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The composition of Amazonian forests: patterns at local and regional scales

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ABSTRACT. An analysis was conducted of floristic patterns contained in 48 1-ha tree plots distributed at 29 sites in seven neotropical countries, with a primary emphasis on the Amazonian region. Analyses were made with family level data, using detrended correspondence analysis and multidimensional scaling to generate two-dimensional ordinations. Dissimilarity values for all pairs of plots were then used to compare forest composition at both local (flooded vs unflooded forests) and regional scales (e.g., western vs central vs eastern Amazonia). The predominate family of trees in a large majority of Amazonian and Guianan forests (by number of stems) is either Palmae or Leguminosae (*sensu latu*), followed by Moraceae and Euphorbiaceae. The forests of western Amazonia are particularly rich in palms, Moraceae, and Myristicaceae, whereas those of eastern Amazonia and the Guianas are rich in Lecythidaceae and Chrysobalanaceae. Dissimilarity between sites increases with distance for both flooded and unflooded forests. The tree communities of flooded and unflooded forests within a region tended to resemble one another more closely than forests of either type resembled the homologous forests of the adjoining regions. Within Amazonia the edaphic properties of each region and its geological history are tightly interrelated. It is therefore difficult to distinguish between evolutionary and ecological interpretations of the results.

KEY WORDS: Amazon, detrended correspondence analysis, flooded forests, forest composition, multi-dimensional scaling, terra firme forest, tropical forests, varzea

INTRODUCTION

The forests of tropical South America remain largely undiagnosed from a compositional standpoint. Vegetation maps as well as botanical diagnoses of the region distinguish only primary divisions of the landscape, such as forest vs

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savannah, and flooded vs non-flooded (terra firme) forest (Braga 1979, Encarnación 1985, Pires & Prance 1985). Efforts to date to discriminate finer divisions have been few (Felfili & da Silva 1993). The UNESCO (1980) map of South American vegetation, to mention but one example, portrays only a scant half-dozen cover types in the Amazon basin. At the same time, it is known that the Amazon region harbours at least 30,000 plant species (Gentry 1982). Is one to believe that so many species are accomodated in only six consociations? Not unless beta-diversity is extremely low, a possibility that is directly contradicted by the findings of Gentry (1981, 1988).

In contrast to the broad-brush approach taken in vegetation maps, inspection of satellite images has recently led Tuomisto *et al.* (1995) to propose that the Peruvian Amazon alone contains perhaps hundreds of distinct cover types. The fact that such widely discrepant views can stand side by side reflects a vacuum of knowledge of floristic patterns within tropical South America, and within Amazonia in particular.

Classifications of Amazonian vegetation have invariably been based on indirect measures, such as climate, topography, hydrology, or gross physiognomy of the vegetation (Braga 1979, Beard 1944, Encarnacion 1985, Holdridge 1967, Kubitzki 1989, Malleux 1975, Pires & Prance 1986), whereas in other parts of the world, composition-based classification systems have become routine (e.g., Barbour & Billings 1988).

In past efforts to classify Amazonian forests, much of the emphasis has been given to distinguishing types of seasonally flooded forests (Encarnación 1985, Junk 1989, Kalliola *et al.* 1991, Klinge *et al.* 1990, Kubitzky 1989, Pires & Prance 1985, Puhakka & Kalliola 1993, Salo *et al.* 1986). Comparatively little emphasis has been given to discriminating Amazonian terra firme forests (Prance 1990, Ruokolainen & Tuomisto 1993, Tuomisto & Ruokolainen 1994, Young & Leon 1989), although preliminary indications from the analysis of satellite images are of a great diversity of such forests (Tuomisto *et al.* 1994, 1995).

Here, we make a first attempt to examine compositional variation in the tree communities of tropical South America, with a primary focus on the Amazon Basin. The data are derived from three sources. First, we draw upon the > 50 permanent tree plots that have been established in the Peruvian Department of Madre de Dios (Dallmeier *et al.* 1991, 1993; Gentry 1988, Terborgh *et al.* 1996). Second, we searched the Neotropical literature for published tree plot data that satisfied certain basic criteria: minimum area of 1 ha, comprehensive inventory comprising ≥ 450 trees ≥ 10 cm dbh, and identifications of all individual trees to at least the family level. Third, we contacted several colleagues who had established tree plots in the region, and were gratified to receive unpublished data for a number of additional sites. In the following report, we apply quantitative techniques to reveal floristic patterns contained in the data from 48 plots, representing 29 localities. Clear geographic and edaphic patterns emerge, allowing some initial generalizations about the organization of the Amazonian tree flora.

