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RESEARCH ARTICLE

Vegetative morphological variation in *Chamaedorea elatior* (Arecaceae), a first approach at species delimitation

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Abstract

Background and aims – *Chamaedorea* is the largest genus of neotropical palms distributed mainly in lowland rainforests and montane cloud forests from Mexico to Bolivia. Species delimitation in this genus remains problematic due to high morphological variation and inconsistent taxonomic treatment of such variation. *Chamaedorea elatior*, a climbing species from southern Mexico and northern Central America, exemplifies these challenges with several historical synonyms and informally recognized morphotypes. This study evaluates the morphological variation in vegetative characters between this species' most characteristic two morphotypes, cespitose and solitary, to evaluate their taxonomic distinctiveness.
Material and methods – Six populations of *C. elatior* were sampled in Mexico and Guatemala, representing both solitary and cespitose morphotypes. Thirteen morphological leaf characters were measured from mature individuals. Data were examined using univariate and multivariate analyses (NMDS, *k*-means clustering, PCA, MANOVA, LDA) to evaluate morphological variation between the morphotypes and populations. Discriminant analyses were also used to assess classification into either morphotype.
Key results – Univariate analyses revealed significant differences between morphotypes in most measured characters, mainly those associated with leaf size. Similarity analyses recovered both morphotypes as being distinct from each other. PCA showed notable separation of the morphotypes along the first component that summarized leaf and median leaflet size. Both MANOVA and LDA confirmed significant differences between morphotypes and resulted in high accuracy classification.
Conclusion – Leaf morphology clearly distinguishes the solitary and cespitose morphotypes of *C. elatior*, supporting their potential delimitation as separate species. The branching habit of the cespitose form further reinforces this distinction. While current results support species-level recognition, additional evidence from reproductive characters, niche, and genetic divergence is recommended to confirm a possible species delimitation.

Keywords

climbing palm, Guatemala, Mexico, morphometrics, systematics

INTRODUCTION

Chamaedorea Willd. is the largest genus of neotropical palms, with around 106 species (POWO 2025). It consists of dioecious, mainly small understory palms with either pinnate or bifid leaves, and solitary flowers in all but three species (Hodel 1992). They occur mostly in rainforests and montane cloud forests, ranging from sea level to

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almost 3,000 m a.s.l. (Hodel 1992; Dransfield et al. 2008). Two centres of diversity for the genus have been proposed based on the vast assortment of species in these areas: the mountainous regions of southern Mexico and Guatemala, and Costa Rica and Panama (Hodel 1992).

Various phylogenetic hypotheses have been proposed at the species level in *Chamaedorea*, expanding our understanding of its interspecific relationships and broad biogeographical history (Thomas et al. 2006; Cuenca and Asmussen-Lange 2007; Cuenca et al. 2008; Cano et al. 2022). However, the considerable variation both between and within species has not been studied in detail, and research on species limits within the genus is lacking (Hodel 1999; Dransfield et al. 2008). This has led to two separate scenarios regarding the same variation problem: a) a high number of synonymies are found within species due to names published based on small differences in local forms and their intermediates; or b) species which notable morphological variation has not been properly recognized beyond informal forms or varieties.

Species delimitation and variation between similar species and species complexes have been studied previously in other palm genera. Traditional morphometric analyses have been used with positive results in the delimitation of taxa (Henderson 2006; Laubengayer et al. 2012; Santos-Hernández et al. 2022). Conversely, in highly variable species complexes, species limits could not be resolved with good fidelity using morphometric data (Borchsenius 1999; Atria et al. 2017). Fewer studies have integrated multiple lines of evidence, mainly morphological, genetic and sometimes environmental data, with varied results (Bacon et al. 2012, 2016; Atria et al. 2020). Despite the recognized variation between and within *Chamaedorea* species, few studies have explored species limits in this genus. Bacon and Bailey (2006) delimited two similar species, *C. tepejilote* Liebm. and *C. alternans* H.Wendl., based on microsatellite data complemented by morphological differences. In his undergraduate thesis, Ruíz-Castillejos (2011) delimited similar looking *C. glaucifolia* H.Wendl. and *C. plumosa* Hodel using morphometric analyses of the leaves. Another study using morphometry on the leaf, yet unpublished, segregated *C. tenella* H.Wendl. and *C. geonomiformis* H.Wendl. (Pérez-Farrera unpubl. data).

A notable example of a high number of historical synonyms and a lack of formal recognition of varieties or forms is *C. elatior* Mart. This climbing species occurs mainly in lowland tropical humid forests along the Atlantic slope of southern Mexico, Guatemala, and Honduras. It is less commonly found at higher elevations in montane cloud forests of the Sierra Madre Oriental in Mexico (Fig. 1). At least five other species names and varieties have been synonymized under it (Hodel 1992; Dowe and Hodel 2021). Most of these names were initially published based on variations in leaf size (Martius 1849; Wendland 1853; Dammer 1905) or habit differences (Dammer 1905; Gérôme 1911).

