



# The evolutionary history of Fouquieriaceae (Ericales): biogeography, growth habit, habitat colonization, and chromosome evolution

Fabiola Soto-Trejo<sup>1,5</sup> · Susana Magallón<sup>2</sup> · José Arturo De-Nova<sup>3</sup> · Patricia Dávila<sup>1</sup> · Luis A. Sánchez-González<sup>4</sup> · Ken Oyama<sup>5</sup>

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## Abstract

Fouquieriaceae consists of a single genus *Fouquieria* with eleven species occurring in arid and semiarid regions in Mexico and the southwestern USA. A recently developed phylogeny based on chloroplast DNA sequences provided strong support for the monophyly of the genus and the evolutionary species relationships. However, details of its evolutionary history remain unclear. Due to this uncertainty, additional information such as the evolution on its growth habit, reconstruction of the ancestral habitat, and on chromosome evolution is needed for a clear understanding of its evolutionary history. Different hypotheses concerning the shift of growth habits (succulent or woody) and the occupation of the ancestral habitat, and the chromosomal evolution in the family were analyzed. We assessed the ancestral distribution by fitting different biogeographic models. Our results suggest that Fouquieriaceae may have originated in two regions at the margins of the present geographic distribution of the genus: the Sonoran Desert and desert areas south of the Mexican Transvolcanic Belt. However, our results suggest that the ancestral lineage of Fouquieriaceae was originated in desert habitats in central–southern Mexico with a basal chromosome number of  $n = 12$ , and a succulent habit, all of which may have allowed the dispersion of polyploid species to newly developed dry environments during the Late Miocene.

**Keywords** BioGeoBEARS · Chromosomal evolution · *Fouquieria* · Polyploidy · Succulence · Woody

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✉ Fabiola Soto-Trejo  
fabiolasototrejo@gmail.com

- 1 Unidad de Biología, Tecnología y Prototipos, FES-Iztacala, Universidad Nacional Autónoma de México (UNAM), Av. De los Barrios s/n, Los Reyes Iztacala, Estado de México, 54090 Tlalnepantla, CP, Mexico
- 2 Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, 3er Circuito de Ciudad Universitaria, Mexico City, Mexico
- 3 Instituto de Investigación de Zonas Desérticas – Facultad de Agronomía y Veterinaria, Universidad Autónoma de San Luis Potosí, 78377 San Luis Potosí, Mexico
- 4 Museo de Zoología “Alfonso L. Herrera”, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apdo. Postal 70-399, 04510 Mexico City, Mexico
- 5 Escuela Nacional de Estudios Superiores (ENES) Unidad Morelia, UNAM, Antigua carretera a Pátzcuaro no. 8701, Col. Ex-hacienda San José de la Huerta, 58190 Morelia, Michoacán, Mexico

## Introduction

Mexican dry environments, including deserts, savannas, and seasonal tropical dry forests, are widespread and characterized by high species diversity and endemism (Rzedowski 1978; Trejo and Dirzo 2002). The evolution of these communities is the result of a complex biotic history mostly attributed to relatively recent major geological changes, such as the origin and development of the Transvolcanic Belt from the Miocene to the Pleistocene, the detachment of the Baja California Peninsula during the Pliocene, the subsequent Pleistocene climate changes (Graham 1999; Ferrusquía-Villafranca and González-Guzmán 2005), and a complex topography, all of which has been enhanced due to a disjunct distribution of these dry environments (Rzedowski 1978; Trejo and Dirzo 2002). All these factors promoted the establishment of arid-adapted plant groups, such as the genera *Agave*, *Bursera*, and *Yucca* and the families Cactaceae and Fouquieriaceae, that exhibit numerous endemic species to these Mexican dry habitats (De-Nova et al. 2012, 2018; Hernández-Hernández et al. 2014; Sosa et al. 2018).

Fouquieriaceae is a family that consists of the single genus *Fouquieria*, with eleven species that are endemic to deserts and dry tropical regions throughout Mexico and the southwestern USA (Henrickson 1972). Five species are distributed in central–southeastern Mexico: *Fouquieria fasciculata* is found in the dry environments of Hidalgo and Querétaro; *F. leonilae*, *F. ochoterenae*, and *F. formosa* grow in dry tropical regions in Guerrero, Morelos, and Puebla; and *F. purpusii* is restricted to the driest habitats of the Tehuacán-Cuicatlán Valley, in Puebla and Oaxaca. Five more species are restricted to a single desert area in northern Mexico: *F. burragei*, *F. diguetii*, and *F. columnaris* occur in the Peninsular Baja California Desert; *F. macdougalii* occurs in the Sonoran Desert; and *F. shrevei* is found in a few sites in the Chihuahuan Desert in Coahuila. Finally, *F. splendens* is widespread, occurring on the Baja California Peninsula, as well as in the Sonoran and the Chihuahuan Deserts.

