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 "cuajiotales" given to many areas of these forests, from the common name "cuajiote" 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.

See Commentary on page 10757.

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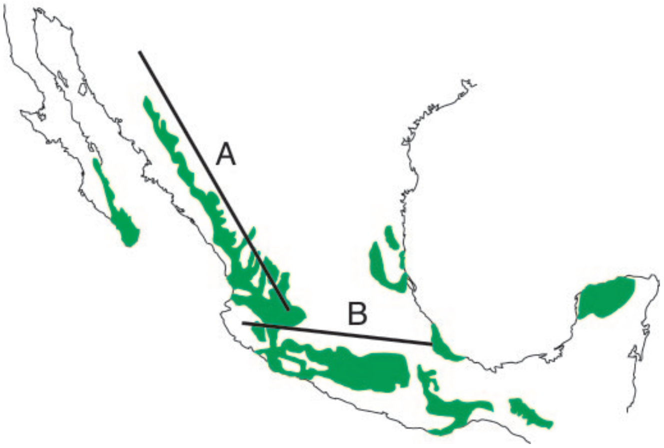

Fig. 1. Distribution of the tropical dry forest in Mexico (modified from ref. 1). The black lines indicate the main axes of the Sierra Madre Occidental (*A*) and the Neovolcanic belt (*B*).

the Aztec name "cuajiote," 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 began 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 tracer 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 $\mathrm{AIC} = 2\,\mathrm{Log}L - 2p$, 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 through Mexico proceeded in the same directions as the geographical expansion of the forest. According to this assumption, older areas of the dry forest should contain more ancestral *Bursera* lineages, whereas newer expansions of the forest should include more recently derived lineages. To investigate the history of *Bursera*'s spatial diversification, I generated maps of current distribution for each *Bursera* species and used these to reconstruct ancestral centers of origin. Maps were generated by using information from herbarium specimens (the Universidad Nacional Autónoma de México herbarium, the Escuela Nacional de Ciencias Biológicas-Instituto Politécnico Nacional herbarium, and the Herbarium of the Institute of Ecology, Bajío México), from published information (27, 28) and from the on-line biodiversity information of the Mexican Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO, www.conabio.gob.mx).

To reconstruct centers of origin of *Bursera* lineages, I divided the part of Mexico where *Bursera* is currently found into 10 subareas (Fig. 4*A*). Previous studies have identified several main biogeographic areas, and I used this information as the criterion for the subdivision (27, 28). Also important was that the maximum number of area distributions that can be handled by the computer program implemented to reconstruct ancestral distributions is 15. The selected areas were: (*i*) the northwestern region, (*ii*) the western region, (*iii*) the subhumid forests of the Pacific coast, (*iv*) the southwestern region, (*v*) the eastern side of the Balsas depression, (*vi*) the western side of the Balsas basin, (*vii*) the tropical dry forests of Oaxaca (excluding the ones in the eastern side of the Balsas basin), (*viii*) the Chiapas region, (*ix*) the Atlantic coast, and (*x*) the central high plateau. Ancestral areas of distribution were reconstructed by using the computer program DIVA (29). Areas *i*, *iii*, *x*, and part of *ix* are currently occupied by other vegetation types such as desert scrub or humid and subhumid tropical forest. They were included because some *Bursera* species are also found there and could provide insight on the historical spread of *Bursera* species in these types of vegetation.

Once the ancestral centers of origin were reconstructed for each internal node in the phylogeny, I investigated which geographic areas contained more ancestral or derived lineages. For this, I counted the number of lineages that, according to the DIVA reconstruction, had diverged in each of the geographic areas at different time intervals. These intervals were every 10 million years (MY) (except 1 of 11 MY) starting at 51 Mya. I also calculated the diversification rates in each area. Because the Kendall/Moran estimator is calculated on phylogenies and no meaningful phylogenies can be constructed for the individual geographic areas, I calculated the speciation rate for every geographic area using the estimator $[\ln(N) - \ln(N_0)/T]$, where N_0 is the initial number of nodes at the beginning of a time interval T, and N is the final number (24).

A common problem with reconstructing ancient areas of distribution is that areas may change their geographic position in time (29). One such problem here is Baja California, which separated from mainland some time between 15 and 4 Mya (30, 31). It is thought to have separated from the coasts of southern Nayarit and northern Jalisco and migrated as an island, which later attached to southern Baja California (32). The southern tip of the peninsula is now home to six *Bursera* species. The calibrated phylogeny of *Bursera* suggests that some of these species may have separated from their congeners long before this land mass separated (13). Thus, to avoid problems of reticulation with DIVA, while constructing the distribution matrix of these species, it was assumed that their distributions were the Western and the Southwestern regions. To avoid reticulation problems, I also did not include the species *B. tecomaca* in this analysis. This species is currently distributed in a small area in the southern state of Guerrero, but fossil information suggests its distribution included Colorado in ancient times (8).

