Plant Syst. Evol. 228: 229–239 (2001)

Plant Systematics and Evolution

Biogeographical affinities among Neotropical cloud forests

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Received February 22, 2001
Accepted May 1, 2001

Abstract. Biogeographical affinities among cloud forests in the Neotropical region were studied through a track approach, by constructing generalised tracks based on the results of a parsimony analysis of endemicity (PAE). Distributional data on 946 genera and 1,266 species of vascular plants (Pteridophyta, angiosperms, and gymnosperms) from 26 cloud forest patches from Colombia, Costa Rica, Cuba, Honduras, Jamaica, Mexico, Peru, Puerto Rico, and Venezuela were analysed; and four localities from eastern and western United States were also included as outgroups. The track analysis identified six generalised tracks: a first one that includes the majority of the cloud forests of Mexico, Central America, the Antilles, and northern Colombia; a second one that includes southern Mexico and northern Central America; a third one that includes the mountains in northwestern South America; a fourth one that includes the mountains in southwestern South America; and two others in western and eastern United States. It is concluded that the Neotropical cloud forests are closely related and that those of the Caribbean subregion exhibit complex relationships, which could be due to the complex tectonic history of the area.

Key words: Neotropics, cloud forests, vascular plants, panbiogeography, track analysis, parsimony analysis of endemicity.

Introduction

The Neotropical region ranges in the Americas, from central Mexico to central Argentina (Morrone 1999, Morrone et al. 1999). This biogeographic region is characterised by its great diversity of ecosystems, which include among others, steppes, grasslands, savannas, moorlands, and dry, moist, and cloud forests (Cabrera and Willink 1973, Dinerstein et al. 1995). Within the Neotropical ecosystems, cloud forests are particularly interesting from a biogeographic viewpoint (Luna et al. 1999). The northernmost stand of cloud forest is found in the Sierra de San Carlos and Gómez Farías (Tamaulipas), in the Mexican Sierra Madre Oriental, between 1,300 and 1,400 m (Briones 1991). The southernmost cloud forest is found in northeastern Argentina, at approximately 27–28° S (Webster 1995). Neotropical cloud forests are characterised by their archipelagic distribution, the presence of endemic taxa, and their high biodiversity, which highlight their biogeographic and biological importance. They have been considered also as one of the main world centres of domestication of certain plants such as corn, beans, peppers and tobacco, which have been clues to the flourishment of Pre-Columbian civilizations.

Neotropical mountains harbour ca. 45,000 species of flowering plants, which when compared to the 250,000 species worldwide, show that they constitute one of the world's great centres of biological diversity (Churchill et al. 1995). Recently, attention has been placed in the study of these Neotropical montane forests, including principally their conservation (Churchill et al. 1995; Hamilton et al. 1995). Notwithstanding, their biodiversity is relatively poorly studied.

Graham (1995) recently argued that the close affinity between the forests of Mexico-Central America and northern South America are due to the arrival of elements by different routes and at various times across the Panamanian land bridge and the North Atlantic. He suggested that the montane vegetation is composed of four biogeographic components, three basically Gondwanic and one Laurasic.

It is becoming increasingly recognised that the Neotropical cloud forests rank high within the world's most threatened ecosystems (Hamilton et al. 1995), and that the damage done to them is far more likely to be irreversible, because they have low resilience to disturbance. These communities have been severely disturbed for centuries by human activities such as forestry, road building, agriculture, farming, colonization, pasture, and fires. The increasing human population has placed pressure on these forests, so that the disturbance is so extensive in several areas that the original vegetation is disappearing quickly (Luna et al. 1988). Many of these forests are today restricted to the most inaccesible slopes and have been partially replaced by grasslands and croplands. It has been proposed that biogeographic analyses can help identify priority areas for biodiversity conservation (Grehan 1993, Morrone and Crisci 1995, Morrone and Espinosa 1998, Espinosa and Morrone 1998).

If taxon-area cladograms for a cladistic biogeographic analysis are not available, Parsimony Analysis of Endemicity or PAE (Rosen 1988; Morrone 1994, 1998) can be used to recognise patterns of biogeographical homology, equivalent to generalised tracks (Craw et al. 1999).