A phylogeny based on chloroplast DNA sequences indicates that Fouquieriaceae is an ancient lineage that diverged from Polemoniaceae at approximately 75.5 Ma during the Late Cretaceous (De-Nova et al. 2018). However, species diversification in Fouquieriaceae occurred during the Miocene–Pliocene, at approximately 12.7 Ma. Regarding the biogeographic history of this family, De-Nova et al. (2018) suggested a North American origin, specifically in the Californian chaparral. Based on this hypothesis, these authors proposed that the extant isolated species of Fouquieriaceae are Miocene or Pliocene relicts, showing stepping-stone migration following a north to south dispersal route, as postulated by Axelrod (1979, 1983). This first dispersal process was then followed during the Neogene by three main vicariant events that promoted most of the diversification in this genus (De-Nova et al. 2018). Currently, most of the Fouquieriaceae species are endemic to mainland Mexico, five of them restricted to small and isolated regions in central–southeastern Mexico, suggesting an alternative geographic origin for the family in this region (Schultheis and Baldwin 1999). Therefore, details of this biogeographic history remain unclear.

Succulence is a morphological adaptation for drought avoidance, and salinity tolerance is often associated with plants living mainly in dry environments (Futuyma 1997; Niklas 1997; Egli and Nyffeler 2009; Ogburn and Edwards 2010; Arakaki et al. 2011; Grace 2019). Both succulent and woody (non-succulent) species are present in Fouquieriaceae (Henrickson 1969, 1972; Fig. 1). The three succulent species, *F. columnaris*, *F. fascicularis*, and *F. purpusii*, show mainly thick stems with unique remarkable anatomical traits, such as the presence of wide rays and axial parenchyma bands enabling water storage (Henrickson 1972; Carlquist 2000). This type of succulence is not found in other closely related families to Fouquieriaceae (Carlquist 2000). On the other hand, woody species in *Fouquieria* possess a cortical

network of water storage tissue that is slightly more developed than in the stems of other succulent species (Henrickson 1969, 1972). Therefore, it seems feasible to ask whether the succulent or woody habit is the ancestral condition in the family, as an additional criterion in the understanding of the evolutionary history of Fouquieriaceae.

Chromosomal rearrangements are frequent in plants and are mainly produced by translocations, aneuploidy, dysploidy, and polyploidy (Stebbins 1971; Levin 2002). Polyploidy has been intensely studied in angiosperm diversification and speciation (Stebbins 1971; Levin 1983, 2002; Otto and Whitton 2000; Hegarty and Hiscock 2007, 2008; Otto 2007; Soltis et al. 2009; Soltis and Soltis 2000, 2016). Fouquieriaceae species in mainland Mexico are diploid ( $n = 12$ ), but the three on Baja California Peninsula are polyploid: *F. columnaris* ( $n = 36$ ), *F. diguetii* ( $n = 24$ ), and *F. burragei* ( $n = 36$ ) (Henrickson 1972). The basal chromosome number  $n = 12$  was suggested to be located close to the lineage ancestral area (Henrickson 1972, Schultheis and Baldwin 1999), suggesting also that polyploidy may add information on the evolutionary history of this plant family.

During the Late Miocene, aridity intensified the enlargement of arid habitats with a consequent reduction and isolation of more humid environments, which may have promoted the diversification of arid-adapted plant groups (Cerling et al. 1997; Graham 1999; Ferrusquía-Villafranca and González-Guzmán 2005; Pound et al. 2012). We therefore hypothesize that Fouquieriaceae may have originated in more mesic environments and then diversified in concert with the expansion of arid environments. Based on this, we expect a colonization from seasonally dry to desert habitats and a shift from a woody to a succulent habit. We expect a shift from low chromosome number in basal taxa occurring in mesic zones to polyploid species in desert environments.

