ORIGINAL ARTICLE

Historical biogeographical patterns of the species of *Bursera* (Burseraceae) and their taxonomic implications

David Espinosa[1]*, Jorge Llorente[2] and Juan J. Morrone[2]

[1]*Herbario, Facultad de Estudios Superiores 'Zaragoza', UNAM, Av. Guelatao 66, Col. Ejército de Oriente, 09230 Mexico, DF,* [2]*Museo de Zoología 'Alfonso L. Herrera', Departamento de Biología Evolutiva, Facultad de Ciencias, UNAM, Apdo. Postal 70-399, 04510 Mexico, DF, Mexico*

ABSTRACT

Aim The plant genus *Bursera*, with 104 species of trees and shrubs, has been used as a model for biogeographical analyses because of its high species richness and large number of endemic species. The biogeographical patterns of *Bursera* and their implications for its phylogenetic classification are reviewed in order that some hypotheses on the historical biogeography of tropical Mexico can be proposed.

Location *Bursera* is found in the south-western USA, most of Mexico, mainly below 1700 m elevation in tropical forests, with some species in xeric shrublands, diversifying along the Pacific slope, Central America, and north-western South America. A few species occur on the Galapagos and Revillagigedo archipelagos, some of which are endemics, whereas in the Antilles species are distributed extensively, with several endemics in the Bahamas, Cuba, Jamaica, and Hispaniola.

Methods Data from specimens in herbaria and the literature were used to construct a matrix of 104 species in 160 areas. Distributional patterns of the species of *Bursera* were inferred applying track analysis, parsimony analysis of endemicity (PAE), and Brooks parsimony analysis (BPA).

Results Track analysis revealed four individual tracks: (1) a circum-Caribbean track, comprising species of the *Bursera simaruba* species group; (2) an Antillean track, including species that have been transferred to *Commiphora* based on their pollen traits; (3) a Mexican Pacific track, including species of the *B. fragilis*, *B. microphylla*, and *B. fagaroides* species groups, called 'cuajiotes'; and (4) a Neotropical Pacific track, including the two species groups assigned to section *Bullockia*, in which the individual track of the *Bursera copallifera* species group is nested within the track of the *B. glabrifolia* species group. The four tracks overlap in a node in the Mexican Pacific slope, where they are highly diversified. PAE allowed us to identify 22 areas of endemism: 12 in Mexico (11 along the Mexican Pacific slope), six in the Antilles, two in Central America, one in South America, and one in the Galapagos. The general area cladogram obtained by BPA has two main clades: one includes the greater Antilles; and the other, 12 Mexican areas of endemism.

Main conclusions *Bursera fragilis*, *B. microphylla*, and *B. fagaroides* species groups can be treated together as a new section within *Bursera*, sect. *Quaxiotea*, because they are segregated from the other groups of sect. *Bursera* based on morphological, anatomical, molecular and geographical evidence.

*Correspondence: David Espinosa, Herbario, Facultad de Estudios Superiores 'Zaragoza', UNAM, Av. Guelatao 66, Col. Ejército de Oriente, 09230 Mexico, DF, Mexico.
E-mail: despinos@servidor.unam.mx

INTRODUCTION

Mexico, one of 12 megadiverse countries that together harbour 70% of the global biodiversity, contains about 10% of the global species richness of the world. This high biodiversity includes genes, species, and ecosystems. Classically, climatic gradients and habitat heterogeneity have been proposed as the main factors that have sustained this biological diversity. In order to account for the high number of species in this country, researchers have recognized two main historical explanations: dispersal and vicariance. According to the dispersal explanation, Mexico contains a high biotic richness because it is located at the transition of the Nearctic and Neotropical regions (Halffter, 1964, 1987; Rzedowski, 1965, 1978, 1992). This hypothesis might explain the high number of supraspecific taxa reasonably well, but not the high number of Mexican species in monophyletic groups, such as *Pinus*, *Quercus* and *Bursera*. Dispersal as conceived by these researchers consists of extension of the areas of distribution, without long-distance dispersal. The second hypothesis is based on a vicariance model and postulates a close relationship between geological/climatic and speciation events (Croizat, 1958, 1964; Rosen, 1978; Halffter, 1987; Liebherr, 1991; Luna *et al.*, 1999). In this model, the high species richness is a result of the complex geological history, with several fragmentation and convergence events (Morrone & Márquez, 2001). Since the earliest analyses using historical approaches, the Mexican biota has been recognized as part of an Antillean–Mesoamerican node (Croizat, 1958), which means an area where two or more ancestral biotas overlap. Another vicariance explanation, based on the refuge model, considers that climatic change through recent geological time, particularly the last 10 Myr, is the causal factor of the richness and endemism (Toledo, 1981). The model proposed by Haffer (1969) may be simplified as an interaction between species fragmentation produced by climatic changes, followed by a prolonged geographic and reproductive isolation, and finally speciation. It can be considered as a particular case of vicariance, in which the event of area fragmentation and the isolation of the derived subareas are climatically induced.

