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The phytogeography of the seasonally dry tropical forests in Equatorial Pacific South America

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ABSTRACT

LINARES-PALOMINO, R., R. T. PENNINGTON & S. BRIDGEWATER (2003). The phytogeography of the seasonally dry tropical forests in Equatorial Pacific South America. *Candollea* 58: 473-499. In English, English and Spanish abstracts.

The origin, current distribution and floristic links of the seasonally dry tropical forest formations in Equatorial Pacific South America (Ecuador, Peru) are assessed by means of multivariate analyses using information from 62 floristic checklists from Neotropical dry forests. Three geographical forest groups are found: (1) coastal Ecuador and Peru plus the Peruvian dry Inter Andean valleys; (2) Central America–Caribbean (including northern South America); and (3) a Bolivian-Argentinean dry forest province. Plate tectonic events, especially the long isolation of South America until the closure of the Isthmus of Panama, the uplift of the Andes and climatic events during the Quaternary are suggested as the causes for these divisions.

RESUMEN

LINARES-PALOMINO, R., R. T. PENNINGTON & S. BRIDGEWATER (2003). Fitogeografía de los bosques tropicales estacionalmente secos en la sudamérica pacífico-ecuatorial. *Candollea* 58: 473-499. En inglés, resúmenes en inglés e español.

El origen, distribución actual y lazos florísticos de las formaciones de bosques tropicales estacionalmente secos en la sudamérica pacífico-ecuatorial (Ecuador y Perú) son evaluados por medio de análisis multivariados usando 62 listas florísticas de bosques secos neotropicales. Se han encontrado tres grupos geográficos de bosques: (1) Ecuador y Perú costero junto con los valles secos interandinos peruanos; (2) América central y el Caribe (incluyendo el norte de Sudamérica); y (3) una provincia de bosques secos boliviano-argentina. Tectónica de placas, especialmente el prolongado aislamiento de Sudamérica hasta antes de la unión del Istmo de Panamá, el levantamiento de los Andes y eventos climáticos durante el Cuaternario son sugeridos como las causas de estas divisiones.

KEY-WORDS: Neotropical region – Phytogeography – Multivariate analysis – Amazon Refuge Theory – Pleistocene climate change – Andes mountains.

Introduction

The Neotropical region is the most species rich area of the planet with a flora of ca. 90.000 species of flowering plants (THOMAS, 1999). Most research describing the level, distribution

and maintenance of this enormous diversity has focused on tropical rain forests because these ecosystems are the most species rich (VALENCIA & al., 1994). However, this concentration on rain forests neglects other more threatened Neotropical ecosystems. Seasonally dry tropical forests (SDTFs) are one example of a formation which has received little attention from conservationists and ecologists, despite being the most endangered ecosystem in the Neotropical region (JANZEN, 1988; MOONEY & al., 1995). This in part reflects the low species diversity of this formation. Although it is true that SDTFs are depauperate in terms of species numbers when compared to tropical rain forest, they have high levels of endemism. Also, due to their widespread destruction (only 0.09% of their original extent remains in Central America, for example) their protection is recognised as a regional conservation priority (GENTRY, 1995; BRIDGEWATER & al., 2003). In addition, recent biogeographic research has hinted that the study of the floras of SDTFs may elucidate patterns of historical vegetation change (PRADO, 1991; PENNINGTON & al., 2000). As such these are scientifically significant ecosystems. Despite these diverse, compelling reasons for study, the floras of SDTF areas are poorly understood, and this lack of detailed floristic information hinders both conservation programmes and the reliable assessment of biogeographic affinities.

A number of thorough quantitative studies have attempted to elucidate floristic links in the Neotropical region (see for instance TER STEEGE & al., 2000, for Amazonia; RATTER & al., 1996 & 2003, for the Brazilian Cerrado; PRADO, 1991, for the Chaco and the Caatingas). However, there are only three studies focused specifically upon SDTFs. GENTRY (1995) made a qualitative comparison of the floristic links between dry forest formations across the Neotropical region. SARMIENTO (1975) carried out a more objective quantitative ordination analysis with similar geographic scope, but the results are of dubious validity because it was conducted at the generic rather than species level. PRADO (2000) carried out a similar quantitative analysis of genera of the seasonal forests of the Chaco and the Caatingas in eastern South America, comparing them to the Cerrados and the Atlantic and Amazon rain forest. His results showed strong floristic affinities among the seasonal forest vegetation types, although the Chaco was shown to be distinct. This resulted in the proposal of a new phytogeographic unit, the Tropical Seasonal Forests Region. This paper presents the first species level biogeographic analysis of Neotropical SDTF based on the floristic comparison of 62 inventories from across the region, and assesses the floristic links between them.

Background: Dry Forests in the Neotropical region

Dry forest formations in their broadest sense have been defined in a variety of ways (PENNINGTON & al., 2000; MURPHY & LUGO, 1995; GENTRY, 1995; SARMIENTO, 1975). This has led to some confusion as to what exactly constitutes a SDTF. This paper will follow the broad definition of PENNINGTON & al. (2000) which describes them as forest formations with an annual precipitation below 2000 mm and showing a significant dry season of at least five to six months in which rainfall totals less than 100 mm. In the Neotropical region, SDTFs occur as disjunct patches scattered across the continent (PENNINGTON & al., 2000; inset in Figure 1), and are of smaller stature and lower basal area than tropical rain forests. They tend to occur on comparatively more fertile soils than savannas (i.e. claylike and with moderate to high pH and nutrient levels, see for instance MURPHY & LUGO, 1986; JOSSE & BALSLEV, 1994), and as such are highly prized for agriculture. As a result, there has been enormous destruction of this ecosystem across its range. The definition of SDTFs followed here excludes the Chaco, which has different climatic conditions (temperature maxima close to 50°C in summer and frosts in winter) and floristic composition (PRADO, 1991, 1993a; PRADO & GIBBS, 1993) and savannas (including the cerrados of Brazil), which usually occur on poorer soils, i.e. acid, dystrophic, with low calcium, magnesium and potassium availability, and often high levels of aluminium (FURLEY, 1999) and have a well developed grassy layer (PENNINGTON & al., 2000).

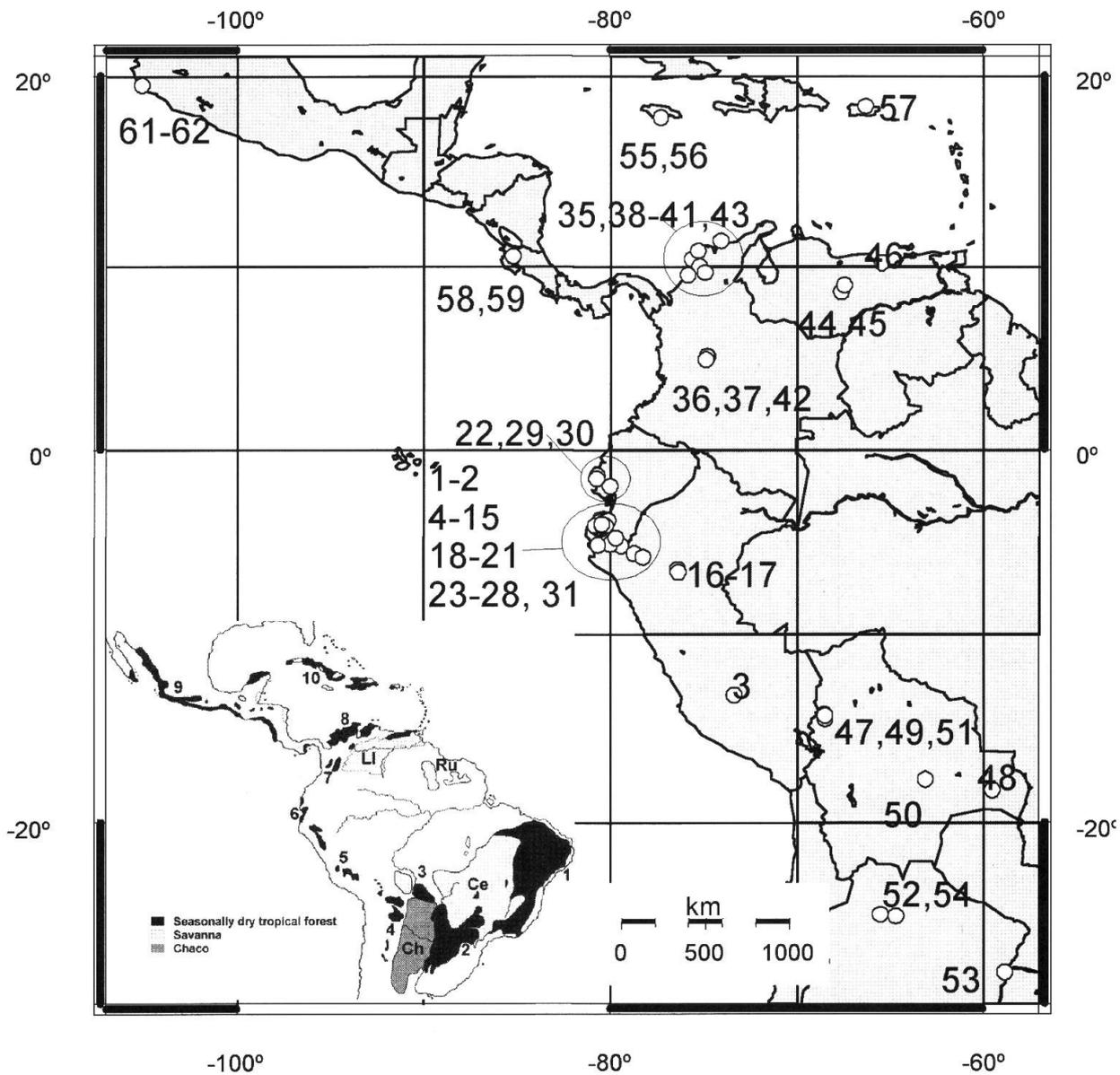


Fig. 1. – Dry forest sites included in the analysis. Numbers refer to the codes given in Table 1. Inset shows the distribution of seasonally dry vegetation in the Neotropical region. **A) Seasonally dry forest:** 1. Caatingas. 2. Misiones Nucleus. 3. Bolivian Chiquitano region. 4. Piedmont Nucleus. 5. Bolivian and Peruvian Inter Andean valleys. 6. Pacific coastal Ecuador. 7. Colombian Inter Andean valleys. 8. Caribbean coast of Colombia and Venezuela. 9. Central America. 10. Antilles. **B) Savannas:** Ce. Cerrado. Ll. Llanos. Ru. Rupununi. Ch. Chaco. (From PENNINGTON & al., 2000).

