left). **A.** Plant total size (TS), rosette width (WR), and peduncle length (LPII). **B.** Length and width of the leaf sheath (LS, WS), width and length of the leaf blade (WLB, LLB). **C.** Length and width of the floral bract (LFB, WFB). **D.** Length and width of the inflorescence (LI, WI). **E.** Number of flowers (NF) in *T. erubescens*. **F.** Number of flowers (NF) in *T. arroyoensis*. Photographs: A–E by Ana Laura Martínez-García; F by Gerardo A. Salazar.

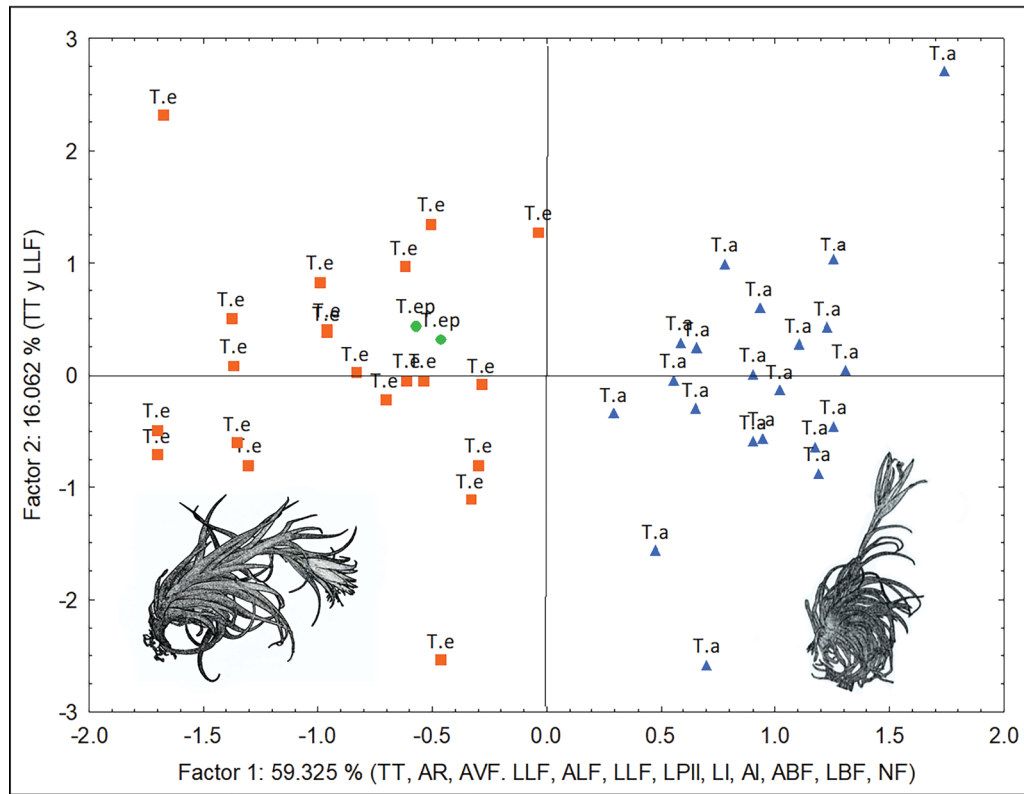


Figure 2 – Factor analysis. Factor 1 (eigenvalue 59.325%) and factor 2 (eigenvalue 16.062%) explain 76.387% of the variance. Character abbreviations correspond to those in table 1. Abbreviations: T.a: *T.erubescens* var. *arroyoensis*, T.e: *T. erubescens* var. *erubescens*, T.ep: *T. erubescens* var. *patentibracteata*. Images of *T. erubescens* and *T. arroyoensis* by Ana Laura Martínez-García.

