New Phytologist

Insights into the historical construction of species-rich Mesoamerican seasonally dry tropical forests: the diversification of *Bursera* (Burseraceae, Sapindales)

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Received: *15 June 2011*
Accepted: *19 August 2011*

New Phytologist (2012) **193**: 276–287
doi: 10.1111/j.1469-8137.2011.03909.x

Key words: aridification, *Bursera*, dated phylogenies, diversification rate, geographical structure, Mesoamerica, niche conservatism, seasonally dry tropical forests.

Summary

- Mesoamerican arid biomes epitomize neotropical rich and complex biodiversity. To document some of the macroevolutionary processes underlying the vast species richness of Mesoamerican seasonally dry tropical forests (SDTFs), and to evaluate specific predictions about the age, geographical structure and niche conservatism of SDTF-centered woody plant lineages, the diversification of *Bursera* is reconstructed.
- Using a nearly complete *Bursera* species-level phylogeny from nuclear and plastid genomic markers, we estimate divergence times, test for phylogenetic and temporal diversification heterogeneity, test for geographical structure, and reconstruct habitat shifts.
- *Bursera* became differentiated in the earliest Eocene, but diversified during independent early Miocene consecutive radiations that took place in SDTFs. The late Miocene average age of *Bursera* species, the presence of phylogenetic geographical structure, and its strong conservatism to SDTFs conform to expectations derived from South American SDTF-centered lineages.
- The diversification of *Bursera* suggests that Mesoamerican SDTF richness derives from high speciation from the Miocene onwards uncoupled from habitat shifts, during a period of enhanced aridity resulting mainly from global cooling and regional rain shadows.

Introduction

The Neotropical Realm is unparalleled in its biotic complexity (Gentry, 1982a; Graham, 2010). The northern Neotropical region geologically corresponds to southwestern Laurasia. It is occupied today by Mexico and Central America, and is here loosely referred to as ‘Mesoamerica’. It includes, but is not limited to, the Mesoamerican Biodiversity Hotspot (Myers *et al.*, 2000), and encompasses a vast diversity of habitats, functional adaptations, and species richness. Substantial efforts to document Mesoamerican biodiversity have been ongoing for centuries (e.g., Sessé & Mociño, 1887; Hernández, 1942; CONABIO, 2008). However, its sheer richness, overlaid on an extensive and physically complex territory, have rendered these fundamental efforts still incomplete. Very little is known about the main evolutionary processes underlying high species richness in different Mesoamerican biomes. Is it caused by high speciation, or by low extinction? Is it derived from temporally circumscribed speciation bursts, or from long-term species accumulation? What is the relative relevance of *in situ* diversification vs the prevalence of immigrants? The main aim of this study is to investigate the evolutionary processes that contribute to high species richness in a particular biome in Mesoamerica.

Arid biomes are prominent in Mesoamerica, providing emblematic landscapes and a substantial part of its biodiversity. While less diverse than wet forests, Mesoamerican arid biomes are richer than their South American counterparts (Gentry, 1982a; Lott *et al.*, 1987; Trejo & Dirzo, 2002; Villaseñor, 2004; Pennington *et al.*, 2009). Seasonally dry tropical forests (SDTFs) encompass a variety of plant associations, from relatively moist tall forests to dry, succulent-rich scrubs, that grow on fertile soils where rainfall is below 1800 mm yr^{-1}, and receive < 100 mm for 5–6 months (Pennington *et al.*, 2009). They are fire- and frost-intolerant, and, in South America, are distributed in small isolated patches separated by areas that are wetter, colder, extremely arid, or at very high elevation (Pennington *et al.*, 2009). Contrary to other biomes (e.g. lowland rainforests; Gentry, 1982a) and biological lineages (e.g. hylid frogs, Wiens *et al.*, 2006), the richest Neotropical SDTFs are distant from the Equator, leading some workers to discuss an ‘inverse latitudinal diversity gradient’ (Gentry, 1995; Trejo & Dirzo, 2002). Lott *et al.* (1987) documented 83–105 spp. km^{-2} at 19°N in Chamela, Mexico, close to the northern end of the distribution of this vegetation type, a substantially higher richness than in sampled South American dry forest sites with equivalent precipitation, and much higher than predicted by the postulated linear relationship between mean annual precipitation and Neotropical plant species richness (Gentry, 1982b; Lott *et al.*, 1987; Trejo & Dirzo, 2002). In particular, Mexican SDTFs have high degrees of endemism and a pronounced species turnover displayed by very low among-site floristic similarity (Trejo & Dirzo, 2002).

After its emergence from the North American epicontinental sea in the early Tertiary, the area corresponding to central and northern Mexico was at least somewhat arid because of its latitudinal position in the descending arm of the Hadley global convection cell and the rain shadows cast by the western and eastern Mexican mountain ranges (Sierra Madre Occidental and Sierra Madre Oriental, respectively) which resulted from orogenic processes starting in the middle Cretaceous and mostly culminating by the late Eocene (Graham, 2010). Between the Miocene and Pliocene, aridity was further enhanced by a global cooling process that resulted in polar ice sheets and local volcanism that enhanced rain shadows (Graham, 2010, pp. 60–66). In response to Miocene aridification, preadapted lineages that existed in North America in the middle Eocene expanded southwards and, together with newly evolved species, represented the onset of the vegetation of the contemporary Sonoran and Chihuahuan Deserts (Graham, 2010, pp. 62–63). Climatic and fossil evidence, as well as molecular clock ages of SDTF-centered lineages (Lavin *et al.*, 2003, 2004; Pennington *et al.*, 2004; Pirie *et al.*, 2009; Schrire *et al.*, 2009), congruently indicate that Neotropical SDTFs may have arisen in North America during the middle Eocene (Pennington *et al.*, 2009).

Considering the early Cenzoic origin, aridity and patchy distribution of South American SDTFs, Pennington *et al.* (2009) postulated that these attributes have shaped the evolution of resident woody plant lineages. Seasonal dryness represents a barrier to potential colonists not adapted to some degree of aridity. Their patchy distribution separated by areas that are difficult to surmount causes limited dispersal of propagules and pollen. These barriers to migration, combined with their prolonged existence, have resulted in a distinctive species composition for each patch. As a consequence, South American SDTFs are compositionally stable, dispersal-limited systems with high among-patch beta diversity, which is positively correlated with geographical distance (Linares-Palomino *et al.*, 2011). SDTF-centered lineages consequently include ancient species and exhibit strong geographic structure in their phylogenies (Pennington *et al.*, 2009). Moreover, South American SDTF lineages exhibit strong niche conservatism where closely related species share the same type of habitat, and habitat shifts are strongly directional: predominantly from SDTFs to other types of vegetation (Pennington *et al.*, 2009). Mesoamerican SDTFs, while sharing with their South American counterparts aridity and origin since at least the Miocene, occupy a variety of physical conditions (e.g. edaphic, altitudinal), a wide latitudinal range, and have a continuous distribution over extensive areas (e.g. the Mexican Pacific slope and the Balsas river basin; Fig. 1), which is unusual for other Neotropical SDTFs (Trejo & Dirzo, 2002).