The genus *Bursera* Jacq. ex L. is found in the south-western USA, in the Colorado, Gila, and Alamo river basins; most of Mexico, mainly below 1700 m a.s.l. in tropical forests, with some species in xeric shrub lands, diversifying along the Pacific slope; and Central American tropical forests towards north-western South America, in the Orinoco (Venezuela) and Magdalena and Atrato (Colombia) river basins, along the Caribbean slope, and the Chocó region (Colombia) and the Guayaquil (Ecuador) and Sechura (Peru) bays on the Pacific slope. A few species occur in the Galapagos and Revillagigedo archipelagos, some of which are endemics, whereas in the Antilles the genus is extensively distributed, with several endemics in Cuba, Jamaica, and Hispaniola (Fig. 1). *Bursera* has been used as a model for biogeographical analyses (Kohlmann & Sánchez-Colón, 1984), because of its high species richness (more than 100 species *sensu* Rzedowski *et al.*,
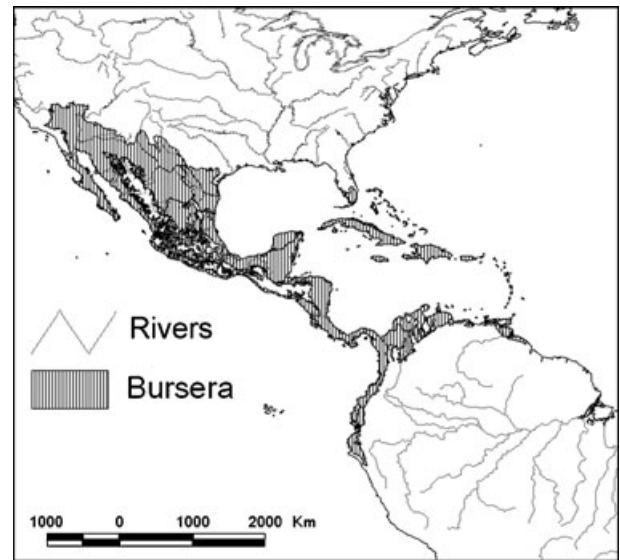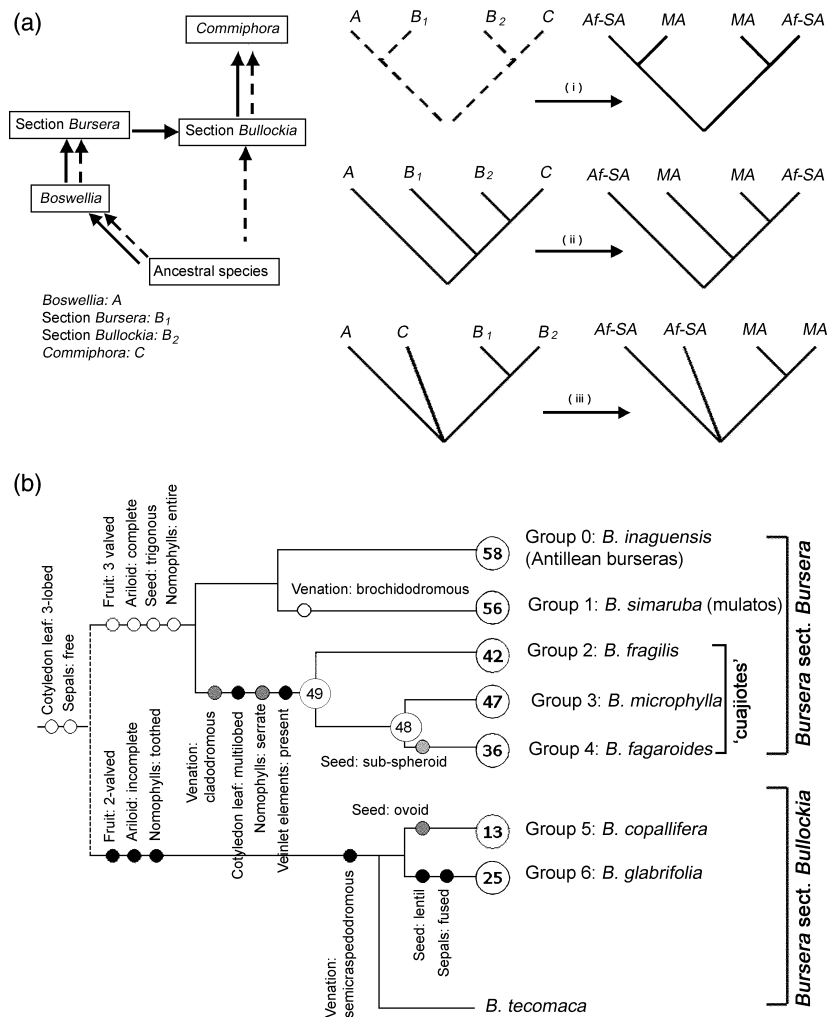

Figure 1 Distribution of the genus *Bursera*. Some species of north-eastern Brazil and the Orinoco river basin have been transferred to *Commiphora*.

2005) and number of restricted-range endemics. McVaugh & Rzedowski (1965) recognized some distributional patterns among species of *Bursera*, involving expansion of areas, ecological affinities, and distributional barriers. Axelrod (1979) associated *Bursera* with the Madro-Tertiary flora, which is composed mainly of elements historically related to the arid lands of North America, whereas others have supported a Caribbean subregion based on the range of *Bursera* among other taxa (Rzedowski, 1978).

Recent studies based on DNA sequences have supported both the monophyletic nature of the two sections of *Bursera*, viz. *Bursera* and *Bullockia*, and the existence of at least four monophyletic species groups assigned to the former: *B. simaruba*, *B. fragilis*, *B. microphylla*, and *B. fagaroides* species groups (Becerra & Venable, 1999; Becerra, 2003; Weeks *et al.*, 2005). Becerra (2003) analysed a sample of 73 Mexican species of *Bursera*, six species of *Commiphora*, and two of *Boswellia*. She found that all species of *Bursera* (sections *Bursera* and *Bullockia*) constituted a monophyletic group: (*Boswellia*, (*Commiphora*, [sect. *Bursera*, sect. *Bullockia*])). Later, Weeks *et al.* (2005) analysed a sample of 48 species from 13 out of 18 genera of Burseraceae (including 12 species of *Bursera*), finding that the two sections of *Bursera* constituted a paraphyletic group: (*Beisellia*, ((*Boswellia*, *Garuga*), (*Triomma*, (*Canarium*, *Dacryodes*, (*Trattinnickia*, *Santiria*)))), (*Crepidospermum*, (*Protium*, *Tetragastris*)), [sect. *Bullockia*, (sect. *Bursera*, *Commiphora*)]). In the latter case, a monophyletic *Bursera* should include *Commiphora*. The Antillean *Bursera* (the *B. inaguensis* species group) were not included in the analysis of Becerra (2003), but, within the Weeks *et al.* (2005) analysis, *B. spinescens* (morphologically related to the *B. inaguensis* group) supports the Antillean burseras being the sister group of the *simaruba* complex. Nevertheless, in both analyses, the two

Figure 2 Hypotheses about the phylogenetic relationships among the two sections of the genus *Bursera* and its close relatives *Commiphora* and *Boswellia*. (a) Rzedowski & Kruse (1979) proposed two histories of evolution (solid and dashed lines), which imply either a paraphyletic or a diphyletic nature of *Bursera* (i and ii); and Gillett (1980) realized that *Commiphora* and *Bursera* are consistently separated entities, thus implying a monophyletic *Bursera* (iii). The biogeographical implications are shown on the right. Af, Africa; SA, southern Asia; and MA, Mesoamerica. (b) The phylogenetic arrangement of *Bursera* adopted in this work is based on both ribosomal DNA sequences (Becerra, 2003; Weeks *et al.*, 2005) and morphological characters (McVaugh & Rzedowski, 1965; Rzedowski & Kruse, 1979; Toledo-Manzur, 1982; Andrés-Hernández, 2001; Andrés-Hernández & Espinosa, 2002). The basal dashed line indicates the conflicting relationships between the sections of *Bursera*, which constitute either a monophyletic (Becerra, 2003) or a paraphyletic (Weeks *et al.*, 2005) group.

groups of section *Bullockia* (the *copallifera* and *glabrifolia* species groups) are monophyletic. The biogeographical implications derived from both hypotheses of the phylogeny of *Bursera* involve the tectonic evolution of Gondwana. Because *Commiphora* (myrrh genus) mainly ranges in western and central Africa, and *Boswellia* (frankincense genus) in southern Asia (Arabian Peninsula to India), the monophyletic or paraphyletic nature of *Bursera* can imply single or multiple vicariant relationships among India, Africa and Tropical America, as illustrated in Fig. 2(a).

The taxonomic structure and some phylogenetic relationships for the species of *Bursera* were proposed by McVaugh & Rzedowski (1965), Rzedowski & Kruse (1979), Toledo-Manzur (1982, 1984), and Andrés-Hernández (2001). The groups best supported by evidence from morphology and ribosomal DNA sequences are combined and summarized in Fig. 2(b) (numbers in the nodes correspond to the clades in Fig. 3). Therein, the relationships supported by ribosomal DNA sequences obtained by Becerra (2003) are shown, and the species not included in their analysis are added to the base of each clade based upon the relationships suggested in the morphological studies. The Antillean species of *Bursera* are grouped as the

sister group of the *simaruba* complex based on Weeks *et al.* (2005), and therein *B. glauca* and *B. nashii* are combined in a single clade because it is probable that these names are synonyms.