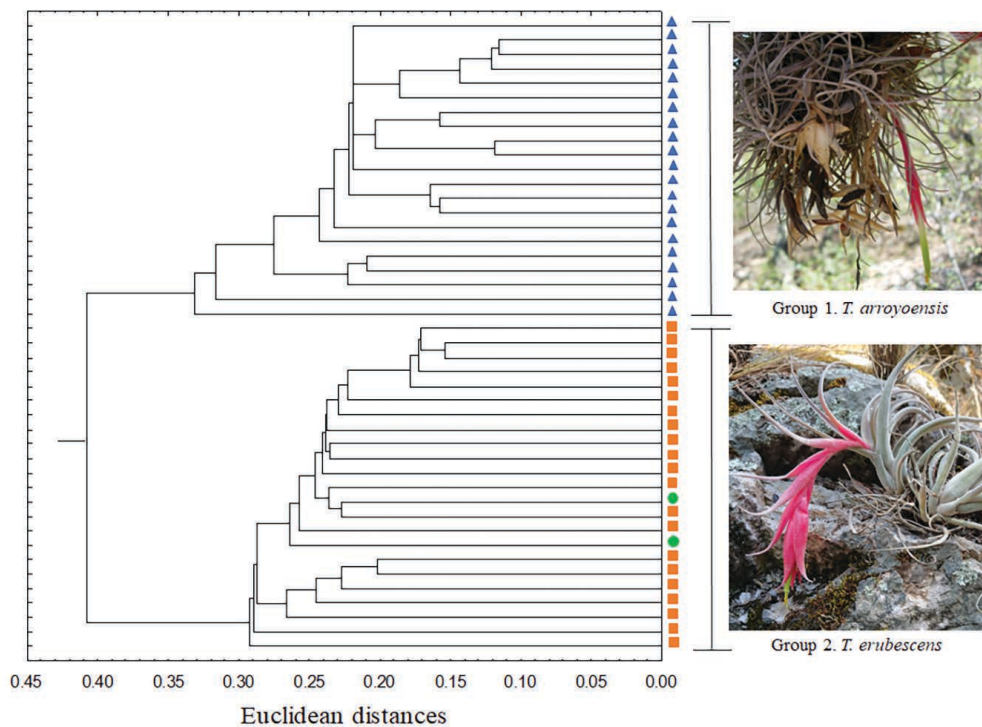


Figure 3 – Dendrogram resulting from the cluster analysis of the Euclidean distance matrix (13 significant morphological characters). Group 1: *T. arroyoensis*, blue triangles; Group 2: *T. erubescens*, orange square (including *T. erubescens* var. *patentibracteata*, green circles). Photographs: *T. arroyoensis* by Gerardo A. Salazar and *T. erubescens* by Ana Laura Martínez-García.

cases, both species were correctly classified based on values of the statistic and supported by morphometry.

Geographic distribution and climate variables

Non-overlapping distribution areas were found for the two resulting taxonomic entities. *Tillandsia erubescens* (including *T. erubescens* var. *erubescens* and *T. erubescens* var. *patentibracteata*) exhibits a very wide geographical distribution throughout the SMOc province in Sonora, Chihuahua, Sinaloa, Durango, Zacatecas, Aguascalientes, Nayarit, and Jalisco; TMVB in Colima, Michoacán, Puebla, Tlaxcala, Estado de México, and Mexico City; the Balsas Basin (BB) in Guerrero and Oaxaca; the SMS in Jalisco; and the southern part of the SMOr in Hidalgo, Querétaro, northern Veracruz, Puebla, and southern San Luis Potosí (fig. 4). In contrast, *T. arroyoensis* is restricted to the northern portion of the SMOr province in Coahuila, Nuevo León, Tamaulipas, and northern San Luis Potosí (fig. 4).

According to the results of the Mantel test (table 3, fig. 5), precipitation ($r = 0.2546$, $p = 0.0001$) and geographic distance ($r = 0.2256$, $p = 0.0024$) are correlated with the morphological differences between the two species. On the other hand, temperature ($r = 0.04744$, $p = 0.2208$) and elevation ($r = 0.03197$, $p = 0.2621$) have no correlation with the morphology of the species.

DISCUSSION

Morphometric delimitation, taxonomic rank, and definition of the three *Tillandsia erubescens* varieties

The statistical analyses allowed two groups to be clearly distinguished. One of them includes all specimens a priori identified as *T. erubescens* var. *arroyoensis* and the other contains the specimens identified as *T. erubescens* var. *erubescens* and *T. erubescens* var. *patentibracteata*. The characters (in order of contribution) that support this grouping were number of flowers (NF), plant total size (TS), those related to the width and length of the leaf sheath and leaf blade (WS, LS, WLB, LLB), and those related to the inflorescence (LP1, LP2, LP3, LP4, LP5, LP6, LP7, LP8, LP9, LP10, LP11, LP12, LP13, LP14, LP15, LP16, LP17, LP18, LP19, LP20, LP21, LP22, LP23, LP24, LP25, LP26, LP27, LP28, LP29, LP30, LP31, LP32, LP33, LP34, LP35, LP36, LP37, LP38, LP39, LP40, LP41, LP42, LP43, LP44, LP45, LP46, LP47, LP48, LP49, LP50, LP51, LP52, LP53, LP54, LP55, LP56, LP57, LP58, LP59, LP60, LP61, LP62, LP63, LP64, LP65, LP66, LP67, LP68, LP69, LP70, LP71, LP72, LP73, LP74, LP75, LP76, LP77, LP78, LP79, LP80, LP81, LP82, LP83, LP84, LP85, LP86, LP87, LP88, LP89, LP90, LP91, LP92, LP93, LP94, LP95, LP96, LP97, LP98, LP99, LP100). These characters are smaller and narrower in the first group (table 4), which agrees with Weber's (1983) original description of *T. erubescens* var. *arroyoensis*, mentioning that all its structures are narrower than in *T. erubescens* var. *erubescens*. We found that the number of flowers per inflorescence is fundamental for differentiating between the two varieties and is herein proposed as a diagnostic character. According to our observations, *T. erubescens* var. *arroyoensis* does not exceed two flowers per inflorescence, whereas *T. erubescens* var. *erubescens* ranges from five to 15. However, the characters associated with the leaf sheath and blade (WS, LS, WLB, and