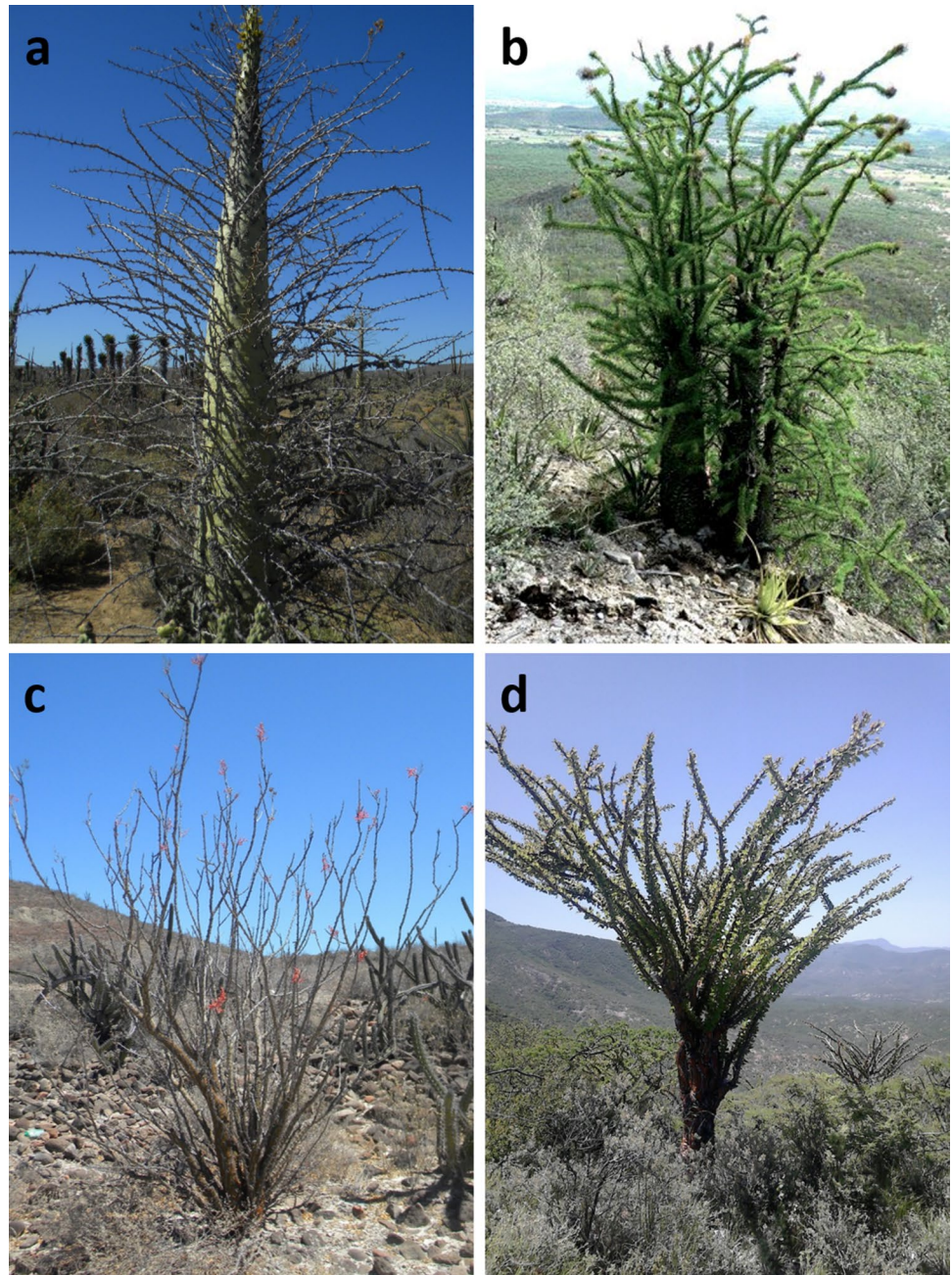
Accordingly, our goal is to integrate evidence from different sources to gain a better and more accurate understanding of the evolutionary history of Fouquieriaceae.

## Materials and methods

### Biogeographic analyses

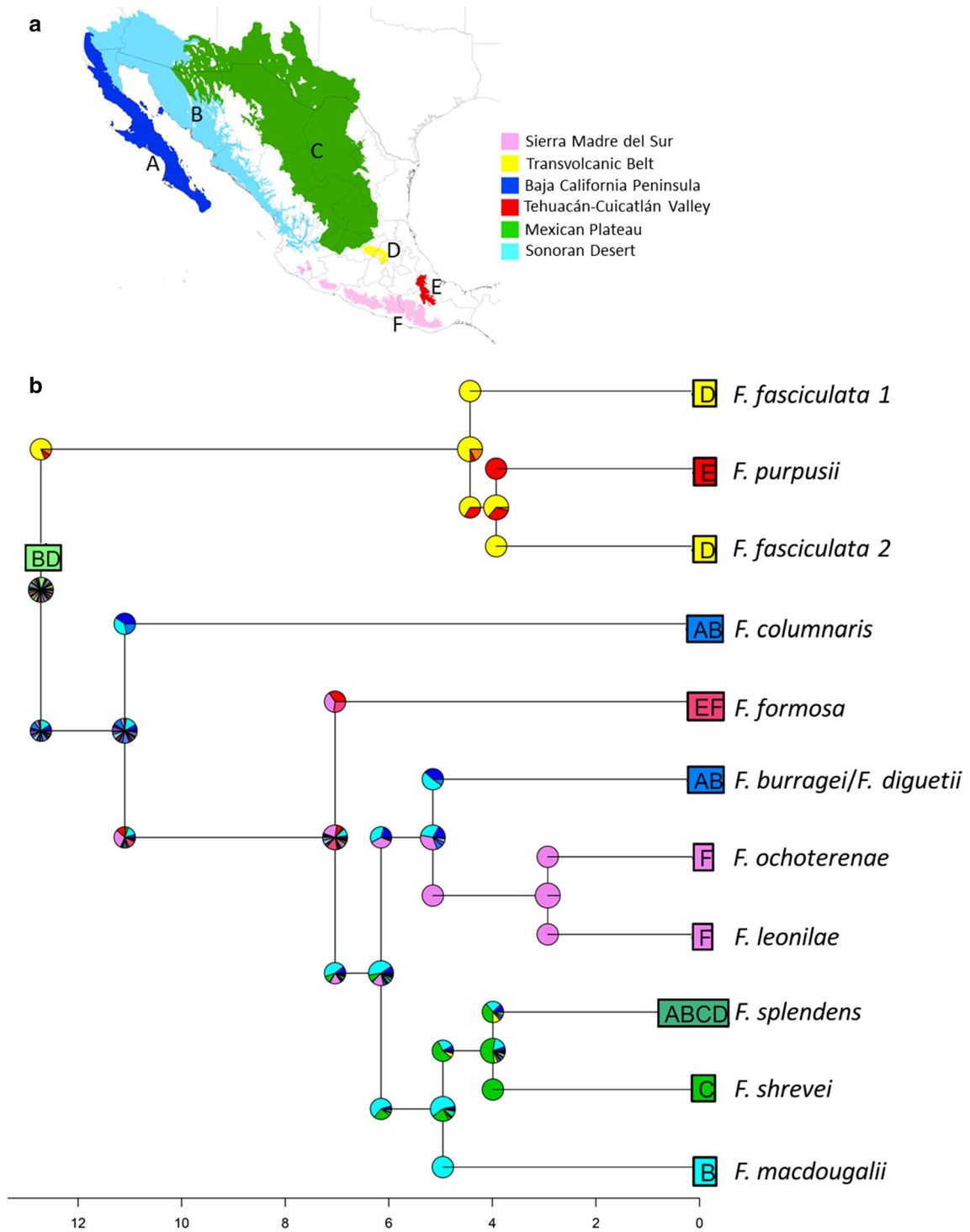
Our analyses were based on a time-calibrated maximum clade credibility tree (MCC tree) previously published in De-Nova et al. (2018), which was pruned to include the 11 taxa of *Fouquieria*. The distribution of these species was summarized in six distributional areas (Fig. 2a) based on the morphotectonic provinces proposed by Ferrusquía-Villafranca (1998): a) Baja California Peninsula, b) Sonoran Desert, c) Mexican Plateau, d) Transvolcanic Belt, e) Tehuacán-Cuicatlán Valley, and f) Sierra Madre del Sur. We used BioGeoBEARS (Matzke 2013; 2014, available at