Code	Site ^a	Lat. S ^b	Long. W	Source	Plot Dimensions (m)	DBH cut-off (cm)	Number of individuals	Number of species
1. Amotape	Tumbes, PE	04°09'	80°37'	MBG, 2002	10(50x2)	10 ^d	377	43
2. Angolo	Piura, PE	04°30'	80°60'	RIOS, 1989	FL ^c	Tree ^e	-	-
3. Apurimac	Apurimac, PE	13°20'	73°20'	WEBERBAUER, 1912	FL ^c	Tree	-	-
4. Baguegra	Amazonas, PE	06°31'	76°22'	BRIDGEWATER & al., 2003	5(10x50)	5	88	26
5. Chulucan	Piura, PE	05°05'	80°10'	WEBERBAUER, 1914	FL ^c	Tree	-	-
6. Elcheco	Piura, PE	04°15'	80°35'	LINARES-PALOMINO, 2002	100x100	10	366	19
7. Elsaue	Tumbes, PE	03°50'	80°28'	LINARES-PALOMINO, 2002	100x100	10	277	19
8. Huancaba	Piura, PE	05°15'	79°23'	WEBERBAUER, 1914	FL ^c	Tree	-	-
9. Ljuanas	Tumbes, PE	03°50'	80°30'	LINARES-PALOMINO, 2002	100x100	10	55	10
10. Marañon	Cajamarca, PE	05°40'	78°42'	WEBERBAUER, 1914	FL ^c	Tree	-	-
11. Miradero	Piura, PE	03°57'	80°29'	LINARES-PALOMINO, 2002	100x100	10	346	22
12. Morropon	Piura, PE	05°10'	79°58'	WEBERBAUER, 1914	FL ^c	Tree	-	-
13. Pasallit	Tumbes, PE	03°57'	80°31'	LINARES-PALOMINO, 2002	100x100	10	524	27
14. Riopiura	Piura, PE	05°13'	80°38'	WEBERBAUER, 1914	FL ^c	Tree	-	-
15. Rquiroz	Piura, PE	04°50'	79°40'	WEBERBAUER, 1914	FL ^c	Tree	-	-
16. Tarapot1	San Martín, PE	06°40'	76°20'	MBG, 2002	10(50x2)	10 ^d	434	75
17. Tarapot2	San Martín, PE	05°51'	78°13'	BRIDGEWATER & al., 2003	4(10x50)	5	88	31
18. Unagato	Tumbes, PE	04°10'	80°47'	LINARES-PALOMINO, 2002	100x100	10	127	6
19. Balneari	Loja, EC	04°06'	80°24'	AGUIRRE & DELGADO, 2001	3(10x50)	5	136	48
20. Bolaspam	Loja, EC	04°11'	80°19'	AGUIRRE & DELGADO, 2001	3(10x50)	5	84	51
21. Cañavera	Loja, EC	04°04'	80°24'	AGUIRRE & DELGADO, 2001	3(10x50)	5	102	51
22. Capeira	Guayas, EC	02°00'N	79°58'	MBG, 2002	10(50x2)	10 ^d	243	42
23. Cazadero	Loja, EC	04°05'	80°26'	AGUIRRE & DELGADO, 2001	3(10x50)	5	57	36
24. Chaguar	Loja, EC	04°00'	80°19'	AGUIRRE & DELGADO, 2001	3(10x50)	5	54	36
25. Gramadal	Loja, EC	04°00'	80°19'	AGUIRRE & DELGADO, 2001	3(10x50)	5	39	7
26. Leonera	Loja, EC	04°05'	80°18'	AGUIRRE & DELGADO, 2001	3(10x50)	5	87	51
27. Maquillo	Loja, EC	04°03'	80°17'	AGUIRRE & DELGADO, 2001	3(10x50)	5	69	36
28. Mauroco	Loja, EC	04°08'	80°25'	AGUIRRE & DELGADO, 2001	3(10x50)	5	108	48
29. Pechiche	Guayas, EC	01°26'	80°41'	JOSSE, 1996	100x100	5	538	37
30. Perromue	Manabí, EC	01°36'	80°42'	MBG, 2002	10(50x2)	10 ^d	272	54

^a PE: Peru, EC: Ecuador, CO: Colombia, VE: Venezuela, BO: Bolivia, ARG: Argentina, JAM: Jamaica, PR: Puerto Rico, CR: Costa Rica, MEX: Mexico. ^b Unless otherwise indicated. ^c FL: Floristic list. ^d Gentry's original dbh cut-off is 2.5 cm. ^e WEBERBAUER (1912, 1914) and RIOS (1989) classify the vegetation as trees, shrubs and herbs.

Code	Site ^a	Lat. S ^b	Long. W	Source	Plot Dimensions (m)	DBH cut-off (cm)	Number of individuals	Number of species
31. Puyango	Loja/El Oro, EC	03°52'	80°04'	KLITGAARD & al., 1999	5x400	5	120	31
32. Sauce	Loja, EC	04°09'	80°23'	AGUIRRE & DELGADO, 2001	3(10x50)	5	81	51
33. Tambillo	Loja, EC	04°09'	80°13'	AGUIRRE & DELGADO, 2001	3(10x50)	5	144	48
34. Ymaurco	Loja, EC	04°05'	80°25'	AGUIRRE & DELGADO, 2001	3(10x50)	5	138	48
35. Bomba	Bolivar, CO	10°21'N	75°34'	MENDOZA, 1999	10(50x2)	1	311	29
36. Bremen	Tolima, CO	05°05'N	74°45'	MENDOZA, 1999	10(50x2)	1	717	7
37. Cardonal	Tolima, CO	05°05'N	74°46'	MENDOZA, 1999	10(50x2)	1	562	8
38. Colorado	Bolivar, CO	09°58'N	75°10'	MBG, 2002	10(50x2)	10 ^d	383	81
39. Colosoi	Sucre, CO	09°30'N	75°48'	MBG, 2002	10(50x2)	10 ^d	238	75
40. Galeraz	Bolivar, CO	10°48'N	75°15'	MBG, 2002	10(50x2)	10 ^d	292	36
41. Monterre	Bolivar, CO	09°37'N	74°54'	MENDOZA, 1999	10(50x2)	1	276	11
42. Santotom	Tolima, CO	04°55'N	74°50'	MENDOZA, 1999	10(50x2)	1	524	42
43. Tayrona	Magdalena, CO	11°20'N	74°02'	MBG, 2002	10(50x2)	10 ^d	238	49
44. Blohmir	Guarico, VE	08°34'N	67°35'	MBG, 2002	10(50x2)	10 ^d	230	51
45. Llano	Guarico, VE	08°56'N	67°25'	MBG, 2002	10(50x2)	10 ^d	274	49
46. Uchire	Anzoátegui, VE	10°09'N	65°25'	GENTRY, 1982, 1995	10(50x2)	10 ^d	222	53
47. Chaquima	La Paz, BO	14°34'	68°28'	MBG, 2002	10(50x2)	10 ^d	331	20
48. Quiapaca	Santa Cruz, BO	18°20'	59°30'	MBG, 2002	10(50x2)	10 ^d	277	55
49. Rioubito	La Paz, BO	14°22'	68°30'	KESSLER & HELME, 1999	FL ^c	10	-	11
50. Santacru	Santa Cruz, BO	17°46'	63°04'	MBG, 2002	10(50x2)	10 ^d	107	36
51. Yanomayo	La Paz, BO	14°24'	68°28'	KESSLER & HELME, 1999	10(50x2)	10	278	59
52. Parqueer	Salta, ARG	24°45'	64°40'	MBG, 2002	10(50x2)	10 ^d	146	31
53. Riachuel	Corrientes, ARG	27°30'	58°50'	MBG, 2002	10(50x2)	10 ^d	339	39
54. Salta	Salta, ARG	24°40'	65°30'	MBG, 2002	10(50x2)	10 ^d	193	22
55. Roundtop	JAM	17°50'N	77°15'	MBG, 2002	10(50x2)	10 ^d	557	54
56. Roundsl	JAM	17°50'N	77°15'	MBG, 2002	10(50x2)	10 ^d	659	48
57. Mogote	PR	18°25'N	66°16'	MBG, 2002	10(50x2)	10 ^d	418	37
58. Guangf	CR	10°30'N	85°10'	MBG, 2002	10(50x2)	10 ^d	171	55
59. Guanup	CR	10°30'N	85°10'	MBG, 2002	10(50x2)	10 ^d	356	47
60. Chamela1	Jalisco, MEX	19°30'N	105°03'	MBG, 2002	10(50x2)	10 ^d	357	79
61. Chamela2	Jalisco, MEX	19°30'N	105°03'	MBG, 2002	10(50x2)	10 ^d	451	80
62. Chamela3	Jalisco, MEX	19°30'N	105°03'	MBG, 2002	10(50x2)	10 ^d	311	81

Within this definition, there are great physiognomic and floristic differences among SDTFs. In a review of SDTF in Central America and the Caribbean, for example, MURPHY & LUGO (1995) pointed out the presence of forests with canopies in the range from 2 m height in drier conditions and up to 40 m in forests on ecologically favorable sites. Floristically the differences are similar with species richness values in the range of six in drier and disturbed forests, rising to 81 in other forests (LINARES-PALOMINO, 2002; GENTRY, 1995). *Leguminosae* is usually the dominant arborescent family in SDTF and *Bignoniaceae* dominates the liana flora. *Capparidaceae*, *Cactaceae* and *Erythroxylaceae* are the only three families conspicuously better represented in dry forests than in wet forests. *Anacardiaceae*, *Flacourtiaceae*, *Euphorbiaceae*, *Myrtaceae*, *Rubiaceae* and *Sapindaceae* are also well represented (GENTRY, 1988, 1995).