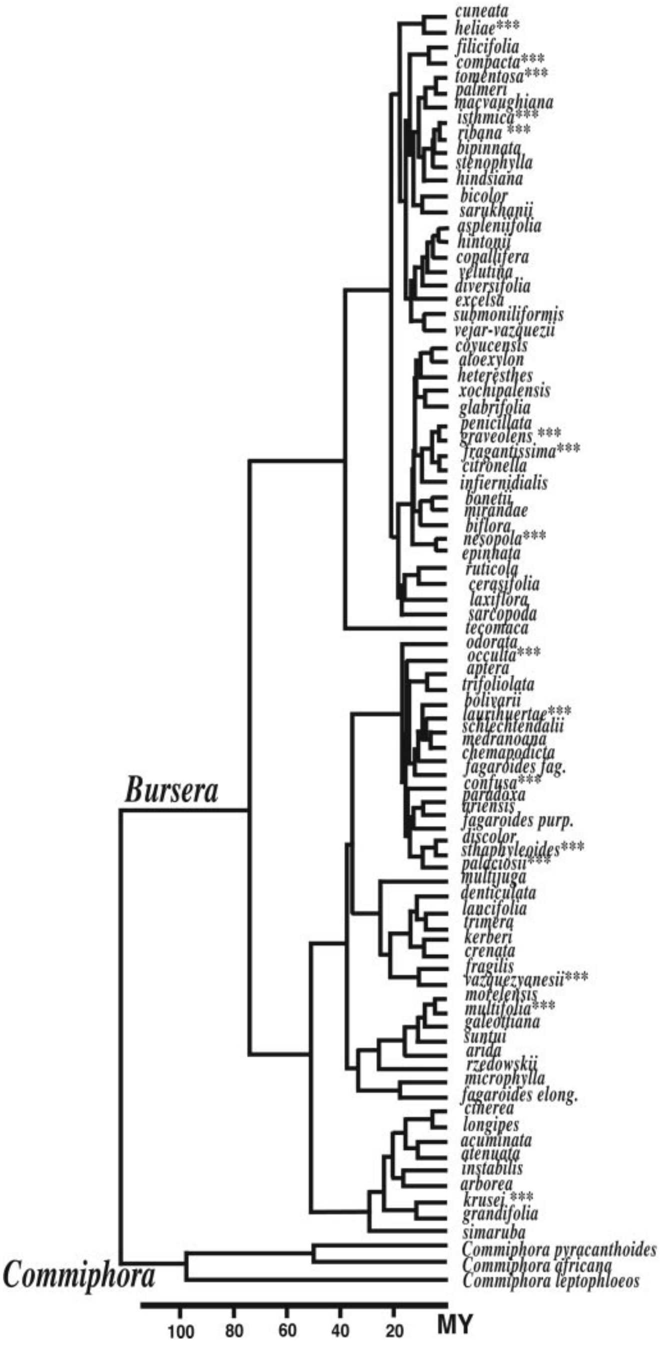

Fig. 2. Time-calibrated phylogeny of *Bursera* (modified from ref. 13). Asterisks indicate species that were added to the phylogeny on the basis of their taxonomic descriptions and for which divergence time is unknown.

Results and Discussion

Fig. 2 shows the time-calibrated phylogeny of *Bursera*. Diversification of extant *Bursera* began in the end of the Cretaceous period, ≈70 Mya, with the division of the genus into the two sections, *Bursera* and *Bullockia*. Nevertheless, the number of diverging lineages in the phylogeny is low until ≈30 Mya, with many of the extant species originating after this time. Between 50 and 30 Mya, the genus went from three to seven major lineages, but in the next 10 MY, they had increased to 14. Between 20 and 5 Mya, 60 more lineages had diverged (Fig. 3).

Results using the γ statistic and diversification rates confirm these patterns. From 60 to 34 Mya (before the raising of the

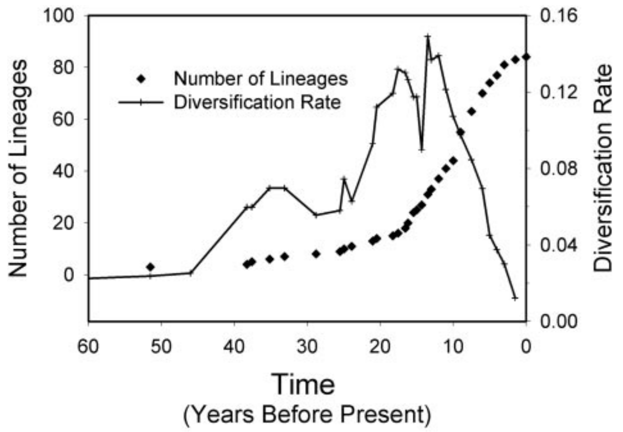

Fig. 3. Number of *Bursera* lineages through time and 10-MY average diversification rates at different times over the last 60 MY.