**Fig. 1** Succulent species: **a** *Fouquieria columnaris* and **b** *F. purpusii*. Woody species: **c** *F. diguetii* and **d** *F. formosa*. Photos: José Arturo De-Nova



<https://github.com/nmatzke/BioGeoBEARS>) to infer the ancestral areas for *Fouquieria*. We undertook a maximum likelihood analysis under six different biogeographic models as follows: a) DEC (dispersal-extinction-cladogenesis; Ree and Smith 2008), b) DIVALIKE (a likelihood interpretation of the Dispersal Vicariance Analysis, DIVA; Ronquist 1997), and c) BAYAREALIKE (a likelihood interpretation of BayArea; Landis et al. 2013). All of these models include anagenetic and cladogenetic processes, in which “dispersal” is modeled as an anagenetic range–expansion process (rate parameter  $d$ ), while “extinction” is modeled as an anagenetic range–contraction process (rate parameter  $e$ ).

These three models display some important differences (see details in Fig. 1 in Matzke 2013): DEC models geographic range change during cladogenesis by assigning equal per-event weights to sympatry, subset sympatry, and vicariance. DIVALIKE allows vicariance, in which both descendants are widespread but disallows subset sympatry, and BAYAREALIKE does not allow any change to geographic range to occur during cladogenesis; instead, the ancestral range is copied to both descendants even if the ancestral range covers several areas. Three additional models were generated by adding the third free parameter  $j$ , which represents the relative per-event weight of founder-event speciation (“jump



**Fig. 2** **a** Map of the six areas based on morphotectonic provinces proposed by Ferrusquía-Villafranca (1998). **b** Estimates of ancestral ranges for Fouquieriaceae under the DIVALIKE+J model ( $d=0.015$ ;  $e=1.0e-12$ ;  $j=0.13$ ;  $\text{LnL}=-30.19$ ). Pie charts at each node show the probability of all possible ancestral states; note the high level of uncertainty in geographic ranges at deeper nodes. The colors of wide-

spread ranges are mixtures of the colors used for the single areas: for example, the range AB is light blue, as its constituent areas are A (dark blue) and B (cyan). The borders between pie slices are black, so a mostly black pie chart indicates dozens or hundreds of tiny pie slices (high uncertainty). A timescale is shown at the bottom, with units in millions of years

dispersal”) during cladogenesis, creating DEC + *j*, DIVA-LIKE + *j*, and BAYAREALIKE + *j* models.

Due to the small size of our study clade, the fitness of each model was compared using the Akaike information criterion corrected for small sample sizes (AICc), as recommended by Burnham and Anderson (2002). AICc was used to calculate the relative likelihood and model weight of each analyzed model.

### Succulence evolution in Fouquieriaceae

To investigate whether succulent or woody habit is the ancestral condition in the family, we used the R packages “corHMM” and “ape” (Paradis et al. 2004), which allowed us to estimate changes among succulent and woody states across the phylogeny using a likelihood method (Beaulieu et al. 2013). Taxa were coded as either succulent or woody based on literature surveys (Henrickson 1972, Carlquist 2000). We estimated the likelihood under the “equal rates” (ER), versus “all rates differ” (ARD) Markov models (Beaulieu et al. 2013). Model selection was performed using AICc.

### Ancestral habitat in Fouquieriaceae

We used BioGeoBEARS to evaluate ancestral habitat in Fouquieriaceae. We defined two broad habitat categories for our analysis: desert habitats and tropical dry forests. Each species was coded according to one of these current habitats. We used the same six basic biogeographic models described above for ancestral habitat inference. In this context, geographic range as required by BioGeoBEARS is represented by the habitat of each species.