Methods

In the past decade, there has been an increase in the number of published floristic studies of Neotropical SDTF. Inventory and floristic lists for woody species in dry forests in Latin America were collated from the published literature and complemented by unpublished studies where these were considered reliable. Reliability was considered to be bad if the species list contained more than 15% of doubtful identifications and/or morphospecies (OLIVEIRA-FILHO & RATTER, 1995). To ensure uniformity among the different lists and if the information was available, only woody species identified as trees or large shrubs with a DBH (Diameter at Breast Height) of at least 1 cm and minimal (potential) heights of 3 m were considered. Exceptions were made for RIOS (1989) and WEBERBAUER (1912, 1914) since both authors refer to the vegetation as trees, shrubs and herbs and only those identified as trees were considered here. SDTFs from Brazil were not included since the analyses by PRADO (1991, 2000) already described these formations and their floristic affinities. Site information for the 62 surveys used in the study is given in Table 1 and they are mapped in Figure 1. Although not all of the floristic studies used the same methodology, a pragmatic approach of including all studies was taken to give maximum geographic coverage. This approach has been used successfully before in vegetation analysis. RATTER & al. (1996) analyzed data from localities which varied "greatly in size and sample methodology" (see also OLIVEIRA-FILHO & RATTER, 1995; RATTER & DARGIE, 1992; OLIVEIRA & NELSON, 2001, for similar approaches). Nomenclature was checked according to BRUMMITT & POWELL (1992), THE PLANT NAMES PROJECT (1999) and W³-TROPICOS (<http://mobot.mobot.org/W3T/Search/vast.html>), as well as relevant literature (see References). All synonyms were changed to the correct names while records not identified to species level were removed. The 'cleaned' floristic lists were then used to form a presence-absence matrix. The floristic data were subjected to multivariate analyses using PC-ORD, version 4 (McCUNE & MEFFORD, 1999). Three different methodological approaches were taken: (1) Detrended Correspondence Analysis, (2) Unweighted Pair-Groups Method using Arithmetic Averages (UPGMA), a cluster analysis using the Sørensen Index as the measure of similarity and (3) Two-Way Indicator Species Analysis (TWINSPAN). These followed OLIVEIRA-FILHO & RATTER (1995) with the difference that all analyses were done using the complete matrix, i.e. without excluding species recorded only at a single site (unicates).

Results and Discussion

In total 517 species were recorded for all the SDTF areas (Appendix 1; the complete matrix is available from the corresponding author). Of these, 317 species were unicates, i.e. species only recorded at one site. This represents ca. 60% of all species. This is a high value, exceeding those reported by similar studies on related vegetation formations (RATTER & al., 1996, 2003; OLIVEIRA-FILHO & RATTER, 1995; RATTER & DARGIE, 1992; but see LENTHALL & al., 1999). SDTFs are well known for their high levels of endemism (BRIDGEWATER & al., 2003), so this very high percentage of unicate species is not unexpected and we

1. North-western Peru (including montane and coastal dry forests)	6. Central America
2. Inter-Andean Peru	7. The Antilles
3. South-western Ecuador	8. Inter Andean Bolivia
4. Inter-Andean Colombia	9. Chiquitos Region in Bolivia
5. Caribbean Colombia and Venezuela (including Costa Rican dry forests)	10. The Piedmont and Misiones nuclei

think it does reflect phylogeographic patterns. However, it is likely to have been inflated by factors such as the geographical sparsity of floristic surveys, the broad geographic area from which they were collated, the unequal methodologies for each survey (different DBH for some studies and unequal survey areas). The inclusion of more floristic information, once it becomes available, will undoubtedly reduce the percentage of unicates.

The most widespread species recorded in this study are *Bursera graveolens*, *Capparis flexuosa* and *Cochlospermum vitifolium*, each with 24 records. All three species are conspicuous representatives of SDTF, although *C. flexuosa* and *C. vitifolium* can also be found occasionally in moist forests (ILTIS, 2001; POPPENDIECK, 1981). The distribution of *B. graveolens* ranges from the South of Mexico to Venezuela and Peru (DALY, 1993), while *C. flexuosa* and *C. vitifolium* have wider distributions in the Neotropical region. The former ranges from tropical Florida in the USA and western Mexico through Mesoamerica and the Antilles to coastal Colombia and Venezuela continuing to Ecuador, Peru, southern Brazil, Bolivia and Argentina (RUIZ-ZAPATA & ILTIS, 1998). The latter ranges from northern Mexico to Peru, Venezuela, West Indies and reaches Central Brazil and Bolivia. *Cochlospermum vitifolium* has been reported to be weedy (POPPENDIECK, 1981) and this ecology could explain its presence in various plots, because several were described as disturbed (e.g. MENDOZA-C, 1999). In this study even the most common species are present in less than half of the total number of plots, with no species being truly cosmopolitan. Only *Tabebuia chrysantha*, *Ceiba trichistandra*, *Eriotheca ruizii*, *Terminalia valverdeae*, *Acacia macracantha*, *Albizia multiflora*, *Caesalpinia glabrata*, *Erythrina smithiana*, *Geoffroea spinosa*, *Guazuma ulmifolia* and *Celtis iguanaea* occur in 15 (24%) or more of the plots. It should be emphasized that of these species, only *G. spinosa* is reported as a 'classic' widespread SDTF species (PRADO & GIBBS, 1993).

The three separate multivariate analyses yielded similar wide geographic patterns, distinguishing three broad groups. These have been assigned to ten phylogeographic subgroups (Table 2).

Agglomerative hierarchical classification (UPGMA)

The cluster analysis of the floristic data shows clear geographical groupings (Figure 2). All the Argentinean and Bolivian sites are separated from the more northern localities in South and Central America. There is also a clear floristic discontinuity in the Central Andes, with distinct northern (i.e. north of southern Peru) and southern (i.e. Argentinean) floristic elements. This supports the findings of SARMIENTO (1975; but see discussion below). Floristically, Bolivia fits within the "southern" group, whilst the "northern" group contains the Central American, Antillean, northern South American, Peruvian Inter-Andean, South-western Ecuadorian and North-western Peruvian sites (Figure 2). These dry forests have been assigned to broader phylogeographic subgroups (Table 2). With the exception of two geographically "misclassified" sites (Venezuelan BLOHMR groups with the eastern Peruvian plots and Peruvian TARAPOT2 with the Bolivian and Argentinean sites), the classification reveals three broad phylogeographical groups:

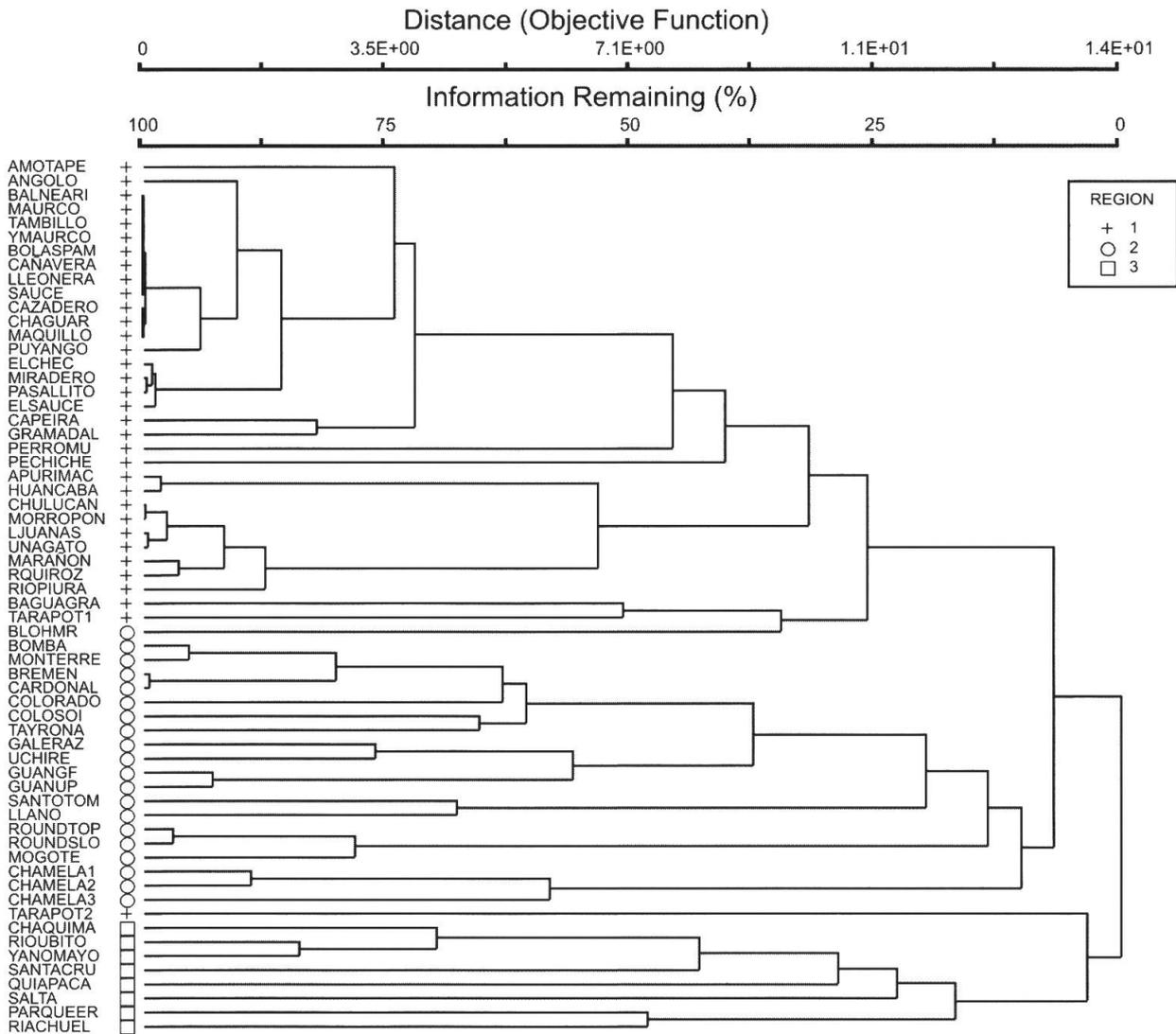


Fig. 2. – UPGMA dendrogram based on the Sørensen Similarity Coefficient: Crosses (Region 1) = Peru and SW Ecuador; Circles (Region 2) = Colombia, Venezuela, Central America and the Antilles; Squares (Region 3) = Bolivia and Argentina.

- **(A) The Equatorial Pacific group of Peruvian and Ecuadorian SDTF (Subgroups 1-3, Table 2).**

This is composed of (1) Peruvian montane dry forest plots from Tumbes and Piura clustered together with the montane dry forest sites from Ecuador, (2) the Peruvian coastal (lowland) dry forests and Inter-Andean dry forests and (3) the isolated Peruvian plots BAGUAGRA and TARAPOT1 which form a cluster clearly distinct from the remaining Peruvian sites. More floristic data are needed to understand more fully the floristic relationships of these isolated SDTF.

- **(B) The Northern SDTF group of Colombian, Venezuelan, Central American and Antillean SDTF (Subgroups 4-7).**

This is composed of (1) the Colombian and Venezuelan dry forests (2) the Antillean sites and (3) the Mexican dry forests. The Costa Rican dry forest plots are grouped in this cluster, which may reflect geographical proximity. These results contradict previous findings (SARMIENTO, 1975; GENTRY, 1995), which suggested a link between the Colombian and Venezuelan dry forests and the coastal Ecuadorian and Peruvian dry forests.