Our main objective is to analyse the main biogeographical patterns among several Neotropical cloud forests, by applying a track approach using PAE.

Material and methods

Taxa. From a data set composed of 1,727 genera and 7,307 species of vascular plants (gymnosperms, angiosperms, and pteridophytes), the taxa present in a single locality were deleted, obtaining a list composed of 946 genera and 1,266 species. These were obtained from field work from 1982 to 2001; published floristic surveys (Shreve 1914; Seifriz 1943; Whittaker 1956; Whittaker and Niering 1965; Howard 1968; Frye 1976; Álvarez del Castillo 1977; Cruz and Erazo 1977; Gutiérrez 1980; Sugden 1982; Luna et al. 1989, 1994; Puig 1989; Haber 1991; Long and Heath 1991; Meave et al. 1992; Kelly et al. 1994; López et al. 1994; Campos and Villaseñor 1995; Ruiz 1995; Silverstone-Sopkin and Ramos-Pérez 1995; Téllez 1995; Michener-Foote and Hogan 1999); Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Conabio) projects (Flores 1992–1994, Santana 1993, Santiago and Jardel 1993); and internet on the www (Dillon 2001). The complete list is available through e-mail upon request to the senior author (ilv@hp.fciencias.unam.mx). This list was carefully checked in order to assess the plant diversity and detect synonyms by consulting the relevant literature or communication with specialists. The units of analysis were 26 Neotropical cloud forest patches from Colombia, Costa Rica, Cuba, Honduras, Jamaica, Mexico, Peru, Puerto Rico, and Venezuela. In addition, four localities from eastern and western United States were included as outgroups (Fig. 1; see Table 1).

Track analysis. The panbiogeographic method was originally developed by Croizat (1958, 1964) and consists basically of plotting distributions of organisms on maps and connecting their discontinuous distributions together with lines named individual tracks, according to their minimal geographical proximity. The summary lines resulting from the coincidence of different individual tracks are considered generalised tracks, which indicate the preexistence of ancestral biotas that