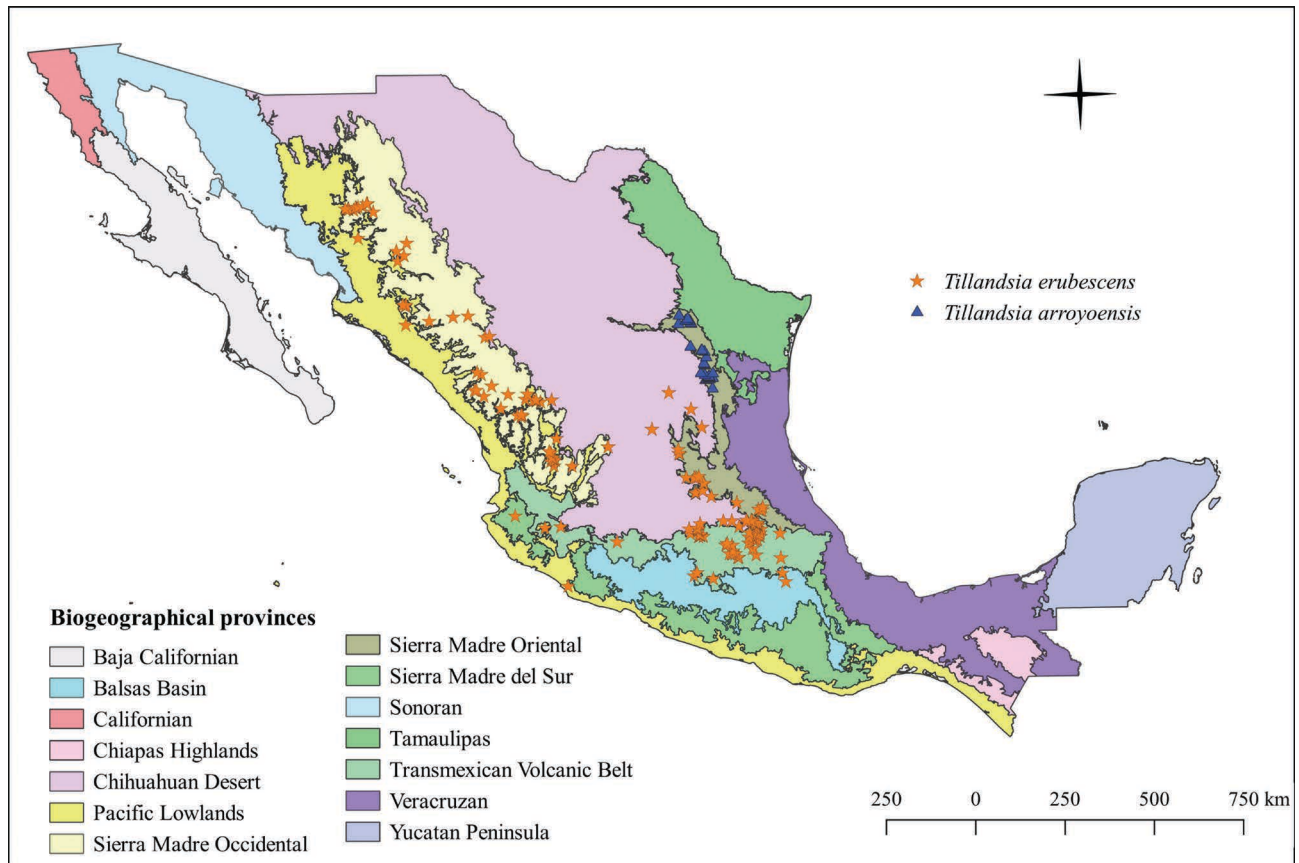


Figure 4 – Geographic distribution of *T. arroyoensis* and *T. erubescens* (including *T. erubescens* var. *patentibracteata*) projected over the Mexican biogeographic provinces. Map generated with QGIS v.3.4 (QGIS Development Team 2020), projecting the coordinates of each record on a layer of the biogeographic provinces of Mexico (Morrone et al. 2017).

Table 3 – Comparative values of the characters of *T. erubescens* var. *arroyoensis*, *T. erubescens* var. *erubescens*, and *T. erubescens* var. *patentibracteata*. All measurements are given in centimetres.

	Morphology vs temperature (°C)	Morphology vs precipitation (mm)	Morphology vs elevation (m)	Morphology vs geographic distance (km)
Mantel statistic	r = 0.04744	r = 0.2546	r = 0.03197	r = 0.2256
Significance	p = 0.2208	p = 0.0001	p = 0.2621	p = 0.0024
	90% 0.0851	90% 0.0927	90% 0.0727	90% 0.0965
Upper quantiles of permutations (null model)	95% 0.1151	95% 0.1226	95% 0.0952	95% 0.1269
	97.5% 0.1416	97.5% 0.1479	97.5% 0.1154	97.5% 0.1540
	99% 0.1746	99% 0.1817	99% 0.1389	99% 0.1838

LLB) enable delimitation of the taxa even if the inflorescence is absent.

The present study agrees with the proposal of Espejo-Serna et al. (2004), recognizing *T. erubescens* var. *arroyoensis* as a taxonomic entity separate from *T. erubescens* var. *erubescens*, since in the three statistical analyses, *T. erubescens* var. *arroyoensis* always formed a separate group without exceeding the values of the other two traditionally recognized varieties. Our study complements the taxonomic proposal of Espejo-Serna et al. (2004) by providing a set of quantitative morphological characters that support the distinction between the two species (table 2).

The morphometric analysis did not support Weber’s (1983) proposal of recognizing *T. erubescens* var.

patentibracteata as a separate taxonomic entity, since in the statistical analysis their measurements always remain within the range reported for *T. erubescens* var. *erubescens* (table 4). Therefore, from a morphometric point of view, there is no basis for recognizing the varieties of the second group as different taxa, however, according to the presented data no specimens are separated from the variety type. Nevertheless, it is important to note that only two specimens identified a priori as *T. erubescens* var. *patentibracteata* (one of them the type), could be included in this study, which contrasts with the large number of specimens that were assigned to *T. erubescens* var. *erubescens*. Consequently, no morphological character was found to support the separation of these varieties as independent taxonomic entities, as

