

Tropical mountain cradles of dry forest diversity

Christopher W. Dick^{*†} and S. Joseph Wright^{*}

^{*}Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panamá; and [†]Department of Ecology and Evolution and University of Michigan Herbarium, University of Michigan, Ann Arbor, MI 48109-1048

Of all ecosystems in tropical America, seasonally dry forests, patchily distributed where relatively fertile soils, annual rainfall <1,600 mm, and strong seasonal drought coincide, are perhaps the least understood and most endangered (1, 2). Mesoamerican dry forest diversity peaks in southwest Mexico, where up to 16% of tree species are local endemics (3). Judith Becerra, in this issue of PNAS (4), presents a novel historical analysis of Mexican dry forests based on a time-calibrated phylogeny of the dry forest tree genus *Bursera*, which was the source of the sacred Mayan incense known as copal. Becerra found that peak diversification of *Bursera* lineages [34–17 million years ago (Ma)] in northwest Mexico followed the uplift of the Sierra Madre Occidental (34–15 Ma), whereas diversification of a southern lineage (peaking at 13.5 Ma) tracked the rise of the Neovolcanic axis (23–2.5 Ma) (Fig. 1). The rising mountains, through their influence on regional climate, permitted dry forests to take hold in Mexico and to spread into Central America.

Becerra's study (4) is an exciting contribution to historical biogeography, which, in the absence of adequate fossils, turns increasingly to plant phylogeny to infer biome histories (5). The dry forest study raises challenging methodological questions. Can the age of a single clade be used to infer the age of a biome? In the neighboring rain forest biome, for example, major clades have radiated at vastly different times, so focus on a single taxon would be misleading. On the side of rain forest youth, the common ancestor of the species-rich ($n > 300$ species) neotropical tree genus *Inga* is apparently less than 6 million years old (6). *Inga* shares the rain forest with trees from several families in the Malpighiales, whose ancestors derive from mid-Cretaceous (94–112 Ma) proto-rain forests (7). As another example, the dry forest legume clade *Leucaena* underwent endemic radiation in southwest Mexico beginning ≈10 million years ago (8), making it younger than *Bursera* but still compatible with Becerra's biogeographic model.

Calibrating the Molecular Clock

The event used to calibrate the timing of diversification within *Bursera* might have to be reexamined. The genus most



Fig. 1. Approximate distribution of seasonally dry forest in Mexico (outlined) (12). Tertiary plant macrofossils in Mexico are known only from a mid-Pliocene (3–5 Ma) site (yellow circle), and from an upper Oligocene (28–24 Ma) site (red circle) (16).

closely related to *Bursera*, *Commiphora*, has several species in Africa and at least one species (*Commiphora leptophloeos*) in South America. Becerra (4) assumed a Gondwanan origin of the family and used the separation of Africa and South America (95–100 Ma) to date disjunct *Commiphora*'s common ancestor (9) and thereby calibrate divergence times across

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the family. Burseraceae is one of nine flowering plant families that comprise the monophyletic species-rich Sapindales (>5,700 species), whose first known fossils appear in Europe ≈65 Ma (10). A 47-million-year lapse between the proposed Gondwanan origin of *Commiphora* (≈112 Ma) (9) and the first fossil Sapindales is hard to reconcile, unless one posits 47 million years of Gondwanan isolation not yet discovered in the fossil record. This seems unlikely.

Transoceanic dispersal of *C. leptophloeos* to South America is an alternative explanation, favored by systematists (10) who posit a North American origin of

Burseraceae during the Paleocene (≈60 Ma) (Fig. 2). The North American dispersal hypothesis is compelling. The most important dry forest tree family, Leguminosae, has numerous recent clades with species in Africa and tropical America, whose geographic distributions can be explained only by oceanic dispersal (8). The dispersal scenario cuts the estimated divergence times of Mexican *Bursera* roughly in half, drawing them closer in time to the radiation of cooccurring *Leucaena* and other dry forest endemic legume clades (8).

Causes of Diversification

Under the North American dispersal model, diversification of Mexican *Bursera* still overlaps with the rising Neovolcanic axis. What are the plausible mechanisms of speciation? In a paper aptly titled “Why mountain passes are higher in the tropics” (11), D. H. Janzen explained how relatively small tropical mountains act as allopatric barriers for lowland populations. Their disproportionate stature owes to the latitudinal gradient in seasonality and hence the physiology of tropical plants. Temperate-zone plants must adapt to warm summers and freezing winters and therefore are able to ascend to cool eleva-

See companion article on page 10919.