METHODS

The plots included in our analysis are primarily Amazonian (39 out of 48 plots), but for reference, we include five sites from former British Guiana (now Guyana), two from the Brazilian Atlantic coastal forest, and two from Central America. Collectively, the sites cover a geographical area that extends from latitude 10 °N to 23 °S, and from the base of the Andes (76 °W) to the mouth of the Amazon (48 °W) (Table 1, Figure 1).

Data sets were not included in the analysis unless they conformed to standard criteria with respect to taxonomic level, sample size and minimum tree diameter (see above). After some preliminary analyses, we decided to delete plots representing swamp forests because these invariably appeared as extreme outliers in the ordinations. Plots in Madre de Dios, Peru have been identified to the species level, and conform to a uniform taxonomic treatment provided by R. Foster (1987, 1990). To avoid over representing Madre de Dios in the data set, we selected 15 plots to represent the flooded and unflooded forests at the principal sites to have been investigated. Few plots outside Madre de Dios have been comprehensively identified to the species level. Some are complete, or nearly complete, at the genus level, while many are determined only to the family level. Therefore, one of the problems we had to resolve the extent to which the statistical relationships between plots and sites were dependent on the taxonomic level of the analysis.

Preparation of the data set

Plot data were first entered at the species level, listing named taxa or morphospecies recognized by the authors. Tree plots are traditionally defined by area, a practice that results in unequal numbers of trees per plot. In order to weight plots equally, we truncated the samples to a standard 450 trees, the number contained in the hectare with the lowest tree density. We did this by first assigning a random number to each tree in each plot, then ranking the random numbers, and finally selecting the first 450 to represent the plot in the analyses. The data sets were then collapsed into genera or families, so that analyses could be conducted at the corresponding taxonomic levels.

Plot data were organized in a standard format in a spreadsheet program (Excel®). We then ordered plots via detrended correspondence analysis (DCA) and multidimensional scaling (MDS), respectively, with the programs CANOCO (ter Braak 1987) and SYSTAT®. Finally, to quantify relationships between ecologically or geographically defined groups of plots, we used bootstrap (internal resampling) methods to compute, using coordinates of the first and second axes of DCA and MDS ordinations, distributions of Euclidian distances within and between all groups of plots. Mean values for the grouped plots were then used in comparisons.

Table 1. Characteristics of sites and plots used in the analysis of the floristic variation of Amazonian forests.

Country/Region	Division	Site	Site number	Abrev-iation	Latitude/Longitude	Reference
Guianan TF						
British Guiana		Moraballi Creek	S5	BGTF1	6°35′N 59°00′W	Davis & Richards (1933, 1934)
British Guiana		Moraballi Creek	S6	BGTF2	6°35′N 59°00′W	Davis & Richards (1933, 1934)
British Guiana		Moraballi Creek	S7	BGTF3	6°35′N 59°00′W	Davis & Richards (1933, 1934)
British Guiana		Moraballi Creek	S8	BGTF4	6°35′N 59°00′W	Davis & Richards (1933, 1934)
Guianan FL						
British Guiana		Moraballi Creek	S9	BGFLO	6°35′N 59°00′W	Davis & Richards (1933, 1934)
E. Amaz. TF						
Brazil	Para	Rio Xingu	S14	XinguTF	3°29′S 51°40′W	Campbell *et al.* (1986)
Brazil	Para	Castanhal	S1	CastaTF	1°20′S 47°50′W	Pires *et al.* (1953)
Brazil	Para	Caxiuana	S44	CaxiTF	3°50′S 51°30′W	Almeida *et al.*
Brazil	Para	Carajas	S28	CarajTF1	6°00′S50°30′W	Salomao *et al.* (1988)
Brazil	Para	Carajas	S29	CarajTF2	6°00′S 50°30′W	Silva *et al.* (1987)
Brazil	Para	Carajas	S30	CarajTF3	6°00′S 50°30′W	Silva & Rosa (1989)
Brazil	Para	Carajas	S31	CarajTF4	6°00′S 50°30′W	Silva *et al.* (1986)
Brazil	Para	Maraba	S32	MarabTF	5°45′S 49°2′W	Salomao (1991)
E. Amaz. FL						
Brazil	Para	Guama River	S2	GuamaVAR	1°20′S 48°30′W	Pires & Koury, (1958)
Brazil	Para	Guama River	S3	BeleIGA	1°20′S48°30′W	Black *et al.* (1950)
C. Amaz. TF						
Brazil	Amazonas	Urucu River	S12	UrucuTF	4°50′S 65°16′W	Peres (1991)
Brazil	Mato Grosso	Aripuana	S43	AripTF	10°10′S 59°27′W	Ayres (1981)
Brazil	Rondonia	Rondonia	S33	RondoTF1	11°00′S 61°57′W	Salomao & Lisboa (1988)