• **(C) The Southern group of Bolivian and Argentinean dry forests (Subgroups 8-10).**

The Bolivian Inter-Andean sites (CHAQUIMA, RIOUBITO and YANOMAYO) are clustered with the Misiones (RIACHUEL) and Piedmont (PARQUEER and SALTA) nuclei, and this group is distinct from the lowland Chiquitano region (SANTACRUZ and QUIAPACA). KESSLER & HELME (1999) reported a similar pattern based on distribution patterns of *Acanthaceae* and *Bromeliaceae*. This pattern is particularly important as it is not consistent with the Argentinean-Bolivian – Peruvian-Ecuadorean connection of the Pleistocenic Arc Model. This model (PRADO, 1991; PRADO & GIBBS, 1993) proposed links between three nuclei of seasonally dry forests in South America during the Pleistocene: (1) the Caatingas of north-eastern Brazil, (2) the Paraguay-Paraná river system in north-eastern Argentina, east Paraguay and south-western Mato Grosso do Sul, and (3) the Subandean Piedmont Forests of north-western Argentina and south-western Bolivia extending along the foothills of the Andes in north-western Bolivia, and entering Peru in dry Inter-Andean valleys such as those of the Apurimac, Huallaga and Marañon rivers, and just reaching south-western Ecuador (PRADO, 2000). The clear placement of all Peruvian sites (with the exception of TARAPOT2 which is the only apparent anomalous site) in group A, and their floristic distinction from the Bolivian and Argentinean sites, suggests that these areas were not as recently linked as PRADO (1991; 2000) has suggested.

Divisive hierarchical classification (TWINSPAN) site hierarchy

Of the three broad groups recognised by UPGMA, only the Equatorial Pacific group could be clearly recognized. The Northern SDTF group was split into two with the Colombian, Venezuelan and Costa Rican sites grouped with the other South American ones and the Mesoamerican sites grouped distinctly apart. The Southern group was scattered between the

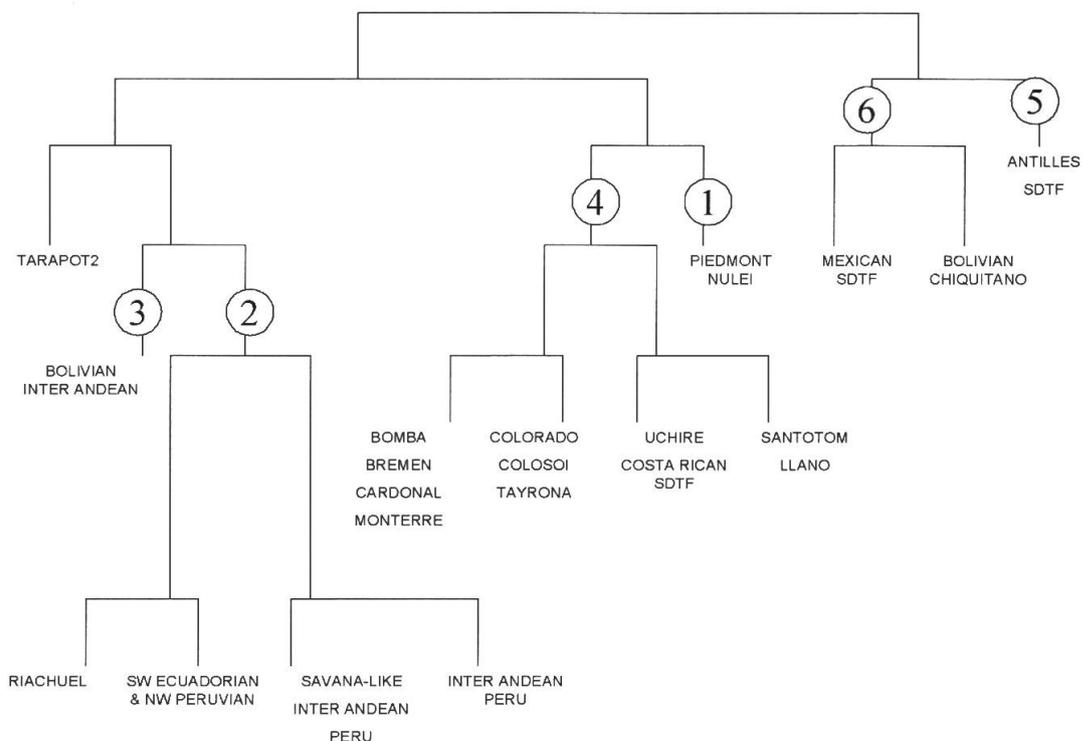


Fig. 3. – TWINSPAN classification. Numbers indicate the six geographically coincident groups produced after four divisions.

other groups, showing no clear resolution. However, six geographically coincident groups were produced after four divisions (Figure 3), which were similar to those obtained by UPGMA.

- **Group 1:** Two Argentinean sites from the Piedmont nucleus (Subgroup 10 from UPGMA).
- **Group 2:** The majority of the sites corresponding to the Equatorial Pacific group, including Peruvian and Ecuadorian sites of subgroups 1 to 3 (UPGMA). There are two anomalously placed sites in this group GALERAZ (Colombia) and BLOHMR (Venezuela), while RIACHUELO (Argentina) is placed as a sister group.
- **Group 3:** Inter-Andean Bolivian sites (UPGMA Subgroup 8).
- **Group 4:** Northern South American sites from Colombia and Venezuela (UPGMA Subgroup 5). The Costa Rican sites are included in this group, again showing a strong affinity with the northern South American dry forests.
- **Group 5:** Antillean sites (UPGMA Subgroup 7).
- **Group 6:** Includes the Mexican sites (UPGMA Subgroup 6). Strangely, the Bolivian Chiquitano Region (UPGMA Subgroup 9) sites cluster with this group. A further level of division separates the Bolivian ones from the Mexican sites.

Ordination (DCA)

The ordination of the complete matrix resulted in a pattern differentiating the three broad phytogeographical groups already referred to above. The exclusion of three outliers, namely ROUNDSLO, ROUNDTOP and MOGOTE, all from the Antilles, resulted in a good spreading of the remaining sites (Figure 4). The Equatorial Pacific group (Peruvian and Ecuadorean forests), the Northern group (Colombian, Venezuelan and Central American forests) and the Southern groups (Bolivian and Argentinean forests) are all recognized. Interestingly, the

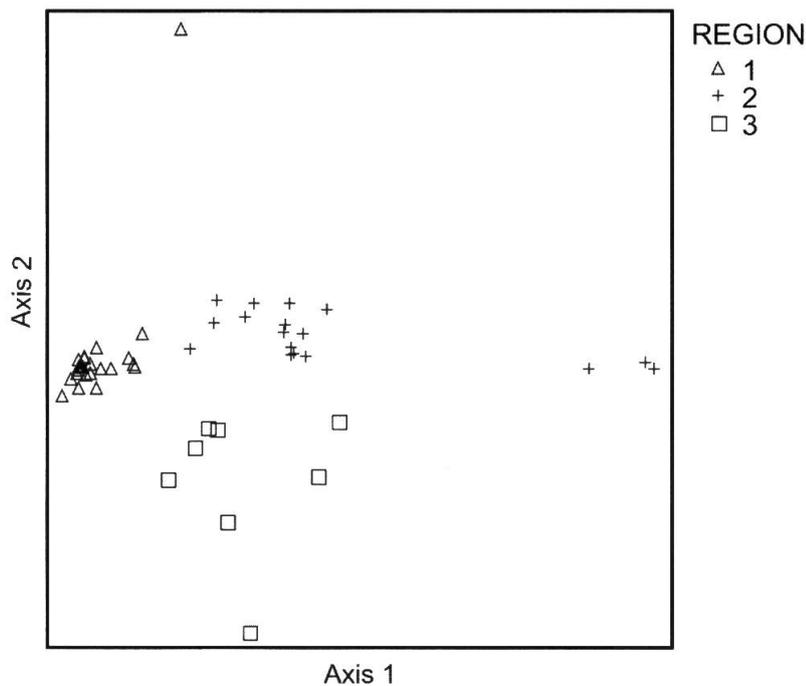


Fig. 4. – DCA output for 59×476 matrix. Triangles (Region 1) = Peru and SW Ecuador; Crosses (Region 2) = Colombia, Venezuela, Central America and the Antilles; Squares (Region 3) = Bolivia and Argentina.

Mexican sites cluster far apart from the rest of the northern group supporting their floristic uniqueness that was already suggested by LOTT (1993). She estimated that around 10% of the flora in coastal Jalisco and Colima in mid-western Mexico was endemic. In Chamela, where the plots from this study are located, her estimate was 16%.

The TARAPOT2 plot clusters alone at the top left of the ordination. This is due to its distinctive floristic composition. BRIDGEWATER & al. (2003) reported that ca. 10% of the species of this site were narrow endemics. In the present study, six out of a total of nine species from BRIDGEWATER & al.'s plot are unicates.

Neotropical Dry Forest Phytogeography

SDTFs in Equatorial Pacific South America

Several authors have noted the high floristic affinities between the dry forest formations in Tumbes and Piura in north-western Peru, and the adjacent forests in south-western Ecuador (BRIDGEWATER & al., 2003; AGUIRRE & DELGADO, 2001; GENTRY, 1992b). The UPGMA and TWINSPAN analyses of this study certainly support this view.

The analyses showed closest floristic affinities between the montane dry forests in Loja (Ecuador) and the montane dry forests in Cerros de Amotape (Peru). This includes the montane dry forests at El Angolo in northern Piura (Peru). The same analysis shows the coastal lowland dry forests in north-western Peru in a cluster with the Peruvian Inter-Andean dry forests. A Detrended Correspondence Analysis (DCA) run only on the Ecuadorian and Peruvian Data (data not shown), supported the closer relationships of the Peruvian montane dry forests to the Ecuadorian dry forests. This coincidence of the two analyses show that there is clear evidence of a floristic relationship between the dry forests in Cerros de Amotape and the dry forests in the Inter-Andean Valleys in Peru. These appear to form a wider phytogeographic unit.

The principal factors explaining the patterns of floristic relationships of Equatorial Pacific SDTFs are probably the physical barriers presented by the Andean Mountains (Figure 5). In this area, there are two main Cordilleras: Western and Central. The Western Cordillera separates the Pacific coastal plain (sites 1, 2, 5-7, 9, 11-14, 18-34 in Table 1) from the valley of the Rio Marañon (sites 8, 10 and 15). This cordillera is punctuated by the Huancabamba Depression in the Peruvian Andes where the lowest point is at 2145m at the Abra de Porculla. This is the lowest pass in the entire Andean chain from Chile to Venezuela. The central cordillera separates the sites in the Marañon drainage from SDTFs at Tarapoto. A much lower mountain chain in the Tarapoto area, the Eastern Cordillera is not considered as a dispersal barrier since its elevation reaches barely 1500 m.