[†]To whom correspondence should be addressed. E-mail: dickc@si.edu.

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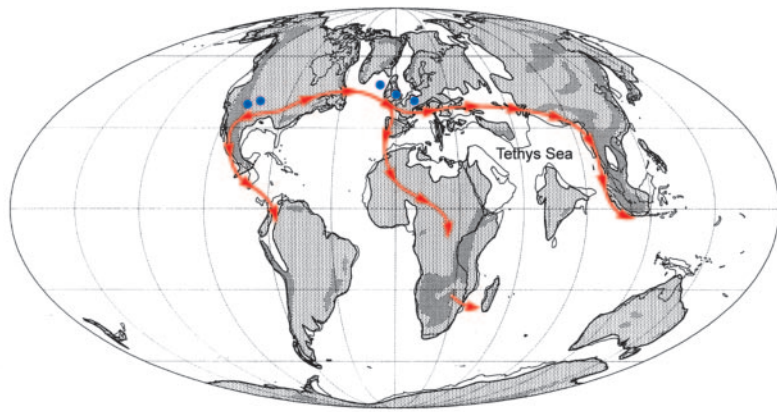


Fig. 2. The North American origin and dispersal hypothesis for Burseraceae modified from ref. 10. Map shows Eocene shorelines (53 Ma) and early Eocene fossil locations of Burseraceae (blue circles).

tions. Temperature-sensitive tropical plants, on the other hand, adapted to a narrow range of warm and aseasonal temperatures, are restricted to the warmth of low altitudes. Moreover, tropical mountains create a mosaic of soil and climatic gradients on their surface that favor adaptive divergence.

Although tropical mountains undoubtedly alter the evolutionary trajectories of subdivided populations, they also define distribution patterns of vegetation through their influence on regional climate. Nowhere is habitat variation more evident than in mountainous Mexico, with its jigsaw puzzle of vegetation types (12). The long finger of dry forest along the Pacific coast is flanked by thorn woodland to the west and conifer or oak woodland to the east. Rain forest or semievergreen forests envelop islands of dry forest along the Gulf Coast. Thus, tropical mountains contribute to sharp climatic gradients and the juxtaposition of dissimilar habitats.

The mosaic of adjacent habitats can lead to ecotonal speciation (13) or “hab-

itat switching.” Habitat switching may be inferred when a clade contains species adapted to dry forest, grassland, and rain forest habitat (8, 14), and it may be frequent during periods of climate change. There have been up to 20 glacial cycles during the past 2 Ma. The longer glacial periods ($\approx 100,000$ yr) were relatively cool and dry in the tropics. The shorter interglacial periods ($\approx 10,000$ – $20,000$ yr) were warmer and wetter and presumably similar to modern climates. Seasonally dry forests likely expanded during the long glacial periods and contracted during the shorter interglacials (15). The dynamic habitat mosaic, like a kaleidoscope turning during periods of climate change throughout the Pleistocene and earlier (15), may be an additional cause of biotic diversification in Mesoamerica.

Becerra (4) suggests that mountain uplift provided climatic conditions necessary for dry forest by blocking cold winds and storms from the north. This hypothesis does not explain how megathermal plants persist in lowlands

north and east of these mountains. An alternative hypothesis is that dry forest expansion was caused by aridity stemming from Miocene cooling (16, 17) and rain shadows created by rising mountains. While promoting adaptive divergence, uplifting mountains also must have provided refuge for lineages that arose earlier and elsewhere, such as the recently discovered genus *Beiselia*, a Mexican dry forest endemic represented by a single species (*Beiselia mexicana*), whose basal phylogenetic position within the Burseraceae implies a Paleocene origin (10). The interplay between mountain uplift and cladogenesis and lineage sorting in tropical dry forests may be examined in other places. The inter-Andean dry forests of Peru, for example, parallel Mexico’s dry forests in species diversity and endemism (18) and could serve as a laboratory to test the generality of Becerra’s important result.

Future of Mexican Dry Forest

What of the future of Mexican dry forests? Because they grow on soils suitable for agriculture and human occupation, $<2\%$ of the pre-Columbian dry forest remains in Mesoamerica, and it is largely unprotected (2). The work of Becerra (4) and colleagues (8, 10) indicates that remnant Mexican dry forests harbor endemic tree lineages and merit urgent conservation measures. In the words of noted botanist A. H. Gentry, “To whatever extent a single neotropical dry forest region is to be given conservation priority, that region should be southwestern Mexico where dry forest diversity and endemism felicitously coincide” (3).

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