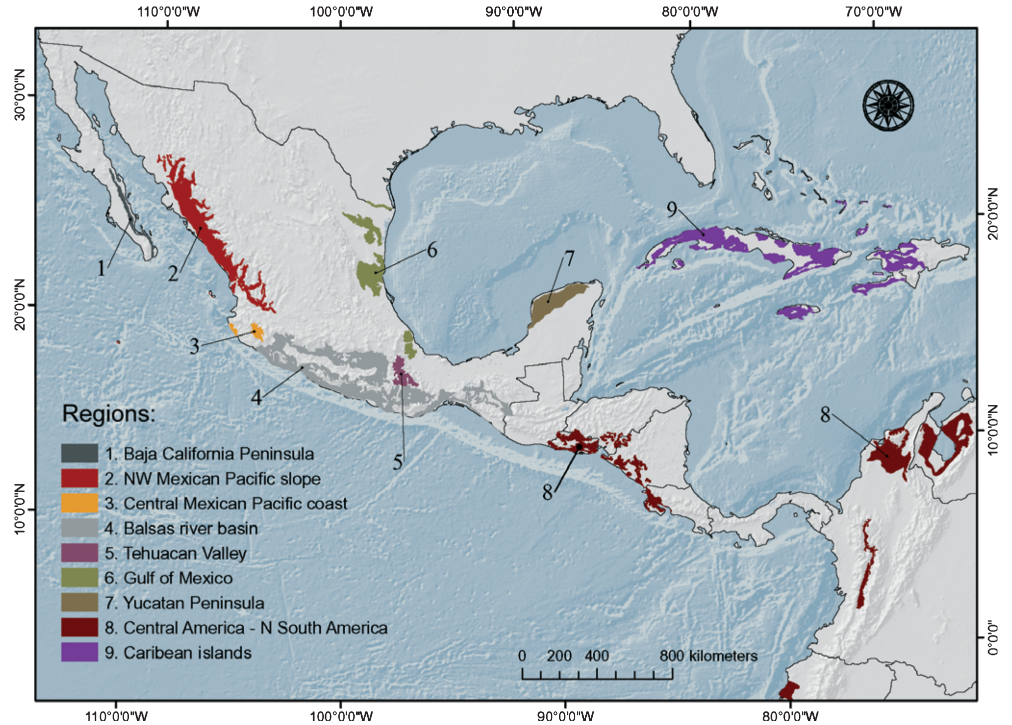

Fig. 1 Main areas of *Bursera* distribution in seasonally dry tropical forests (SDTFs). The colored areas represent nine main disjunct areas of distribution of *Bursera* in SDTFs, delimited mainly by considering species distributions (see main text). SDTFs are continuously distributed among several of these areas. Nevertheless, the distribution of *Bursera* species is discontinuous as a result of altitudinal barriers. Map based on Brown *et al.* (2007).

To document some of the diversification processes underlying the high species richness of Mesoamerican SDTFs, and to evaluate if the old species age, high geographical structure and directionality of habitat shifts observed for South American SDTF-centered lineages prevail in their Mesoamerican counterparts, we use the genus *Bursera* (Burseraceae, Sapindales) as a study system. *Bursera* is arguably the most distinctive physiognomic component of Mesoamerican SDTFs. It includes *c.* 107 species which, except for *B. tonkinensis* from northern Vietnam, are approximately distributed between northern Mexico and northern South America (Fig. 1). *Bursera*'s diversification has been linked with the southward expansion of SDTFs in North America in response to the uplift of the Sierra Madre Occidental and the Mexican Transvolcanic Belt (Becerra, 2005; Cevallos-Ferriz & González-Torres, 2005; Dick & Wright, 2005). The strong association of *Bursera* with SDTFs has prompted attempts to reconstruct the history of this vegetation type in Mexico on the basis of the diversification of *Bursera* (Becerra, 2005; but see, e.g. Dick & Wright, 2005).

Here we estimate phylogenetic relationships for a nearly complete representation of *Bursera* species based on one plastid and four nuclear molecular markers. To document the diversification process leading to *Bursera* species diversity, we estimate the timing of lineage splitting and test for significant diversification heterogeneity among phylogenetic branches and through time. To evaluate specific predictions about SDTF-centered lineages (Pennington *et al.*, 2009), we obtain the average age of *Bursera* species; conduct tests of geographical structure; and reconstruct habitat shifts. We expect the following: a pre-Pliocene age for most *Bursera* species, particularly for those centered in SDTFs; the presence of geographical structure in its phylogeny; and directional habitat shifts predominantly from SDTFs to other vegetation types.

Materials and Methods

Taxa and data

Ninety-three species of *Bursera*, from a total of *c.* 106, were sampled from their natural distributions in the American continent. Species of *Commiphora* and representatives of the main lineages within Burseraceae were also included. Species of *Searsia* and *Rhus* (Anacardiaceae) were included as outgroups. Data for phylogenetic analyses are the nucleotide sequences of phosphoenolpyruvate carboxylase (fourth intron of the *PEPC* gene), nuclear nitrate reductase (third intron of the *NIAi3* gene), internal and external transcribed spacers (*ITS* and *ETS* of the nuclear ribosomal DNA, respectively), from the nuclear genome; and the *psbA-trnH* intergenic spacer, from the plastid genome. Previously published and newly generated sequences were combined (Supporting Information, Table S1). DNA extraction, amplification and sequencing followed Rosell *et al.* (2010; details provided in Methods S1). Sequence alignments are available in TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S11329).

Phylogenetic analyses

The sequences of each locus were aligned with MUSCLE (Edgar, 2004), and adjusted with Se-Al v.2.0a11 Carbon (Rambaut, 2002). The best fit model for each locus was identified with the Akaike Information Criterion (AIC) implemented in ModelTest v3.06 (Posada & Crandall, 1998), as follows: TVM+G for *ETS*; GTR+I+G for *ITS*; K91uf+G for *PEPC*; HKY+G for *NIAi3*; and HKY+G for *psbA-trnH*. Parsimony analyses were conducted independently for each locus, using NONA (Goloboff, 1999) spawned in WinClada (Nixon, 2002), and resulted in trees displaying weakly supported incongruences (results available from the authors). Each of the five loci, and a concatenated five-loci matrix, were analyzed with MrBayes v3.1.2 (Huelsenbeck & Ronquist, 2001). Details of Bayesian phylogenetic analyses are provided in Methods S1. The maximum *a posteriori* (MAP) tree topology derived from the five-loci analysis was used as a working hypothesis of phylogenetic relationships.