We review the biogeographical patterns of *Bursera* and their implications for its phylogeny, in order to propose some hypotheses on the historical biogeography of tropical Mexico.

MATERIAL AND METHODS

Data matrix

A matrix of 160 rows (areas) by 104 columns (species) was obtained. (See Appendix S1 in Supplementary Material for the list of areas, and Appendix S2 for the matrix of presence–absence of species × areas.) The 104 species and their 60 components, based upon the molecular phylogeny *sensu* Becerra (2003), are drawn in Fig. 3. The set of species includes the 82 Mexican species accepted by Rzedowski *et al.* (2005) and *B. ribana*. *Bursera diversifolia* was excluded from this analysis, since its hybrid origin and identity have not yet been clarified. The other 22 species are not present in Mexico.
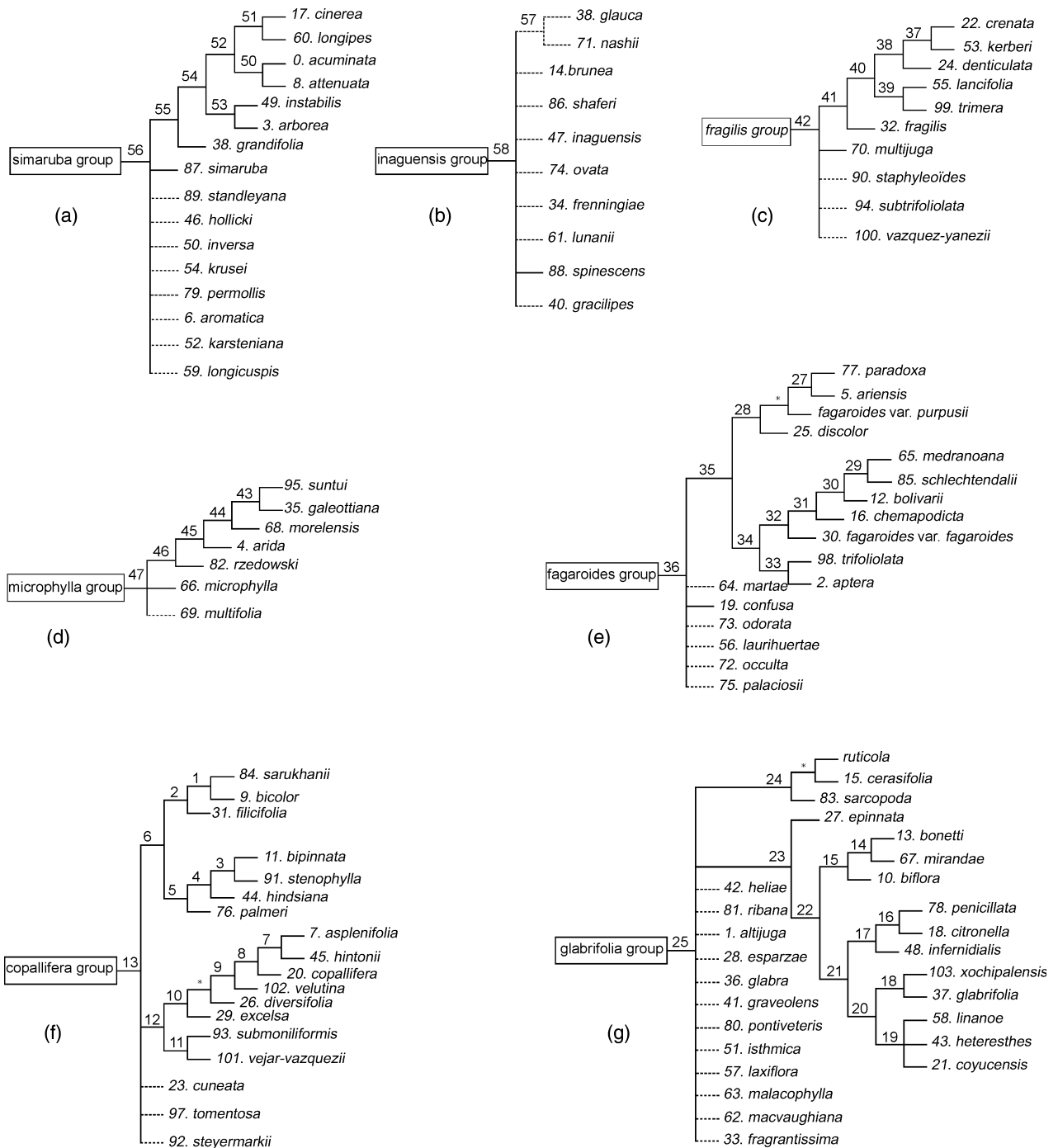
Figure 3 The main groups adopted in this work. Numbers correspond to each clade of Fig. 2b: (a) simaruba group (node 56); (b) inaguensis (node 58); (c) fragilis (node 42); (d) microphylla (node 47); (e) fagaroides (node 36); (f) copallifera (node 13); (g) glabrifolia (node 25). Species not included in Becerra's (2003) analysis are added at the basal level of each clade, indicated by dashed lines. Nodes were numbered in order to apply BPA. Nodes with *, such as those that relate *B. diversifolia* and varieties of *B. fagaroides*, were not included in the BPA, owing to the difficulty of identifying herbarium specimens. Species groups continuing clade 58, the *B. inaguensis* species group, were not included in Becerra's (2003) analysis and therefore are shown as a polytomy. Only *B. nashii* and *B. glauca* were joined in a clade, 59, since their strong similarity suggests their synonymy.

Distributional data for each species were obtained from Standley (1923, 1937), Urban (1928), Miranda (1941, 1942a,b, 1943, 1947, 1948), Standley & Steyermark (1946), McVaugh & Rzedowski (1965), Rzedowski (1968), Porter (1974), Correll (1979), Guevara-Féfer & Rzedowski (1980), Proctor (1982), Toledo-Manzur (1982, 1984), Kohlmann &

Sánchez-Colón (1984), Liogier (1985), Rzedowski & Ortíz (1988), Moncada-Ferrara (1989), Johnson (1992), Rzedowski & Guevara-Féfer (1992), Dávila *et al.* (1993), Daly (1993, 1997), Rzedowski & Calderón de Rzedowski (1996, 2000a,b, 2002), Reyes-García & Sousa (1997), Cuevas & Rzedowski (1999), León de la Luz *et al.* (1999), Diego-Pérez (2000), Jiménez & Cruz (2001), and Rzedowski *et al.* (2004, 2005). Other data were obtained from specimens loaned from the following herbaria: National Herbarium of Mexico (Mexico City), Instituto de Ecología AC, CR Pátzcuaro (IEB, Pátzcuaro, Michoacán), Gray Herbarium (Cambridge, Massachusetts), Royal Botanic Gardens Kew, Missouri Botanical Garden (St Louis), New York Botanical Garden (New York), and the United States National Herbarium (Washington DC).