The variation in this species was previously summarized in four informally recognized forms by Hodel (2013): 1) the most common form, a solitary palm with deeply bifid juvenile leaves and adult pinnate leaves with strongly reflexed apical leaflets that help it attain a robust climbing habit; 2) a cespitose form with aerial branching stems, pinnate juvenile and mature leaves, and a weaker climbing habit; 3) another solitary form with pinnate juvenile and mature leaves characterized by their narrow, linear leaflets; and 4) a variant of the first solitary form, with larger bifid blades retained a few years into maturity but that eventually produces its typical pinnate leaves. The distribution and habitat of these forms are also distinct

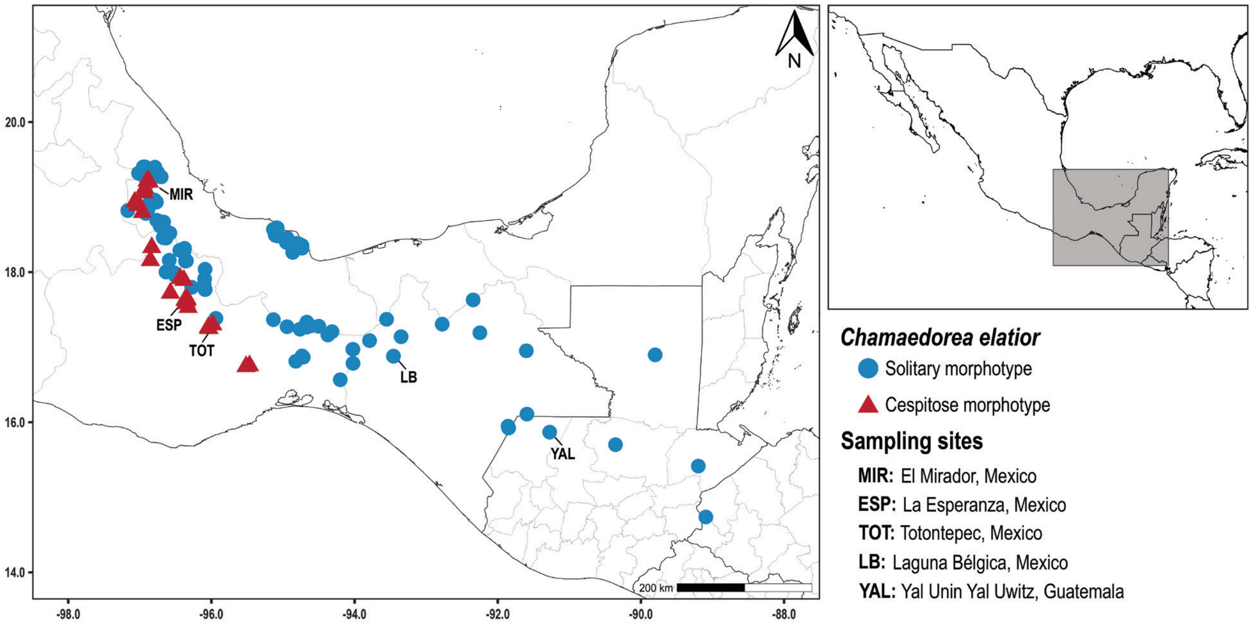

Figure 1. Geographic distribution and sampling sites of *Chamaedorea elatior*. Points represent distribution of herbarium specimens from Villar-Morales (2020) and GBIF data.

Table 1. Forms of *Chamaedorea elatior* according to Hodel (2013) and Pérez-Farrera et al. (2021). * Probably based on the area described in Hodel (2013).

	(1) Solitary form	(2) Cespitose form	(3) *Chamaedorea tacanensis*	(4) Solitary with early flowering
Habit	Solitary	Cespitose, branching	Solitary	Solitary
Juvenile leaves	Bifid	Pinnate	Pinnate	Bifid
Mature leaves (after flowering)	Pinnate	Pinnate	Pinnate	Bifid, then pinnate
Habitat	Lowland rainforest	Montane cloud forest	Montane cloud forest	Lowland rainforest
Elevation (m a.s.l.)	50–1,200	1,000–1,900	1,200–1,900	below 600*
Distribution	Atlantic slope of Guatemala, Honduras, Mexico	Atlantic slope of Mexico	Pacific slope of Guatemala and Mexico	Atlantic slope of Mexico

between them (Table 1). The third form would eventually be segregated as a distinct species, *C. tacanensis* Pérez-Farr., Villar-Mor. & Hodel, based on morphological and genetic characteristics (Pérez-Farrera et al. 2021).

Dowe and Hodel (2021) proposed that the various forms of *C. elatior* could be elevated to formal taxonomical status given proper research. The delimitation and recognition of *C. tacanensis* proved this point and added to the ongoing discussion of species limits within *Chamaedorea*, especially in *C. elatior*. With now two climbing species in the genus that resemble each other superficially, a reassessment of the variation within *C. elatior* is desirable. Following the publication of *C. tacanensis*, Hodel's (2013) forms of *C. elatior* were reduced to three. However, for this study, we compared only two of these forms based on habit differences: solitary and cespitose (Fig. 2). The recognition of the remaining form, characterized by its early flowering, will be discussed further below. This study aims to evaluate the vegetative morphological variation between these two most well-known forms, or morphotypes, of *C. elatior*, and determine whether there is sufficient variation to delimit these as distinct species.

MATERIAL AND METHODS

Species distribution

Presence points of *C. elatior* in Mexico were taken from the compiled and revised database of herbarium material from Villar-Morales (2020). Central American distribution in Guatemala and Honduras was obtained from the Global Biodiversity Information Facility (GBIF 2024). The total distribution map was visualized in R v.4.3.1 (R Core Team 2024).

Sampling

We sampled six populations of *C. elatior* in five localities from Mexico and Guatemala corresponding to both solitary and cespitose morphotypes (Fig. 1; Suppl. material 1). A single locality, El Mirador, Veracruz,

