

Timing the origin and expansion of the Mexican tropical dry forest

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Macroevolution examines the temporal patterns of biological diversity in deep time. When combined with biogeography, it can provide unique information about the historical changes in the distribution of communities and biomes. Here I document temporal and spatial changes of diversity in the genus *Bursera* and relate them to the origin and expansion of the tropical dry forests of Mexico. *Bursera* is very old, highly adapted to warm dry conditions, and a dominant member of the Mexican tropical dry forest. These characteristics make it a useful indicator of the history of this vegetation. I used a time-calibrated phylogeny to estimate *Bursera*'s diversification rate at different times over the last 60 million years. I also reconstructed the geographic center and time of origin of all species and nodes from information on current distributions. Results show that between 30 and 20 million years ago, *Bursera* began a relatively rapid diversification. This suggests that conditions were favorable for its radiation and thus, very probably for the establishment of the dry forest as well. The oldest lineages diverged mostly in Western Mexico, whereas the more recent lineages diverged in the south-central part of the country. This suggests that the tropical dry forest probably first established in the west and then expanded south and east. The timing of the radiations in these areas corresponds to that suggested for formations of the mountainous systems in Western and Central Mexico, which have been previously recognized as critical for the persistence of the Mexican dry forest.

Bursera | Mexico | speciation rate | diversification

The tropical dry forest is one of the four most extensive types of vegetation of Mexico (1). In its natural state, it is a dense community dominated by low- to medium-sized trees that lose their leaves during the dry season. A desolate and brownish-gray stationary aspect, which usually lasts ≈ 6 months, makes a remarkable contrast with the profuse greenness of the forest during the rainy season. This forest is widespread on the Pacific slopes of Mexico covering great extensions from central Sonora and southeastern Chihuahua to the southern state of Chiapas and continuing on to Central America. In northern Mexico, it develops mostly on the west side of the Sierra Madre Occidental at altitudes from 0 to 1,900 m. In the south, it runs along the coast of Nayarit and Colima and then penetrates deeply along the Santiago and Balsas rivers and their tributaries (Fig. 1). Its geographic distribution is largely defined by precipitation, which is absent during several months of the year, and by temperature, with the extreme minimum most often above 0°C and the annual mean varying between 20°C and 29°C , depending on the location.

Although the tropical dry forest contains a high diversity of plants, two groups dominate the woody elements: legumes and the genus *Bursera* (Burseraceae) (2, 3). The prominence of *Bursera* is particularly striking along the Balsas River depression, which is one of the major extensions of the dry forest. Here, this genus often becomes the absolute dominant woody taxon, surpassing legumes both in diversity and abundance and validating the name “cuajotales” given to many areas of these forests, from the common name “cuajote” given to *Bursera* species (1, 4). *Bursera* is also very prominent on the Pacific and

Atlantic coasts, including the Yucatan peninsula, the southern tip of Baja California, and the northern states of Sonora and Sinaloa (1, 5).

Due to a scant fossil record, the history of the Mexican dry forest is still sketchy. Although the floral affinities with other parts of the world, as well as the importance of the endemic elements, have been well established, little is yet known about the timing of the origin of this vegetation and the directions of its historical expansion or contraction. In the western U.S., studies of fossil plants, reptiles, and amphibians indicate that the climate at the end of the Eocene became seasonal and drier (6, 7). Unfortunately, there are no Tertiary floras or faunas known for western Mexico that would indicate similar trends in aridity. For the late Oligocene and middle Miocene, it has been suggested that major mountain building, such as that in the Rocky Mountains, changed the climates and established the modern biogeographic provinces of North America (8, 9).