Distributions of 104 species of *Bursera* were mapped and superimposed on a map of basins (Comisión Nacional del Agua, 1998) digitalized by CONABIO (2005). Each species was recorded in at least one basin. Most species occur extensively in one basin below 1700 m altitude, and a few species range up to 2000 m. The Ameca, Lerma-Santiago and Balsas river basins on the Pacific Slope, and Pánuco and Grijalva along the Gulf of Mexico had to be divided into sub-basins corresponding to subsidiary rivers, however, since several species occupy only parts of the original basins. Cuba and Hispaniola were also split into subareas (see Appendix S1). Thus, a set of 160 areas of southern USA, Mexico, Central America, northern South America, and the Antilles, Galapagos, and Revillagigedo archipelagos was considered in the analysis. The names of islands, regions and geographical traits, particularly those outside Mexico, were adopted from Webster's New Geographical Dictionary (Stevenson, 1988). The Lesser Antilles were fused into a single area, because only *B. simaruba* has been recorded there and it occurs throughout all of the islands of this archipelago.

Phylogenetic information about species of *Bursera* was based mainly on Becerra (2003), supported by DNA sequences analysed by parsimony. Some morphological and anatomical characters were mapped on the cladogram, especially those that agree with the molecular structure (Fig. 3). All species not included in the molecular phylogeny (Becerra, 2003) were assigned to a particular group based on morphological evidence from McVaugh & Rzedowski (1965), Rzedowski & Kruse (1979), Daly (1993), Andrés-Hernández (2001), and Rzedowski *et al.* (2005).

Track analysis

Individual tracks for each monophyletic group of *Bursera* were drawn and oriented applying the baseline concept (oldest geological trait on the species range) and/or phylogeny (locating the root of each cladogram) criteria (Craw *et al.*, 1999).

Analysis of endemism

A parsimony analysis of endemicity (PAE) (Rosen, 1988; Morrone, 1994) was undertaken in order to detect areas of endemism. Matrices were analysed using NONA version 1.16 (Goloboff, 1993) and WINCLADA version beta 0.9.99 (Nixon, 1999), with a heuristic algorithm (tree bisection and reconnection, 100 replications). Species resulting as synapomorphies were interpreted as endemic species supporting the areas of endemism (Morrone, 1994).

Cladistic biogeography

Areas of endemism were constructed by fusion of those areas supported by endemic (synapomorphic) species from the PAE. Nodes were coded as components, and a matrix of 60 components (columns), numbered upon the nodes of Fig. 3(a–g), by 23 areas of endemism (rows) were constructed, coding missing areas with '?' (see Appendix S3), following Brooks parsimony analysis (Brooks, 1981), and using NONA version 1.16 (Goloboff, 1993) and WINCLADA version beta 0.9.99 (Nixon, 1999).

RESULTS

Track analysis

Seven distinct tracks were obtained. The *B. simaruba* species group forms a circum-Caribbean track (Fig. 3a, node 56, and Fig. 4a). Herein, *B. simaruba* shows the widest distribution, ranging through almost the total extent of the track. The baseline can be located in the Caribbean Sea, despite the fact that the main massing is located in the lower portion of the Santiago river basin, where eight of the 16 species of the group are present. A second track is formed by all species closely related to *B. inaguensis*. It includes 10 species from the Greater Antilles and Bahamas islands, most of them being endemic to a single island or to a part of Cuba or Hispaniola (Fig. 3b, node 58, and Fig. 4b). The third track, consisting of species of the *B. fragilis* species group, is largely confined to non-coastal Mexican Pacific areas (Fig. 3c, node 42, and Fig. 4c). The *B. microphylla* species group shows a Mexican Pacific track, closely associated with the driest areas in the total range of *Bursera* (Fig. 3d, node 47, and Fig. 4d). The fifth track is that of the *B. fagaroides* group, and is the most widespread Pacific Mexican track. The group is more diverse than the two other groups of the 'cuajiotes' clade (Fig. 3e, node 36, and Fig. 4e). The *B. fragilis*, *B. microphylla* and *B. fagaroides* species groups all have their main massings on the Balsas river basin; however, the phylogenies for each group locate the oldest relationship on the Sierra Madre Occidental, which is the oldest geological trait along continental Mexico.

The two tracks for the groups of sect. *Bullockia* mainly range on the Neotropical Pacific slope (Fig. 3f–g, nodes 13 and 25, Fig. 4f,g). The track of the *B. copallifera* group (Fig. 3f, node 14, and Fig. 4f) is strictly continental, even clearly peninsular, whereas the *B. grabrifolia* group (Fig. 3g, node 15, and Fig. 4g) extends to the Baja California peninsula and the Galapagos and Revillagigedo archipelagos. The specimens reviewed from Cuba, all collected in botanical gardens, have probably been introduced.
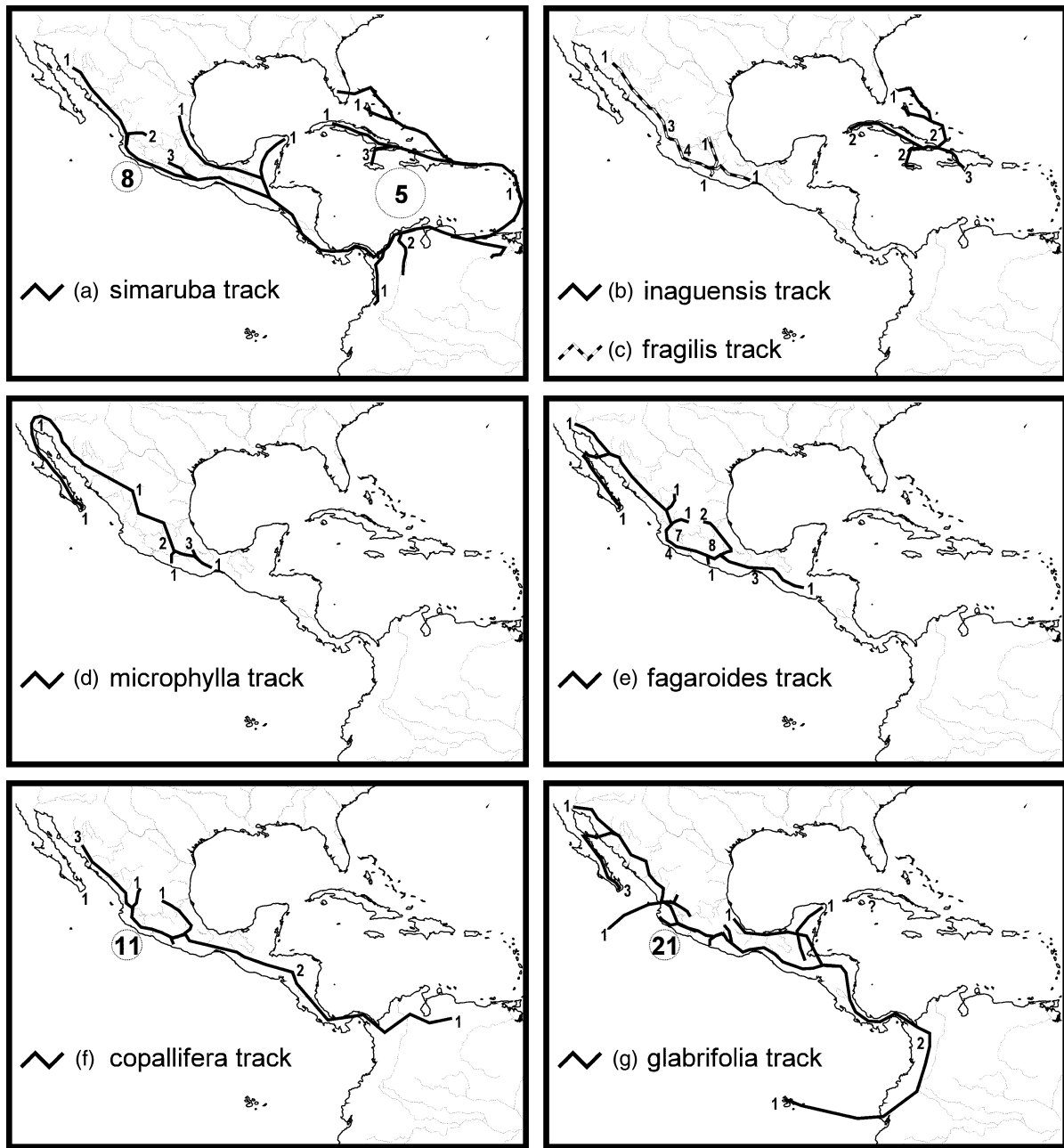
Figure 4 Individual tracks of (a) *B. simaruba* (clade 56 from Fig. 3a); (b) *B. inaguensis* (clade 58 from Fig. 3b); (c) *B. fragilis* group; (d) *B. microphylla* group; (e) *B. fagaroides* group; (f) *B. copallifera* group; (g) *B. glabrifolia* group. Numbers in each area or circle represent their species richness.