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 Nevolcanic 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

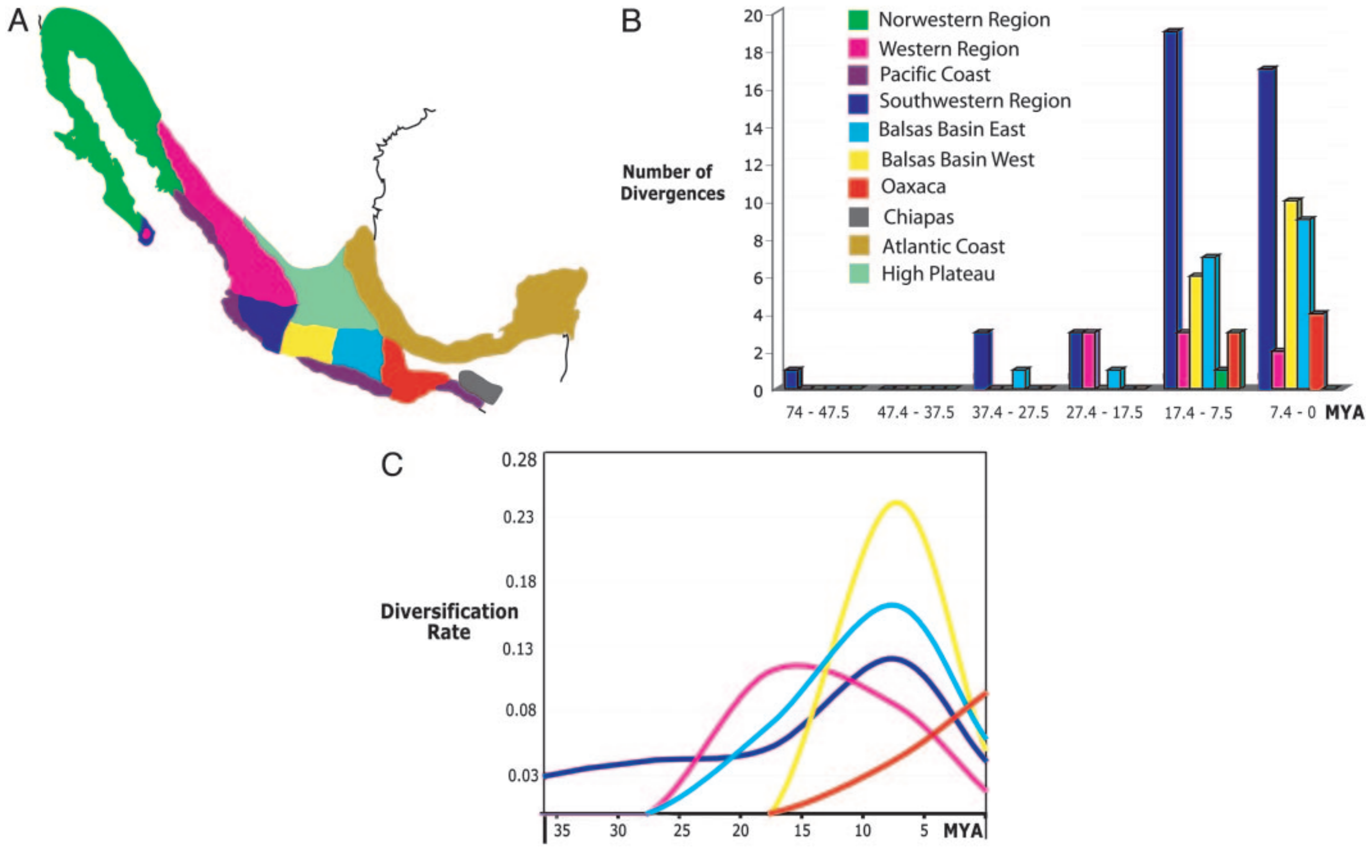

Fig. 4. *Bursera*'s historical expansion in Mexico. (*A*) The distribution of *Bursera* was divided into 10 subareas. (*B*) Number of lineages that have diverged in each subarea of distribution at different time intervals. Some of the subareas have not had speciation events. (*C*) Diversification rates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

observed after the beginning of the uplift of the Sierra Madre Occidental and the Neovolcanic belt.