### Chromosome number evolution in Fouquieriaceae

Chromosome numbers for the *Fouquieria* taxa were obtained from Henrikson (1972). To elucidate the role of chromosome number change in the evolutionary history of the family, we used probabilistic models as implemented in

ChromEvol v.2.0 (Mayrose et al. 2010). This program infers the most likely basal chromosome numbers via a likelihood-based method using ancestral state reconstruction. The eight chromosome evolutionary models implemented were analyzed with 10,000 simulations, and the best-fitting model was selected using the Akaike information criterion.

## Results

### Biogeographic analyses

We reviewed the charts generated by BioGeoBEARS to infer the probable biogeographic events that shaped the evolutionary history of Fouquieriaceae (Fig. 2b). Log-likelihood (LnL) and AICc values for the six assessed models are presented in Table 1. There were no significant differences in model performance: LnLs ranged from −35.48 (BAYAREALIKE) to −30.19 (DIVALIKE + J). The best-fitted model was DIVALIKE + J, with 45% of the weight, while DEC + J recorded 41% of the model weight. Ancestral range estimates corresponding to the DIVALIKE + J showed high uncertainty at some of the deeper nodes. These biogeographic estimations suggested that diversification in *Fouquieria* may have occurred in two widely separated areas corresponding to the Transvolcanic Belt and the Sonora Desert (areas BD) during the Late Miocene (Fig. 2b).

### Succulent habit evolution in Fouquieriaceae

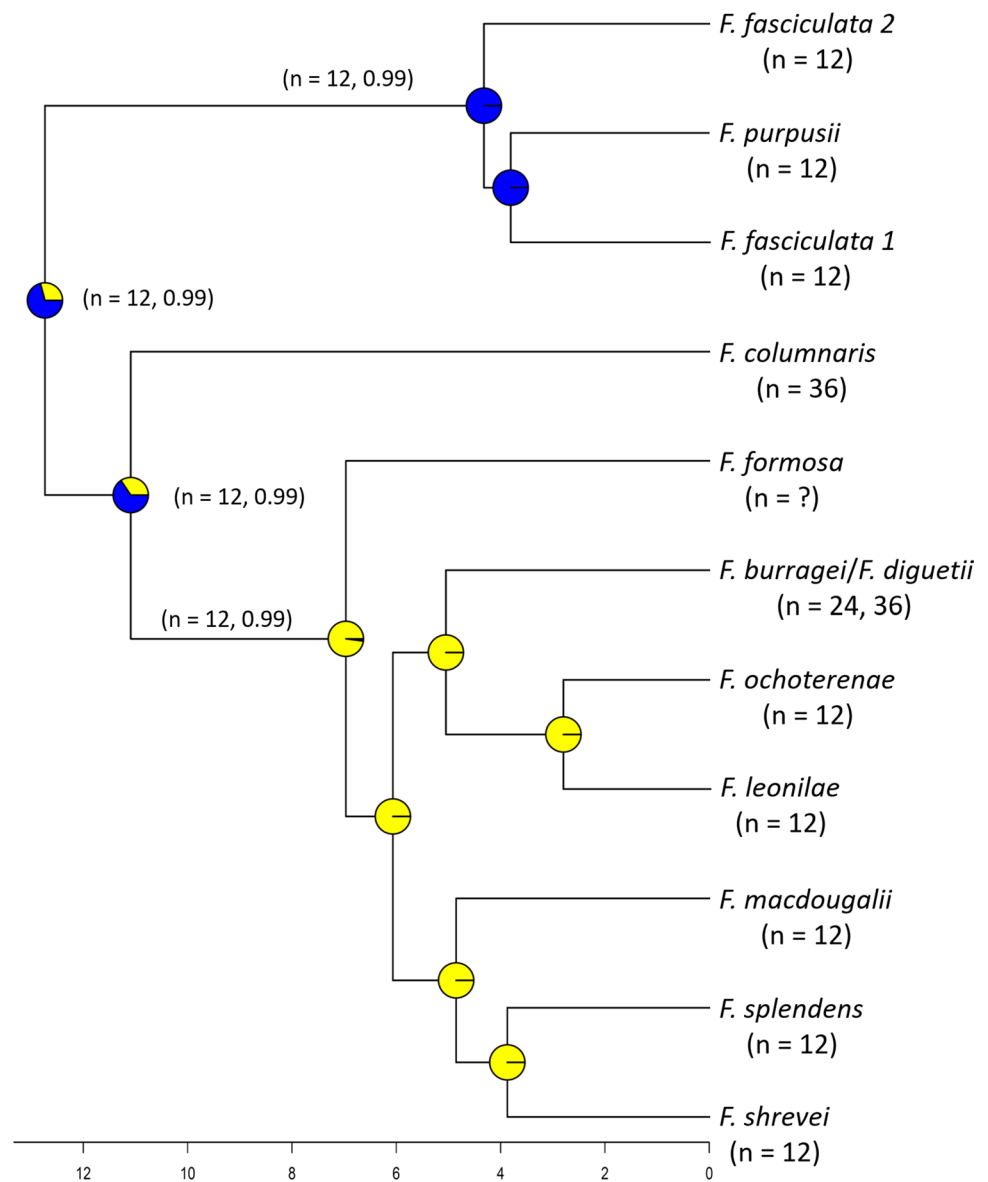
Our estimations of shifts between succulent and woody habits along the phylogeny showed that the model ER (all rates were equal among states) was preferred over an ARD model (ER: LnL = −4.17, AICc = 10.78; ARD: LnL = −3.83, AICc = 13.16). Based on the ER model, a succulent habit was suggested to be the ancestral state for Fouquieriaceae (Fig. 3), and the shift to a woody state may have occurred between 11.09 and 7.04 Ma, in the Late Miocene.