Parsimony analysis of endemicity

The parsimony analysis produced more than 1000 most parsimonious trees (length = 224, consistency index (CI) = 0.45, and retention index (RI) = 0.70). A consensus tree was obtained and the species and components were mapped. A first clade includes all the Antilles, the Gulf of Mexico, Central America, and South American areas along the Caribbean slope. A second clade includes all the areas of the Pacific slope from the basins of the Colorado and Gila rivers to Nicaragua. The Antillean–Central and South American clade consists of nine areas of endemism. Two are on Cuba, Oriente to Camagüey Cays and Western Cuba, and two are on Hispaniola, located at the Northern and Barahona peninsulas. The other five areas are Jamaica, the Peninsula of Osa (Costa Rica), Motagua river basin (Guatemala) (only if *B. steyermarkii* is not a synonym of *B. tomentosa*), the Gulf of Venezuela and the basin of the Orinoco River, and the Galapagos Islands. The Mexican Pacific clade consists of 11 areas of endemism (Table 1). Two of them are

Table 1 Areas of endemism of *Bursera*. Species with * are non-synapomorphic, but have a retention index close to 1.0. For codes of basins and areas see Appendix S1

Region	Major areas	Endemics	Minimal areas	Endemics
Caribbean areas of endemism	Greater Antilles		Bahamas	*B. frenningiae*
			West Cuba	*B. shaferi*
			Hispaniola, Peninsula of Barahona	*B. gracilipes, B. ovata, B. spinescens*
			Hispaniola, Gonave Gulf	*B. brunea*
			Hispaniola, Northern Peninsula	*B. nashii*
			Jamaica	*B. aromatica, B. holickii, B. lunanii*
	Caribbean South America	*B. glabra**	(Northern Colombia and Venezuela)	*B. inversa, B. karsteniana*
	Central America		Motagua basin river	*B. permollis, B. steyermarkii*
	South Pacific areas		Galapagos	*B. malacophylla*
			Peninsula of Osa and Dulce Gulf (Southern Costa Rica)	*B. standleyana*
Gulf of Mexico slope			Moctezuma basin river	*B. medranoana*
Mexican Pacific slope			Coast of Chiapas	*B. longicuspis*
	Gulf of Baja California: Sonoran-Baja California	*B. hindsiana, B. microphylla**	El Cabo	*B. cerasifolia, B. epinnata*
			Sonora	*B. fragilis, B. laxiflora*
	SW Mexican Pacific slope areas		Tuito	*B. vazquezyanesii*
			Bolaños	*B. multifolia, B. subtrifoliolata*
	S Mexican Pacific slope areas		Papagayo	*B. tecomaca, B. krusei*
			Armería–Coahuayana and Chacala basin rivers	*B. confusa, B. macvaughiana, B. occulta, B. palaciosii, B. ribana*
			Western Balsas	*B. coyucensis, B. crenata, B. fragrantissima, B. infernidialis, B. paradoxa, B. sarukhanii, B. staphyleoides, B. trifoliolata*
		B. linanoe, B. submoniliformis	Eastern Balsas	*B. bolivarii, B. chemapodicta, B. longipes, B. martae, B. rzedowski, B. suntui, B. vejar-vazquezii, B. xochipalensis*
			Tehuacán–Cuicatlán Valley (upper Papaloapan basin river)	*B. arida, B. biflora*
			Tehuantepec basin river	*B. heliae, B. isthmica, B. laurihuertae*

closely related and are located around the Gulf of California, south-eastern Baja California peninsula, from the Cabo region to La Paz Bay, whereas on the Pacific coast, the basins of the Mayo, Fuerte, and Sonora rivers and the Yaqui Valley constitute a distinct area of endemism. Other groups of areas of endemism are ranged in the south-western Mexican Pacific: one of them is part of the Santiago river basin, the Northern Bolaños river at the boundary of Jalisco and Zacatecas states; the Tuito river basin is supported by the recently described *B. vazquezyanesii*; and the basins of the Armería and Coahuayana rivers are supported by four species. The Balsas basin is divided into two areas of endemism, western Balsas (lower basin), and eastern Balsas (upper basin). South of the Balsas river, the Papagayo basin is supported by two species, whereas a single species supports the basin of Tehuantepec.