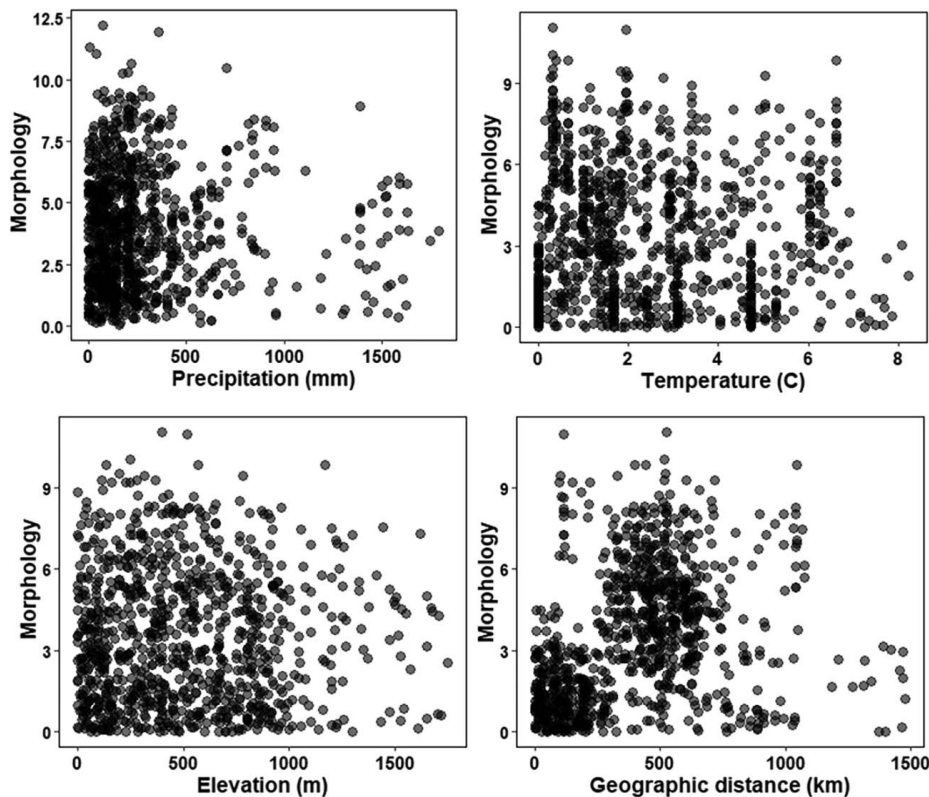


Figure 5 – Scatterplot of the Mantel test for morphology vs climatic variables (precipitation and temperature), elevation, and geographic distance.

Table 4 – Summary of the Mantel test results.

Character	<i>T. arroyoensis</i>	<i>T. erubescens</i>	<i>T. erubescens</i> var. <i>patentibracteata</i>
TS	7.5–20	15–30	25–27
WR	5.4–14.5	5–26	15–16
WS	0.7–1.5	1.2–3.1	1.2–1.4
LS	1–2.7	1.8–5	2–2
WLB	0.4–1	1.1–2.8	1.1–1.2
LLB	7–13.5	9–25	18–18
LPII	5.5–16	13–28	20–22
LI	3.5–10	5.5–10.2	7–7.5
WI	1–2	2.5–4	2.7–4
NF	1–3	4–12	3–5
WFB	0.8–2	1.3–2.5	1.5–1.9
LFB	3.4–6	4–8.7	4.8–4.8
TS/LLB	0.72–82	1.16–2.111	1.389–1.5
TS/LI	2–3.2	2.142–4.142	1.389–1.5
LI/LLB	0.340–1	0.28–0.967	0.389–0.417
LLB/LS	3.592–13.4	3.2–8	9–9

these two specimens are not separated from *T. erubescens* var. *erubescens* by the analysis. Therefore, we consider that *T. erubescens* var. *patentibracteata* could be considered a synonym of the type variety. However, this proposal should be further investigated by including more specimens, if they are found, in future studies.

The relationship between morphology and floral visitors is well-known (Benzing 1998), and although there are no specific data on the pollination syndrome of these three taxa, previous studies report that species with exerted stamens are mostly pollinated by hummingbirds (Carranza-Quiceno & Estévez-Varón 2008; Barfuss et al. 2016). Observations of hummingbirds visiting the flowers of *T. erubescens* var. *erubescens* were made, both in the field and in cultivation (Claudia Hornung-Leoni pers. obs.).

Geographic distribution and climatic variables

The two taxonomic entities recovered herein (i.e. *T. erubescens* and *T. arroyoensis*) showed non-overlapping geographic ranges. *T. erubescens* is widely distributed in SMOc, TMVB, BB, SMS, and in the southern part of the SMOr, while *T. arroyoensis* is restricted to the northern part of the SMOr province. The wide distribution of *T. erubescens* could be due to its epiphytic and epilithic lifestyle, which could have allowed it to colonize a wider variety of niches available in different types of vegetation, such as pine oak and oak forests, as well as xerophilous scrub. The exclusively epiphytic lifestyle of *T. arroyoensis*, together with its presence only in pine oak and oak forests, could be associated with its narrower geographic distribution (Granados Mendoza 2008).