The Huancabamba depression has been postulated by some authors as a biogeographical barrier for the dispersal of montane organisms (e.g. *Fuchsia*, BERRY, 1982; *Loasaceae*, WEIGEND, 2002). It might actually constitute a dispersal opportunity for lowland dry forest vegetation, usually found at low altitudes, to cross the Andean mountain chain. This is suggested by dry vegetation formations in the Mantaro valley in Central Peru, which can be found at altitudes as high as 2800 m (WEBERBAUER, 1936) and dry forests at Manu-Parobamba in Cusco and the Apurimac valley in southern Peru are found at altitudes between 2000 m – 2500 m (M. P. NUÑEZ, pers. comm.; R. T. PENNINGTON, unpubl. data). This indicates that dry forest species may be able to cross the 2145m of the Abra de Porculla pass; SDTF vegetation grows within a few kilometres of the summit of the pass (BRIDGEWATER & al., 2003). The dispersal of dry forest plants across the western Cordillera in this area may have occurred recently, and may still be happening for some organisms. This may explain the high floristic similarity between the Pacific coastal dry forests and those of the Marañon valley as already suggested by BRIDGEWATER & al. (2003).

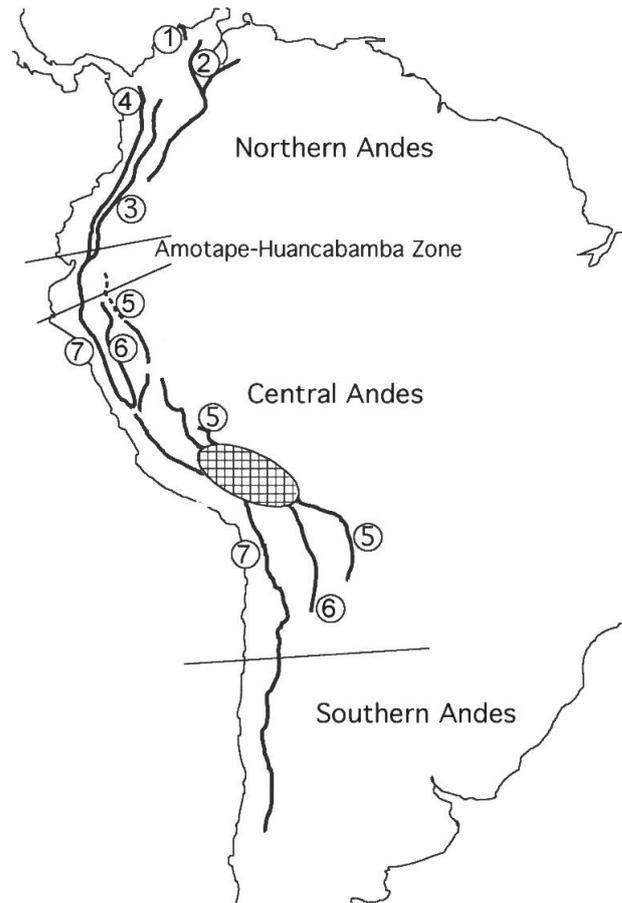


Fig. 5. – Simplified division of the Andes. In the Northern Andes: 1. Cordillera (C.) of Santa Marta. 2. Eastern C. 3. Central C. 4. Western C. In the Central Andes: 5. Eastern C. 6. Central C. 7. Western C. Hatched area represents the Peruvian-Bolivian Altiplano region. Stippled line shows mountain ranges below 2000 m in the Tarapoto area.

In contrast, floristic links with the SDTFs situated to the east of the central cordillera Andes (e.g. Tarapoto) are weak. The Central Cordillera has no discontinuities in its range, and organisms on either side may have been gradually isolated since the uplift of the mountain range began some 23 Ma ago (BURNHAM & GRAHAM, 1999). The relationships of the Tarapoto sites are unstable in all analyses, and although they are represented by only two floristic lists, we consider that this instability reflects their unique flora. It seems conceivable that the SDTFs in this area have been isolated for a long geological period, allowing a considerable number of endemic species to accumulate.

Equatorial Pacific SDTFs: The Latin American context

The multivariate analysis of 62 samples from representative dry forests in Latin America showed strong support for the division of these dry forest formations into three broad phytogeographical groups: (1) a Central American–Caribbean group (including northern South America), (2) an Ecuadorian-Peruvian group, and (3) a Bolivian-Argentinean group. This differs from the phytogeographical divisions for dry plant formations suggested by SARMIENTO (1975). He proposed four original floristic stocks which provided the material for the development and evolution of the current South American arid floras, two of them being tropical dry forest formations, the other two being subtropical formations. He suggested an almost continuous dry forest formation from southern Mexico, through Central America, to northern South America southwards

to Peru as one stock and the dry forests in north-eastern and Central Brazil and the Chaco forests of Bolivia and Paraguay as a second. Moreover, he indicated a major division of the South American dry floras to be located in central Andean Peru. The analyses presented here shift this division further south, between southern Inter Andean Peru and north-western Inter Andean Bolivia.

The origin of each of the three phytogeographical groups presented here cannot be easily explained by single factors as they have arisen from a complex interplay of Cenozoic geological and climatological history in Latin America. Although recent Quaternary glacial and inter-glacial events have undoubtedly impacted the floras of these regions (HAFFER, 1979; COLINVAUX & al., 1996; HOOGGHIEMSTRA & CLEEF, 1995; MAYLE & al., 2000), plate tectonic events (RAVEN & AXELROD, 1974; HAMMEL & ZAMORA, 1993; BURNHAM & GRAHAM, 1999; GOLDBLATT, 1993; ROMERO, 1993) and the Andean uplift (YOUNG & al., 2002; LUTEYN, 2002; GENGLER-NOWAK, 2002; TAYLOR, 1995) have also been crucial in shaping present day distribution patterns in the Neotropical region.

An important factor in explaining the clear separation of the Central American-Caribbean SDTFs is the isolation of South America from any other landmass for approximately 80 million years, beginning with the rifting from Africa and ending with the closure of the Isthmus of Panama approximately 3.5 – 3.1 Ma (BURNHAM & GRAHAM, 1999). There is geological evidence that brief connections between northern South America and *proto* Central America might have existed in the latest Eocene/early Oligocene (35 – 33 Ma) (ITURRALDE-VINENT & MACPHEE, 1999), but little paleobotanical and paleozoological evidence exists to support migration events, and it is thought that these connections would never have been continuous. However, this possible migration route offers one explanation for the apparent close floristic link of Costa Rican SDTFs, and the rest of Mesoamerican and Caribbean sites, with northern South American sites in the multivariate analyses. A second, perhaps more likely explanation is relatively recent dispersal of species along the Isthmus of Panama since its closure. From the Eocene-Oligocene transition, through the middle Miocene, and especially during high sea-level stands in the late Miocene, an epicontinental sea in the present-day Orinoco river basin might have isolated north-western South America from the rest of the continent (ITURRALDE-VINENT & MACPHEE, 1999). This may have reinforced the floristic differences between northern South American sites and the rest of the continent, which are demonstrated in this study.

Several authors have proposed a dynamic relationship between moist/wet forests and dry vegetation formations (savannas and dry forests) in the Neotropical region during glacial and inter-glacial cycles in the Quaternary (e.g. HAFFER, 1982; PRADO & GIBBS, 1993). The moist/wet forests have been proposed as expanding their geographical range during inter-glacial cycles (such as that of the present day), in which more humid and warm climates are predominant. As a consequence, the dry vegetation formations, once more widespread in distribution, have receded to areas of low rainfall, forming dry forest and savanna refugia. During glacial maxima, evidence suggests that the climate was drier and cooler by around 2–8°C (BURNHAM & GRAHAM, 1999) and the sea level lower by around 100 – 200 m (GREGORY-WODZICKI, 2000). These events would have been important factors in promoting the retreat of moist/wet forests into refugia and the expansion of drier vegetation formations around the region.

This model of Pleistocene vegetation shifts may be a more recent factor reinforcing the separation between coastal Pacific and Andean SDTFs in Ecuador and Peru, and those in Colombia and Venezuela. GENTRY (1982b) postulated that the super-humid Chocó region in western Colombia may have always kept these areas separate. The Chocó presently has a high record of precipitation (around 11.6 m/year) and during drier glacial maxima it may have remained a moist barrier to the expansion of the drier Pacific vegetational formations from South America and Caribbean Colombia and Venezuela. It has been proposed as a glacial rain forest refuge by several authors (HAFFER, 1969, 1982; GENTRY, 1982b; PRANCE, 1973, 1982).

Pleistocene vegetation history in central Amazonia may also explain the floristic dissimilarities between the northern South American sites and the SDTFs in southern South America.

Palynological evidence indicates much of Amazonia remained humid throughout the Pleistocene (COLINVAUX & al., 1996). Species characteristic of dry forests are sparsely distributed in Amazonia, which is suggestive of once more extensive ranges in drier glacial times (PENNINGTON & al., 2000). However, the floristic division between SDTF sites south and north of the Amazon basin suggests that recent migration of species right across the basin may have been limited. A migration route has been hypothesized which might have linked the Caatingas in north-eastern Brazil with other seasonal ecosystems in the Roraima – Rupununi savannas (in Guyana and the Roraima State in Brazil) (PRADO, 2000). This hypothesis has been based on plant distribution data and even suggests links of the Caatingas with the Caribbean and Central America (PRADO, 1991). However, the inclusion of the Caatingas in the Tropical Seasonal forests Region (PRADO, 2000) implies that the relationships of this area lies to the south and not with the Caribbean.

Andean uplift events and Quaternary climatic changes may have been important factors causing the weak floristic affinities between the Ecuadorian-Peruvian and the Bolivian-Argentinean phytogeographic groups. Orographic factors could have caused isolation of the SDTFs of the dry Inter-Andean valleys of southern Peru from those located in more southern regions, especially the ones in the Bolivian Andes. Even though up to 10 Ma the elevation of the Bolivian Altiplano was only half of its present height of 4000 m, organisms still had to disperse across at least two (Eastern and Central), and possibly three (Western) of the Cordilleras (see Figure 5) to cross between northern Peru and Bolivia. This suggests that the high peaks of the Andes have played a role in isolating these different SDTF areas for over 10 million years. It is probable that the links of dry Inter-Andean valleys of La Paz with the Chiquitos region (or even the Piedmont or Misiones nuclei) reflect past extension of Chiquitano forests during dry periods of glacial cycles. For instance, species distribution and floristic studies in Chaco forests and SDTF in the Misiones Nucleous in Paraguay have established ranges reaching into neighbouring Argentina, Brazil and Bolivia, but not to more northern areas (PRADO, 1993b; SPICHIGER & al., 1992, 1995). They suggest climatic and orographic causes for the present forest distribution patterns (RAMELLA & SPICHIGER, 1989; SPICHIGER & al., 1995).