Cladistic biogeographical analysis

Brooks parsimony analysis produced three most parsimonious trees (Fig. 5a–c) (length = 64, CI = 0.65, and RI = 0.67). The areas of endemism involved in the Nelson consensus tree are shown in Fig. 6(a). All trees reveal two main clades. The first clade groups all the Greater Antilles (Jamaica, Cuba, Hispaniola, and Bahamas). The second clade groups all Mexican areas of endemism: El Cabo, Sonora, Bolaños, Tuito (southern Banderas bay), Armería–Coahuayana (coast of Jalisco, Colima and Michoacán states), Papagayo (south of Balsas, flowing into the Acapulco bay), Western and Eastern Balsas, Tehuantepec (Oaxaca state), and Salado (xeric land located at the boundary between Puebla and Oaxaca states, also called Tehuacán–Cuicatlán valley).
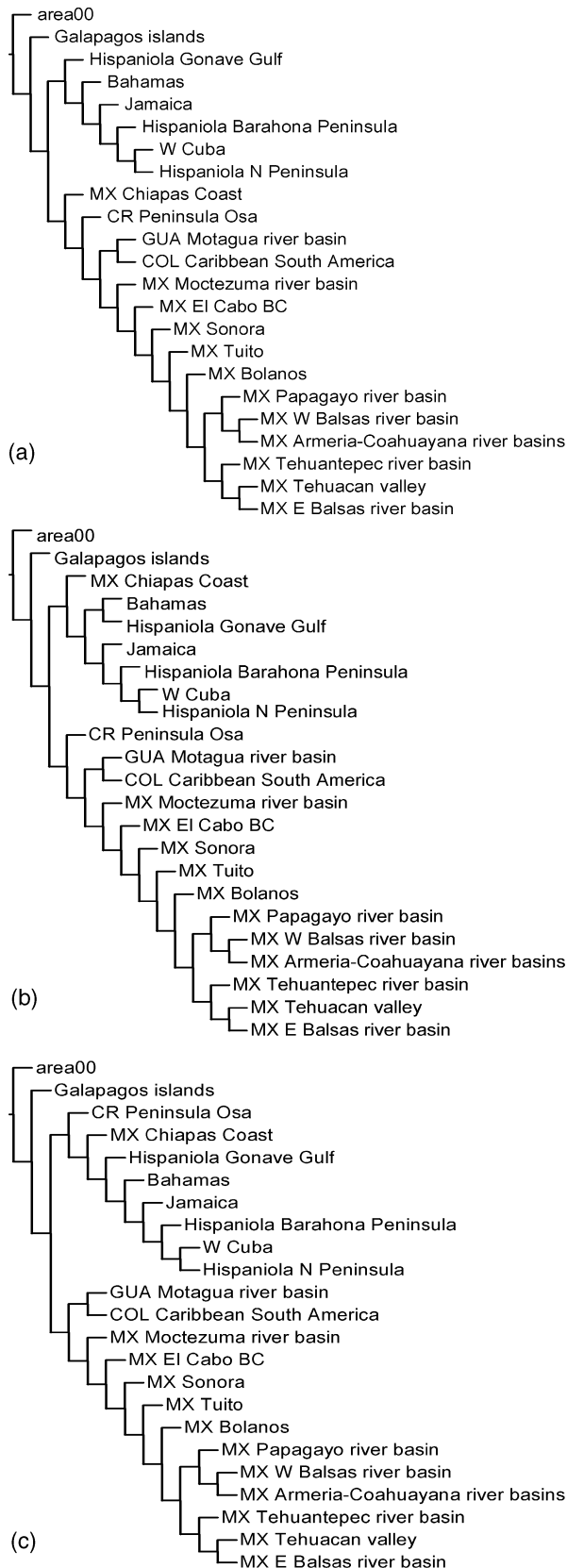
(a)

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area00
Galapagos islands
Hispaniola Gonave Gulf
Bahamas
Jamaica
Hispaniola Barahona Peninsula
W Cuba
Hispaniola N Peninsula
MX Chiapas Coast
CR Peninsula Osa
GUA Motagua river basin
COL Caribbean South America
MX Moctezuma river basin
MX El Cabo BC
MX Sonora
MX Tuito
MX Bolanos
MX Papagayo river basin
MX W Balsas river basin
MX Armeria-Coahuayana river basins
MX Tehuantepec river basin
MX Tehuacan valley
MX E Balsas river basin
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(b)

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area00
Galapagos islands
MX Chiapas Coast
Bahamas
Hispaniola Gonave Gulf
Jamaica
Hispaniola Barahona Peninsula
W Cuba
Hispaniola N Peninsula
CR Peninsula Osa
GUA Motagua river basin
COL Caribbean South America
MX Moctezuma river basin
MX El Cabo BC
MX Sonora
MX Tuito
MX Bolanos
MX Papagayo river basin
MX W Balsas river basin
MX Armeria-Coahuayana river basins
MX Tehuantepec river basin
MX Tehuacan valley
MX E Balsas river basin
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(c)

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area00
Galapagos islands
CR Peninsula Osa
MX Chiapas Coast
Hispaniola Gonave Gulf
Bahamas
Jamaica
Hispaniola Barahona Peninsula
W Cuba
Hispaniola N Peninsula
GUA Motagua river basin
COL Caribbean South America
MX Moctezuma river basin
MX El Cabo BC
MX Sonora
MX Tuito
MX Bolanos
MX Papagayo river basin
MX W Balsas river basin
MX Armeria-Coahuayana river basins
MX Tehuantepec river basin
MX Tehuacan valley
MX E Balsas river basin
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Figure 5 Three general area cladograms (a–c) resulting from BPA for 11 areas of endemism of *Bursera* in Mexico.

DISCUSSION

The patterns of distribution of *Bursera* show different aspects of the natural history of the genus. Individual track components reveal factors that should be taken into account when the taxonomic structure of *Bursera* is revised.

The *B. simaruba* species group conforms to an eminently circum-Caribbean track, which supports the well-recognized Caribbean subregion (Rapoport, 1968; Cabrera & Willink, 1973; Rzedowski, 1978; Takhtajan, 1986; Coscarón & Coscarón-Arias, 1995; Liebherr, 1997; Morrone *et al.*, 1999; Morrone, 2001, among others). The *B. simaruba* group ranges throughout the Antilles, the southern peninsula of Florida, northwestern South America (including the Orinoco, Gulf of Venezuela, Magdalena, and Atrato basins and the Chocó region), Central America, and Yucatan peninsula extending towards the Gulf of Mexico slope (reaching the basin of the Pánuco river); along the Mexican Pacific slope, it reaches the continental coast of the Gulf of California (Sea of Cortez) in the Sonora river basin, where it is represented by *B. grandifolia*. It is associated with tropical semi-deciduous forests and tropical rain forests mainly on the coastal plains, which are the moistest areas through the range of the genus. Indeed, only *B. acuminata* and *B. grandifolia* penetrate the Santiago river basin, and *B. longipes*, in the upper Balsas, is the only non-coastal species.

The track of the Antillean *Bursera* species group is composed of species with three-valved fruit, and leaflets with entire margins. Therefore, they can be considered as part of *Bursera* sect. *Bursera*. Moncada-Ferrara (1989) transferred the Cuban species of this group to *Commiphora* based on pollen characters; however, Weeks *et al.* (2005) found *B. spinescens* (a member of the *B. inaguensis* species group) to be the sister group of the *simaruba* complex.