According to the Mantel test, the precipitation distance matrix has a strong correlation with the dissimilarity matrix of morphology. This is, as the samples become more different in terms of precipitation, they also become more different in terms of morphology. It has been reported that within the microenvironmental conditions inherent to epiphytes, including the genus *Tillandsia*, the availability of water (which is taken in pulses during rainfall events, including mist and dew), is the environmental factor that most influences its distribution (Benzing 1998). This can cause displacements or even the disappearance of species in certain areas (Benzing 1998; Cach-Pérez et al. 2014). This could also explain the wide distribution of *T. erubescens*, which is distributed along the sites with the highest levels of precipitation. The morphology dissimilarity matrix also had a strong significant correlation with the geographic separation of the samples, that is, the more the samples were physically separated, the more the morphology of the specimens differed. This may be due to the fact that each group, even when it is present in similar climatic conditions, is immersed in a different niche, which could eventually favour the morphological differentiation between both species. In contrast, the species dissimilarity matrix did not have a significant correlation with the dissimilarity matrix of temperature or elevation. This suggests that, at least within the range in which these species are recorded, as temperature or elevation changes, the morphology does not necessarily change as well. This is consistent with the values obtained for temperature and elevation, which are similar in the species' distribution zones (17°C and from 1100 to 2900 m).

The remarkable environmental heterogeneity of the mountainous tropical forests of North and Central America, together with the complex climate history of these regions during the late Miocene and Pliocene, which included an increment in seasonality and aridity induced by a global cooling trend (Antonelli & Sanmartín 2011), could have promoted high rates of diversification of the subgenus *Tillandsia*, resulting in the current high richness of species present in this region (Granados Mendoza et al. 2017).

Previous studies have recovered *T. erubescens* and *T. arroyoensis* as sister species (Granados Mendoza et al. 2016). It could be hypothesized that their common ancestor was widely distributed and that climate changes during the Pleistocene could produce geographic isolation as a result of expansion, fragmentation, and divergence between its populations. This could eventually give rise to what we currently recognize as *T. erubescens* and *T. arroyoensis*. These kinds of speciation events have been reported to have occurred in different types of vegetation currently distributed in Mexico and North America (Graham 1999; Metcalfe et al. 2000), such as hummingbirds and flying squirrels inhabiting pine oak forest and mountain cloud forest (Kerhoulas & Arbogast 2010; Cavender-Bares et al. 2011; Ornelas et al. 2013, 2015). It should, however, be noted that this speciation hypothesis needs to be formally evaluated using, among other evidence, a dated phylogeny.

On the other hand, it has been proposed that the SMOr province is not a natural biogeographic unit and it could be divided into southern and northern portions. The southern part comprises crasicaule, microphyllous, and rosetophyllous

scrubland vegetation types (Salinas-Rodríguez et al. 2018) and is represented by several endemic species of mammals, birds, and cacti (León-Paniagua et al. 2004; Navarro et al. 2004; Del Conde Juárez et al. 2009). The northern part contains the highest mountains, with temperate forests dominated by oak, pine, and chaparral communities (Salinas-Rodríguez et al. 2018) and it is characterized by several taxa of coleopterans, mammals, reptiles, amphibians, and gymnosperms (Luna-Vega et al. 1999; Márquez & Morrone 2004; Medina-Romero 2009). The presence of *T. arroyoensis* in the north of the SMOc province supports the idea of this biogeographic division.

Although it is thought that the Bromeliaceae as a whole is not yet exposed to anthropic threats, some species have been systematically depleted since they are used indiscriminately by the human communities that inhabit the areas in which they are distributed (Espejo-Serna & López-Ferrari 2018). The correct delimitation of the species will allow a better estimation of the diversity of this group, its distribution area, and the problems that it is facing, as well as will promote studies or programs that address aspects of its conservation and sustainable use. Despite the fact that the advance in the floristic knowledge of this important family has been constant in recent years, more studies are required in groups as *Tillandsia* in which complexes of species of difficult delimitation and recognition are presented (Espejo-Serna & López-Ferrari 2018), indicating a morphological, ecological diversity, genetics, among others, that have not been yet sufficiently explored.

CONCLUSION

This study provides morphometric evidence for the recognition of two traditionally defined species within the green corollas clade of the *T. erubescens* group based on a set of quantitative characters. Through the use of linear morphometry, it was possible to recognize two species: *T. arroyoensis* and *T. erubescens*, from the three varieties originally proposed. The characters that enable them to be differentiated are the total size and the sheath and leaf blade (AVF, LVF, ALF, LLF) and the number of flowers. *T. erubescens* var. *erubescens* and *T. erubescens* var. *patentibracteata* are considered synonymous because no significant differences were found that would allow them to be separated. We conclude that precipitation and geographic distance play an important role in the morphological divergence between species. The distribution of *T. arroyoensis* and *T. erubescens* shows a geographic delimitation that divides the species and suggests that they are separated by geographic barriers; however, more studies are needed to explain the cause of this separation.

SUPPLEMENTARY FILE

Supplementary file 1 – Details of the 44 specimens used in the morphometric analysis.