Divergence time estimation

Estimation of *Bursera* divergence times was done in two steps. First, the age of crown group Burseraceae was estimated using *rbcL* and *atpB* sequences for a representation of 28 order-level eudicot clades, and including the crown group of Burseraceae (Table S2). Ages were estimated with the uncorrelated lognormal relaxed clock available in BEAST v1.4.8 (Drummond & Rambaut, 2007), calibrated with the earliest fossil tricolpate pollen grains plus 17 fossil-derived minimum-age constraints (Table S3). In the second step, the mean age and credibility interval of the Burseraceae crown node estimated previously were assigned as root height priors to the *Bursera* data set, and used to estimate divergence times among *Bursera* species. Dating was conducted with the same method as described earlier, and included five fossil-derived minimum age constraints (Table S4). Dating analyses are described in detail in Methods S1.

Diversification rate analyses

The absolute rate of diversification (r) of *Bursera*, sections *Bursera* and *Bullockia*, and several internal clades were calculated using a maximum likelihood estimator that accounts for the possibility of extinction (Magallón & Sanderson, 2001). Because absolute rates of speciation (λ) and extinction (μ) are unknown, diversification rates were calculated under no extinction, and under a high relative extinction rate ($\varepsilon = \mu/\lambda = 0.0$ and 0.9, respectively).

The presence of significant diversification rate changes was evaluated among the branches of the phylogenetic tree, and through time. Significant phylogenetic rate heterogeneity within crown group *Bursera* was assessed with SymmeTREE v1.1 (Chan & Moore, 2005), a method that, by calculating the combined probability of the observed tree balance given constant stochastic branching (equal rates Markov, ERM), identifies whether, and in which branch, significant diversification increases have occurred

(Chan & Moore, 2002). Because our phylogenetic analysis included only 93 of the 106 known American *Bursera* species, 13 missing species were manually inserted into the MAP topology on the basis of taxonomy and morphology (Table S5). The test was based on one million ERM simulated trees, with polytomies resolved through one million taxon size-sensitive random resolutions. Significant cumulative whole-tree probabilities of diversification rate change were identified through tail probability values of the 0.025 and 0.975 frequentiles of the M_Π statistic (Chan & Moore, 2002). Significant diversification rate shifts were located through *P*-values associated to the Δ_1 and Δ_2 statistics for each internal node, using 150 species for quick shift statistic calculation (Chan & Moore, 2005).

Significant temporal diversification rate heterogeneity was tested with a maximum likelihood model-selection method that fits time-constant and time-variable birth–death likelihood (BDL) models, which differ by being rate-constant or rate-variable through time; allowing one or two temporal rate changes; encompassing extinction; and considering that diversification is diversity-dependent, to a lineage through time (LTT) plot (Rabosky, 2006a,b). Model selection is based on the difference in AIC scores between the best-fitting rate-constant and rate-variable models (ΔAIC_{RC}). The LTT plot can be used to identify the time(s) of diversification change. The BDL method was implemented with LASER v2.3 (Rabosky, 2006b), using a LTT plot derived from the *Bursera* dated phylogeny obtained with BEAST (Fig. 2). The test was conducted using yuleSim to determine the significance of the observed ΔAIC_{RC} statistic by simulating 1000 trees with the same number of taxa as in the input tree, and speciation rate estimated under the pure-birth model.

Tests of geographical structure

Geographical structure among *Bursera* species was evaluated through randomization tests and phylogenetic community structure analyses (Webb, 2000; Irwin, 2002; Lavin, 2006). We identified nine main disjunct areas of distribution of *Bursera* in SDTFs: (1) Baja California Peninsula; (2) NW Mexican Pacific slope; (3) central Mexican Pacific coast; (4) Balsas river basin; (5) Tehuacán Valley; (6) Gulf of Mexico; (7) Yucatán Peninsula; (8) Central America-northern South America; and (9) the Caribbean islands (Fig. 1). These areas were delimited by considering observed *Bursera* species distributions, and modifying the SDTF nuclei defined by Lott & Atkinson (2006), accounting for observations by Toledo Manzur (1982) and Dick & Wright (2005). Whereas SDTFs are continuous over some of these areas, the distribution of *Bursera* species is discontinuous because of their inability to surmount high mountains that transverse these regions. These nine geographical units were mapped onto the *Bursera* MAP tree using parsimony optimization with MacClade v4.07 (Maddison & Maddison, 2005). The observed number of area transformations was then compared with the distribution of the number of transformations of the same character states mapped onto 1000 random trees generated with MacClade. If observed area transformations involved substantially fewer steps than those on random trees, a strong geographic phylogenetic structure was inferred.

The phylogenetic structure of each area was quantified using PHYLOCOM (Webb, 2000; Webb *et al.*, 2002, 2008). The net relatedness index (NRI) and the nearest taxa index (NTI) were estimated from *Bursera* phylogenetic relationships as depicted in the MAP tree. High, low, and negative NRI and NTI values indicate that sister species have a high probability of occupying the same (aggregated distribution), random, or different areas (over-dispersed distribution), respectively. Significance of NRI and NTI values were determined through a frequency distribution of these values calculated for 10 000 randomly assigned geographical areas on the phylogeny.

Direction of habitat shifts

Field observations and species distribution data obtained from published taxonomic accounts were used to determine the main vegetation type preference of each sampled species of *Bursera*. We then transformed all the listed vegetation types into four main categories: seasonally dry tropical forests, tropical rainforests, xerophytic scrubs, and oak forests. The ancestral vegetation type of *Bursera*, and the direction of shifts, were reconstructed using the maximum likelihood approach available in Mesquite v2.74 (Maddison & Maddison, 2010), which incorporates branch length information into ancestral state inference. Reconstructions assumed all transformations to be equiprobable (Mk1 model). The procedure ‘trace over trees’ was used to summarize reconstructions over a set of 1000 chronograms chosen randomly from among those sampled by BEAST (after the burn-in), including only *Bursera* species. Trees were rooted with *Commiphora*, for which a seasonally dry tropical forest was specified as its preferred vegetation type.

Results

Phylogeny estimation

The aligned combined dataset for the five loci contained 109 taxa, including 93 *Bursera* species (Table S1). Bayesian Monte Carlo Markov chains (MCMC) for the five combined loci reached stationarity at *c.* 400 000 generations. The effective sample size (ESS) of almost all estimated parameters is well above 200. The ‘compare’ plot produced by AWTY (Wilgenbusch *et al.*, 2004; available from the authors) suggests that parallel MCMC runs achieved topological convergence. Thirty-one phylograms topologically identical to the MAP topology were found, and one, including PP values, is shown in Fig. S1. Bayesian analysis recognized *Bursera* (posterior probability (PP) = 1.0) and *Commiphora* (PP = 1.0) as monophyletic, forming a sister pair (PP = 1.0). The deepest split within *Bursera* separates sections *Bursera* and *Bullockia* (PP = 1.0 each). The deepest split within section *Bursera* separates the Simaruba group (PP = 1.0) – the ‘mulatos’, including a nested Caribbean clade (PP = 1.0), from the ‘cuajiotes’ (*Bursera*s with exfoliating bark; PP = 1.0) consisting of the sister Fagaroides and Microphylla groups (PP = 0.97