The tracks of the three groups of 'cuajiotes' (*B. fragilis*, *B. microphylla*, and *B. fagaroides* species groups) are related to the history of the dry lands of Mexico and the south-western USA, whereas the *B. simaruba* species group is related to subhumid tropical forests. The two groups of sect. *Bullockia* constitute typical elements of the tropical deciduous forests along the Pacific slope, whereas tracks of *B. microphylla* and *B. fragilis* species groups are usually found in the driest parts of the generic range: the Arizona–Sonora desert, Central Plateau, and Tehuacán–Cuicatlán valley. The *B. microphylla* species group track agrees with the pattern found by Axelrod (1979) and Morafka *et al.* (1992), who recognized the close relationships among arid lands of North America. Both *B. microphylla* and *B. fragilis* species groups show their basal species in the Sonora Desert, but are highly diverse in the Balsas and neighbouring areas. The third group of 'cuajiotes', the *B. fagaroides* species group, is more diversified and widespread, extending toward the Central Plateau of Mexico and the entire Mexican Pacific coast. Andrés-Hernández (2001) and Andrés-Hernández & Espinosa (2002) found cladodromous venation and veinlet elements, particularly tracheoblasts, to be synopomorphies of the 'cuajiotes' (see Fig. 2b, node 49). Tracheo-
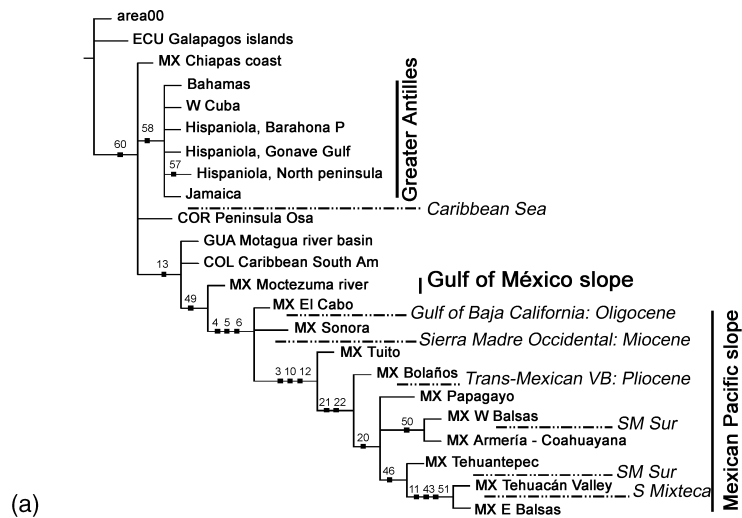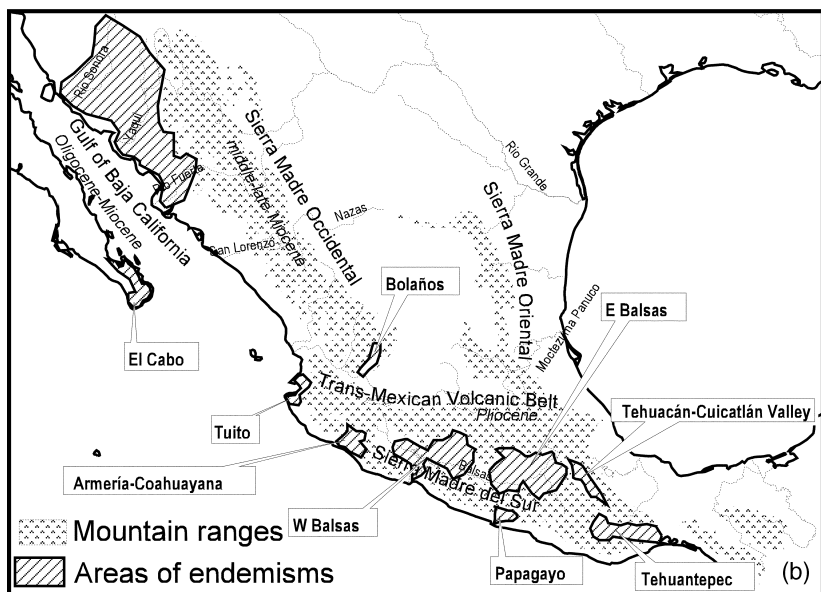
Figure 6 Areas of endemism of *Bursera* in Mexico. (a) Nelson consensus cladogram obtained from the three trees 5a to c (numbers 1, 2, 3, …, 60 correspond to components drawn in Figs 3 and 4); (b) map of the areas of endemism obtained from the analysis.

blasts have been interpreted as an adaptative character that could be related to hydric stress (Metcalfe, 1979); however, all extant species of 'cuajiotes' have veinlet elements, no matter where they live, whether in xeric or subhumid environments. This means that the ancestral species could have evolved early in dry lands, and its descendents could have expanded their distributions into moister environments. There are other characters that strongly support the 'cuajiotes' clade, for example the fact that the multilobate cotyledons and protophylls are always toothed with cladodromous venation. The clade is also supported in the molecular phylogeny obtained by Becerra (2003). Thus, the *B. fragilis*, *B. microphylla* and *B. fagaroides* species groups can be treated together as a new section in the genus *Bursera*, since they are segregated from the other groups of sect. *Bursera* (*B. simaruba* and *B. inaguensis*) based on morphological, anatomical, molecular, and geographical evidence. This clade is named here as *Quaxiotea*, reviving the concept of Toledo-Manzur (1982) who called it

'cuajiotes' (náhuatl: *quauitl*, tree; *xiotl*, leprosy), a term used in folk taxonomy based on the papery bark.

The track of the *B. glabrifolia* group, highly diversified in the Baja California peninsula and on the Galapagos and Revillagigedo archipelagos, suggests a presence earlier than the displacement of the Baja California peninsula in the Oligocene, whereas the track of *B. copallifera* implies a later evolutionary history.

The track of the whole genus Bursera coincides with the upper American segment of the track of tribe Protiae (Burseraceae) (Croizat, 1952). However, the genera of Protiae (*Tetragastris* and *Protium*) are largely vicariant with *Bursera*, since they are more diversified in those areas of Central and South America where *Bursera* is represented by just a few species.

Areas of endemism

The Sonora area of endemism of *Bursera* (Table 1 and Fig. 6a,b) occupies most of the Sonora province, recognized

as an area of endemism by several authors (Goldman & Moore, 1945; Cabrera & Willink, 1973; Marshall & Liebherr, 2000; Morrone, 2001; Morrone et al., 2002). Adjacent areas in the Sonora and Cabo region are paraphyletic, since there are no species diagnosing them as areas of endemism. *Bursera acuminata* is almost endemic to coastal Sinaloa, between Sonora and the basin of Santiago, but additional records are needed to confirm this pattern. The Cabo region is mainly supported by two species, but a recent study has proposed two other species for the area (Pérez, 2001), which could clarify some patterns of *Bursera* within the peninsula.

The Bolaños area of endemism belongs to the large Lerma–Santiago river basin, which can be divided into three areas: lower Santiago, closely related to coastal areas; central Santiago, where the Bolaños area is nested, strongly related to Balsas areas, particularly to western Balsas; and Lerma, more related to upper Panuco (Moctezuma river basin). The great Santiago basin, however, appears as paraphyletic, because the three subareas are related partially to other areas of endemism, but do not present any endemic species that support them as areas of endemism.

Tuito basin, southern Banderas bay, is located at the limit of the Transmexican Volcanic Belt. Armería–Coahuayana is a highly diverse area, and contains more species than the Papagayo, an area closely related to it. Several endemics of the Papagayo river basin range on segregated habitats. *Bursera tecomaca* is a microendemism of the upper basin, in the Salto Valadez canyon (above 1000 m altitude), whereas *B. krusei* ranges in the lower basin (below 500 m altitude).