The Sierra Madre Occidental and the Neovolcanic belt were also developing during the Oligocene and early Miocene and, in theory, their formation could also have triggered the establishment of modern biomes in West and Central Mexico, as is presumed to have happened contemporaneously in the U.S. The last uplift of the Sierra Madre Occidental occurred between 34 and 15 million years ago (Mya) (8, 10, 11), whereas the Neovolcanic axis was formed in several stages in a west–east progression that started in the west ≈ 23 Mya and ended 2.5 Mya (10). These two mountainous systems are currently critical in providing the climatic conditions that maintain this forest by blocking the cold fronts from the North. In the present study, I investigate the possible effects of the uplift of the Western Sierra Madre and the Neovolcanic belt on the temporal and spatial diversification of the genus *Bursera* and relate this diversification to the origin and expansion of the tropical dry forests in Mexico.

The Genus *Bursera*

The genus *Bursera* comprises ≈ 100 species distributed from Southern U.S. to Peru. It reaches its maximum diversity in the Pacific slopes of Mexico, where ≈ 84 species occur and ≈ 80 are endemic (2, 3, 12). They are typically low- to medium-size trees. The genus is relatively well known taxonomically, and it has been divided into two sections, *Bursera* and *Bullockia* (2, 4).

Bursera is highly adapted to the warm and dry conditions of the tropical dry forest. All of its species are deciduous, including those that are present in tropical subhumid and humid forests. Most species are cold-sensitive, and their distributions are limited by freezing temperatures. As with other members of these forests, many *Bursera* species have succulent trunks, and some display a spectacular brightly colored bark that exfoliates in colorful papery sheets or flakes. This trait is responsible for

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Abbreviations: mya, million years ago; AIC, Akaike information criterion; MY, million years.

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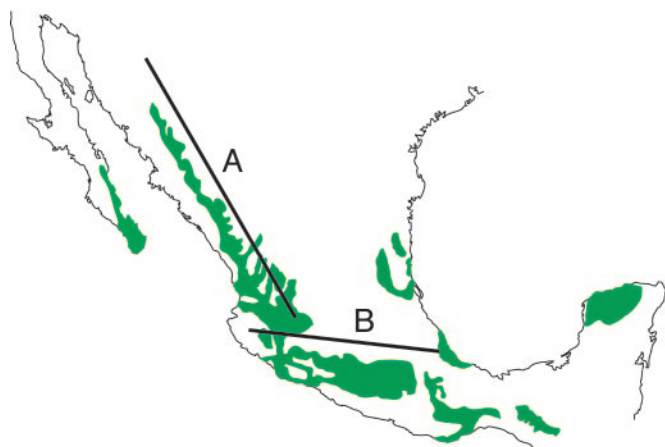


Fig. 1. Distribution of the tropical dry forest in Mexico (modified from ref. 1). The black lines indicate the main axes of the Sierra Madre Occidental (A) and the Neovolcanic belt (B).

the Aztec name “cuajote,” meaning “leprous tree,” which is still applied to these plants in some regions of Mexico (4).

Bursera is an old genus, whose distribution at one time extended across central North America. Fossil leaves of *B. serrulata*, a relative of the modern *Bursera tecomaca* (13), are abundant in the early Oligocene beds of Florissant, in Colorado (14). Fossil pollen of *Bursera* is also present in these beds (15). Another fossil species belonging to the section *Bullockia*, *Bursera inaequilateralis*, is known from the Eocene Green River, Colorado–Wyoming, and provides evidence that the genus had begun diversifying by at least 45 Mya (16). That *Bursera* is old, highly adapted to the ecological and climatic conditions of the dry forest, and of great physiognomic importance in the tropical dry forests today suggests that its evolution and diversification could be tied to the history of these forests and thus could be a powerful indicator of their historical expansion in Mexico.

Materials and Methods

This study took advantage of a robust time-calibrated DNA phylogeny that I recently produced for *Bursera* (13). This phylogeny was reconstructed by using sequences from the internal transcribed spacer (ITS) region, the external transcribed spacer (ETS) region, and the 5S nontranscribed region of nuclear ribosomal DNA (2, 3). Divergence times for the phylogeny were calibrated by using the ITS, ETS, and 5S sequences with biogeographic and fossil data (13).