Table 1. *contd.*)

Country/Region	Division	Site	Site number	Abrev-iation	Latitude/ Longitude	Reference
Brazil	Rondonia	Rondonia	S34	RondoTF2	11°15′S 62°50′W	Maciel & Lisboa (1989)
C. Amaz. FL						
Brazil	Amazonas	Japura River	S10	JapuVAR	2°00′S 66°W	Ayres (1986)
W. Amaz. TF						
Peru	Madre de Dios	Manu River	S21	ManuUT	11°45′S 71°30′W	Terborgh *et al.* (unpubl. data)*
Peru	Madre de Dios	Manu River	S22	ManuUR	11°45′S 71°30′W	Terborgh *et al.* (unpubl. data)
Peru	Madre de Dios	Manu River	S23	PakiTF1	11°45′S 71°30′W	Dallmeier *et al.* (1993)
Peru	Madre de Dios	Manu River	S25	PakiTF2	11°45′S 71°30′W	Dallmeier *et al.* (1993)
Peru	Pasco	Cabeza de Mono	S37	MonoTF	10°20′S 75°18′W	A. Gentry (unpubl. data)
Peru	Loreto	Mishana	S38	MishaTF	3°47′S 73°30′W	A. Gentry (unpubl. data)
Peru	Madre de Dios	Tambopata River	S41	TamboTF	12°49′S 69°43′W	A. Gentry (unpubl. data)
Bolivia	Beni	Rio Ivon	S4	IvonTF	11°45′S 66°02′W	Boom (1986)
Ecuador	Napo	Yasuni Nat'l Park	S13	YasuTF	0°32′S 76°27′W	Balslev *et al.* (1987)
Ecuador	Napo	Cuyabeno	S47	YasuTF	0°0′S 76°10′W	Valencia *et al.* (1993)
W. Amaz. FL						
Peru	Madre de Dios	Manu River	S15	ManuLS	11°45′S 71°30′W	Terborgh *et al.*
Peru	Madre de Dios	Manu River	S16	Manu3	11°45′S 71°30′W	Terborgh *et al.* (unpubl. data)
Peru	Madre de Dios	Manu River	S17	Manu2	11°45′S 71°30′W	Terborgh *et al.* (unpubl. data)
Peru	Madre de Dios	Manu River	S18	Manu12	11°45′S 71°30′W	Terborgh *et al.* (unpubl. data)
Peru	Madre de Dios	Manu River	S19	ManuOTO	11°45′S 71°30′W	Terborgh *et al.* (unpubl. data)
Peru	Madre de Dios	Manu River	S20	ManuSAL	11°45′S 71°30′W	Terborgh *et al.* (unpubl. data)
Peru	Madre de Dios	Manu River	S24	PakiFLO	11°45′S 71°30′W	Dallmeier *et al.* (1993)
Peru	Loreto	Yanamono	S36	YanamFLO	3°16′S 72°54′W	A. Gentry (unpubl. data)

Table 1. *contd.*)