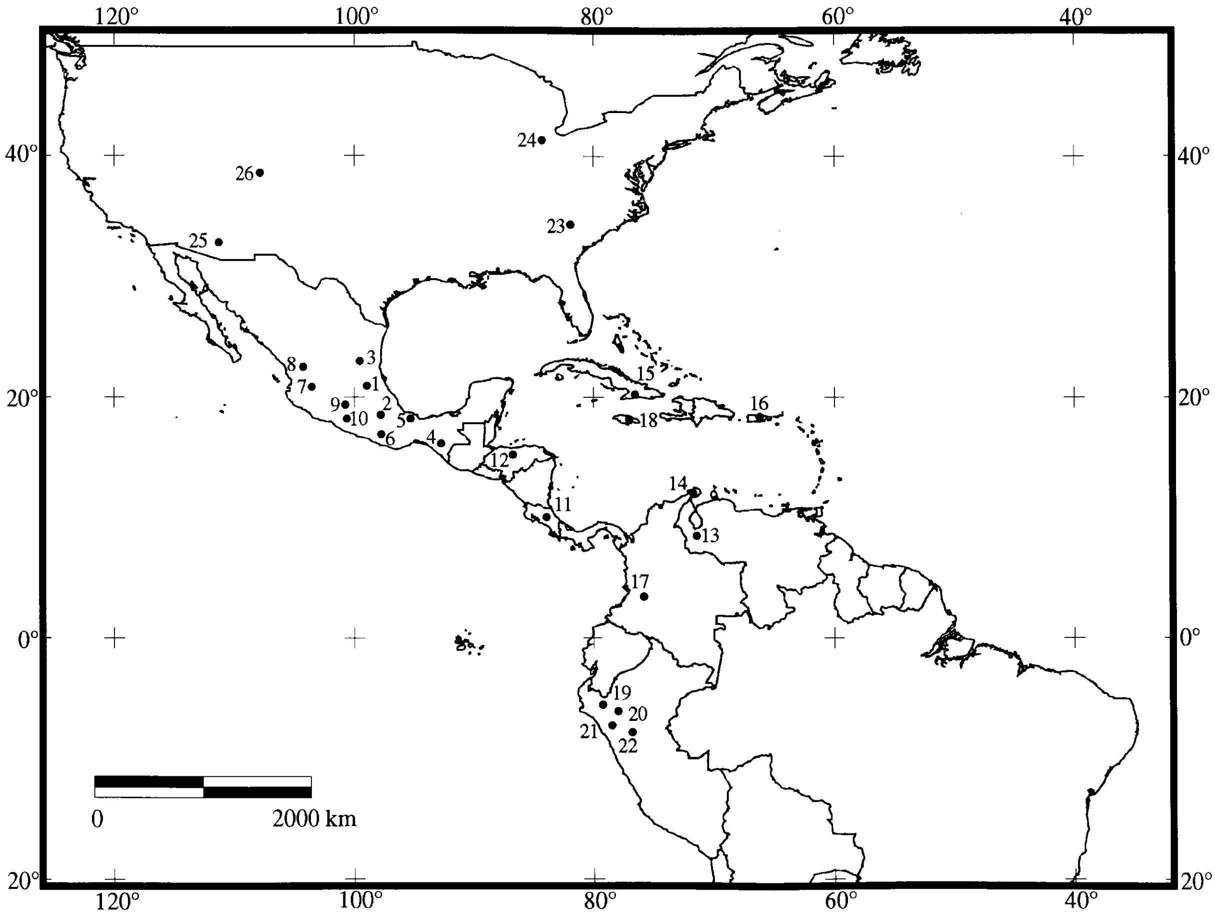

Fig. 1. Cloud forest localities analysed: 1. Tlanchinol, Hidalgo, Mexico; 2. Huautla de Jiménez, Oaxaca, Mexico; 3. Gómez Farías, Tamaulipas, Mexico; 4. El Triunfo, Chiapas, Mexico; 5. Volcán San Martín, Veracruz, Mexico; 6. San Jerónimo Coatlán, Oaxaca, Mexico; 7. Sierra de Manantlán, Jalisco and Colima, Mexico; 8. Sierra de San Juan, Nayarit, Mexico; 9. Ocuilan, Morelos-Mexico, Mexico; 10. Omiltemi, Guerrero, Mexico; 11. Monteverde, Costa Rica; 12. San Juancito, Honduras; 13. La Montaña, Venezuela; 14. Serranía de Macuira, Colombia; 15. Turquino, Cuba; 16. Luquillo Mountains, Puerto Rico; 17. Cerro del Torrá, Chocó, Colombia; 18. Blue Montain, Jamaica; 19. Canchaque, Peru; 20. Parque Nacional de Cutervo, Peru; 21. Bosque Monteseco, Peru; 22. Bosque Cachil, Peru; 23. Great Smoky Mountains, eastern United States; 24. Sandhill Woodlot, Michigan, northeastern United States; 25. Santa Catalina Mountains, western United States; 26. Needle Mountains, southwestern Colorado, western United States

were fragmented in the past due to tectonic and climatic changes. The areas where two or more generalised tracks intersect are nodes, which suggest that different ancestral biotic and/or geological components interrelated in space/time (Morrone and Crisci 1995, Craw et al. 1999).

Parsimony Analysis of Endemicity or PAE (Rosen 1988; Cracraft 1991; Myers 1991; Morrone 1994, 1998; Posadas 1996) classifies areas (analogous to taxa) by their shared taxa (analogous to characters) according to the most parsimonious cladogram. Data for PAE consist of area x taxa matrices and the resulting cladograms represent nested sets of areas. Cladistic information is incorporated by adding supraspecific natural groups –genera in this study- to the matrix (Cracraft 1991, Morrone and Crisci 1995). Craw et al. (1999) considered PAE as a method that allows recognition of generalised tracks, through the discovery of nested sets of areas. In order to undertake this analysis, taxa were coded for their absence (0) or presence (1) in each area of endemism

Table 1. Units of the analysis, mountain systems where they are located, and literature consulted. Mexican floristic provinces based on Rzedowski (1978)