**Table 1** Maximum log-likelihood (LnL) of *Fouquieria* range data under each model, and resulting AICc and model weights

Model	LnL	<i>D</i>	<i>E</i>	<i>J</i>	<i>K</i>	<i>n</i>	AICc	Model weight (%)
DEC	−33.92	0.017	0.0030	0.00	2	10	71.85	2.9
DEC + J	−30.29	0.013	1.0e−12	0.14	3	10	66.58	41.00
DIVALIKE	−34.59	0.024	0.0048	0.00	2	10	73.19	1.15
DIVALIKE + J	−30.19	0.015	1.0e−12	0.13	3	10	66.37	45.00
BAYAREALIKE	−35.48	0.023	0.15	0.00	2	10	74.95	0.62
BAYAREALIKE + J	−31.85	0.0087	0.0092	0.16	3	10	69.71	8.6

*D* dispersal, *E* extinction, *J* jump dispersal, *K* number of parameters, *n* number of data, AICc Akaike Information Criterion corrected for small sample size

**Fig. 3** Estimated shifts between succulent and woody habit along of the Fouquieriaceae phylogeny. A model ER in which all rates are equal among states was preferred over an ARD model (ER: LnL = -4.17, AICc = 10.78; ARD: LnL = -3.83, AICc = 13.16). Succulent habit (blue) and woody habit (yellow). A timescale is shown at the bottom, with units in millions of years



### Estimation of ancestral habitat

The DIVALIKE + J model was selected as the best-fitting model (LnL = -6.42, AICc = 18.85) (Fig. 4). The model indicated that the common ancestor of the extant species of Fouquieriaceae occurred in desert habitats. Furthermore, our results also showed at least two independent events of recolonization of desert habitats, one in *F. burragei/diguetii* to Baja California and Sonora, and the other in the *F. shrevei-F. splendens* clade to the Mexican Plateau.

### Chromosome number evolution in Fouquieriaceae

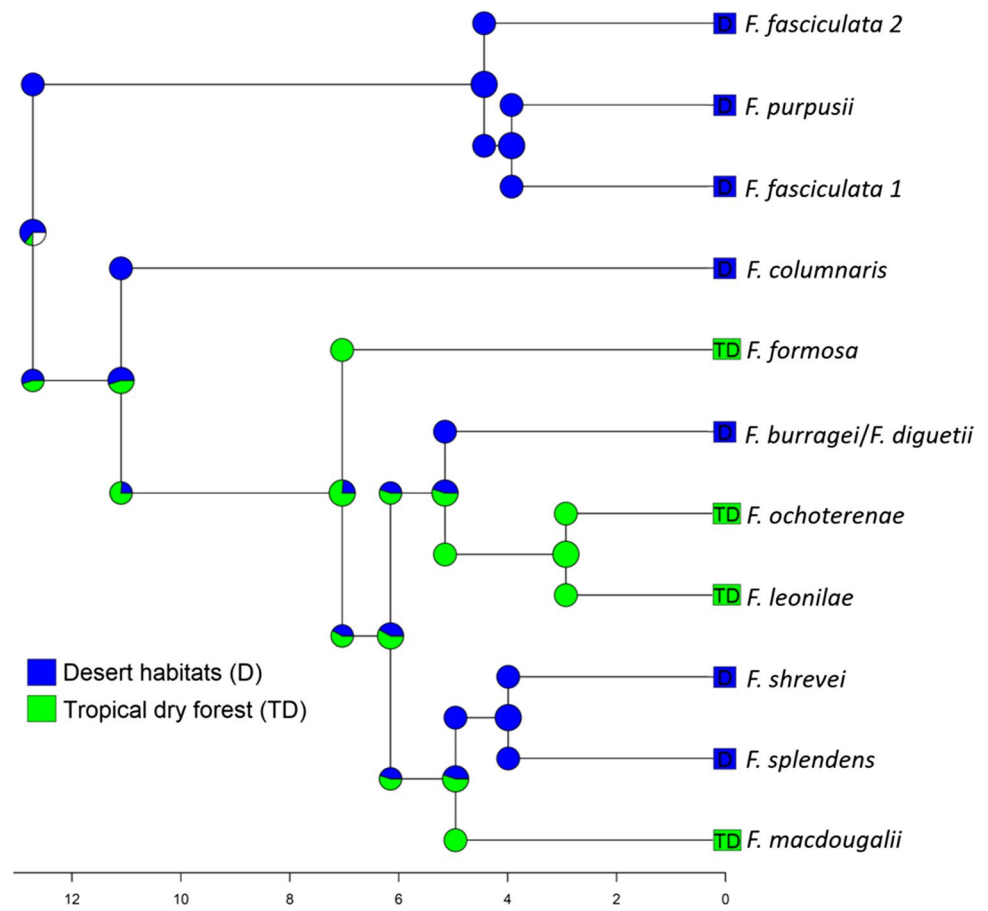
Our reconstruction of the evolution of ploidy numbers in Fouquieriaceae selected the model “CONST\_RATE\_DEMI” (LnL = -8.597; AIC = 23.19), which suggests that

