

Commentary

Molecular systematic perspectives on biome origins and dynamics

Phylogenetic reconstructions of diverse tropical groups have yielded biological insights that extend well beyond the field of systematics, illuminating such topics as biome assembly and plant–insect coevolution. In this issue of *New Phytologist*, De-Nova *et al.* (pp. 276–287) present a rigorous time-calibrated phylogeny of the Neotropical tree genus *Bursera* in order to estimate lineage ages, and to investigate how geography and ecology have structured its species diversification. Because *Bursera* is a dominant component of Mesoamerican seasonally dry tropical forests (SDTFs), the study provides evidence relating to the origin and expansion of this important biome. The study also sets the record straight on the age of a well-known plant–herbivore interaction.

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Seasonally dry tropical forests (SDTFs) and *Bursera* trees

SDTFs occur on fertile soils and maintain a more or less continuous woody canopy. They are patchily distributed in lowland tropical regions and experience several leafless months in the dry season (< 100 mm per month). Despite the arid conditions, fire is not a natural feature of SDTFs and most of its species, which often include succulents, have few adaptations to fire. This sets SDTF apart from both grassland and wooded savannas (Pennington *et al.*, 2009). Because of their good soils, SDTFs have been largely displaced by agriculture, and are considered the most threatened type of tropical forest in the world.

Like other tropical American SDTFs, Mesoamerican dry forests are dominated by the legume family (Leguminosae or Fabaceae), but *Bursera* (Burseraceae) is a characteristic and often

dominant element, especially in some areas of Mexico (Fig. 1). Burseraceae is a pantropical family of trees with aromatic terpenoid resins, which are often maintained at high-pressure in specialized leaf canals and in bark. The resins have found their way into the fabric of human culture as the source of biblical frankincense and myrrh, and the Mesoamerican incense copal, which is derived from *Bursera* and *Protium* species. Flea beetles (*Blepharida*) counter *Bursera*'s ‘squirt defense’ by chewing at the canals to reduce the pressure, and by evolving metabolic pathways that enable them to digest the toxins (Speight *et al.*, 2008). The *Bursera* and *Blepharida* phylogenies are topologically congruent (Becerra, 2003) and because *Blepharida* and *Bursera* relatives occur both in Africa and tropical America, Becerra (2003) inferred that the *Bursera*–*Blepharida* interaction originated 112 million yr ago (Ma), when the future continents were still connected as part of the Gondwana landmass.

There are an estimated 106 species of *Bursera* distributed from Mexico to Peru and the Caribbean. Most of the species (*c.* 80) are endemic to various SDTF nuclei in Mexico. Using a phylogeny calibrated with fossil and biogeographic evidence, including a presumed Gondwanan (97.5 Ma) origin of the sister genus *Commiphora*, Becerra (2005) inferred a mid-Miocene (*c.* 15 Ma) origin of clades located near the western Sierra Madre mountains, with subsequent radiation along the more southern Mexican Transvolcanic belt. Because the timing of two major pulses of *Bursera* speciation appeared to overlap in time and space with the uplift of the two mountain chains, Becerra (2005) proposed that these mountains created the climatic conditions necessary for *Bursera* speciation and for the expansion of Mexican SDTFs.

De-Nova *et al.* have built upon previous work in many ways, including: increasing the taxonomic sampling to include 93 out



Fig. 1 *Bursera moreletensis* behind a line of columnar cacti and mimosoid legume shrubs in the seasonally dry tropical forest (SDTF) biome in Mexico. Photograph taken in the Valley of Tehuacán, Puebla, courtesy of Rosalinda Medina.

of the 106 known species; using several additional genome regions in phylogenetic estimation; increasing the number of fossil calibration points to 17; and excluding biogeographic calibration points such as hypotheses of Gondwana vicariance.