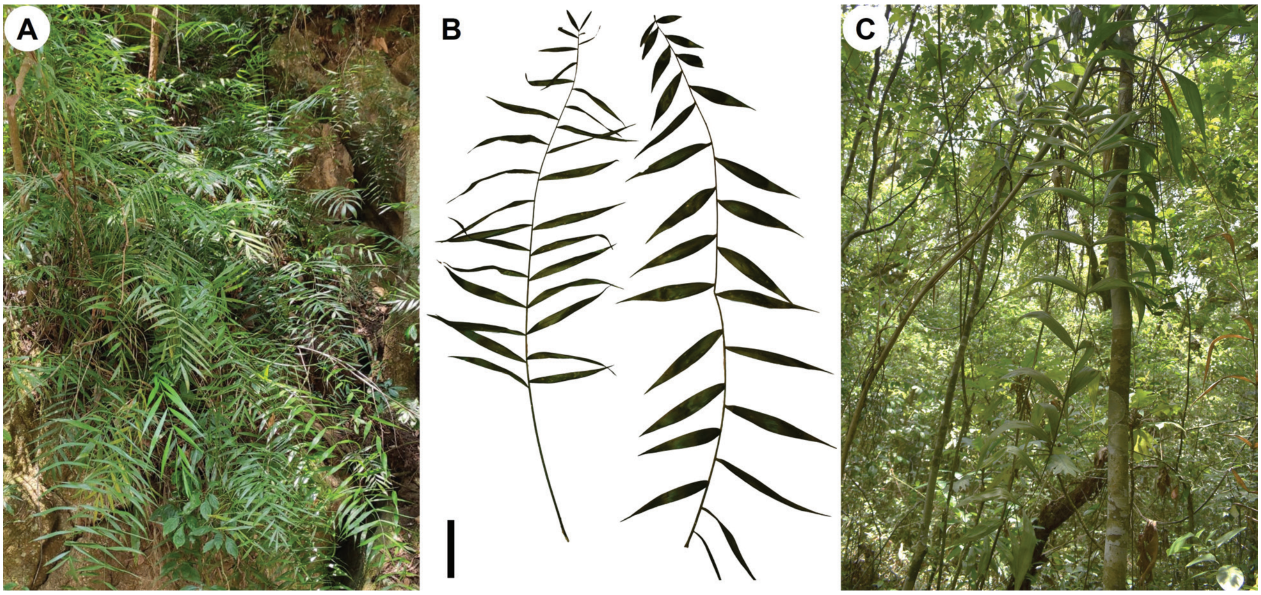

Figure 2. *Chamaedorea elatior* morphotypes. **A**. Cespitose morphotype. **B**. Leaves of cespitose (left) and solitary (right) morphotypes. Scale bar = 10 cm. **C**. Solitary morphotype. Photographs by María Fernanda Martínez Velarde (A) and Diego Villar-Morales (C).

Mexico had both morphotypes growing in syntopy, while in the others only one of them was found. Morphotypes were recognized and assigned on the field by their habit, either solitary or cespitose with above-ground branching. We collected leaves from different individuals, with an average of 10 plants sampled per population. Leaves of *C. elatior* show significant morphological changes as the plant grows and acquires its scandent habit as an adult (Standley and Steyermark 1958). The typical, reflexed apical leaflets are seen in mature individuals with fully pinnate leaves, and as such only these leaves were sampled to avoid variation regarding the age of the individuals and leaf maturity as much as possible.

To avoid confusion, we have used the term "morphotype" in contrast to "form" used by previous authors (Hodel 2013; Dowe and Hodel 2021). We consider this term to reflect better the framework of this study since sampling and evaluations were based on morphological, specifically habit, differences. Our cespitose morphotype corresponds to the previously mentioned cespitose form and our solitary morphotype would compare to the first solitary form of Hodel (2013). Although we were unable to visit the locality of the remaining solitary form described by Hodel (2013) from the isthmus of Tehuantepec, we consider it to be a rare, local variant of our solitary morphotype for a number of reasons that will be discussed afterwards. Field exploration in the area where this form inhabits has been made problematic due to recent fires and an uprise in violence.

We could not consistently find reproductive structures, either inflorescences or infructescences, during the sampling field trips. Most solitary plants had already lost their male inflorescences or were in advanced state of decomposition to properly measure them, while only a few individuals in some populations had immature fruits. Similarly, we did not observe measurable flowering and fruiting structures in the cespitose populations, except for very few fruiting plants in La Esperanza. As a result, due to the small and inconsistent sample size comparative statistical analyses could not be performed with reproductive characters.

Morphometric analyses

To evaluate the morphological variation among populations and morphotypes, we measured 13 morphological characters from the leaves, most of which have been used in previous studies (Atria et al. 2017; Santos-Hernández et al. 2022): petiole length (PL), petiole width (PW), rachis length (RL), width of the rachis at its middle length (mRW), width of the rachis between the most distal leaflets (aRW), leaflet number on one side of the rachis (LN), basal leaflet length (bLL), basal leaflet width (bLW), basal leaflet insertion length (bLI), median leaflet length (mLL), median leaflet width (mLW), median leaflet insertion length (mLI), and distance between median leaflets (mLD). All variables were log-10 transformed before the analyses. All statistical analyses were performed in R v.4.3.1 (R Core Team 2024) using RStudio v.2023.12.1 (RStudio Team 2023).

Univariate methods were used to study the variation between both morphotypes. Student's t-test was performed for all characters considering both morphotypes using the stats base package in R. For a multivariate approach using *Q*-type analyses, we first explored the structure of the data and summarized its variation by applying a non-metric multidimensional Scaling (NMDS) on a distance matrix obtained with the Euclidean measure. Clustering of the data was also analysed via a non-hierarchical *k*-means cluster analysis which does not form nested clusters iteratively as in hierarchical clustering, instead finding all clusters simultaneously as partitions of the data (Jain 2010). To assess the optimal number of clusters, we used the Calinski-Harabasz index (Caliński and Harabasz 1974). Both NMDS and *k*-means cluster analyses were done using the R package vegan v.2.6-8 (Oksanen et al. 2024).

Under a *R*-type multivariate approach, we first examined all variable's contribution to total variance in a simplified manner with a Principal Component Analysis (PCA). Components with eigenvalues greater than 1.0 were extracted and plotted in a scatterplot. A priori grouping (solitary vs cespitose morphotypes) was first evaluated with a MANOVA to assess differences in group centroids. We calculated the partial eta-squared measure (η^2) to quantify the effect of the morphotype on the variance of the leaf characters, using the R package effectsize v.1.0.0 (Ben-Shachar et al. 2024).