Conclusion

Both, ancient (Tertiary) and more recent (Pleistocene) geological and climatic events explain the origin and present distribution of the SDTF in the Neotropical region. Although plate tectonic events and especially Andean orogeny seem to have played a major factor, glacial and post-glacial events cannot be totally discounted. Amazonian speciation models predict similar scenarios (BUSH, 1994; COSTA, 2003). Recent cladistic vicariance and molecular biogeographic analyses on SDTF have reached similar conclusions as in this study (PENNINGTON & al., submitted).

On a regional scale, more detailed inventory in SDTFs is required to reveal more clearly the patterns outlined here. Particularly critical areas to be surveyed are on the border between Inter Andean Bolivia and southern Peru and in Inter Andean and eastern Peru (the Tarapoto area). Although many of the areas evaluated in the present analysis have been declared as threatened (e.g. in Colombia, MENDOZA-C., 1999 and INSTITUTO NACIONAL ALEXANDER VON HUMBOLDT, 1998; in Ecuador, DODSON & GENTRY, 1991; GENTRY, 1992b; and in Bolivia, PARKER & al., 1993), the importance of the Tarapoto area in Peru should be highlighted. It has never been included in any conservation or natural protected area. In the analyses presented here, one plot from Tarapoto shows uncertain relationships, emphasizing the area's unique flora. SDTF in the Tarapoto valley is severely damaged and requires urgent study and conservation.

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http://www.aquarius.geomar.de/omc/omc_intro.html.

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APPENDICES

Species Matrix

The number of sites recorded for each species is given, with unicates highlighted in bold.

ACHATOCARPACEAE

***Achatocarpus gracilis* H. Walter 1**

A. nigricans Triana 2

A. praecox Griseb. 3

ANACARDIACEAE

***Astronium balansae* Engl. 1**

***A. fraxinifolium* Schott ex Spreng. 1**

A. graveolens Jacq. 10

A. urundeuva (Allemão) Engl. 3

***Comocladia engleriana* Loes. 1**

Loxopterigyum huasango Spruce ex Engl. 8

***Mauria suaveolens* Poepp. & Endl. 1**

Metopium brownei (Jacq.) Urb. 2

Schinopsis brasiliensis Engl. 2

***S. glabra* (Engl.) F.A. Barkley & E. Mey. 1**

***S. peruviana* Engl. 1**

Schinus molle L. 3

***S. piliferus* I.M. Johnst. 1**

Spondias mombin L. 7

S. purpurea L. 2

***S. radlkoferi* Donn. Sm. 1**

ANNONACEAE

***Annona holosericea* Saff. 1**

***A. muricata* L. 1**

***A. nutans* (R.E. Fr.) R.E. Fr. 1**

***A. palmeri* Saff. 1**

***Oxandra espiantana* (Spruce ex Benth.) Baill. 1**

Sapranthus palanga R.E. Fr. 2

APOCYNACEAE

***Aspidosperma australe* Müll. Arg. 1**

***A. cuspa* (Kunth) S.F. Blake ex Pittier 1**

***A. cylindrocarpon* Müll. Arg. 1**

***A. excelsum* Benth. 1**

A. parvifolium A. DC. 2

A. polyneuron Müll. Arg. 5

***A. pyriformis* Mart. 1**

***A. rigidum* Rusby 1**

Plumeria rubra L. 2

***Rauvolfia tetraphylla* L. 1**

***Tabernaemontana catharinensis* A. DC. 1**

***T. cymosa* Jacq. 1**

ARALIACEAE

***Pentapanax angelicifolius* Griseb. 1**

***Sciadodendron excelsum* Griseb. 1**

ARECACEAE

***Attalea phalerata* Mart. ex Spreng. 1**

***A. tessmannii* Burret 1**

***Copernicia tectorum* (Kunth) Mart. 1**

***Phytelephas aequatorialis* Spruce 1**

***Syagrus romanzoffiana* (Cham.) Glassman 1**

S. sancona H. Karst. 2

Thrinax parviflora Sw. 2

ASTERACEAE

Barnadesia arborea Kunth 7

***Cnicothamnus lorentzii* Griseb. 1**

Fulcaldea laurifolia (Bonpl.) Poir. ex Less. 8

***Tessaria integrifolia* Ruiz & Pav. 1**

Vernonanthura patens (Kunth) H. Rob. 7

***Vernonia baccharoides* Kunth 1**

BETULACEAE

Alnus jorullensis Kunth 2

BIGNONIACEAE

***Adenocalymna inundatum* C. Mart. ex DC. 1**

***Arrabidaea corallina* (Jacq.) Sandwith 1**

***A. fagoides* Bureau 1**

***A. pubescens* (L.) A.H. Gentry 1**

***A. viscida* (Donn. Sm.) A.H. Gentry 1**

***Crescentia cujete* L. 1**

***Cydista diversifolia* (Kunth) Miers 1**

Godmania aesculifolia (Kunth) Standl. 2

***Jacaranda acutifolia* Bonpl. 1**

***J. obtusifolia* Bonpl. 1**

Macfadyena unguis-cati (L.) A.H. Gentry 2

Mansoa hymenaea (DC.) A.H. Gentry 2

Memora patula Miers 1**Parabignonia chodatii (Hassl.) A.H. Gentry 1***Tabebuia billbergii* (Bureau & K. Schum.) Standl. 5*T. chrysantha* (Jacq.) G. Nicholson 19**T. donnell-smithii Rose 1****T. heptaphylla (Vell.) Toledo 1***T. heterophylla* (DC.) Britton 3*T. impetiginosa* (Mart. ex DC.) Standl. 3**T. incana A.H. Gentry 1***T. ochracea* (Cham.) Standl. 6*T. rosea* (Bertol.) A. DC. 2**T. roseoalba (Ridl.) Sandwith 1***Tecoma castanifolia* (D. Don) Melch. 11**Xylophragma seemannianum (Kuntze) Sandwith 1****BOMBACACEAE***Cavanillesia platanifolia* (Bonpl.) Kunth 11*Ceiba insignis* (Kunth) P.E. Gibbs & Semir 2*C. pentandra* (L.) Gaertn. 2*C. trichistandra* (A. Gray) Bakh. 18**Chorisia integrifolia Ulbr. 1****C. speciosa A. St.-Hil. 1***Eriotheca discolor* (Kunth) A. Robyns 2*E. ruizii* (K. Schum.) A. Robyns 22*Ochroma pyramidale* (Cav. ex Lam.) Urb. 13**Pachira quinata (Jacq.) W. S. Alverson 1***P. rupicola* (A. Robyns) W.S. Alverson 11*P. trinitensis* Urb. 2**Pseudobombax guayasense A. Robyns 1****BORAGINACEAE****Bouyeria venosa (Miers) Stearn 1***Cordia alliodora* (Ruiz & Pav.) Oken 6**C. collococca L. 1****C. elaeagnoides A. DC. 1****C. eriostigma Pittier 1***C. iguaguana* Melch. ex I.M. Johnst. 2*C. lutea* Lam. 4*C. macrantha* Chodat 13**C. nodosa Lam. 1***C. sericalyx* A. DC. 2*Patagonula americana* L. 2*Saccellium lanceolatum* Bonpl. 2**BUDDLEJACEAE****Buddleja americana L. 1****BURSERACEAE***Bursera excelsa* (Kunth) Engl. 1**B. fagaroides (Kunth) Engl. 1****B. glabra (Jacq.) Triana & Planch. 1***B. graveolens* (Kunth) Triana & Planch. 24*B. simaruba* (L.) Sarg. 13**CACTACEAE****Armatocereus cartwrightianus (Britton & Rose) Backeb. ex A.W. Hill 1****A. matucanensis Backeb. Ex A. W. Hill 1****Browningia microsperma (Werderm. & Backeb.) W.T. Marshall 1****B. riosaniensis (Backeb.) G. D. Rowley 1****Monvillea euchlorus (Weber ex K. Schum) Backeb. 1***Opuntia brasiliensis* (Willd.) Haw. 2**O. excelsa Sánchez-Mej. 1****Pachycereus pecten-aboriginum (Engelm. ex S. Watson) Britton & Rose 1***Pereskia guamacho* F.A.C. Weber 4**CANELLACEAE***Canella winterana* (L.) Gaertn. 2**CAPPARACEAE****Belencita nemorosa (Jacq.) Dugand 1****Capparis avicennifolia Kunth 1****C. baduca L. 1****C. ecuadorica H.H. Iltis 1***C. eustachiana* Jacq. 3*C. flexuosa* (L.) L. 24**C. hastata Jacq. 1***C. indica* (L.) Druce 3*C. odoratissima* Jacq. 7*C. petiolaris* Kunth 3*C. prisca* J.F. Macbr. 2**C. retusa Griseb. 1***C. scabrida* Kunth 11**C. sprucei Eichler 1***Crataeva tapia* L. 2*Forchhammeria pallida* Liebm. 2**Morisonia americana L. 1****M. oblongifolia Britton 1****CAPRIFOLIACEAE****Sambucus nigra L. 1**

CARICACEAE

- Carica quercifolia* (A. St.-Hil.) Hieron. 1
Jacaratia mexicana A. DC. 1
Elaeodendron trichotomum (Turcz.) Lundell 1

CELASTRACEAE

- Gyminda latifolia* (Sw.) Urb. 1
Maytenus clarendonensis Britton 1
M. elliptica (Lam.) Krug & Urb. 1
M. emarginata (R&P) Loes. 1
M. jamaicensis Krug & Urb. 1
M. macrocarpa (Ruiz & Pav.) Briq. 1
M. retusa Briq. 1

CHRYSOBALANACEAE

- Licania arborea* Seem. 1

COCHLOSPERMACEAE

- Cochlospermum orinocense* (Kunth) Steud. 1
C. vitifolium (Willd.) Spreng. 24

COMBRETACEAE

- Bucida buceras* L. 1
Combretum fruticosum (Loefl.) Stuntz 1
Terminalia triflora (Griseb.) Lillo 2
T. valverdeae A.H. Gentry 16