The Balsas river basin, with 48 species of *Bursera*, is a geographically complex area, and may contain four other areas of endemism in addition to those proposed here. The division into western (lower) and eastern (upper) Balsas only represents the most evident and best-supported pattern of endemism. It has previously been recognized by Toledo-Manzur (1984) for *Bursera*, and also supported by the distribution of the lizard genus *Sceloporus* (Smith, 1941). The barrier that split the distribution of endemics of the two subareas of the Balsas river basin is the Sierra de Taxco, located at 100° W longitude. This mountain range involves an abrupt change of elevation, which implies that the western Balsas are warmer and drier than the eastern Balsas. In addition, there are other smaller nested areas that need to be confirmed by additional exploration of some areas not yet sufficiently sampled. Some canyons, such as the Zopilote and Yextla (upper Balsas), contain microendemics. Furthermore, most endemic species are homopatrid (having the same geographical distribution) but locally allotopic in relation to other species. Indeed, each basin of a particular subsidiary river may contain about 15 species, but there are hardly ever more than eight species in a single locality.

The Tehuacán–Cuicatlán valley (upper Papaloapan) was also proposed as a floristic province by Rzedowski (1978). Miranda (1948) suggested that this area was once part of the basin of the Balsas, which coincides with the relationships of *Bursera* species. Endemic species of this area are frequently allopatric and occupy only a small nested portion of this area.

A similar pattern occurs in the species inhabiting the Balsas basin.

The Tehuantepec area of endemism is characterized by *B. laurihuertae*. This area marks the eastern limit of a set of species of *Bursera* that ranges along the western and southern Mexican Pacific.

Biogeographical relationships among the areas

The area cladograms show two main clades, summarized in Fig. 6(a) by the Nelson consensus, which seem to be correlated with the geological history: an Antillean clade related to the tectonic evolution of the Greater Antilles; and a second clade related to the historical biogeography of the Mexican subhumid tropics. The historical relationships among the Antillean clade and the Central and South American areas of endemism are not yet clear, because the phylogenetic information on the involved species is poor. The *B. inaguensis* species group (Figs 3b & 4b) only supports the Greater Antilles clade.

The second clade includes all Mexican areas of endemism supported by the clade *Quaxiotea* (Fig. 2b, component 49, Fig. 3c–e), which includes the *B. fragilis*, *B. microphylla* and *B. fagaroides* species groups (Fig. 6a). The split at the base of the Mexican clade represents a first division between Pacific and Gulf of Mexico slopes (Fig. 6a). The Mexican Pacific clade is supported by component 6 of the *B. copallifera* group. The basal area of this clade is El Cabo, at the tip of the peninsula of Baja California, followed by the Sonora area. The two areas are separated by the Sea of Cortés, and are segregated from the remaining Mexican areas of endemism by the Sierra Madre Occidental, which was formed during middle to late Miocene times, whereas the Sea of Cortés (or Gulf of Baja California), which splits the Cabo and Sonora areas, is dated to the Oligocene, when the displacement of California towards the north-west occurred (Craw et al., 1999). Later vicariance and convergence events have been inferred between the late Miocene and Pleistocene (Riddle et al., 2000).

Components 3, 10 and 12 from the *B. copallifera* species group (Figs 3f & 6a) support a clade composed of all areas ranged on the Mexican Pacific slope from the Santiago river basins southwards. The Tuito and Bolaños areas north of the Transmexican volcanic belt are separated, and a clade supported by component 20 of the *glabrifolia* species group (Figs 3g & 6a,b) has two subclades. The first one is composed of the most diverse areas: western Balsas, Armería–Coahuayana, and Papagayo river basins; the second one in turn is composed of the eastern Balsas, Tehuacán–Cuicatlán valley, and Tehuantepec river basins. Together they represent 80% of the total species diversity of *Bursera*, indicating that these areas had a complex tectonic and climatic evolution.

The southern Mexican Pacific clade is highly diversified. The Balsas river basin alone harbours nearly 50 species, which represents half of the total richness of the genus. Many of these 50 species are endemic to just a part of it. Many sister species are endemic, but mutually allopatric. This can be explained by the action of the Sierra Madre del Sur, Sierra de Taxco and

Sierra Mixteca as vicariant events on the Pacific slope in southern Mexico. Armería–Coahuayana, Papagayo and Tehuantepec are located south of Sierra Madre del Sur, whereas Balsas, western and eastern, and Tehuacán–Cuicatlán Valley range north of this barrier. Sierra de Taxco splits the Balsas river basin into the western Balsas (lower Balsas) and eastern Balsas (upper Balsas). The Tehuacán–Cuicatlán Valley is isolated from the other areas by the Sierra Mixteca, bordering the eastern Balsas, and the Sierra Madre del Sur, bordering the Tehuantepec basin. However, most of the microendemics could be explained by palaeoclimatic vicariance (even by present climatic vicariance), since their distributions are frequently restricted to canyons that could have acted as climatic refuges. Many of these areas show displaced distribution of their rainy seasons from the rest of the eastern Balsas climate, which might imply reproductive isolation by phenology. This hypothesis needs to be tested.

The non-coastal areas (western and eastern Balsas, Tehuacán–Cuicatlán and Tehuantepec) are closely related, and the consensus tree (Fig. 6a,b) supports an early connection between the Balsas and Tehuacán–Cuicatlán valley (Salado river), and the upper Papaloapan, which currently flows into the Gulf of Mexico. In turn, the coastal areas are closely related among themselves, but the segregation of Tehuantepec and Sonora areas, if repeated in other taxa, would make it necessary to split the complex Coastal Pacific province, as proposed in several biogeographical classifications of Mexico and North America (Rzedowski, 1978).

The relationships of the Santiago river basin are even more uncertain, owing to the paraphyletic relationships of its subareas, but the relationships of Bolaños suggest a history more related to areas located south of the Sierra Madre Occidental. The main stream of the Santiago river flows along the physiographic limits between the Sierra Madre Occidental and the Transmexican Volcanic Belt.

Finally, it is noteworthy that all clades of the general area cladograms are supported mainly by the components of sect. *Quaxiotea* and *B. copallifera* and *B. glabrifolia* species groups. This is an expected pattern if it is considered that the track is mainly circum-Caribbean, and that the primitive groups of 'cuajiotes' are more related to the history of the arid lands of North America.

ACKNOWLEDGEMENTS

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from http://www.Blackwell-Synergy.com:

Appendix S1 Areas of 104 species of *Bursera* spread along the southern USA, Mexico, Central America, northern South America, and the Antilles, Galapagos, and Revillagigedo archipelagos.

Appendix S2 Matrix of 104 species of *Bursera* occurring in 159 areas (plus an out area). Numbers of species correspond to those in Fig. 3.

Appendix S3 Data matrix of 60 components × 24 areas (23 areas of endemism and one out area). Numbering corresponds to components in Fig. 3.

BIOSKETCHES

David Espinosa is interested in the historical biogeography of Mexico, biogeographical classification, and the taxonomy and distribution of the genus *Bursera* (Burseraceae).

Jorge Llorente-Bousquets has interests in the history and theory of comparative biology and has edited and published several books on the topic in Spanish, Portuguese, and Italian. His major interests are now in the history of biogeography, particularly during the 18th to 20th centuries. For 30 years he studied Mexican butterflies, faunistic methodology, and problems in inventories.

Juan J. Morrone is interested in phylogenetics, historical biogeography, and evolution. He has published several papers and books on the historical biogeography of Latin America and systematics of Curculionoidea (Insecta: Coleoptera).

Editor: Chris Humphries