<https://doi.org/10.5091/plecevo.84524.suppl>

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REFERENCES

- Antonelli A. & Sanmartín I. 2011. Why are there so many plant species in the Neotropics? *Taxon* 60(2): 403–414. <https://doi.org/10.1002/tax.602010>
- Barfuss M.H.J., Till W., Leme E.M.C., Pinzon J.P., Manzanares J.M. & Halbritter H. 2016. Taxonomic revision of Bromeliaceae subfam. Tillandsioideae based on a multi-locus DNA sequence phylogeny and morphology. *Phytotaxa* 279(1): 1–97. <https://doi.org/10.11646/phytotaxa.279.1.1>
- Benzing D.H. 1998. Vulnerabilities of tropical forest to climate change: the significance of resident epiphytes. *Climate Change* 39: 519–540.
- Cach-Pérez M.J., Andrade J.L. & Reyes-García C. 2014. La susceptibilidad de las bromeliáceas epífitas al cambio climático. *Botanical Sciences* 92(2): 157–168.
- Caputo P., Campo I. & De Luca P. 1996. Morphometric variation in *Lomelosia crenata* (Dipsacaceae). *Plant Systematics and Evolution* 201: 223–232. <https://doi.org/10.1007/BF00989063>
- Carranza-Quiceno J.A. & Estévez-Varón J.V. 2008. Ecología de la polinización de Bromeliaceae en el dosel de los bosques neotropicales de montaña. *Boletín Científico Museos de Historia Natural* 12: 38–47.
- Castello L.V. & Galetto L. 2013. How many taxa can be recognized within the complex *Tillandsia capillaris* (Bromeliaceae, Tillandsioideae)? Analysis of the available classifications using a multivariate approach. *PhytoKeys* 23: 25–39. <https://doi.org/10.3897/phytokeys.23.4507>
- Castillo-Batista A.P., Ponce-Saavedra J. & Montero-Castro J.C. 2017. Análisis morfométrico de *Cestrum guatemalense*, *C. mexicanum* y *C. pacayense* (Solanaceae). *Revista Mexicana de Biodiversidad* 88: 56–64. <https://doi.org/10.1016/j.rmb.2017.01.021>
- Cavender-Bares J., Gonzalez-Rodriguez A., Pahlich A., Koehler K. & Deacon N. 2011. Phylogeography and climatic niche evolution in live oaks (*Quercus* series *Virentes*) from the tropics to the temperate zone. *Journal of Biogeography* 38: 962–981. <https://doi.org/10.1111/j.1365-2699.2010.02451.x>

- Chew-Taracena T.L. 2010. Filogenia molecular y morfometría de las *Tillandsia* pseudobulbosas del subgénero *Tillandsia* (Tillandsioideae: Bromeliaceae). PhD thesis, Instituto de Ecología A.C., Mexico.
- CONABIO 2020. Sistema Nacional de Información sobre Biodiversidad. Registros de ejemplares. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Ciudad de México, México. Available from: <https://enciclovida.mx/especies/> [accessed 3 Mar. 2020].
- Costa A.F., Rodrigues P.J.F.P. & Wanderley M.G.L. 2009. Morphometric analysis and taxonomic revision of the *Vriesea paraibica* complex (Bromeliaceae). *Botanical Journal of the Linnean Society* 159: 163–181. <https://doi.org/10.1111/j.1095-8339.2008.00919.x>
- De la Estrella M., Aedo C. & Velayos M. 2009. A morphometric analysis of *Daniellia* (Fabaceae-Caesalpinioideae). *Botanical Journal of the Linnean Society* 159: 268–279. <http://doi.org/10.1111/j.1095-8339.2008.00894.x>
- De Luna E. 2020. Integrando análisis morfométricos y filogenéticos: de la sistemática fenética a la morfometría filogenética. *Acta Botánica Mexicana* 127: e1640. <https://doi.org/10.21829/abm127.2020.1640>
- Del Conde Juárez H., Contreras R. & Luna-Vega I. 2009. Biogeographic analysis of endemic cacti of the Sierra Madre Oriental, Mexico. *Biological Journal of the Linnean Society* 97: 373–389. <https://doi.org/10.1111/j.1095-8312.2009.01212.x>
- de Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology* 56: 879–886. <https://doi.org/10.1080/10635150701701083>
- DIVA-GIS Development Team 2021. DIVA –GIS A geographic information system for the analysis of species distribution data. Available from <https://www.diva-gis.org/> [accessed 28 June 2021].
- Egan A.N. 2015. Species delimitation and recognition in the *Pediomelum megalanthum* complex (Fabaceae) via multivariate morphometrics. *PhytoKeys* 44: 65–87. <https://doi.org/10.3897/phytokeys.44.8750>
- Espejo-Serna A. & López-Ferrari A.R. 2018. La familia Bromeliaceae en México. *Botanical Sciences* 96(3): 533–554. <https://doi.org/10.17129/botsoci.1918>
- Espejo-Serna A., López-Ferrari A.R., Ramírez-Morillo I., Holst BK., Luther H.E. & Till W. 2004. Checklist of Mexican Bromeliaceae with notes on species distribution and levels of endemism. *Selbyana* 25: 33–86.