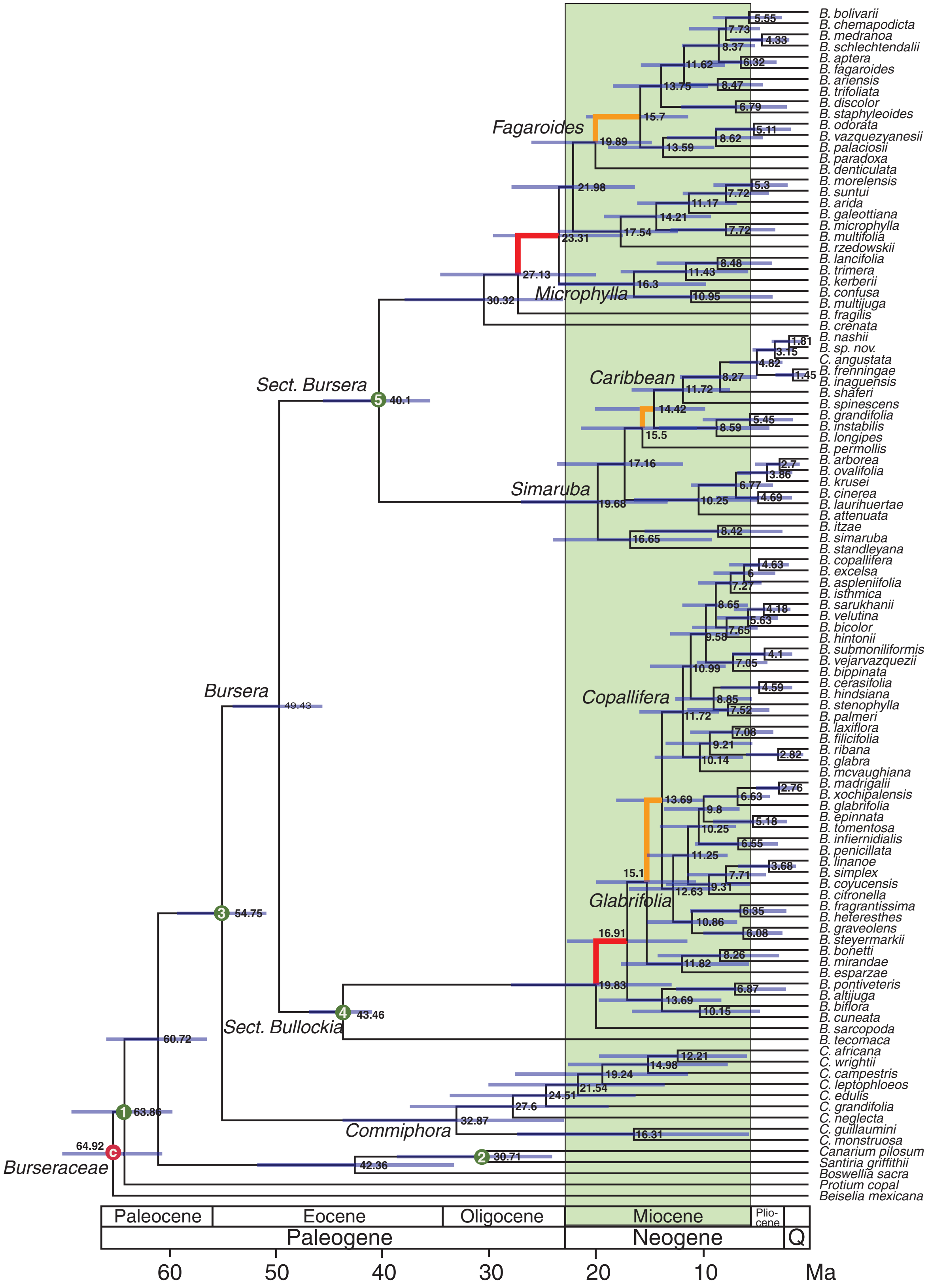

Fig. 2 Timing of *Bursera* diversification. Chronogram derived from the maximum clade credibility tree estimated with the uncorrelated lognormal method in BEAST. Mean ages and their 95% highest posterior density (HPD) are shown next to nodes. The red node (C) represents the calibration node. Green numbered nodes were constrained with fossil-derived minimal ages as shown in Supporting Information, Table S4. Branches marked in red and orange were identified by SymmeTREE as having significant and marginally significant increases in diversification, respectively.

and 1.0, respectively), and the members of the Fragilis group, forming an early diverging grade (Fig. S1).

Independent Bayesian analyses of the five loci (results available from the authors) found low resolution at deep levels in the phylogeny, but the sections inside *Bursera*, and the genus *Commiphora*, were always monophyletic. Whereas the trees obtained with ITS, *NIAi3*, and *psbA-trnH* resolved *Bursera* as the monophyletic sister of *Commiphora*, trees obtained with ETS and PEPC found *Bursera* to be paraphyletic, with section *Bursera*, and section *Bullockia*, respectively, more closely related to *Commiphora*. These relationships are weakly supported.

Divergence time estimation

The uncorrelated lognormal dating analyses in BEAST provided an ESS of > 300 for the age of crown Burseraceae, and estimated a mean age of 57.43 million yr (Myr) (63.35–51.77, 95% highest posterior density (HPD); results available from authors). This estimate falls within the stratigraphic interval containing the oldest fossil remains of Burseraceae (*Bursericarpum aldwickense*, Ypresian, Eocene; Collinson, 1983; Table S4).

The combined MCMCs of the uncorrelated lognormal dating analyses for Burseraceae provided ESS > 200 for age parameters. The mean age for crown Burseraceae is 64.92 Myr (60.33–69.67; Fig. 2). Ages of clades within *Bursera*, and their associated errors, are available in Table 1 and Fig. 2. The average stem group age of *Bursera* species is 7.92 Myr (SD = 6.10). The average age of *Bursera* species that typically inhabit SDTFs is 7.49 Myr (SD = 5.31); of species from xerophytic scrubs is 6.54 Myr (SD = 2.40); and from tropical rainforests is 11.16 Myr (SD = 4.75). Species from oak forests are older, being on average 13.37 Myr (SD = 13.44). This average age is strongly influenced by the early split of *B. tecomaca*, 43.46 Myr ago. The average age of oak forest *Bursera* species, excluding *B. tecomaca*, is 8.35 Myr (SD = 2.37).