The new analysis has produced a much younger estimate for the age of the *Bursera* (*c.* 50 Ma; see table 1 in De-Nova *et al.*). The fact that *Bursera* may be > 60 million yr younger than the prior estimates does not come as a surprise. In a careful phylogenetic analysis of the Burseraceae, Weeks *et al.* (2005) estimated that the family shared a common ancestor with the Anacardiaceae *c.* 60 Ma, which would make the Burseraceae, and all of its subclades, much too recent to be of Gondwanan origin. Because most of the relevant fossils occurred in high latitudes, Weeks *et al.* (2005) hypothesized that the family originated in North America at a time when frost intolerant ('boreotropical') vegetation covered much of that continent. Boreotropical dispersal has supplanted Gondwana vicariance as a preeminent explanation for many pantropical plant distributions (Davis *et al.*, 2002). The weight of the evidence points to an Eocene origin for *Bursera*, which suggests that the notion of an ancient 112 million yr history of coevolution between *Bursera* and *Blepharida* (Becerra *et al.*, 2009) should be discarded (Speight *et al.*, 2008).

Despite this and other discrepancies in the revised set of divergence time estimates (see table 1 in De-Nova *et al.*), the timing of diversification in both studies overlaps with mountain uplift events. As De-Nova *et al.* point out, however, the mountain building spans such a broad time frame (starting from the middle Cretaceous for the Sierra Madres) that it would be remarkable to not find some overlap. Uncertainty around geological and molecular clock estimates makes it difficult to find strong correlations, let alone causal relationships, between specific geological events and the origin of the SDTF biome.

Biome dynamics

De-Nova *et al.* dated the origin of most *Bursera* species to the Miocene, and they report an average species age of > 7 Ma. Such old species are unusual in the tropical plant literature (but see Dick *et al.*, 2003; Pennington *et al.*, 2010). Most species in the Neotropical tree genus *Inga* (Fabaceae; *c.* 300 species), for example, originated during the last two million yr of the Pleistocene (Richardson *et al.*, 2001). The method used by De-Nova *et al.* estimates the age of the common ancestor of putative sister species and may overestimate individual species ages, particularly if the actual sister species has not been sampled (or is extinct). Nevertheless, these are very old species, and it is intriguing to imagine seasonally dry forests in the Miocene with many of the same species as today, found in the same geographic locations, but under global temperatures that were warmer than the present day.

De-Nova *et al.* found evidence of phylogenetic clustering of *Bursera* species with respect to geographic distribution. This strong signal of phylogenetic geographic structure, where sister species are likely to be found sharing the same SDTF nucleus, has also been found in legumes of South American SDTFs (Pennington *et al.*, 2009). There were few evolutionary transi-

tions in *Bursera* to non-SDTF habitats, and migration among SDTF nuclei was rare. This suggests that non-SDTF habitats pose a barrier to migration, even over evolutionary time scales, and perhaps that even if propagules reach a new SDTF area, establishment is infrequent. The limited interchange of species between the SDTF nuclei has resulted in high beta (among site) diversity in *Bursera*, and in the woody plant component of the SDTF as a whole (Linares *et al.*, 2011). The high phylogenetic geographic structure found in Neotropical SDTFs may not be duplicated in Neotropical rain forests such as the Amazon (Pennington *et al.*, 2009), where the geographic structure of plant phylogenies is much lower. This may partly reflect the fact that dispersal – even across major oceans – has been important in shaping tropical rain forests communities over evolutionary time scales (Pennington & Dick, 2004).

In *Bursera*, habitat switching most frequently occurs from the SDTFs to more xeric habitats, with a single transition to wetter forests. This phylogenetic niche conservatism may reflect physiological trade-offs that largely confine *Bursera* to the SDTF biome. For example, trade-offs between growth and drought tolerance might keep *Bursera* from competing in wetter forests (Engelbrecht *et al.*, 2007). Or, as in the case of Amazonian Burseraceae in the genus *Protium*, the trade-off may involve production of chemical defenses at the expense of faster growth. This was shown experimentally for *Protium* found in white-sand forest in the Amazon basin (Fine *et al.*, 2006). A similar experimental approach may uncover some of the physiological trade-offs that restrict *Bursera* and some legume clades to the SDTF biome.

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