Units	Mountain system	Source
1. Tlanchinol, Hidalgo, Mexico	Sierra Madre Oriental	Luna et al. 1994, Mayorga et al. 1998, Alcántara and Luna 2001
2. Huautla de Jiménez, Oaxaca, Mexico	Serranías Meridionales	Ruiz 1995
3. Gómez Farías, Tamaulipas, Mexico	Sierra Madre Oriental	Puig 1989
4. El Triunfo, Chiapas, Mexico	Serranías Transístmicas	Long and Heath 1991
5. Volcán San Martín, Veracruz, Mexico	Mexican Gulf coast	Álvarez del Castillo 1977
6. San Jerónimo Coatlán, Oaxaca, Mexico	Serranías Meridionales	Campos and Villaseñor 1995
7. Sierra de Manantlán, Jalisco and Colima, Mexico	Serranías Meridionales	Santana 1993, Santiago and Jardel 1993
8. Sierra de San Juan, Nayarit, Mexico	Serranías Meridionales	Téllez 1995
9. Ocuilan, Morelos-México, Mexico	Serranías Meridionales	Luna et al. 1989
10. Omiltemi, Guerrero, Mexico	Serranías Meridionales	Flores 1992–1994, Meave et al. 1992
11. Monteverde, Costa Rica	Cordillera de Tilarán	Haber 1991
12. San Juancito, Honduras	Central American Sierra	Cruz and Erazo 1977
13. La Montaña, Venezuela	Cordillera de Mérida, Northern Andes	Kelly et al. 1994
14. Serranía de Macuira, Colombia	Andean Cordillera	Sugden 1982
15. Turquino, Cuba	Sierra Maestra	Seifriz 1943, Gutiérrez 1980, López et al. 1994
16. Montañas de Luquillo, Puerto Rico	Luquillo Mountains	Howard 1968
17. Cerro del Torrá, Chocó, Colombia	Cordillera Occidental	Silverstone-Sopkin and Ramos-Pérez 1995
18. Blue Montain, Jamaica	Blue Montain Range	Shreve 1914
19. Canchaque, Peru	Andean Cordillera	Dillon 2001
20. Parque Nacional de Cutervo, Peru	Cordillera de Tarros	Dillon 2001
21. Bosque Monteseco, Peru	Cordillera de los Andes Occidentales	Dillon 2001
22. Bosque Cachil, Peru	Andean Cordillera	Dillon 2001
23. Great Smoky Mountains, eastern United States	Appalachian Mountains	Whittaker 1956
24. Sandhill Woodlot, Michigan, eastern United States	Ingham County	Frye 1976
25. Santa Catalina Mountains western United States	Rocky Mountains	Whittaker and Niering 1965
26. Needle Mountains, SW Colorado, western United States	Rocky Mountains	Michener-Foote and Hogan 1999

in the data matrix. The cladistic analysis was carried out with the heuristic search option in Nona (Goloboff 1994) through Winclada (Nixon 1999). The cladogram was rooted with a hypothetical area coded all zeros.

Results and discussion

The analysis of the original data matrix yielded a single most parsimonious cladogram, with 5,952 steps, CI = 0.37, and RI = 0.33 (Fig. 2). The six major clades supported by the congruent distributions of two or more taxa were identified as generalised tracks (Fig. 3; Appendix 1). The first track (F), supported by the congruent distribution of two genera (node 14 included in Fig. 2), includes the majority of the cloud forests in Mexico, Central America, the Antilles, and northern Colombia. A second one (C), supported by the presence of two species (node 8), includes southern Mexico and northern Central America. Another group, which includes the northern Andean forests, is only supported by one genus (*Axinea*, node 9 in Fig. 2) and contains two clades. One clade is in northwestern South America, in the Cordillera Oriental of the Andes in the Atlantic slope (D), and diagnosed by two genera and two species (node 10, Appendix 1). The other clade is located in southwestern South America, along the Peruvian Andes, in the Pacific slope (E), and is supported by the congruent distribution of 10 genera and 18 species (node 11 in Fig. 2). Two other generalised tracks are localised in western United States, along the Rocky Mountains (A), supported by three genera and eight species (node 4), and eastern United States, along the Appalachian mountains (B), supported by seven genera and 18 species (node 5). The genera and species diagnosing the nodes in the cladogram are detailed in Appendix 1.