Diversification analyses often assume that all extant species have been sampled in the phylogeny (17). However, the published calibrated *Bursera* phylogeny included only 65 of the ≈ 84 species reported for Mexico. To include the missing taxa, three species were added to the phylogeny by sequencing the internal and external transcribed tracers and 5S regions and by doing parsimony analysis with the same procedures as in Becerra (4). Their times of divergence were calculated based on their branch lengths. Sixteen more species were placed in their most likely position in the phylogeny on the basis of taxonomic information, because DNA data were unavailable (18–20). In the past, taxonomic information has often been a good predictor of phylogenetic relationships derived from analysis of DNA sequences (4), and all of these added species exhibit clear affinities to others already in the phylogeny. Because there is no information for divergence times of these 16 species, I assigned their nodes to be halfway along the branch to which each species was added (21). Because the nodes of the added species most often (12 of 16) fell very close to nodes for which age had been

estimated, if the species were accurately placed, then their assumed divergence time would not be far from what DNA calibration results would give.

Because this study concerns the Mexican dry forests, and also because of their poor systematic understanding, this study included neither the nine endemic species reported for the West Indies region nor the five species endemic to Central and South America.

Estimation of Time of Diversification and Diversification Rates in *Bursera*. One assumption of this study is that *Bursera*'s diversification could be an indicator of the time of origin of the Mexican dry forest. Because *Bursera* is old and highly adapted to ecological and climatic conditions of the dry forest, it is reasonable to assume that this community also included a substantial number of *Bursera* species in the past. To estimate *Bursera*'s diversification in time, I plotted the number of lineages through time starting 60 Mya. If there has been an increase in the speciation rate caused by the uprising of the Sierra Madre Occidental and the Neovolcanic axis, then an apparent acceleration in diversification rate is expected some time after the formation of these mountains. To test for significant departures from a constant speciation rate, I used the γ statistic, which compares the relative position of nodes in a phylogeny to those expected under a constant speciation rate model (22). Under a constant speciation rate model, γ follows a standard normal distribution. Positive values signify that nodes are closer to the tips of the phylogenetic tree than is expected under the constant speciation rate model, i.e., there has been an increase in diversification rate during the time window tested. Negative values signify an apparent deceleration. Therefore, accelerated diversification can be tested by rejecting a null hypothesis of a constant speciation rate at the 5% level, i.e., $\gamma < 1.645$ (one-tailed test). I calculated γ for: (i) the interval beginning 60 Mya, starting with two lineages, and ending 34 Mya; (ii) the interval beginning 34 Mya and ending 15 Mya; and (iii) the interval beginning 34 Mya and ending 1.5 Mya.

To have an estimate of the number of *Bursera* lineages diverged per unit of time and compare them at different times, I also calculated diversification rates for different time intervals using the Kendall/Moran estimator. According to this estimator, for a time window starting at time 0 and finishing at time t , the per-lineage speciation rate is $b = (n - m)/B$, where m and n are the number of lineages at the start and the end of the time interval, respectively, and B is the summed durations of all branches falling within the time interval (23, 24).

An increase in the diversification rate during the uplift of the Sierra Madre Occidental and the Neovolcanic axis would lead to a positive significant value of γ and an increased value of the Kendall/Moran estimator. However, although higher diversification values could be the result of an increase in the speciation rate, constant clade extinction will also cause a significant increase in the apparent diversification rate (22, 25). To more rigorously test for increased diversification during the time window of 33.1–15.43 Mya (the closest nodes to 34 and 15 Mya), I compared the likelihoods of five models of diversification (21, 25). These assumed (i) zero extinction and constant diversification, (ii) constant extinction and diversification, (iii) zero extinction but two separate diversification rates switching at time T , (iv) constant extinction and two separate diversification rates changing at time T , and (v) two separate diversification and extinction rates switching at time T . I used the Akaike information criterion (AIC) to select the best model to fit the *Bursera* data (26). The model with the highest AIC is chosen where $AIC = 2 \text{ Log}L - 2p$, L is the likelihood, and p is the number of parameters.