the chromosome duplication rate equals a demi-duplication rate. The ancestral chromosome number inferred for Fouquieriaceae was  $n = 12$  ( $p = 0.99$ ), but changes in the chromosome number were suggested to have occurred in two different events since the Late Miocene in *F. columnaris* at approximately 11.09 Ma, and in *F. burragei* and *F. diguetii* at approximately 5.15 Ma (Fig. 3). All these changes occurred in Baja California and Sonora deserts.

### Discussion

Our biogeographic analyses showed high uncertainty at deeper nodes for identifying the ancestral geographic range of Fouquieriaceae (Fig. 2). This may be partially explained by several reasons, including the small number

**Fig. 4** Estimation of ancestral habitat across the Fouquieriaceae phylogeny. The DIVA-LIKE+J model was selected as the best-fitting model (LnL = -6.42, AICc = 18.85). A timescale is shown at the bottom, with units in millions of years



of species in the family, the relatively widespread distributional range of some species (e.g., *Fouquieria splendens*), and the tendency of sister species to show allopatric ranges, as in the case of *F. purpusii* and *F. fasciculata* (see Soto-Trejo et al. 2017). In addition, the split between extant Fouquieriaceae and its sister family Polemoniaceae occurred approximately 99–75 Ma during the Cretaceous (Bremer et al. 2004; De-Nova et al. 2018; Rose et al. 2018), making difficult the inclusion of some of the closest relatives of *Fouquieria* in ancestral geographic range estimations. Despite this uncertainty, the best-fitting biogeographic model suggested an ancestral range for Fouquieriaceae in two widely separated areas: the Sonoran Desert and central–southern Mexico in the Transvolcanic Belt. Therefore, diversification may have occurred from a widespread ancestor, resulting in the distribution of sister clades on different dry areas. This ancestral range reconstruction partially agrees with previous findings by De-Nova et al. (2018), since our analyses also recovered a relatively small region within the Transvolcanic Belt (Hidalguense Desert), as an ancestral geographic range. However, our analyses testing for multiple models suggest dispersal as the main driver for the diversification in the family, in contrast to the results in De-Nova et al. (2018).

Due to this uncertainty, additional information is needed for a clear understanding of the Fouquieriaceae ancestral geographic range, such as the evolution of its growth habit, reconstruction of the ancestral habitat, and its chromosome evolution. This additional data may add to the estimation of the biogeographic origin of the family and probably to a more accurate evolutionary history.

Diversification in Fouquieriaceae occurred throughout the Late Miocene and Pliocene (De-Nova et al. 2018). The rapid expansion of aridity during the Late Miocene may have been a primary driver of the global diversification of succulent plant lineages (Arakaki et al. 2011). In North American deserts, evolutionary radiations of succulent plant groups such as cacti and agaves coincide with the establishment of a northern desert, which was presumably caused by increased volcanic activity (Ferrusquía-Villafranca and González-Guzmán 2005; Hernández-Hernández et al. 2014; Eguiarte et al. 2021). Our ancestral habit reconstructions revealed that succulence may well be the ancestral condition in Fouquieriaceae, suggesting that the ancestor of *Fouquieria* was likely a succulent-stemmed plant with abundant parenchyma, a condition unique to this family (Henrickson 1969, 1972; Schultheis and Baldwin 1999; Carlquist 2000). Therefore, this supports the evolution from a succulent habit

to a woody habit in the family, which would be unusual, as it may be an evolutionary reversion (Schultheis and Baldwin 1999). In other groups with both succulent and woody members, an ancestrally woody habit has been shown to give rise to a succulent habit, as in Apocynaceae (Fishbein et al. 2018), Cactaceae, (Altesor et al. 1994; Edwards and Donoghue 2006) and *Euphorbia* (Horn et al. 2012). In woody *Fouquieria* species, water storage capacity is limited, but they have an extremely responsive nature of drought deciduousness of leaves. Most of these species (e.g., *F. leonilae*, *F. ochoteranae*, and *F. formosa*) inhabit mainly seasonally dry environments, such as dry tropical forests or tropical scrublands, which are often characterized by short pluvial periods alternating with long dry periods. Thus, the woody species of Fouquieriaceae drop their leaves when moisture availability falls, and the new leaves grow soon after the onset of the rainy season. Since the common ancestor of Fouquieriaceae is suggested to have been a dry-adapted lineage, extant species show a diversity of drought survival strategies for their persistence in dry environments, which may have facilitated the expansion of this taxon to tropical dry forests since the Late Miocene and Pliocene and probably enhanced the diversification of the group. Contrary to our expectations, the reconstruction of the ancestral habitat indicates that the common ancestor of the extant species of Fouquieriaceae inhabited desert habitats; thus, the earliest diverging lineages should be located in central–southern and/or northern Mexico, where these desert habitats are widespread. The clade including *F. fasciculata* and *F. purpusii* inhabit desert environments of central–southern Mexico, while *F. columnaris* occurs in arid regions of northern areas of the Baja California Peninsula and in a small area in the Sonoran Desert. Given the magnitude of the disjunction between species in these two clades, the identification of the ancestral range of the family remains elusive and possibly widespread. Most taxa in the woody species clade inhabit dry tropical forests, which are widely distributed in Mexico and originated at least 20 Ma (Rzedowski 1978; Trejo and Dirzo 2002; Becerra 2005), suggesting dispersal into tropical dry forest habitats during the Late Miocene. Furthermore, it seems that two independent events of recolonization of desert habitat occurred, as in *F. burragei*/*F. diguetii* at Baja California and Sonora and in *F. shrevei* at the Mexican Plateau and in the widely distributed *F. splendens*.