Diversification rate analyses

Absolute diversification rates of *Bursera* were estimated as 0.0484 net speciation events per million yr (sp Myr^{-1}) under a high relative extinction rate (ε = 0.9), and 0.0803 sp Myr^{-1} under no extinction (ε = 0.0). Diversification rates estimated for clades within *Bursera* are shown in Table 1. The M_{Π} statistic in SymmeTREE detected significant diversification rate heterogeneity in the tree with tail probabilities of 0.0040 and 0.0289 for the 0.025 and 0.975 frequentiles, respectively. The Δ_1 statistic detected two branches where significant rate increases occurred (Fig. 2): the branch subtending the most recent common ancestor (MRCA) of *B. cuneata* and *B. copallifera* (P = 0.0364), corresponding to section *Bullockia*, excluding *B. tecomaca* and *B. sarcopoda*, and here referred to as the 'nearly *Bullockia* clade'; and the branch subtending the MRCA of *B. multijuga* and *B. bolivarii* (P = 0.0430), corresponding to the 'cuajiotes', excluding *B. crenata* and *B. fragilis*, and here referred to as the 'nearly cuajiotes clade'. The Δ_2 statistic detected a significant rate change in the former branch (P = 0.0476), but a marginally significant one in the latter (P = 0.0516). Marginally significant rate changes were also detected in the branches subtending the

Table 1 Ages and diversification rates estimated for *Bursera*, including clades identified as resulting from significant (**) or marginally significant (*) diversification rate increase, as detected by SymmeTREE

Clade	Crown group mean age (95% HPD)	Stratigraphic interval	Age estimated by Becerra (2005)	Number of species	r (ε = 0.0)	r (ε = 0.9)
Burseraceae	64.92 (60.33–69.67)	Early Paleocene (Danian)	NA	–	–	–
Bursera – *Commiphora* split	54.75 (50.61–58.96)	Early Eocene (Ypresian)	> 100	–	–	–
Bursera	49.43 (45.38–53.77)	Early Eocene (Ypresian)	> 70	106	0.0803	0.0484
Section *Bursera*	40.1 (35.31–45.33)	Middle Eocene (Bartonian)	*c.* 50	59	0.0844	0.0465
Microphylla clade	17.54 (12.17–23.41)	Early Miocene (Burdigalian)	*c.* 35	9	0.0858	0.0304
Fagaroides clade	19.89 (14.62–25.88)	Early Miocene (Burdigalian)	< 20	16	0.1045	0.0434
Simaruba clade	19.68 (13.15–26.84)	Early Miocene (Burdigalian)	*c.* 30	26	0.1303	0.061
Caribbean clade	11.72 (7.36–16.51)	Middle Miocene (Serravallian)	NA	11	0.1455	0.0546
Nearly cuajiotes clade** (MRCA *B. multijuga* – *B. bolivarii*)	23.31 (17.30–29.45)	Latest Oligocene (Chattian)	NA	31	0.1176	0.0572
Nearly Fagaroides clade* (MRCA *B. paradoxa* – *B. bolivarii*)	15.70 (11.23–20.78)	Middle Miocene (Langhian)	NA	15	0.1283	0.0524
Approximately Carribean clade* (MRCA *B. longipes* – *B. nashii*)	14.42 (9.64–19.94)	Middle Miocene (Langhian)	NA	14	0.1349	0.0541
Section *Bullockia*	43.46 (40.74–46.61)	Middle Eocene (Lutetian)	*c.* 40	47	0.0726	0.0384
Section *Bullockia* after *B. tecomaca*	19.83 (12.77–27.77)	Early Miocene (Burdigalian)	> 20	–	–	–
Glabrifolia clade	12.63 (8.85–16.76)	Middle Miocene (Serravallian)	< 20	16	0.1646	0.0684
Copallifera clade	11.72 (8.36–15.79)	Middle Miocene (Serravallian)	*c.* 20	21	0.2006	0.0893
Nearly *Bullockia* clade** (MRCA *B. cuneata* – *B. copallifera*)	16.91 (11.30–22.55)	Early Miocene (Burdigalian)	NA	45	0.1841	0.0967
Glabrifolia plus Copallifera clades* (MRCA *B. steyermarkii* – *B. copallifera*)	13.69 (9.65–17.95)	Middle Miocene (Langhian)	NA	36	0.2111	0.1061

HPD, highest posterior density; MRCA, most recent common ancestor; NA, not applicable.

MRCA of *B. paradoxa* and *B. bolivarii*, corresponding to the Fagaroides clade excluding *B. denticulata*, and here referred to as the 'nearly Fagaroides clade' ($P\Delta_1$ = 0.0762 and $P\Delta_2$ = 0.0952); the MRCA of *B. steyermarkii* and *B. colpallifera*, corresponding to the Glabrifolia plus Copallifera clade ($P\Delta_1$ = 0.0835, $P\Delta_2$ = 0.0975); and the MRCA of *B. longipes* and *B. nashii*, corresponding to the Caribbean clade plus *B. longipes*, *B. instabilis* and *B. grandifolia*, and here referred to as the 'approximately Caribbean clade' ($P\Delta_1$ = 0.0989; Fig. 2). The absolute diversification rates associated with these rate increases are shown in Table 1.

The BDL analysis rejected the null hypothesis of temporally homogeneous diversification rates within *Bursera* (ΔAIC_{RC} = 33.0863; $P < 0.001$, Table S6). The yule3rate model, which includes two diversification rate shifts and no extinction, was found to fit the data best (AIC = −50.6052). The (log) number of lineages and the rate shifts under the best rate-variable model were plotted as a function of time (Fig. 3). According to the scenario suggested by the yule3rate model, *Bursera* started to diversify with a rate r_1 = 0.0481 sp Myr^{-1}. A shift in diversification rate occurred at ts_1 = 19.89 Myr, increasing to r_2 = 0.1312 sp Myr^{-1}, followed by a shift at ts_2 = 4.10 Myr, decreasing to r_3 = 0.0214 sp Myr^{-1}.

Tests of geographical structure

Randomization tests with MacClade detected significant geographical structure in phylogenies ($P < 0.01$, Fig. 4). The nine main distribution areas of *Bursera* in STDFs were optimized with a minimum of 88 transformations on the MAP tree, while optimization on each of 1000 random trees yielded a range of 96–108 steps, indicating that sister species in *Bursera* have a high likelihood of being confined to the same geographical region. The phylogenetic community structure analysis in PHYLOCOM (Table 2) showed that most of the geographic structure is condensed in four STDF units: Caribbean islands, Balsas river basin, Baja California Peninsula, and Tehuacán Valley, with significant positive NTI values ($P < 0.05$), indicating that shared area of occupancy predicts phylogenetic relatedness.

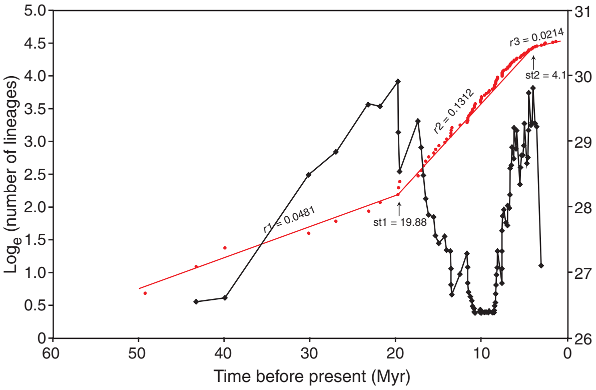

Fig. 3 Diversification analysis of *Bursera*. The red line indicates the lineage through time (LTT) plot derived from nodal divergence times obtained from uncorrelated lognormal dating in BEAST. The black line indicates likelihood of changes of diversification rate through time under the best-fit diversification model.