Clade F includes some tracks that agree with our previous work (Luna et al. 1999) that included 24 Mexican cloud forest patches. Nevertheless, the relationship between the Mexican cloud forests from the Serranías Transístmicas and the Sierra Madre Oriental

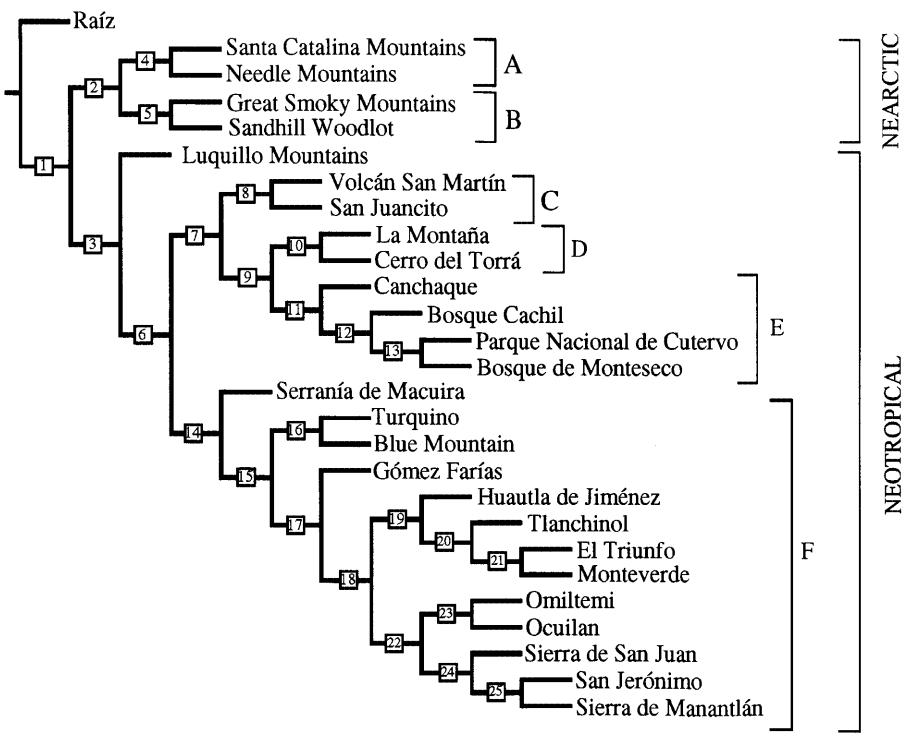

Fig. 2. Cladogram obtained by PAE. Raíz = root

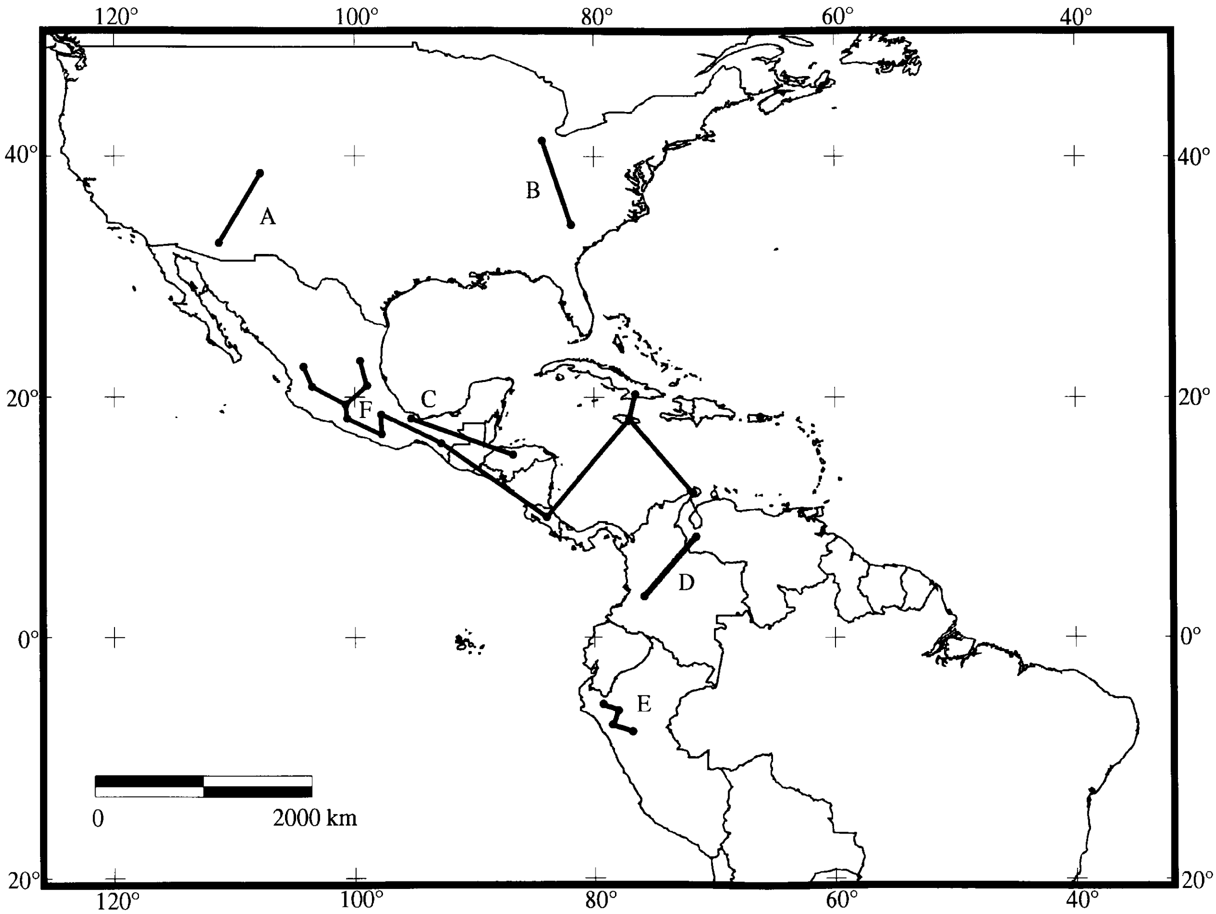

Fig. 3. Generalised tracks obtained in the analysis

may be obscured, since many of these localities were excluded from the present analysis.

The existence of several generalised tracks evidences the complex nature of the Neotropical region. It is relevant to note that all of the Neotropical tracks were included in a larger track (C, D, E, F), supported by the congruent distribution of five genera, *i.e. Begonia*, *Elaphoglossum*, *Epidendrum*, *Miconia*, and *Peperomia* (node 3 in Fig. 2), thus corroborating the naturalness of the Neotropical region as a biogeographic unit. It is interesting to note that many of the species of these genera are typical elements of the cloud forests (Rzedowski 1978, 1996; Luna et al. 1994; Alcántara and Luna 1997), and that they are represented in the Neotropical cloud forests by exclusive and preferential species. Another five genera present in the clade excluding Puerto Rico, are *Cestrum*, *Passiflora*, *Piper*, *Pleurothallis*, and *Tillandsia*, that are also typical and frequent components of cloud forests (node 6 in Fig. 2). The complexity of the Caribbean subregion has been considered by previous authors to be due to its complex geobiotic history (Rosen 1976, 1985; Pregill 1981; Hedges 1982; Guyer and Savage 1986; Donnelly 1988; Thomas 1993; Briggs 1994; Ortega et al. 1994; Llorente 1996). On the other hand, it has been suggested that cloud forests represent extremely diverse and heterogeneous ecosystems, with different biotic affinities (Rzedowski 1978, Meave et al. 1992). Future studies should be addressed to test whether this vegetation type does really represent a natural biogeographic unit, as suggested by our analysis, or it has a hybrid or complex origin.

When we compare the cladogram obtained in this work with the cladogram of Luna et al.

(1999), we note that both confirm the naturalness of the patterns described. In the present case, we only include some representative localities of Mexico, instead of the 24 taken in the former work.

This work has been partially supported by projects DGAPA-PAPIIT IN205799, CONACyT 31879N, and National Geographic Society 6590-99. The useful suggestions by Pauline Ladiges and two anonymous reviewers are greatly acknowledged.