Since 13.5 Mya, diversification of the genus has decreased steadily. By 1.5 Mya, the Kendall/Moran estimator is only 0.012 species per million years, and the value of γ is negative for the time interval of 34–1.5 Mya, indicating a significant deceleration ($\gamma = -2.92$ $P < 0.01$, two-tailed test).

Thus, according to these results, between 30 and 20 Mya, conditions were favorable for the radiation of *Bursera*. Because all extant *Bursera* species are highly adapted to dry, warm, and seasonal climate, it seems reasonable to deduce that the dry forest had also began developing at this time. By 13.5 Mya, *Bursera* was at its peak rate of diversification. Diversification results do not preclude the possibility that the dry forest had already originated before, and that for some reason *Bursera*'s representation in this vegetation was low, but they definitely suggest that the minimum age of the dry forest in Mexico is between 30 and 20 MY.

The Sierra Madre Occidental and the Neovolcanic belt have often been considered crucial to providing the ecological conditions for the persistence of the tropical dry forest by blocking the cold storms and winds from the north. Most of the floral elements in this forest are not adapted to freezing conditions and at present, the forest occurs where the absolute minimum temperature is above 0°C. The diversification rates are highest between 20 and 7.5 MY. These estimates of diversification times for *Bursera* are concurrent with the highest activity in mountain building in Western Mexico, when both the Sierra Madre Occidental and the Neovolcanic axis were being formed. This coincidence suggests that the mountain uprising may have been critical in providing the conditions not only for the persistence but also for the original establishment of this vegetation type in Mexico.

Only 5 of the 10 geographic areas investigated appear to have been important centers of diversification. The southwestern region seems to have functioned as a major engine for *Bursera*'s speciation. According to the DIVA reconstruction, ≈60% of *Bursera*'s lineages originated here (Fig. 4*B*). In contrast, areas such as the Atlantic and Pacific coasts, the high plateau, the northwestern region, and the Chiapas regions have one or zero divergence events each. The timing of diversification of *Bursera* has differed geographically as well. Lineages that are between 30 and 17 MY old diverged mostly in the west of the country (western and southwestern regions), whereas the newest lineages tend to occur in the south on both sides of the Balsas basin and continue to be produced in the southwestern region as well. The southwestern region has a particularly high rate of diversification at the end of the formation of the Sierra Madre when the Neovolcanic axis was also beginning in the west. If *Bursera*'s spatial diversification progressed after the geographic expansion of the tropical dry forest, the forest was first established in the west in the last 30 MY and then expanded southeast to the Balsas depression and the north of Oaxaca. My results thus suggest that *Bursera* diversified as the Sierra Madre Occidental and later the Neovolcanic belt were formed, creating conditions for the establishment and persistence of the tropical dry forest. From the south of Mexico, the forest probably expanded to Central America, where fossil evidence seems to suggest that it invaded only after 2.5 Mya (33).

Although diversification is still active in *Bursera*, in the last 7.5 MY, rates have decreased in all but one of the geographic areas studied. One possible reason for this decline is that incipient speciation is hard to recognize, so there may be new cryptic species awaiting taxonomic description. However, this does not seem very plausible. To maintain diversification rates similar to the ones between 30 and 7.5 Mya, taxonomists would have to have overlooked ≈80 species that diverged in the last 7.5 MY. Another possibility, perhaps more plausible, is that the opportunity for speciation of *Bursera* is in decline as the possibilities for further geographical expansion of the tropical dry forest have declined. The Sierra Madre Occidental completed its last uprising ≈15 Mya, and the western side of the Neovolcanic belt has not had extensive additions in the last 5 MY. The most recent significant extensions to the belt are along its most eastern side, and it is only close to those last extensions, in the Oaxaca area, where diversification rates are still increasing. Further evidence for species saturation in the tropical dry forest is that recently derived species that originated in the dry forest are currently distributed in more arid or more humid environments where other kinds of vegetation persist. DIVA results show that those arid or more humid environments function as diversity sinks, places that maintain *Bursera* species, but where speciation does not occur (Fig. 4*C*).

Even though the tropical dry forest is one of the four most extensive types of vegetation in Mexico, there has been little information on its time of origin and historical directions of expansion. By calculating *Bursera*'s diversification rates at different times and by reconstructing the species centers of divergence, I have shown that the tropical dry forest probably originated between 30 and 20 Mya, and that it was first established in the west and from there expanded to south and central Mexico.

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