***Bursera*'s Historical Geographic Expansion in Mexico.** The second assumption in this study is that *Bursera*'s historical spread

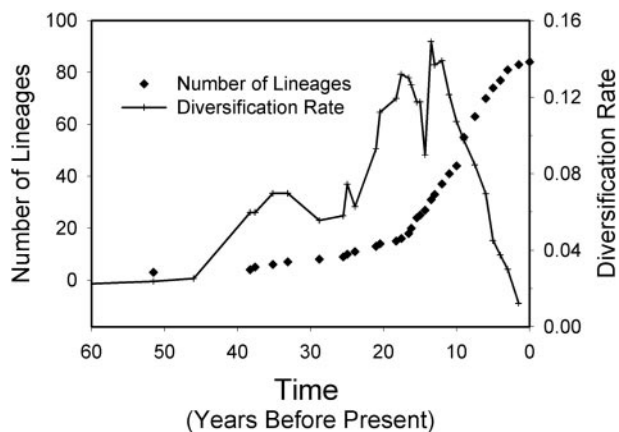


Fig. 3. Number of *Bursera* lineages through time and 10-MY average diversification rates at different times over the last 60 MY.

Sierra Madre Occidental and the Neovolcanic axis), the value of the γ statistic was very close to zero, suggesting no acceleration in diversification up to this time ($0.27 P < 0.5$). However, between 34 and 15 MY, after the uplifting of the Sierra Madre Occidental and of the west portion of the Neovolcanic Belt, the statistic increased, indicating a statistically significant acceleration in the apparent diversification rate toward the end of this time window ($\gamma = 1.91, P < 0.03$).

The Kendall/Moran estimates calculated for overlapping 10-MY time intervals are also low before 34 MYa: between 0.02 and 0.07

species per million years (Fig. 3). They start to increase after 30 MY. By 20 MYa, the rate is 0.11 species per million years and by 18 MYa, it reached 0.13 species per million years. Between 17 and 15 MYa, there was a brief decline in the speciation rate, which coincides with the end of the uprising of the Western Sierra Madre. Then it increases again to its maximum value of 0.15 species per million years at 13.5 MY, when the Neovolcanic belt was in active formation.

A higher diversification rate caused by a higher speciation rate after the rise of the Sierra Madre was confirmed by evaluation of the five models of diversification rates. The constant extinction and diversification model fitted the data better than the zero-extinction constant diversification model, as expected given the apparent acceleration of diversification (AIC = -28.30 and -28.62 , respectively). However, the zero-extinction model with two separate diversification rates provided the best fit to the data (AIC = -27.08). Adding two separate nonzero extinction rates had a similar likelihood, but the AIC value was penalized, because little likelihood was gained at the expense of adding two extra parameters (AIC = -30.80). The model with two diversification rates and one constant-extinction rate gave a better fit than the model with two diversification and two nonzero extinction rates but worse than the two diversification and zero-extinction rate (AIC = -28.46). This was because the fitted extinction rate (0.031) was low enough to not improve the fit over a model with zero extinction enough to outweigh the cost of adding the extra parameter. The best-fitting model suggests a diversification rate shift between 26 and 20 MYa (the likelihoods for all these years are very similar) involving more than tripling the speciation rate (before 26–20 MYa = 0.051, after 26–20 MYa = 0.179). Hence it appears that an increase in speciation rate was indeed leading to the accelerated clade diversification