We then used a Linear Discriminant Analysis (LDA) to further test differences in the morphotype grouping and find the variables with the higher discrimination power. Our a priori classification of the individuals was evaluated using the confusion matrices produced by this analysis, testing its accuracy without cross-validation and with cross-validation via two methods: jack-knifing and Monte Carlo (1,000 repeats using 40% of the data as test). LDA and jack-knife cross-validation was done with the R package MASS v.7.3-60 (Ripley et al. 2024), while Monte Carlo cross-validation was done with the R package caret v.7.0-1 (Khun et al. 2024). Additionally, we repeated the discriminant analysis with population grouping as to compare its results with the morphotype grouping. The same evaluation of the accuracy via confusion matrices was done as in the previous grouping.

RESULTS

According to the univariate analyses between groups, there were highly significant differences ($p < 0.001$) in almost all variables among both morphotypes of *C. elatior* (Suppl. material 2). The only characters with lower or no significance correspond to the basal leaflets: insertion (bLI; $p < 0.01$) and length and width (bLL and bLW, respectively; both $p > 0.1$) (Suppl. material 2). Based on the significant differences, the solitary morphotype can be distinguished from the cespitose by having longer

Table 2. MANOVA results using different statistics.

Morphotype	Value	Approx F	p
Pillai's Trace	0.872	24.11	**< 0.001**
Wilks' Lambda	0.128	24.11	**< 0.001**
Hotelling-Lawley Trace	6.814	24.11	**< 0.001**
Roy's Largest Root	6.814	24.11	**< 0.001**

leaves (RL), thicker axes (PW, mRW, aRW), larger leaflet insertions (bLI, mLI), and larger median leaflets with longer distance between them (mLL, mLW, mLD) but shorter petioles (PL).

On the NMDS plot most specimens gathered in two more or less defined groups along the horizontal axis: most cespitose individuals are found on the left of the axis, whereas almost all solitary individuals are on the right of the axis (Fig. 3A). About half of the specimens from Totontepec (cespitose) form a small cluster located between the two large groups and even located on the right side of the horizontal axis, suggesting certain similarity with solitary individuals rather than to other cespitose ones. Individuals from El Mirador grouped together according to their morphotype, not the locality. *K*-means clustering resulted in an optimal number of groups (*k*) of two (highest C-H index: 43.56). These two groups correspond mostly to the a priori assigned morphotypes, the only exceptions being certain specimens in the cespitose populations of La Esperanza (2 individuals) and Totontepec (5 individuals) that were grouped with the solitary individuals (Fig. 3B). All previously assigned solitary individuals were grouped together. As in the NMDS, El Mirador plants were clearly separated according to their morphotype.

The PCA showed that the first five principal components explained 91% of the variation in the data (PC1: 58.1%, PC2: 18.2%, PC3: 6.4%, PC4: 5.1%, PC%: 3.2%). We show only the components with an eigenvalue higher than 1.0, being that the first (7.56) and the second (2.37). The variables with the highest contribution to the PC1 were those concerned with the overall size of the leaf and median leaflets: rachis length (RL), petiole width (PW), and median leaflet length (mLL) and width (mLW). For PC2, the variables with the highest contribution were leaflet number (LN) and the ones measured from the basal leaflets: length (bLL), width (bLW), and insertion (bLI) (Suppl. material 3A). In a scatterplot of the first two principal components (Fig. 4), individuals of each morphotype are distributed on different sides along the first component axis with certain overlap occurring between the cespitose Totontepec population and solitary populations. Specimens from the same population group together with varying degrees of overlap happening within the same morphotype. As with the previous *Q*-type analyses, the individuals from El Mirador are clearly separated from each other according to their morphotype.

Significant differences between morphotypes with all variables measured were found by the MANOVA analysis ($p < 0.001$; Table 2). The proportion of total variance explained by the grouping is high ($\eta^2 = 0.87$), suggesting that morphotype differences account for most of the variation in the leaf characters.