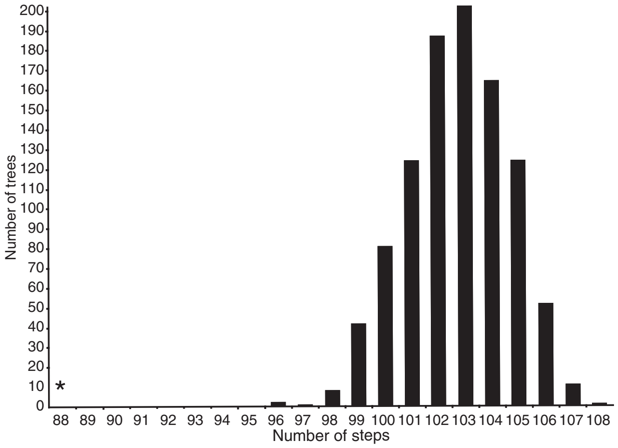

Fig. 4 Test of geographical structure. Histogram showing the number of shifts for seasonally dry tropical forest (STDF) optimized via parsimony on 1000 random equiprobable phylogenetic trees of *Bursera*. The analysis optimized nine geographical areas (see main text) with a minimum of 88 transformations on the maximum *a posteriori* tree. Optimizations on each of 1000 random trees yielded a range of 96–108 steps. The observed reconstruction falls outside this distribution (asterisk), and is considered indicative of substantial geographical structure.

Direction of habitat shifts

The vegetation type that each *Bursera* species most commonly occupies is shown in Fig. 5. Of the 93 sampled species of *Bursera*, 70 (75.27%) typically inhabit SDTFs; 13 (13.98%) occupy xerophytic scrubs; seven (7.53%) inhabit oak forests; and three (3.22%) occupy tropical rainforests. A SDTF was reconstructed as the ancestral vegetation type of *Bursera* (LH: 0.9478) and of its two sections (section *Bursera*: LH = 0.9769; section *Bullockia*: LH = 0.9181). A SDTF was reconstructed as the most likely state for most internal nodes (Fig. 5). Shifts to other vegetation types always involved a change from SDTF to a different vegetation type, except for one possible reversion. There were nine shifts to xerophytic scrubs: one in the Glabrifolia clade (occurring after 5.18 Myr); three in the Copallifera clade (the first after 7.08 Myr, the second after 4.59 Myr, and the third after 2.82 Myr); two in section *Bullockia* outside the Glabrifolia and Copallifera clades (one after 10.15 Myr, and another after 6.87 Myr); two in the Fagaroides clade (one after 5.11 Myr, and another after 4.33 Myr); and one in the Microphylla clade (between 17.54 and 14.21 Myr) with an apparent reversion to SDTF (between 7.72 and 5.3 Myr). There were seven shifts to oak forests: two in the Copallifera clade (one after 7.52 Myr, and another after 7.05 Myr); three in section *Bullockia* outside the Glabrifolia and Copallifera clades (the first after 43.46 Myr, the second after 11.82 Myr, and the last after 10.15 Myr); and two in the Fagaroides clade (one after 8.47 Myr and the other after 5.11 Myr). A single shift to tropical rainforest was reconstructed, occurring within the Simaruba clade (between 19.68 and 16.65 Myr; Fig. 4).

Table 2 Net relatedness and nearest taxa indices estimated with PHYLOCOM using the independent swap algorithm for 1000 runs

Area	Accesions (*n*)	NRI[a]	Quantile[b]	NTI[c]	Quantile[b]
Baja California Peninsula*	7	0.7294	799	1.9384	980
NW Mexican Pacific slope	18	0.3494	641	0.0176	512
Central Pacific coast	34	0.0672	547	0.8613	817
Balsas river basin*	44	0.4428	681	3.2771	1000
Tehuacan Valley*	19	0.2253	598	1.7152	959
Gulf of Mexico	7	1.0017	844	1.0895	868
Yucatán Peninsula	4	1.4247	912	1.5073	941
Central America-northern South America	11	1.2945	900	0.6533	759
Caribbean islands*	8	7.2856	1000	3.9990	1000

NRI, net relatedness index; NTI, nearest taxa index.

[a] Quantifies the degree of aggregation in the phylogeny of the sampled areas. Higher values indicate phylogenetic structure.

[b] The number of random trees in which NRI and NTI measures were lower than the actual estimate (≥ 950 is significant*).

[c] Quantifies the degree to which the sister group of any given taxon inhabits the same area. Higher values indicate phylogenetic structure.