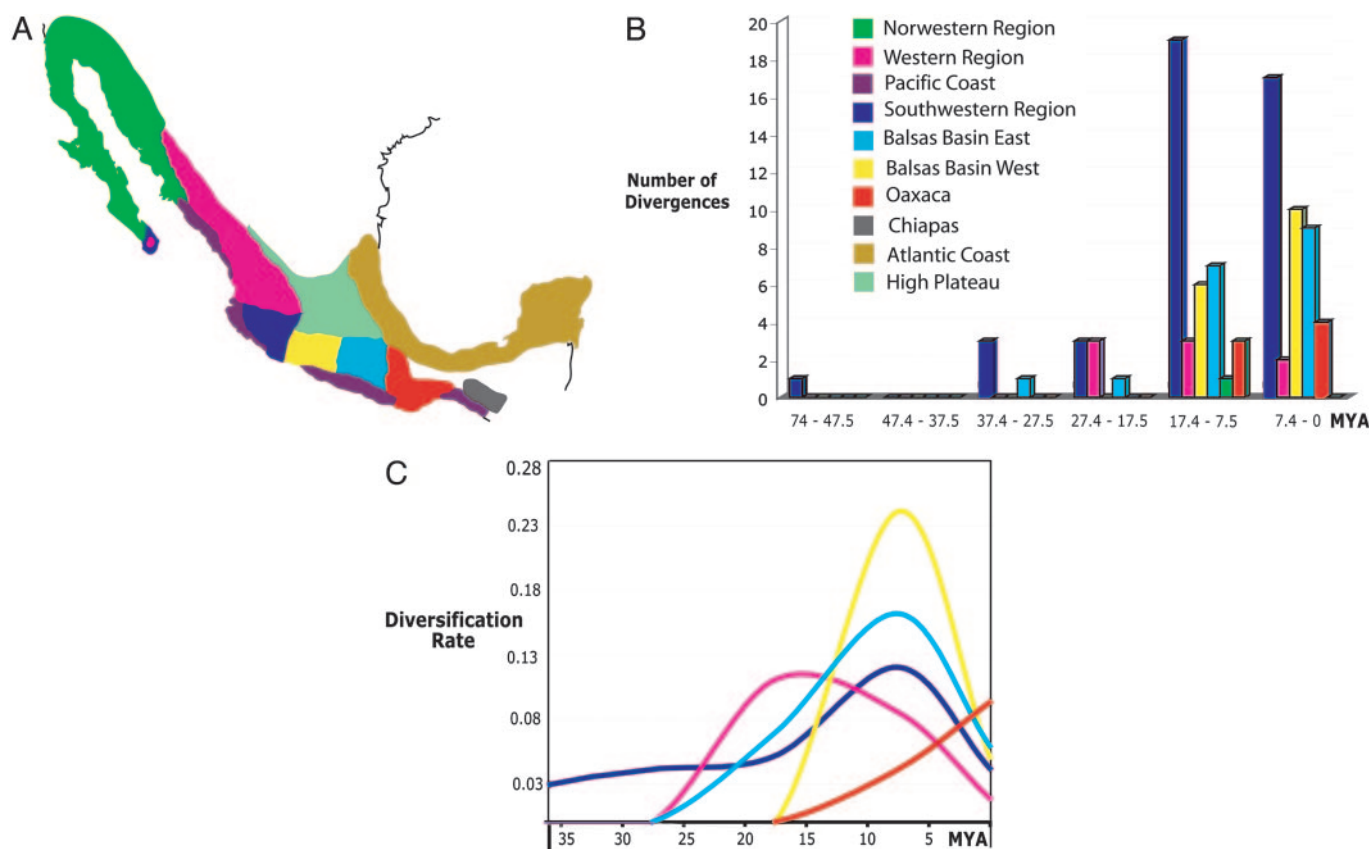


Fig. 4. *Bursera*'s historical expansion in Mexico. (A) The distribution of *Bursera* was divided into 10 subareas. (B) Number of lineages that have diverged in each subarea of distribution at different time intervals. Some of the subareas have not had speciation events. (C) Diversification rates in each subarea of distribution at different time intervals.