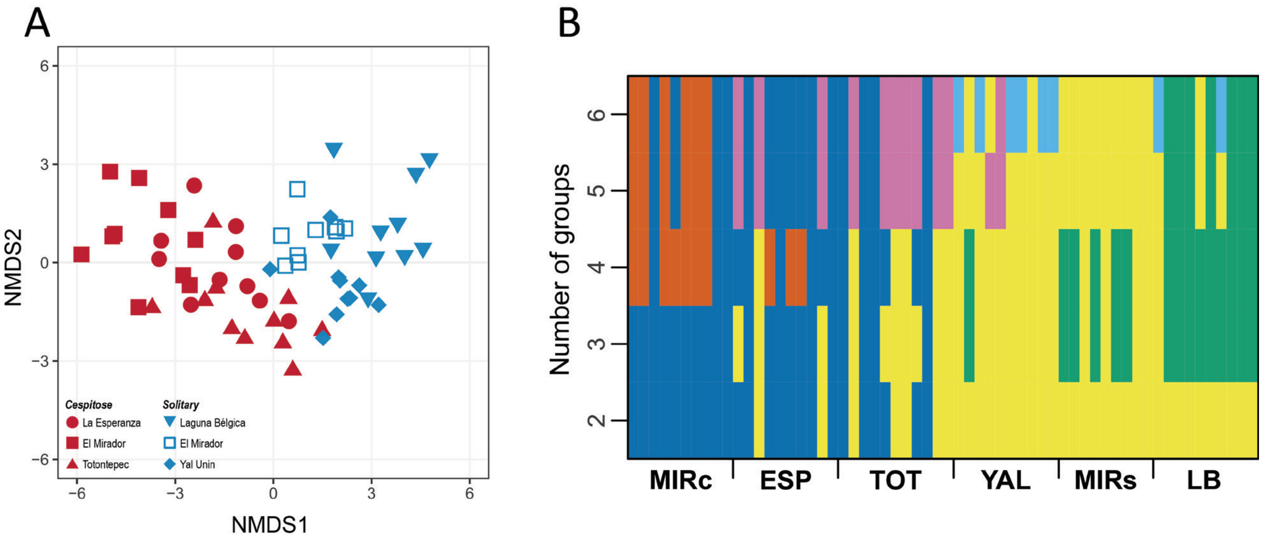

Figure 3. *Q*-type analyses plots. **A**. NMDS plot using Euclidean dissimilarity. **B**. *K*-means cluster analysis for various groups (*k* = 2–6). Populations are shown on the horizontal axis; each bar corresponds to a measured individual. Abbreviations of populations correspond to Fig. 1 and Suppl. material 1.

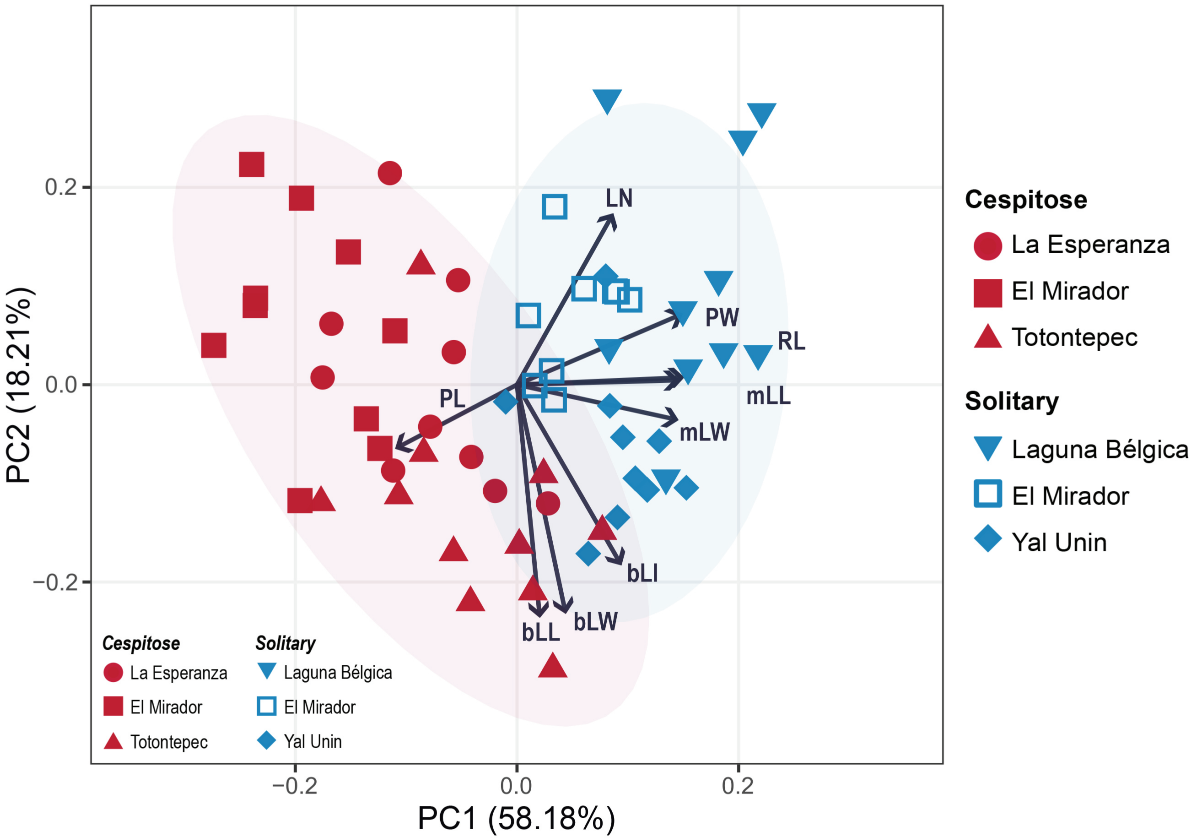

Figure 4. PCA biplot of first two principal components. Abbreviations of variables are explained in the text.