CONNARACEAE

- Connarus venezuelanus* Baill. 1

CONVOLVULACEAE

- Ipomoea phillomega* (Vell.) House 1
I. wolcottiana Rose 2

DILLENIACEAE

- Curatella americana* L. 1

EBENACEAE

- Diospyros ierensis* Britton 1
D. tetrasperma Sw. 2

ELAEOCARPACEAE

- Sloanea terniflora* (Moc. & Sessé ex DC.) Standl. 1

ERYTHROXYLACEAE

- Erythroxylum areolatum* L. 1

- E. confusum* Britton 2
E. deciduum A. St.-Hil. 1
E. glaucum O.E. Schulz 1
E. orinocense Kunth 1
E. ruizii Peyr. 1
E. subracemosum Turcz. 1
E. ulei O.E. Schulz 1

EUPHORBIACEAE

- Adelia spinosa* (Chodat & Hassl.) Pax & K. Hoffm. 1
Ateramnus lucidus (Sw.) Rothm. 1
Cnidoscopus spinosus Lundell 1
Croton eluteria Sw. 1
C. lechleri Müll. Arg. 1
Drypetes alba Poit. 1
D. amazonica Steyerm. 1
D. lateriflora (Sw.) Krug & Urb. 2
Hura crepitans L. 6
Jatropha platanifolia Standl. 2
J. standleyi Steyerm. 1
Margaritaria nobilis L. f. 2
Pachystroma longifolium (Nees) I.M. Johnst. 1
Sagotia racemosa Baill. 1
Sapium haematospermum Müll. Arg. 1
S. laurifolium (A. Rich.) Griseb. 1
S. pedicellatum Huber 1

FABACEAE

- Acacia farnesiana* (L.) Willd. 1
A. glomerosa Benth. 4
A. macracantha Humb. & Bonpl. ex Willd. 15
A. polyphylla DC. 1
A. riparia Kunth 11
A. tamarindifolia (L.) Willd. 1
A. tortuosa (L.) Willd. 1
A. visco Lorentz ex Griseb. 1
Acosmium cardenasii H.S. Irwin & Arroyo 1
Albizia dubia Britton & Killip 1
A. multiflora (Kunth) Barneby & J.W. Grimes 15
A. niopoides (Spruce ex Benth.) Burkart 1
A. occidentalis Brandegee 1
A. pistaciifolia (Willd.) Barneby & Grimes 1
A. tomentosa (Micheli) Standl. 1
Amburana cearensis (Allemão) A.C. Sm. 1
Anadenanthera colubrina (Vell.) Brenan 7
Andira inermis (W. Wright) Kunth ex DC. 1

Apoplanesia paniculata C. Presl 2

***Bauhinia aculeata* L. 1**

***B. divaricata* L. 1**

***B. glabra* Jacq. 1**

Caesalpinia coriaria (Jacq.) Willd. 3

C. eriostachys Benth. 3

C. glabrata Kunth 18

***C. platyloba* S. Watson 1**

***C. pluviosa* DC. 1**

C. sclerocarpa Standl. 3

C. spinosa (Molina) Kuntze 2

Calliandra taxifolia (Kunth) Benth. 7

Cassia fistula L. 2

***C. moschata* Kunth 1**

Centrolobium ochroxylum Rose ex Rudd 11

***Chloroleucon bogotense* Britton & Killip 1**

C. mangense (Jacq.) Britton & Rose 2

***C. tenuiflorum* (Benth.) Barneby & Grimes 1**

***C. tortum* (Mart.) Pittier 1**

***Copaifera chodatiana* Hassl. 1**

***C. officinalis* (Jacq.) L. 1**

***Coursetia ferruginea* (Kunth) Lavin 1**

***Cyathostegia mathewsii* (Benth.) Schery 1**

***Cynometra oaxacana* Brandegee 1**

***Dalbergia retusa* Hemsl. 1**

Entada polystachya (L.) DC. 2

***Enterolobium contortisiliquum* (Vell.) Morong 1**

E. cyclocarpum (Jacq.) Griseb. 2

***Erythrina eggersii* Krukoff & Moldenke 1**

***E. pallida* Britton 1**

***E. poeppigiana* (Walp.) O.F. Cook 1**

E. smithiana Krukoff 17

E. velutina Willd. 8

Geoffroea spinosa Jacq. 20

***Gleditsia amorphoides* (Griseb.) Taub. 1**

***Gliricidia brenningii* (Harms) Lavin 1**

Hymenaea courbaril L. 2

***Inga feuillei* DC. 1**

Leucaena trichodes (Jacq.) Benth. 5

Lonchocarpus atropurpureus Benth. 13

***L. cochleatus* Pittier 1**

L. constrictus Pittier 2

***L. costaricensis* (Donn. Sm.) Pittier 1**

***L. crucisrubierae* Pittier 1**

***L. eriocarinalis* Micheli 1**

***L. nudiflorens* Burkart 1**

***L. parviflorus* Benth. 1**

***Lysiloma microphylla* Benth. 1**

Machaerium arboreum (Jacq.) Vogel 2

M. capote Triana ex Dugand 3

***M. latialatum* Pittier 1**

***M. microphyllum* (E. Mey.) Standl. 1**

M. millei Standl. 14

***M. peruvianum* J.F. Macbr. 1**

Mimosa acantholoba (Humb. & Bonpl. ex Willd.) Poir. 11

Myroxylon balsamum (L.) Harms 4

Parapiptadenia excelsa (Griseb.) Burkart 2

***Parkinsonia praecox* (Ruiz & Pav.) Hawkins 1**

***Peltogyne purpurea* Pittier 1**

Piptadenia constricta (M. Micheli) Macbr. 2

***P. flava* (Spreng. ex DC.) Benth. 1**

***P. peruviana* (J.F. Macbr.) Barneby 1**

***P. viridiflora* (Kunth) Benth. 1**

Piscidia carthagenensis Jacq. 13

Pithecellobium dulce (Roxb.) Benth. 3

P. excelsum (Kunth) Mart. 13

***P. roseum* (Vahl) Barneby & Grimes 1**

***Platymiscium cochabambense* Rusby 1**

***P. lasiocarpum* Sandwith 1**

P. pinnatum (Jacq.) Dugand 2

***P. pubescens* Micheli 1**

***Poeppigia procera* C. Presl 1**

Prosopis juliflora (Sw.) DC. 5

P. pallida (Humb. & Bonpl. ex Willd.) Kunth 2

***Pseudopiptadenia pittieri* (Harms) G. P. Lewis 1**

Pterocarpus floribundus (Benth.) Kuntze 3

***P. orbiculatus* DC. 1**

P. rohrii Vahl 4

***Senegalia turbacensis* Britton & Killip 1**

Senna bicapsularis (L.) Roxb. 2

S. mollissima (Humb. & Bonpl. ex Willd.) H.S. Irwin & Barneby 12

***S. spectabilis* (DC.) H.S. Irwin & Barneby 1**

***Tipuana tipu* (Benth.) Kunze 1**

***Zygia longifolia* (Willd.) Britton & Rose 1**

FLACOURTIACEAE

***Casearia aculeata* Jacq. 1**

***C. corymbosa* Kunth 1**

***C. decandra* Jacq. 1**

***C. gossypiosperma* Briq. 1**

***C. guianensis* (Aubl.) Urb. 1**

C. praecox Griseb. 2

C. sylvestris Sw. 3

***C. tremula* (Griseb.) Griseb. ex C. Wright 1**

***C. zizyphoides* Kunth 1**

***Hecatostemon completus* (Jacq.) Sleumer 1**

***Phyllostylon brasiliensis* Capan. 1**

***Prockia pentamera* A.H. Gentry 1**

***Xylosma intermedia* (Seem.) Triana & Planch. 1**

HERMANDIACEAE

Gyrocarpus americanus Jacq. 3

HIPPOCRATEACEAE

Hippocratea volubilis L. 3

***Pristimera verrucosa* (Kunth) Miers 1**

***Salacia elliptica* (Mart. ex Roem. & Schult.) G. Don 1**

JUGLANDACEAE

***Juglans australis* Griseb. 1**

JULIANACEAE

***Amphipterygium adstringens* (Schltdl.) Standl. 1**

LAURACEAE

***Nectandra acutifolia* (Ruiz & Pav.) Mez 1**

N. laurel Klotzsch ex Nees 8

Ocotea aurantiodora (Ruiz & Pav.) Mez 4

***O. puberula* (Rich.) Nees 1**

LECYTHIDACEAE

***Gustavia angustifolia* Benth. 1**

Lecythis magdalenica Dugand 2

LOGANIACEAE

***Strychnos fendleri* Sprague & Sandwith 1**

MALPHIGIACEAE

***Dicella macroptera* Mart. ex A. Juss. 1**

***Bunchosia nitida* (Jacq.) DC. 1**

***Malpighia emarginata* Sessé & Moc. ex DC. 1**

MALVACEAE

***Hibiscus pernambucensis* Arruda 1**

MELIACEAE

***Cedrela fissilis* Vell. 1**

C. odorata L. 2

Guarea glabra Vahl 2

Swietenia humilis Zucc. 2

Trichilia acuminata (Humb. & Bonpl. ex Roem. & Schult.) C. DC. 2

T. carinata M.E.Morales-Puentes 2

***T. claussenii* C. DC. 1**

T. elegans A. Juss. 4

***T. glabra* L. 1**

T. hirta L. 12

***T. moschata* Sw. 1**

T. oligofoliata M.E.Morales-Puentes 2

T. pallida Sw. 2

T. pleeana (A. Juss.) C. DC. 2

***T. rubra* C. DC. 1**

***T. trifolia* L. 1**

MORACEAE

Brosimum alicastrum Sw. 2

***B. guianense* (Aubl.) Huber 1**

***Cecropia obtusifolia* Bertol. 1**

***Clarisia biflora* Ruiz & Pav. 1**

Ficus citrifolia Mill. 2

***F. cotinifolia* Kunth 1**

***F. cuatrecasana* Dugand 1**

***F. eliadis* Standl. 1**

F. jacobii Vázq. Avila 12

F. obtusifolia Kunth 12

***F. perez-arbelaezii* Dugand 1**

F. pertusa L. f. 14

***F. trigona* L. f. 1**

***F. velutina* Humb. & Bonpl. ex Willd. 1**

Maclura tinctoria (L.) D. Don ex Steud. 13

Sorocea sprucei (Baill.) J.F. Macbr. 3

MYRSINACEAE

***Rapanea laetevirens* Mez 1**

MYRTACEAE

***Blepharocalyx gigantea* Lillo 1**

***Calyptanthes pallens* Griseb. 1**

C. zuzygium (L.) Sw. 2

Eugenia uniflora L. 2

***Hexachlamys edulis* (O. Berg) Kausel & D. Legrand 1**

Myrcia ovalifolia (O. Berg) Kiaersk. 1
M. splendens (Sw.) DC. 1
Myrcianthes discolor (Kunth) McVaugh 1
M. pungens (O. Berg) D. Legrand 1
Myrciaria cauliflora (Mart.) O. Berg 1
Myrrhinium loranthoides (Hook. & Arn.) Burret 1
Psidium rostratum McVaugh 1
P. rutidocarpum Ruiz & Pav. 1
P. sartorianum (O. Berg) Nied. 2