Appendix 1. List of genera and species that support the nodes in the cladogram

NODE	GENERA/SPECIES
1	–
2	–
3	*Begonia, Elaphoglossum, Epidendrum, Miconia,* and *Peperomia*
4	*Abies concolor, Acer glabrum, Aquilegia, Artemisia, Picea engelmannii, Pinus ponderosa, Pinus strobiformis, Pseudotsuga, Pseudotsuga menziesii, Salix scouleriana,* and *Senecio callosus*
5	*Acer rubrum, Acer saccharum, Adiantum pedatum, Amelanchier arborea, Amelanchier laevis, Aralia, Arisaema triphyllum, Athyrium, Carya cordiformis, Carya ovalis, Cornus alternifolia, Cornus florida, Fraxinus americana, Hamamelis, Hamamelis virginiana, Liriodendron, Liriodendron tulipifera, Monarda, Polystichum acrostichoides, Quercus alba, Quercus velutina, Sanguinaria, Sanguinaria canadensis, Smilacina racemosa,* and *Trillium*
6	*Cestrum, Passiflora, Piper, Pleurothallis,* and *Tillandsia*
7	–
8	*Calea urticifolia* and *Cirsium subcoriaceum*
9	*Axinaea*
10	*Blechnum schomburgkii, Diplopterygium, Diplopterygium bancroftii, Palicourea demissa, Paragynoxys,* and *Polypodium fraxinifolium*
11	*Abutilon dianthum, Achyrocline, Achyrocline alata, Barnadesia, Barnadesia hutchisoniana, Bocconia integrifolia, Bomarea distichifolia, Brachyotum, Calceolaria calycina, Cranichis longipetiolata, Dalea weberbaueri, Delostoma, Delostoma integrifolium, Fuchsia ayavacensis, Gardoquia, Hyptis eriocephala, Iochroma, Iochroma grandiflorum, Ipomoea purpurea, Miconia denticulata, Monactis, Monactis flaverioides, Myrsine manglilla, Philoglossa, Siphocampylus, Siphocampylus keissleri, Stenomesson,* and *Vriesea cylindrica*
12	*Asplundianthus, Asplundianthus sagasteguii, Begonia acerifolia, Calceolaria pinnata, Croton abutiloides, Dioscorea glandulosa, Hedyosmum scabrum, Manettia peruviana, Maytenus jelskii, Muehlenbeckia tiliifolia, Brandbyge, Otholobium, Otholobium munyense, Palicourea methystina,* and *Viola arguta*
13	*Allophylus densiflorus, Alonsoa meridionalis, Alternanthera mexicana, Aulonemia, Aulonemia longiaristata, Axinaea nitida, Baccharis latifolia, Bomarea purpurea, Brachyotum coronatum, Calceolaria tripartita, Centropogon pilosulus, Chionanthus pubescens, Cissus obliqua, Citronella incarum, Dalea coerulea, Dioscorea syringaefolia, Doryopteris, Erythrina edulis, Fernandezia, Fuchsia andrei, Heliopsis, Heliopsis buphthalmoides, Hoffmannia obovata, Jacquemontia, Lepechinia radula, Lycopersicon, Lycopersicon hirsutum, Mandevilla glandulosa, Miconia adinantha, Nectandra discolor, Nephelea, Oncidium macranthum, Oxalis lotoides, Passiflora cumbalensis, Passiflora mollissima, Pavonia sepium, Persea subcordata, Phaseolus polyanthus, Physalis peruviana, Piper acutifolium, Polystichum montevidense, Rhipsalis micrantha, Salvia oppositiflora, Saurauia peruviana, Schistocarpha sinforosi, Schmardaea, Schmardaea microphylla,*

Appendix 1 (continued)