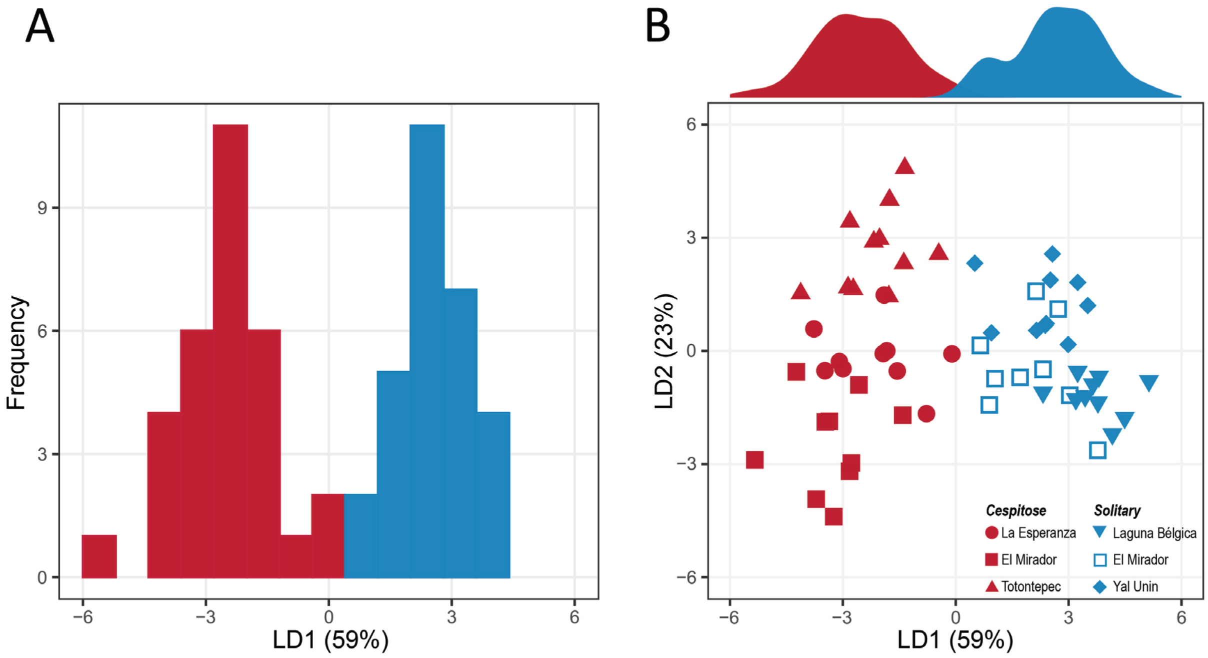

Figure 5. Linear discriminant analysis plots. **A**. Considering morphotype grouping. **B**. Considering population grouping.

Table 3. Confusion matrix obtained from discriminant analyses when considering morphotype grouping. Rows indicate assigned individuals and columns predictions. Numbers shown for each assignation correspond to non-cross-validated LDA, jack-knife validated LDA, and Monte Carlo validated LDA, respectively. Monte Carlo cross-validation numbers are shown in average. Highest numbers are shown in bold.

	Cespitose	**Solitary**
Cespitose	**31 / 29 / 29.4**	0 / 2 / 1.9
Solitary	0 / 1 / 1.4	**29 / 28 / 27.2**

Table 4. Confusion matrix obtained from discriminant analyses when considering population grouping. Rows indicate assigned individuals and columns predictions. Abbreviations of populations correspond to Fig. 1 and Suppl. material 1. Numbers correspond to non-cross-validated, jack-knife validated, and Monte Carlo validated LDA, respectively. Monte Carlo cross-validation numbers are shown in average. Highest numbers are shown in bold.

	MIR-C	**ESP**	**TOT**	**MIR-S**	**LB**	**YAL**
MIR-C	**9 / 8 / 6.6**	1 / 1 / 2.1	0 / 0 / 0.5	0 / 1 / 0.7	0 / 0 / 0	0 / 0 / 0.1
ESP	0 / 2 / 2	**10 / 6 / 5.6**	0 / 1 / 1.5	0 / 1 / 0.6	0 / 0 / 0.1	0 / 0 / 0.2
TOT	0 / 0 / 0.1	1 / 3 / 2.6	**10 / 8 / 8.1**	0 / 0 / 0	0 / 0 / 0.1	0 / 0 / 0.1
MIR-S	0 / 0 / 0.1	0 / 0 / 0.2	0 / 0 / 0.1	**8 / 5 / 5.2**	0 / 1 / 1.0	1 / 3 / 2.4
LB	0 / 0 / 0	0 / 0 / 0.1	0 / 0 / 0	0 / 1 / 1.3	**10 / 8 / 7.7**	0 / 1 / 1
YAL	0 / 0 / 0	0 / 0 / 0.3	0 / 1 / 0.6	0 / 1 / 1.9	0 / 1 / 1	**10 / 7 / 6.3**

Table 5. Best characters at discriminating between morphotypes according to statistical analysis. Character abbreviations as in Material and methods.

Analysis	**Best discriminating characters**
t-student test	All except bLI, bLL, and bLW
LDA (morphotypes)	RL, PW, mRW
LDA (populations)	RL, PW, mRW

In the LDA analysis considering the two morphotypes, the highest discrimination was given by rachis length (RL), petiole width (PW), and median rachis width (mRW), all characters associated with leaf size (Suppl. material 3B). The specimens form two groups clearly separated from each other (Fig. 5A). Although a single cespitose specimen from El Mirador graphically appears separated from the rest of its group, this was attributed to its rather short and thin rachis compared to the rest. Regarding classification, specimens were classified correctly to their a priori assigned morphotype in the discriminatory analyses with high accuracy (LDA: 100%, jack-knife LDA: 95%, MC-LDA: 94%) (Table 3).

Considering the six populations, the LDA's first dimension accounted for 59% of the total variance, the second 23%, and the third 11%, amounting to more than 90% of it. The variables with the highest discrimination coefficient along the first dimension are the same as for the LDA between morphotypes (RL, PW, mRW), while leaflet number (LN), petiole width (PW), and median leaflet width (mLW) had the highest coefficients along LD2 (Suppl. material 3C). The scatterplot of the first two linear discriminants shows distinct clusters corresponding to the morphotypes along the first axis, with overlap between corresponding morphotype populations (Fig. 5B). Cespitose populations show a higher degree of separation along the second axis in comparison with the solitary populations, the coefficients indicating that specimens from El Mirador have thinner petioles and less, narrower leaflets than those from La Esperanza and especially Totontepec. Although this variation is noteworthy to mention, the separation between morphotypes explains more of the variance, as inferred by the dimensions (59% vs 23%).

When considering populations rather than morphotypes, individuals were mostly classified to their own population, followed by classification to other populations of the same morphotype (Table 4). In only very few cases in the cross-validated analyses specimens were classified to a different morphotype population, mostly two cespitose individuals were predicted to belong to a solitary population, and one solitary specimen predicted in a cespitose population. Notably, no specimens from Totontepec were predicted to belong to solitary populations. The accuracy of the classification among populations varied between methods (LDA: 95%, jack-knife LDA: 70%, MC-LDA: 65.8%).