NYCTAGINACEAE

Bougainvillea modesta Heimerl 1
B. pachyphylla Heimerl ex Standl. 1
B. peruviana Bonpl. 13
B. stipitata Griseb. 1
Guapira fragrans (Dum. Cours.) Little 3
G. obtusata (Jacq.) Little 2
G. pacurero (Kunth) Lundell 1
Neea virens Poepp. ex Heimerl 1
Pisonia aculeata L. 14
P. zapallo Griseb. 1
Reichenbachia hirsuta Spreng. 1

OCHNACEAE

Ouratea guildingii (Planch.) Urb. 1
O. laurifolia (Sw.) Engl. 1

OLACACEAE

Ximenia americana L. 4

OLEACEAE

Chionanthus domingensis Lam. 1
Schrebera americana (Zahlbr.) Gilg 5

OPILIACEAE

Agonandra brasiliensis Miers ex Benth. & Hook. f. 2
A. excelsa Griseb. 9
A. racemosa (DC.) Standl. 1

PHYTOLACCACEAE

Gallesia integrifolia (Spreng.) Harms 3
Phytolacca dioica L. 1
Seguieria aculeata Jacq. 3

POACEAE

Guadua chacoensis (Rojas) Londoño & P. M. Peterson 1

POLYGONACEAE

Polygala jamaicensis Chodat 1
Coccoloba barbadensis Jacq. 1
C. coronata Jacq. 1
C. densifrons C. Mart. ex Meisn. 1
C. diversifolia Jacq. 3
C. krugii Lindau 2
C. lehmannii Lindau 2
C. obovata Kunth 1
C. padiformis Meisn. 3
C. ruiziana Lindau 12
C. scandens Casar. 1
C. swartzii Meisn. 1
Podopterus cordifolius Rose & Standl. 2
Ruprechtia aperta Pendry 1
R. apetala Wedd. 1
R. fusca Fernald 1
R. jamesonii Meisn. 1
R. laxiflora Meisn. 2
R. ramiflora C.A. Mey. 3
Triplaris americana L. 5
T. cumingiana Fisch. & C.A. Mey. ex C.A. Mey. 13
T. setosa Rusby 1

RHAMNACEAE

Colubrina elliptica (Sw.) Brizicky & W.L. Stern 1
C. heteroneura (Griseb.) Standl. 1
C. retusa (Pittier) R.S. Cowan 1
Krugiodendron ferreum (Vahl) Urb. 2
Rhamnidium elaeocarpum Reissek 2
Ziziphus mauritiana Lam. 2
Z. saeri Pittier 1
Z. sarcomphalus (L.) M.C. Johnst. 1
Z. thyriflora Benth. 14

ROSACEAE

Prunus subcorymbosa Ruiz ex Koehne 1
P. tucumanensis Lillo 1

RUBIACEAE

Alseis eggersii Standl. 1
A. peruviana Standl. 2

Calycophyllum candidissimum (Vahl) DC. 1
C. spruceanum (Benth.) Hook. f. ex K. Schum. 1
Chomelia spinosa Jacq. 3
Coutarea hexandra (Jacq.) K. Schum. 1
Exostema mexicanum A. Gray 1
Guettarda divaricata (Humb. & Bonpl. ex Roem. & Schult.) Standl. 1
Hintonia latiflora (Sessé & Moc. ex DC.) Bullock 1
Palicourea guianensis Aubl. 1
Pogonopus speciosus (Jacq.) K. Schum. 1
Randia aculeata L. 11
R. armata (Sw.) DC. 3
R. lasiantha (Standl.) Standl. 1
R. purdiei Hook. f. 1
Rondeletia stipularis (L.) Druce 1
Simira cordifolia (Hook. f.) Steyererm. 2
S. ecuadorensis (Standl.) Steyererm. 2
S. rubescens (Benth.) Bremek. ex Steyererm. 5

RUTACEAE

Amyris pinnata Kunth 2
Angostura pilocarpoidea (Rusby) Albuq. 1
Dictyoloma peruvianum Planch. 1
Esenbeckia almawillia Kaastra 1
E. berlandieri Baill. ex Hemsl. 1
E. densiflora (Chodat & Hassl.) Hassl. 1
Metrodorea flavida K. Krause 1
Pilocarpus peruvianus (J.F. Macbr.) Kaastra 1
P. racemosus Vahl 1
Zanthoxylum acuminatum (Sw.) Sw. 1
Z. fagara (L.) Sarg. 4
Z. mantaro (J.F. Macbr.) J.F. Macbr. 1
Z. rhoifolium Lam. 1
Z. rigidum Humb. & Bonpl. ex Willd. 2

SALICACEAE

Salix humboldtiana Willd. 6

SAPINDACEAE

Allophylus edulis (A. St.-Hil., Cambess. & A. Juss.) Radlk. 3
A. lorentensis Standl. ex J.F. Macbr. 1
Cupania dentata DC. 1
C. latifolia Kunth 1
C. vernalis Cambess. 1
Exothea paniculata (Juss.) Radlk. 2
Hypelate trifoliata Sw. 2

Melicoccus bijugatus Jacq. 2
Paullinia sessiliflora Radlk. 1
Sapindus saponaria L. 11
Serjania rhombea Radlk. 1
Talisia intermedia Radlk. 1
T. oliviformis Radlk. 2
T. stricta (H. Karst. & Triana) Triana & Planch. 1
Thouinia paucidentata Radlk. 1
Thouinidium decandrum (Bonpl.) Radlk. 2

SAPOTACEAE

Chrysophyllum gonocarpum (Mart. & Eichler) Engl. 2
C. lucentifolium Cronquist 1
C. marginatum (Hook. & Arn.) Radlk. 2
Pouteria glomerata (Miq.) Radlk. 2
Pradosia colombiana (Standl.) Penn. ex T. J. Ayers & Boufford 1
P. montana T.D. Penn. 1
Sideroxylon capiri (A. DC.) Pittier 2
S. foetidissimum (Jacq.) 1
S. obtusifolium (Humb. ex Roem. & Schult.) T.D. Penn. 2
S. salicifolium (L.) Lam. 2

SAXIFRAGACEAE

Escallonia pendula (Ruiz & Pav.) Pers. 2

SIMAROUBACEAE

Recchia mexicana Moc. & Sessé ex DC. 2

SOLANACEAE

Acnistus arborescens (L.) Schltdl. 10
Solanum confertiseriatum Bitter 1
S. granuloso-leprosum Dunal 1
Vassobia breviflora (Sendtn.) Hunz. 1

STERCULIACEAE

Guazuma ulmifolia Lam. 15

STYRACACEAE

Styrax tarapotensis Perkins 1

THEOPHRASTACEAE

Jacquinia aristata Jacq. 1

TILIACEAE

Apeiba tibourbou Aubl. 2

Heliocarpus americanus* L. 1H. pallidus* Rose 2*Luehea candida* (Moc. & Sessé ex DC.) Mart. 3***L. speciosa* Willd. 1***Muntingia calabura* L. 2**ULMACEAE*****Ampelocera macphersonii* Todzia 1***Celtis iguanaea* (Jacq.) Sarg. 16***C. loxensis* C.C. Berg 1*****C. pubescens* Spreng. 1*****C. schippii* Standl. 1***Phyllostylon rhamnoides* (J. Poiss.) Taub. 4**URTICACEAE*****Urera baccifera* (L.) Gaudich. ex Wedd. 1*****U. elata* (Sw.) Griseb. 1****VERBENACEAE*****Citharexylum chartaceum* Moldenke 1*****C. fruticosum* L. 1*****Cornutia grandifolia* (Schltdl. & Cham.) Schauer 1*****Petrea pubescens* Turcz. 1*****Rehdera trinervis* (S.F. Blake) Moldenke 1***Vitex compressa* Turcz. 2*V. gigantea* Kunth 2***V. orinocensis* Kunth 1****VOCHYSIACEAE*****Vochysia venezuelana* Stafleu 1****ZYGOPHYLLACEAE***Bulnesia arborea* (Jacq.) Engl. 3*B. carrapo* Killip & Dugand 2

Number of species considered for each site in the matrix for the multivariate analysis.

<i>Site</i>	<i>N° species</i>	<i>Site</i>	<i>N° species</i>
EQUATORIAL SOUTH AMERICA		NORTHERN SOUTH AMERICA	
North-western Peru		Inter Andean Colombia	
AMOTAPE	20	BREMEN	22
ANGOLO	48	CARDONAL	21
BAGUAGRA	27	SANTOTOM	19
CHULUCAN	5	Caribbean Colombia	
ELCHECO	15	BOMBA	16
ELSAUCE	17	COLORADO	23
LJUANAS	9	COLOSOI	24
MIRADERO	14	GALERAZ	17
MORROPON	7	MONTERRE	19
PASALLIT	13	TAYRONA	24
RIOPIURA	4	Venezuela	
TARAPOT1	26	BLOHMR	24
TARAPOT2	9	LLANO	15
UNAGATO	6	UCHIRE	17
Inter Andean Peru		SOUTHERN SOUTH AMERICA	
APURIMAC	8	Inter Andean Bolivia	
HUANCABA	8	CHAQUIMA	18
MARAÑON	11	RIOUBITO	11
RQUIROZ	10	YANOMAYO	36
South-western Ecuador		Lowland Bolivia	
BALNEARI	39	QUIAPACA	23
BOLASPAM	46	SANTACRU	17
CAÑAVERA	46	Argentina	
CAZADERO	38	PARQUEER	18
CHAGUAR	38	RIACHUEL	22
GRAMADAL	6	SALTA	11
LLEONERA	46	ANTILLES	
MAQUILLO	38	Jamaica	
MAURCO	39	ROUNDTOP	33
PUYANGO	28	ROUNDSLO	18
SAUCE	46	Puerto Rico	
TAMBILLO	39	MOGOTE	14
YMAURCO	39	CENTRAL AMERICA	
Coastal Ecuador		Costa Rica	
CAPEIRA	29	GUANGF	21
PECHICHE	30	GUANUP	18
PERROMUE	13	Mexico	
		CHAMELA1	28
		CHAMELA2	18
		CHAMELA3	45