- Faria A.P.G., Wendt T. & Brown G.K. 2010. A revision of *Aechmea* subgenus *Macrochordion* (Bromeliaceae) based on phenetic analyses of morphological variation. *Botanical Journal of the Linnean Society* 162: 1–27. <https://doi.org/10.1111/j.1095-8339.2009.01019.x>
- Fick S.E. & Hijmans R.J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37(12): 4302–4315. <https://doi.org/10.1002/joc.5086>
- Freudenstein J.V., Broe M.B., Folk R.A. & Sinn B.T. 2017. Biodiversity and the species concept – lineages are not enough. *Systematic Biology* 66: 644–656. <https://doi.org/10.1093/sysbio/syw098>
- Fritsch P.W., Schiller A.M. & Larson K.W. 2009. Taxonomic implications of morphological variation in *Cercis canadensis* (Fabaceae) from Mexico and adjacent parts of Texas. *Systematic Botany* 34: 510–520. <https://doi.org/10.1600/036364409789271254>
- Gage E. & Wilkin P. 2008. A morphometric study of species delimitation in *Sternbergia lutea* (Alliaceae, Amaryllidoideae) and its allies *S. sicula* and *S. greuteriana*. *Botanical Journal of the Linnean Society* 158: 460–469. <https://doi.org/10.1111/j.1095-8339.2008.00903.x>
- García-Cruz K.V. 2015. Variación morfológica de tricomas foliares en especies del género *Tillandsia* (Bromeliaceae) en Hidalgo, México. Bachelor degree thesis, Universidad Autónoma del Estado de Hidalgo, Mexico.
- Gardner C.S. 1986. Preliminary classification of *Tillandsia* based on floral characters. *Selbyana* 9(1): 130–146. <https://doi.org/10.15468/dl.888q6e>
- GBIF 2020. Global Biodiversity Information Facility. Available from <https://www.gbif.org/es/species/> [accessed 15 Feb. 2020].
- González-Rocha E., Castillo-Rivera M.A., López-Ferrari A.R. & Espejo-Serna A. 2018. A multivariate analysis of the *Pitcairnia palmeri* group (Bromeliaceae: Pitcairnioideae). *Phytotaxa* 351: 219–228. <https://doi.org/10.11646/phytotaxa.351.3.3>
- Google Earth 2020. Available from <https://www.google.com/earth/> [accessed 13 Apr. 2020].
- Graham A. 1999. Late Cretaceous and Cenozoic history of the North American vegetation (North of Mexico). Oxford University Press, Oxford.
- Granados Mendoza C. 2008. Sistemática del complejo *Tillandsia macdougallii* (Bromeliaceae). Master's thesis, Universidad Nacional Autónoma de México, Mexico.
- Granados Mendoza C., Salazar G.A. & Flores-Cruz M. 2016. A new species of the Mexican *Tillandsia erubescens* group (Bromeliaceae). *Phytotaxa* 260(1): 57–65. <https://doi.org/10.11646/phytotaxa.260.1.6>
- Granados Mendoza C., Granados-Aguilar X., Donadio S., et al. 2017. Geographic structure in two highly diverse lineages of *Tillandsia* (Bromeliaceae). *Botany* 95(7): 641–651. <https://doi.org/10.1139/cjb-2016-0250>
- Guarçoni E.A.E. & Costa A.F. 2017. The reestablishment of *Dyckia oligantha* and *D. nana* (Bromeliaceae, Pitcairnioideae), belonging to the *D. macedoi* complex. *Phytotaxa* 306(1): 49–65. <https://doi.org/10.11646/phytotaxa.306.1.4.49>
- Hodálová I. & Marhold K. 1998. Morphometric comparison of *Senecio germanicus* and *S. nemorensis* (Compositae) with a new species from Romania. *Botanical Journal of the Linnean Society* 128(3): 277–290. <https://doi.org/10.1111/j.1095-8339.1998.tb02122.x>
- INEGI 2021. Instituto Nacional de Estadística, Geografía e Informática. Climatología. Available from <https://www.inegi.org.mx/temas/climatologia/> [accessed 30 June 2021].
- Kerhoulas N.J. & Arbogast B.S. 2010. Molecular systematics and Pleistocene biogeography of mesoamerican flying squirrels. *Journal of Mammalogy* 91: 654–667. <https://doi.org/10.1644/09-MAMM-A-260.1>
- León-Paniagua L., García E., Arroyo-Cabrales J. & Castañeda-Rico S. 2004. Patrones biogeográficos de la mastofauna. In: Luna-Vega I., Morrone J.J. & Espinosa-Organista D. (eds) Biodiversidad de la Sierra Madre Oriental: 469–486. Las prensas de Ciencias, UNAM, México.
- Luna-Vega I., Alcántara-Ayala O., Espinosa-Organista D. & Morrone J.J. 1999. Historical relationships of the Mexican cloud forests: a preliminary vicariance model applying parsimony analysis of endemism to vascular plant taxa. *Journal of Biogeography* 26: 1299–1305. <https://doi.org/10.1046/j.1365-2699.1999.00361.x>