DISCUSSION

Vegetative morphological delimitation

All but two of the analysed morphological characters of leaves showed significant differences between the solitary and cespitose morphotypes of *C. elatior*, and both morphotypes were significantly distinct when all variables were compared in the MANOVA analysis. In the similarity and ordination analyses, the morphotypes could be distinguished separately with only minor overlap between them. Specimens were classified to their previously assigned morphotype with high accuracy in the discriminant analyses. If populations were considered for the discriminant analyses instead of morphotypes, the classification still separated the latter with high accuracy. The variables that most distinguish between morphotypes are related to the overall size and robustness of the leaves (Table 5), with the solitary form's being larger with bigger leaflets and longer insertions to the rachis. The cespitose morphotype, though smaller in leaves and leaflets, has longer petioles.

Certain morphological overlap was observed, mainly between some cespitose Totontepec and solitary specimens, both in the similarity analyses (NMDS and *k*-means clustering) and in the PCA. According to our raw data and the PCA coefficients, leaves of Totontepec specimens were the most robust and with the largest leaflets within the cespitose populations, but not so as in the solitary populations. This would explain their similarity with solitary specimens and their resulting position and clustering in the *Q*-type analyses. The discriminant analyses, however, group this population clearly with the other cespitose ones.

The most striking character used to recognize morphotypes in the field, the branching of the cespitose morphotype, was not considered in the analyses because of its lack of variance and evident segregation power. Mature individuals of the cespitose morphotype can produce branches well above ground, one on every other node, forming a dense clump above the ground and nearby smaller vegetation. No other *Chamaedorea* species are known to produce proper aerial branches, other cespitose (clustering) species form new stems (branches) from buds on proximal nodes below or just above the ground (Fisher 1974; Hodel 1992). Nevertheless, much work is still needed in characterizing the branching of many palm species.

The only other species in the genus known to also present a solitary and cespitose habit is *C. tepejilote*; however, the variation in this species has been associated to its cultivation history, the solitary habit a result of domestication (Castillo Mont et al. 2017). Although *C. elatior* is used in some areas in Mexico for handcrafting or as ornamental, its extraction is irregular, and no serious domestication effort has been recognized (Contreras Cortés et al. 2018; Rendón-Aguilar et al. 2022). Considering this, the presence of two habits in *C. elatior* does not seem to be a consequence of cultivation nor related to human activity. In view of the uniqueness of its branching habit, and pending proper development studies, this difference should be considered an important character that could enhance species delimitation of both morphotypes.

Chamaedorea elatior's morphotypes are also segregated geographically and possibly ecologically (Table 1). According to previous knowledge and herbaria records, the solitary morphotype inhabits lowland tropical humid forests usually below 800 m a.s.l., with some populations extending up to about 1,200 m. In contrast, the cespitose morphotype is found in tropical montane cloud forests from 1,000 to 1,900 m a.s.l. (Hodel 2013; Villar-Morales 2020). In certain localities in Oaxaca and Veracruz, Mexico, the solitary morphotype can be found in tropical forests on the foot of the mountains and lowlands extending beyond, while the cespitose morphotype has been registered a few hundred meters uphill in montane forests on the slopes of the mountains. Though geographically very near, the difference in altitude and thus vegetation is notorious.

El Mirador is the only locality to our knowledge where both morphotypes have been found living in syntopy. Their coexistence in this site has been registered historically, as we located specimens collected by Liebmann in the 1840s (at C herbarium) corresponding to both morphotypes in the same area. This locality is geographically near the species's northern limit, and only very few populations of both morphotypes are known to exist beyond it. Furthermore, El Mirador is on the upper boundaries of altitudinal range of the solitary morphotype and on the lower range of the cespitose one. This could explain their presence in this area, probably being a contact zone where both morphotypes can inhabit given the proper altitudinal range for each of them. The vegetation type there has been registered in diverse collected specimens as montane cloud forest (or synonyms sensu Gual-Díaz and González-Medrano 2014) though it is at a lower altitude and less dense and humid as the others sampled here in La Esperanza and Totontepec. Although montane cloud forests are variable in environmental characteristics and composition (Gual-Díaz and González-Medrano 2014), a proper compositional and ecological study of the site could lead to a better understanding of its uniqueness regarding this syntopy.

Chamaedorea species are known to occur sympatrically in many areas (Hodel 1992). However, very few research has been done on how species limits are maintained in these instances. Differences in pollinators and flowering time have been proposed in other species in the genus (Luna et al. 2005; Bacon and Bailey 2006), as well as in other understory palms (Knudsen 1999; Borchsenius 2002; Borchsenius et al. 2016). Different reproductive timing could also be keeping the morphotypes distinct in El Mirador, since immature fruits were only found in some solitary plants. However, records of the cespitose morphotype both in El Mirador and other sites are very limited and incomplete to properly assess its phenology and compare it with its solitary counterpart. Ecological studies pending, our results suggest that the variation found in the leaf characters has little correlation with environmental factors and could be evidence of underlying genetic divergence. This could perhaps be kept through certain means of reproductive isolation that can only be seen in this locality due to their cohabitation.

As stated previously, we have considered only two morphotypes in this study based on their habit differences, a solitary and a cespitose one. Hodel (2013) described a third form that resembles the solitary morphotype but differs in size and developmental characteristics. We believe this to be a rare variant of the solitary morphotype, rather than a completely different form, based on our current knowledge of *C. elatior* and the following reasons. First, bifid juvenile leaves of similar size were seen in other localities visited in Veracruz, Mexico. Second, the more robust size is only noted in its bifid leaves with no reference to a distinction in its pinnate leaves (Hodel 2013). Third, both its habitat and altitudinal range fall in the range of our solitary morphotype. Fourth, we have seen herbarium material of *C. elatior* from Uxpanapa, Veracruz and Los Chimalapas, Oaxaca that border the reported site and all are quite similar in appearance. Though we did not include herbarium material in this study due to its incompleteness and difficulty in assessing homology between leaflets, no material could be accurately referred to this form since all specimens were pinnate.