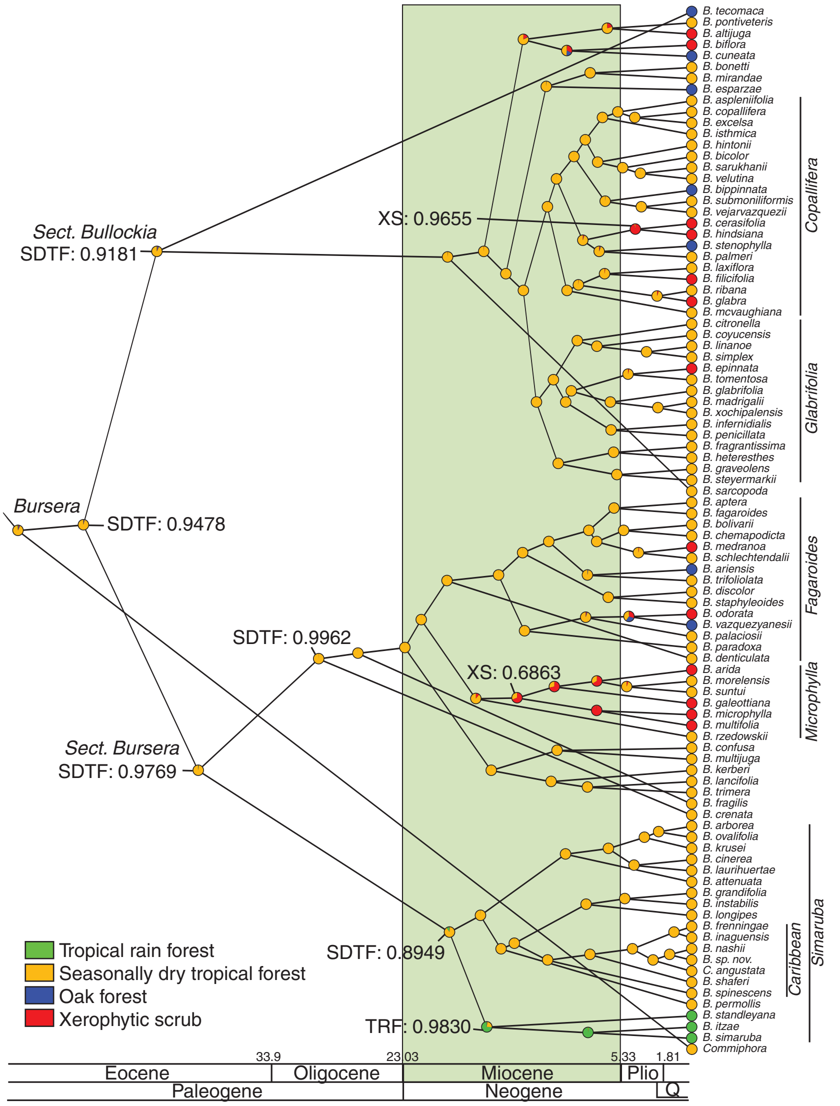

Fig. 5 Reconstruction of habitat shifts. The Mk1 model reconstructed seasonally dry tropical forest (SDTF) as the ancestral habitat for *Bursera*, and for most of the internal nodes in the phylogeny. Shifts to xerophytic scrubs (XS) and to oak forest occurred independently in nearly all clades within *Bursera*, whereas shifts to tropical rain forest (TRF) occurred only in the Simaruba clade.

Discussion

Time and mode of diversification in *Bursera*

Our phylogenetic results are based on a nearly complete species-level representation of *Bursera*, a sample of major lineages within Burseraceae, and the combined sequences of one plastid and four nuclear markers. The Vietnamese *B. tonkinensis* is apparently more closely related to *Commiphora* than to *Bursera* (Weeks & Simpson, 2007); hence, its absence in these analyses is unlikely to compromise the phylogenetic, dating and diversification results.

The origin of family Burseraceae, represented by the divergence of *Beiselia mexicana* from the remainder of the family, is here estimated in the earliest Paleocene (Danian; 64.92 Myr). This age is slightly older than the one estimated by Weeks *et al.* (2005; 60 ± 1.9 Myr), and both fall within the same stratigraphic interval. The divergence of *Bursera* and *Commiphora* occurred in the earliest Eocene (Ypresian; very close to the age estimated by Weeks & Simpson, 2007), soon followed by the split between sections *Bursera* and *Bullockia* (Fig. 2). Most of the ages here obtained are much younger than previous estimates (Becerra, 2003, 2005), including the split between *Commiphora* and *Bursera* (*c.* 45 Myr younger) and the divergence of sections *Bursera* and *Bullockia* (*c.* 20 Myr younger; Table 1). These age differences, most likely the result of different calibration strategies, suggest the need for a reconsideration of the postulated > 100 Myr association between the sister pairs *Diamphidia-Blepharida* herbivores and their *Commiphora-Bursera* hosts (Becerra, 2003).

Whereas the genus *Bursera* is *c.* 50 Myr old, most of its extant species are much younger – namely, the Microphylla, Fagaroides and Simaruba clades, within section *Bursera*, and section *Bullockia* after the divergence of *B. tecomaca*, all started to generate extant species between 20 and 17.5 Myr ago, a time when the Miocene aridification trend reached its peak (Graham, 2010). Sections *Bursera* and *Bullockia* exhibit parallel waiting times between their differentiation in the earliest Eocene and the onset of their radiation in the Miocene (Fig. 2). The crown groups of both sections were here constrained to have fairly old minimal ages. If these minimal ages are incorrect, the long temporal separation between each clade's differentiation and radiation, and their inferred diversification modes might be artifactual. We nevertheless believe that the long temporal separation between the origin and the diversifications of sections *Bursera* and *Bullockia* are real, because (1) two independent evaluations (Weeks *et al.*, 2005 and this study) found similarities between the early-middle Eocene *B. inaequalateralis*, and the early Oligocene *B. serrulata*, and members of sections *Bullockia* and *Bursera*, respectively; (2) other fossils confidently assigned to Burseraceae are older than the two previous fossils; (3) ages estimated for the crown nodes of sections *Bursera* and *Bullockia* (40.1 and 43.46 Myr, respectively) are older than their minimal age constraints (33.9 and 40.4 Myr, respectively); and (4) the crown groups of each of the two sections and their respective diversifications are each separated by a long phylogram branch (Fig. S1).

The absolute diversification rate estimated for *Bursera* is similar to that of angiosperms as a whole ($r = 0.089$, given $\varepsilon = 0.0$; Magallón & Sanderson, 2001), and lower than that of Sapindales ($r = 0.1114$ with $\varepsilon = 0.0$, and $r = 0.0879$ with $\varepsilon = 0.9$; Magallón & Castillo, 2009). However, several of its subclades have very high rates (e.g. $r = 0.2006$ and 0.2111 in the Copallifera and Glabrifolia plus Copallifera clades, respectively; Table 1). Two significant rate increases led to the diversification of the nearly *Bullockia* clade and the nearly cuajiotes clade *c.* 17 and 23 Myr ago (Fig. 2), which together generated over 70% of *Bursera*'s extant species. Absolute diversification rates associated with these clades include some of the highest within the genus (Table 1). The independent radiations within *Bursera* are unlinked from habitat shifts, as indicated by the fact that most of the reconstructed habitat shifts took place long after the most likely time when an increase in diversification occurred; that the branches where habitat shifts were reconstructed were not detected as having increased diversification rates (Fig. 5); and that the starting and ending nodes of all branches where increased rates were detected (see earlier; Figs 2, 5) were reconstructed as a SDTF.

The test for temporal diversification rate heterogeneity identified a model with no extinction and two rate shifts as best fitting the LTT *Bursera* plot (Fig. 3). The first rate change was an increase at 19.89 Myr, during the early Miocene. The second rate change was a decrease 4.01 Myr ago, during the early Pliocene. This rate decrease, which appears as a flattening of the LTT plot as it approaches the present (Fig. 3), might nevertheless be an artifact of the 13 species that were not included in this analysis, especially considering that some of them have been taxonomically associated with species younger than 5 Myr. Clearly, high speciation played the major role in *Bursera's* diversification. However, the existence of Tertiary fossil representatives of sections *Bursera* and *Bullockia*, outside *Bursera's* present-day natural distribution, suggests that extinction also had a role, albeit possibly a minor one, in *Bursera's* evolution. Furthermore, we wonder if a rate-variable diversification model that includes extinction can be confidently rejected in favor of a pure birth one, because according to BDL model selection, the AIC score of the latter is only slightly smaller than that of the former (−50.61 and −49.98, respectively; see Quental & Marshall, 2009).