	Solanum asperolanatum, Solanum cucullatum, Solanum poeppigianum, Stigmaphyllon bogotense, Styrax ovatus, Tillandsia tovarensis, Tristerix, Tristerix longebracteatus, Turpinia heterophylla, Vernonia scorpioides, and *Weinmannia cymbifolia*
14	*Dendropanax* and *Malvaviscus*
15	–
16	*Besleria lutea, Brunellia comocladifolia, Brunfelsia, Cyrilla, Dichaea glauca, Fagara, Garrya fadyenii, Haemocharis, Heterotrichum, Isochilus linearis, Juniperus barbadensis, Lobelia assurgens, Marattia alata, Meriania leucantha, Peperomia verticillata, Stelis ophioglossoides,* and *Viburnum villosum*
17	*Cornus disciflora, Crusea, Dahlia, Peperomia collocata and Trichilia havanensis*
18	*Adiantum andicola, Alnus acuminata, Clethra mexicana, and Peperomia quadrifolia*
19	*Carex donnell-smithii, Cyathea fulva, Osmanthus, Osmanthus americanus, Rhynchostele, Rhynchostele rosii,* and *Vaccinium leucanthum*
20	*Hansteinia, Smilax mollis, and Styrax glabrescens*
21	*Achimenes pedunculata, Aegiphila valerii, Alfaroa, Amphitecna, Arpophyllum giganteum, Billia hippocastanum, Brassia, Brassia verrucosa, Calyptranthes pallens, Casearia corymbosa, Casearia tacanensis, Catopsis nutans, Chamaedorea tepejilote, Chomelia, Chomelia protracta, Costus scaber, Cupania aff. Macrophylla, Desmopsis, Dioscorea racemosa, Epidendrum laucheanum, Epidendrum pseudoramosum, Epidendrum trachythece, Epiphyllum thomasianum, Exothea, Exothea paniculata, Forchhammeria, Geonoma seleri, Gibsoniothamnus, Gibsoniothamnus cornutus, Hasseltia, Hauya, Heisteria, Heisteria acuminata, Hirtella, Hyptis urticoides, Ipomoea lindenii, Juanulloa mexicana, Justicia aurea, Koanophyllon pittieri, Liabum bourgeavi, Lunania mexicana, Marattia excavata, Maxillaria cucullata, Miconia desmantha, Miconia globulifera, Monnina sylvatica, Nectandra sinuata, Nidema, Nidema boothii, Oerstedella, Onoseris onoseroides, Ophioglossum, Ornithocephalus, Pecluma ferruginea, Pelexia, Physalis aff. angulata, Pilea aff. auriculata, Piper glabrescens, Platymiscium, Pleuropetalum, Pseudolmedia, Secchium, Sideroxylon capiri, Sloanea ampla, Smilax velutina, Solanum trizygum, Solanum wendlandii, Spathiphyllum, Stemmadenia galeottiana, Synedrella, Synedrella nodiflora, Tapirira, Tillandsia brachycaulos, Tillandsia compressa, Tradescantia zebrina, Trigonidium, Tripogandra serrulata, Trophis mexicana, Verbesina turbacensis,* and *Xylosma quichense*
22	*Rumfordia* and *Rumfordia floribunda*
23	*Cranichis subumbellata, Heliocereus, Quercus crassifolia, Solanum demissum,* and *Tillandsia prodigiosa*
24	*Crotalaria longirostrata, Crotalaria quercetorum, Cunila, Cunila pycnantha, Ilex brandegeana, Quercus elliptica, Smilax moranensis, Tephrosia,* and *Tephrosia langlassei*
25	*Ardisia compressa, Asclepias auriculata, Asclepias pellucida, Astragalus guatemalensis, Calceolaria mexicana, Clidemia matudae, Cologania biloba, Commelina tuberosa, Cordia prunifolia, Costus pictus, Crotalaria bupleurifolia, Crotalaria mollicula, Desmodium jaliscanum, Drymaria gracilis, Encyclia chondylobulbon, Euphorbia ariensis, Guardiola, Guardiola tulocarpus, Hyptis oblongifolia, Marina, Panicum parviglume, Peperomia mexicana, Piper umbellatum, Ponthieva ephippium, Prunus cortapico, Quercus magnoliifolia, Quercus vicentensis, Rondeletia jurgensenii, Russelia coccinea, Sommera grandis, Stanhopea martiana, Trigonospermum, Trigonospermum melampodiodes, Valeriana sorbifolia, Vallesia, Vallesia mexicana,* and *Zornia*

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