- Marhold K. 1996. Multivariate morphometric study of the *Cardamine pratensis* group (Cruciferae) in the Carpathian and Pannonian area. *Plant Systematics and Evolution* 200(3/4): 141–159.
- Márquez J. & Morrone J.J. 2004. Relaciones biogeográficas basadas en la distribución de Coleoptera (Insecta). In: Luna I., Morrone J.J. & Espinosa-Organista D. (eds) Biodiversidad de la Sierra Madre Oriental: 375–392. Las Prensas de Ciencias, UNAM, México
- Mascarenhas I., Silveira L. & Paganucci L. 2014. Morphological analyses suggest a new taxonomic circumscription for *Hymenaea courbaril* L. (Leguminosae, Caesalpinioideae). *PhytoKeys* 38: 101–118. <https://doi.org/10.3897/phytokeys.38.7408>
- McGarigal K., Cushman S. & Stafford S. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York. <https://doi.org/10.1007/978-1-4612-1288-1>
- Medina-Romero M.A. 2009. Regionalización biogeográfica de la Sierra Madre Oriental. Master's thesis, Universidad Autónoma del Estado de Hidalgo, Mexico.
- Menini Nieto L., van den Berg C. & Forzza R.C. 2019. Linear and geometric morphometrics as tools to resolve species circumscription in the *Pseudolaelia velozicola* complex (Orchidaceae, Laeliinae). *Plant Ecology and Evolution* 152(1): 53–67. <https://doi.org/10.5091/plecevo.2019.1531>
- Metcalf S.E., O'Hara S.L., Caballero M. & Davies S.J. 2000. Records of late Pleistocene-Holocene climatic change in Mexico a review. *Quaternary Science Reviews* 19: 699–721. [https://doi.org/10.1016/s0277-3791\(99\)00022-0](https://doi.org/10.1016/s0277-3791(99)00022-0)
- Morrone J.J., Escalante T. & Rodríguez-Tapia G. 2017. Mexican biogeographic provinces: map and shapefiles. *Zootaxa* 4277(2): 277–279. <https://doi.org/10.11646/zootaxa.4277.2.8>
- Navarro A.G., Garza-Torres H.A., López de Aquino S., Rojas-Soto O.R. & Sánchez-González L.A. 2004. Patrones biogeográficos de la avifauna. In: Luna-Vega I., Morrone J.J. & Espinosa-Organista D. (eds) Biodiversidad de la Sierra Madre Oriental: 439–467. Las prensas de Ciencias, UNAM, México.
- Neves B., Uribe F.P., Jacques S.S.A., Zanella C.M. & Costa A.F. 2018. Species boundaries in the *Vriesea incurvata* (Bromeliaceae) complex after a broad morphometric and taxonomic study. *Systematic Botany* 43(4): 870–888. <https://doi.org/10.1600/036364418X697670>
- Oksanen J., Blanchet F.G., Friendly M., et al. 2020. Vegan community ecology package version 2.5-7, November 2020. Available from <https://cran.r-project.org/web/packages/vegan/> [accessed 3 Jul. 2021].
- Ornelas J.F., Sosa V., Soltis D.E., et al. 2013. Comparative phylogeographic analyses illustrate the complex evolutionary history of threatened cloud forest of Northern Mesoamerica. *PLoS ONE* 8(2): 1–11. <https://doi.org/10.1371/journal.pone.0056283>
- Ornelas J.F., González de León S., González C., Licona-Vera Y., Ortiz-Rodríguez A.E. & Rodríguez-Gómez F. 2015. Comparative palaeodistribution of eight hummingbird species reveal a link between genetic diversity and Quaternary habitat and climate stability in Mexico. *Folia Zoologica* 64:245–258. <https://doi.org/10.25225/fozo.v64.i3.a6.2015>
- Orozco C.I. 1991. Análisis multivariado del complejo de tres especies de *Brunellia* (Brunelliaceae). *Annals of the Missouri Botanical Garden* 78: 970–994.
- Otieno D.F., Balkwill K. & Paton A.J. 2006. A multivariate analysis of morphological variation in the *Hemizygia bracteosa* complex (Lamiaceae, Ocimeae). *Plant Systematic and Evolution* 261: 19–38. <https://doi.org/10.1007/s00606-006-0429-6>
- Pedersen H.Æ. 2010. Species delimitation and recognition in the *Brachycorythis helferi* complex (Orchidaceae) resolved by multivariate morphometric analysis. *Botanical Journal of the Linnean Society* 162: 64–76. <https://doi.org/10.1111/j.1095-8339.2009.01015.x>
- Pinheiro F., Dantas-queiroz M.V. & Palma-Silva C. 2018. Plant species complexes as models to understand speciation and evolution: a review of South American studies. *Critical Reviews in Plant Sciences* 37: 54–80. <https://doi.org/10.1080/07352689.2018.1471565>
- Pinzón J.P., Ramírez-Morillo I.M. & Fernández-Concha G.C. 2011. Morphometric analyses within the *Tillandsia utriculata* L. complex (Bromeliaceae) allow for the recognition of a new species, with notes on its phylogenetic position. *The Journal of the Torrey Botanical Society* 138: 353–365. <https://doi.org/10.2307/41475102>
- Ponsie M.E., Johnson S.D. & Edwards T.J. 2009. A morphometric analysis of the *Bonatea speciosa* complex (Orchidaceae) and its implications for species boundaries. *Nordic Journal of Botany* 27: 166–177. <https://doi.org/10.1111/j.1756-1051.2008.0a0259>
- QGIS Development Team 2020. QGIS Geographic Information System. Open Source Geospatial Foundation. Available from <http://qgis.osgeo.org> [accessed 22 July 2020].
- R Core Team 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from <https://www.R-project.org> [accessed 1 Jul. 2021].
- Rohlf J. 2018. TpsDig2. Available from <https://life.bio.sunysb.edu/morph/soft-dataacq.html> [accessed 19 Aug. 2019].
- Salinas-Rodríguez M.M., Sajama M.J., Gutiérrez-Ortega J.S., Ortega-Baes P. & Estrada-Castillón A.E. 2018. Identification of endemic vascular plant species hotspots and the effectiveness of the protected areas for their conservation in Sierra Madre Oriental, Mexico. *Journal for Nature Conservation* 46: 6–27. <https://doi.org/10.1016/j.jnc.2018.08.012>
- Schlechtendal D.F.L. 1844 [1845]. *Plantae Leiboldianae. Monocotyleae Reliquae. Linnaea* 18: 410–456.
- StatSoft Inc. 2004. STATISTICA (data analysis software system) version 7.0. Available from <https://www.statsoft.com> [accessed 15 Jan. 2020].
- Thiers B. continuously updated. Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available from <http://sweetgum.nybg.org/science/ih> [accessed 12 Oct 2020].
- Uribe F.P., Neves B., Jacques S.S.A. & Costa A.F. 2020. Morphological variation in the *Vriesea procera* complex (Bromeliaceae, Tillandsioideae) in the Brazilian Atlantic Rainforest, with recognition of new taxa. *Systematic Botany* 45(1): 53–68. <https://doi.org/10.1600/036364420X15801369352306>
- Weber W. 1983. Species novae Bromeliacearum IV. *Feddes Repertorium* 94: 604–607.

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