The combined results of dating analyses, diversification tests and ancestral habitat reconstruction indicate that several independent lineages within *Bursera* began their diversification consecutively, and without involving habitat shifts, into extant diversity during the first half of the Miocene, in a process characterized by increased speciation. This reconstructed evolutionary history is congruent with the postulated expansion of SDTFs as a consequence of enhanced aridity in northern and central Mexico during the Miocene, mainly derived from global cooling and the rain shadow cast by the final uplift of the Sierra Madre Occidental in the Eocene (Graham & Dilcher, 1995; Dick & Wright, 2005; Graham, 2010). Nevertheless, we think that there are no simple links among Mesoamerican aridification, the expansion of SDTFs, and *Bursera* diversification. Mesoamerican aridification seems the consequence of complex interactions among global tectonics that resulted in cooling and drying starting in the middle Eocene; regional orogeny that caused the uplift of the Sierra Madre Occidental and Sierra Madre Oriental, and their rain shadows, mainly between the late Cretaceous and the late Eocene; and local post-Eocene volcanism and block faulting, including the uplift of the Mexican Transvolcanic Belt in the Miocene, which altered local drainage systems and enhanced rain shadows (Graham, 2010, pp. 60–66). Given these complex and prolonged interactions, it seems difficult to postulate a single causal event, let alone a narrow time interval, when Mesoamerican aridity set in, triggering the expansion of SDTFs. Furthermore, we lack elements to evaluate if the expansion of SDTFs in Mesoamerica and the diversification of *Bursera* occurred synchronously. It is possible that the expansion of this vegetation type (or its Tertiary equivalent) predated the diversification of any of the plant lineages that currently inhabit it. Our expectation regarding the pre-Pliocene age of most *Bursera* species is based on the simple assumption that, by the onset of the Pliocene, arid conditions were fully established in Mesoamerica.

Predictions for seasonally dry tropical forest-centered lineages

Based on the premise that the physical attributes and patchy distribution of South American SDTFs shape the evolutionary history of resident woody plant lineages, Pennington *et al.* (2009) predict the old age of their species; a high geographic structure in their phylogenies; and niche conservatism with habitat shifts predominantly from SDTFs to other vegetation types. The results here obtained for *Bursera* indicate that these predictions hold for Mesoamerican SDTFs. A substantial proportion of *Bursera* species are endemic to, or preferentially inhabit, SDTFs. All but four sampled *Bursera* species predate the Pleistocene, and the average age of *Bursera* species centered in SDTFs is 7.49 Myr (late Miocene).

The prediction that sister pairs of SDTF-centered woody plant lineages will occupy the same SDTF nucleus (Pennington *et al.*, 2009) was supported by randomization tests and analyses of phylogenetic community structure for *Bursera*. The geographic structure of *Bursera* suggests a limited historical dispersal among Mesoamerican SDTFs. However, it is somewhat weak in comparison with, for example, the South American robinioid legumes *Coursetia* and *Poissonia* (Schrire *et al.*, 2009). One possible interpretation is that the environmental and physical attributes of South American SDTFs are less pronounced in Mesoamerica. Specifically, Mesoamerican SDTFs usually occupy extensive continuous areas, and the barriers among disjunct nuclei are usually less pronounced as those separating South American SDTF patches. These differences would allow greater dispersal among Mesoamerican SDTF nuclei and, hence, cause weaker phylogenetic geographical structure.

Some of the highest levels of *Bursera* phylogenetic community structure were detected in the Balsas river basin and the Tehuacán Valley, both in central western Mexico, and in the Baja California Peninsula and the Caribbean islands. These four SDTF nuclei are present-day hotspots of *Bursera* diversification, as exemplified by the high number of species they house, including recent discoveries (e.g. Rzedowski & Calderón de Rzedowski, 2008; León de la Luz & Pérez-Navarro, 2010) and numerous endemics.

The observation that most *Bursera* species typically inhabit SDTFs, together with the reconstruction of SDTF as the ancestral vegetation type for the genus and for most internal tree nodes, documents a high degree of phylogenetic niche conservatism. Habitat shifts are relatively infrequent, and, except for a reversion, all occurred from SDTFs to other vegetation types. The largest number of shifts were into xerophytic scrubs – a harsher, drier environment than SDTFs, and occurred independently in all major lineages within *Bursera*, except for the Simaruba clade. The number and distribution of shifts in the phylogeny suggest that, whereas the possibility to occupy drier environments may be a generalized preadaptation across *Bursera* resulting from a plesiomorphic tolerance of aridity, the preadaptations to occupy substantially wetter environments may be phylogenetically restricted.

Conclusions

The reconstructed evolutionary history of *Bursera* provides insights of the processes that led to high species richness in Mesoamerican SDTFs. *Bursera* differentiated in the earliest Eocene, and soon after, split into its two main lineages. In the early Miocene, these two lineages initiated in parallel and without involving habitat change the diversifications that gave rise to most of their extant species. These diversifications took place in a context of enhanced aridity in north and central Mexico, resulting from complex and temporally extended interactions among global tectonics, regional orogenic activity, and local volcanism (Graham & Dilcher, 1995; Dick & Wright, 2005; Graham, 2010). The main process driving *Bursera's* diversification was high speciation. The late Miocene average age of *Bursera* species, the presence of geographic structure in its phylogeny, and unequivocal niche conservatism conform to predictions derived from attributes of South American SDTFs (Pennington *et al.*, 2009).

The reconstructed evolutionary history of *Bursera* indicates that at least some of the high species richness of Mesoamerican SDTFs derives from increased within-habitat speciation rates, from the early Miocene onwards, in the context of enhanced aridity. This scenario agrees with previous suggestions that lineages mostly restricted to dry environments in Mexico resulted from long periods of isolated evolution rather than rapid species generation (Rzedowski, 1962).

Acknowledgements

We thank R.T. Pennington and C. Hughes for critical discussions; P. Fine, M. Lavin and an anonymous reviewer for useful observations; J.E. Morales Can, M.E. Véliz Pérez, R. Ramírez Delgadillo and J. Pérez de la Rosa for field work help; J. Pérez Camacho and C. Martínez Habibe for species samples; V. Patiño for help with ancestral reconstructions; P. Maeda for contributing Fig. 1; S.R.S. Cevallos Ferriz and L. Calvillo Canadell for geological information; and R. Tapia and G. Ortega Leite for technical help. The Coordinación de la Investigación Científica, Universidad Nacional Autónoma de México, provided postdoctoral funding to J.A.D.N. This research was partially funded by grants NSF-DEB 0919179 to A.W.; CONACyT 2004-C01-46475 to L.E.E. and M.E.O.; and PAPIIT-UNAM 202310 to S.M.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Maximum likelihood phylogenetic tree for *Bursera* species.

Table S1 List of species and GenBank accessions for *Bursera* phylogenetic analysis

Table S2 List of species and GenBank accessions for eudicot phylogenetic analysis

Table S3 Fossil calibration and constraints for eudicot dating analysis

Table S4 Fossil calibration and constraints for *Bursera* dating analysis

Table S5 List of *Bursera* species inserted in phylogenetic diversification analysis

Table S6 Fit of birth-death likelihood (BDL) diversification models to *Bursera*

Methods S1 Detailed description of methods.

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