Our chromosome evolutionary analysis in Fouquieriaceae suggests that the most likely ancestral chromosome number in Fouquieriaceae is  $n = 12$ , as suggested by Henrickson (1972). Polyploid taxa in the family may have been involved in demi-polyploidization (i.e., the formation of polyploids via the fusion of gametes of different ploidy). Diploids are ancestral, and the diploid *Fouquieria* species are endemic to mainland Mexico with the exception of the widespread *F. splendens*. These results support the hypothesis that the

ancestral lineage of Fouquieriaceae probably originated in dry environments from central–southern Mexico, in or near where these diploids are currently distributed (Schultheis and Baldwin 1999; De-Nova et al. 2018).

Many studies have recognized that closely related diploid and polyploid species differ in their geographic ranges, with the polyploids found in more extreme climatic environments than their diploid relatives (Löve and Löve 1949; Ehrendorfer 1980; Lewis 1980; Levin 2002; Soltis et al. 2010). For example, diploids and polyploids in *Brachypodium distachyon* (Poaceae) are geographically structured throughout its range and are associated with aridity gradients, where polyploids are more efficient in the use of water than diploids (Manzaneda et al. 2012). Polyploids within *Fouquieria* include the tetraploid *F. diguetii* ( $n = 24$ ), as well as the hexaploids *F. burragei* ( $n = 36$ ) and *F. columnaris* ( $n = 36$ ), all of which are distributed mainly in the Baja California Peninsula. A recent phylogeographic study undertaken by Martínez et al. (2020) suggested that polyploid *F. columnaris* may have had a continuous geographic distribution in the Baja California Peninsula and mainland Mexico before the formation of the Gulf of California. His results indicated that fragmentation events and the occurrence of new habitats during the detachment of the Baja California Peninsula from the Mexican mainland, probably enabled the establishment of new polyploid lineages.

The close phylogenetic relationship between the allopatric polyploids *F. diguetii*/*F. burragei* in Baja California and the diploid *F. leonilae* and *F. ochoteranae* in Sierra Madre Sur may be explained by both vicariant and ecological factors. The Baja California Peninsula and the southwestern region of mainland Mexico are currently distant areas, but they were probably closer during the Pliocene (c. 6 Ma) via the cape region of Baja California (Oskin et al. 2001; Wilson and Pitts 2010; Umhoefer 2011). Presently, the dominant vegetation in the Cape Region of Baja California is distinctively different from the shrublands of most the peninsula ecosystems. The floristic composition in this region shows a clear dry tropical affinity and high species richness, similar to the dry tropical communities at comparable latitudes in mainland Mexico (León de la Luz et al. 2000). During the detachment of the Baja California Peninsula, the topographic features, as well as the shape of both spatial and environmental scenarios, were modified (Shreve 1937; León de la Luz et al. 2000), providing ecological conditions for the establishment of new polyploid lineages (Stebbins 1971; Ehrendorfer 1980; Levin 1983; Morton 1993; Lumaret et al. 1997; Soltis & Soltis 1999; 2000; Soltis et al. 2010; but see Martin and Husband 2009).

Regarding the most widespread species, diploid *F. splendens* appears to have spread across most of the northern deserts during the Pleistocene, maintaining gene flow over large areas probably through hummingbird-mediated



pollination (Redfern, 2008). In contrast, the diploid *F. shrevei* is restricted to small and isolated areas in gypsum soils in central and southeastern Coahuila. The extreme specialization of this species has probably led to intense genetic drift and reduced gene flow among its populations; patchiness of gypsum deposits has probably promoted genetically differentiated populations (Aguirre-Liguori et al. 2014). Therefore, the divergence approximately 3.99 Ma of *F. shrevei* could have occurred by an ecological speciation process, probably associated to the colonization of gypsum soils (De-Nova et al. 2020).

In summary, our results suggest that the ancestral succulent lineage of Fouquieriaceae probably occurred in dry environments in central–southern Mexico during the Miocene, followed by a subsequent expansion and divergence of the polyploid species into the Baja California Peninsula. These results do not support Fouquieriaceae as an ancient element derived from California chaparral and other communities, as postulated by Axelrod (1979, 1983). Studies including more taxa endemic to dry habitats might provide a better understanding of the patterns and causes of high and unique diversity in arid and semiarid environments in Mexico.

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## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Consent for publication** All authors consent to publish.

**Consent to participate** All authors consent to participate.

**Ethical approval** All authors have contributed to and approved the final manuscript.

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