The central difference of this form is that it retains its bifid, otherwise juvenile, leaves for a certain period of time after attaining maturity (i.e. flowering) but will eventually produce its typical pinnate leaves (Hodel 2013; Dowe and Hodel 2021). This distinction is thus best interpreted as developmental rather than morphological. The difference between juvenile and mature leaves in palms has been described by Tomlinson (1960), but no studies have been done to understand the developmental processes responsible for it. In only one experiment in the palm *Caryota mitis* Lour., juvenile leaves were induced in a mature individual by administering gibberellin (Fisher 1976). If such a change is mediated by gibberellin or similar hormones in *Chamaedorea* is unknown. Although rare, other species in the genus can also flower before their leaves attain their maximum number of leaflets or even develop pinnate leaves after years of flowering and bifid leaf production (Hodel 1992).

Scandent habit of *Chamaedorea elatior*

No research has been done on the habit of scandent species of *Chamaedorea*. Still, field observations on *C. elatior* have shown the solitary morphotype to have a more vigorous climbing habit than the cespitose one, as it can reach higher heights in the canopy and has stronger supports. The latter was noticed during this study, since pulling on stems from below to reach the leaves proved harder in the solitary form. The cespitose morphotype, on the other hand, has more of a scrambling habit, covering a wider area and entangling with more plants but not reaching as high. The solitary morphotype's larger leaves might have an adaptive value and could be related to its habit, as shown in other climbing palms. When comparing leaf morphology between *Desmoncus orthacantos* Mart. (a strong climber) and *D. polyacanthos* Mart. (a weaker climber), Isnard et al. (2005) mention that larger leaves provide *D. orthacantos* with a larger range to encounter support points in the vegetation and can ensure its attachment to wider support points (i.e. branches). Although *C. elatior*'s climbing habit is different in various ways from that of species in *Desmoncus* Mart., considering the first lacks more specialized structures as spines or cirri, certainly trends in leaf size appear to be similar.

With no spines nor proper acanthophylls in a cirrus, climbing habit in *C. elatior* seems to be facilitated by its reflexed leaflets, especially distal ones, and their hardened, callose bases acting as support (Acevedo-Rodríguez 2020). During sampling, we noticed that leaves would lose some leaflets, at the insertion to the rachis, when pulled down with force from under the canopy. This suggests that the main point of support is indeed the hardened base of the leaflets. The length of the leaflet insertion to the rachis was seen in situ to be proportional to the size of this callose base, longer insertions had larger bases. This could amount to the previous hypothesis in that the solitary morphotype, as a stronger climber than the cespitose one, would have a more sizeable support system based on its significantly longer leaflet insertions.

Toward species delimitation

Traditional morphometrics have been shown to be a reliable tool in delimiting taxa in palm species (Henderson 2006; Laubengayer et al. 2012; Santos-Hernández et al. 2022). Our analyses on the morphological variation of the leaf show that the solitary and cespitose morphotypes of *C. elatior* are significantly distinct from each other. Though not properly included in our analyses for reasons mentioned previously, the branching habit of the cespitose morphotype is unique and is often used as the main difference to segregate them (Hodel 2013).

Though variation in reproductive structures could not be properly studied between morphotypes, we consider that the observed differences in vegetative characters are indicative of probable evolutionary distinctiveness between them, especially considering their cohabitation in the same habitat while maintaining their unique morphology (in El Mirador). Patterns observed when analysing vegetative characters were comparable when including reproductive characters in *Geonoma* Willd. (Borchsenius 1999) and *Gaussia* H.Wendl. (Santos-Hernández et al. 2022). Differences in leaf morphology were likewise confirmed by genetic divergence between similar species *Chamaedorea glaucifolia* and *C. plumosa*

(Ruíz-Castillejos 2011). A targeted comparative exploration of reproductive structures, phenology, and other lines of evidence would add to our growing knowledge of variation in the morphotypes of *C. elatior* and permit a more satisfactory morphological delimitation.

Reproductive morphology has been used in *Chamaedorea* mainly to delimit artificial subgenera based on floral characters (Hodel 1992, 1999); however, these characters seem to not diverge substantially between closely related species. Similarly, floral variation has been proposed to be useful in delimiting or recognizing certain monophyletic groups within the genus (Askgaard et al. 2008), but no research has been done in intraspecific variation within these groups. In the segregation of *C. tacanensis* from *C. elatior*, only certain quantitative differences were observed in characters pertaining to the inflorescences' axes (Pérez-Farrera et al. 2021). The main distinction was in the longer peduncles of *C. tacanensis*, but all other inflorescence characters overlapped to a certain degree (Pérez-Farrera et al. 2021). According to initial and incomplete observations during field work, we expect a similar pattern to occur among the morphotypes studied, mostly on size and number of the axes and probably not in flower or fruit morphology.

Based on the current evidence, the recognition of these morphotypes as separate species seems valid; however, we consider that more lines of evidence are desirable to properly delimit these forms within *C. elatior* with a more robust, integrative approach (Dayrat 2005; Padial et al. 2010). Preliminary climatic niche divergence and genetic results on nuclear loci of the same populations sampled in this study have shown noteworthy variation that can deepen our understanding of *C. elatior* and corroborate the findings presented here.

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SUPPLEMENTARY MATERIALS

Supplementary material 1

Localities of *Chamaedorea elatior* sampled in this study.
https://doi.org/10.5091/plecevo.160648.suppl1

Supplementary material 2

Boxplots comparing 13 leaf characters analysed in the two morphotypes of *Chamaedorea elatior*.
https://doi.org/10.5091/plecevo.160648.suppl2

Supplementary material 3

Coefficients of 13 leaf characters of *Chamaedorea elatior* on different analyses.
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