Country/Region	Division	Site	Site number	Abrev-iation	Latitude/ Longitude	Reference
Peru	Madre de Dios	Madre de Dios River	S39	CuzcoFLO1	12°35′S 69°7′W	P. Nuñez & O. Phillips (unpubl. data)
Peru	Madre de Dios	Madre de Dios River	S40	CuzcoFLO2	12°35′S 69°7′W	P. Nuñez & O. Phillips (unpubl. data)
Peru	Madre de Dios	Tambopata River	S42	TamboFLO	12°49′S 69°43′W	A. Gentry (unpubl. data)
Bolivia	Beni	Beni	S26	BeniFLO1	14°38′S 66°18′W	Dallmeier *et al*. (1991)
Bolivia	Beni	Beni	S27	BeniFLO2	14°38′S 66°18′W	Dallmeier *et al*. (1991)
Brazil	Acre	Acre	S48	AcreVAR	7°38′S 72°40′W	Campbell & Stone (1992)
Atlantic						
Brazil	Sao Paulo	Sao Paulo	S35	S. Paulo	23°27′S 45°4′W	Silva & Filho (1982)
Brazil	Bahia	Bahia	S46	Bahia	15°00′S 41°W	Mori *et al*. (1983)
Cent. Amer.						
Panama	Canal Zone	Barro Colorado Is.	S11	BCITF	9°10′N 79°51′W	Thorington *et al*. (1982)
Costa Rica	Heredia	La Selva	S45	CRTF	10°24′N 84°0′W	Heaney & Proctor (1990)

*Here and further down in Table: Data of Terborgh, J., Foster, R. B., Gentry, A. H. & Nantez, V. P.

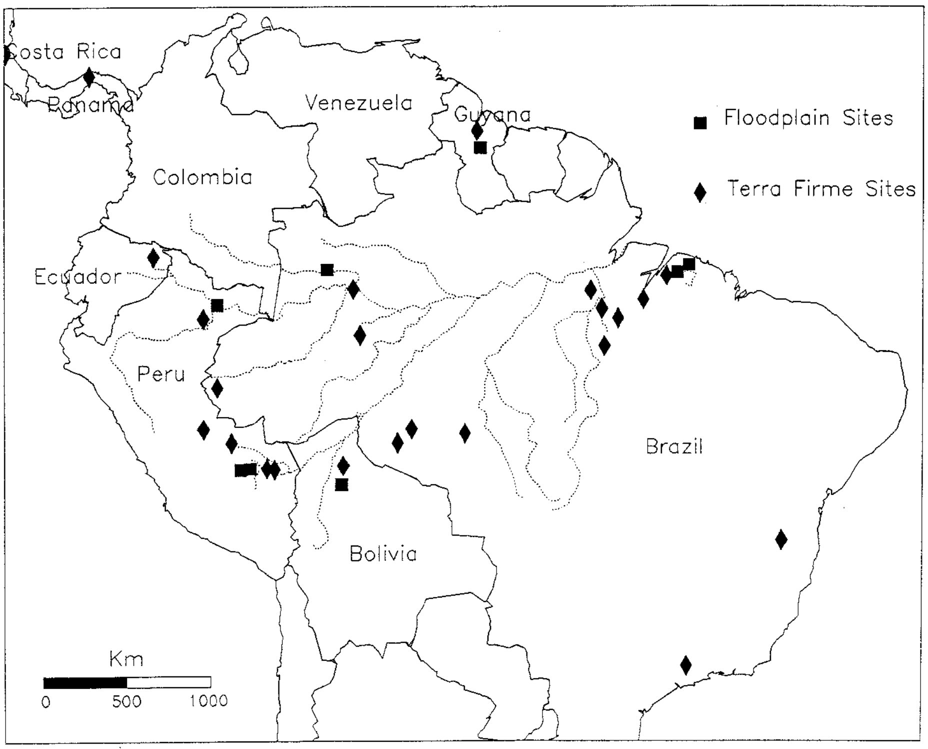

Figure 1. Geographical locations of plots used in the analysis. Some points represent two or more plots.

RESULTS

Preliminary analyses

Preliminary analyses revealed that similarity between sites invariably decreased in data sets compared at the family (total 92), generic (total 554) and species levels (total 1951). Consequently, ordinations based on generic and species level data were of little utility or interpretability. Clustering of sites was particularly pronounced with species-level data, because sites sharing only a few species tended to group tightly together relative to those sharing no species at all. Therefore, for the purpose of broad, continent-wide comparisons of the kind reported here, species, and even genus-level data are not appropriate. All of the results presented below are consequently based on family-level data. Unless the density of sampling is high enough to create more continuity between sites at the species level than was the case here, analysis at higher taxonomic levels is preferable. In a practical sense, this is a positive result, because it places the compositional analysis of Amazonian forests within the reach of a sizeable number of field workers.

To be confident of the robustness of the results generated by ordination of family-level data, we conducted a number of preliminary analyses using various truncated and transformed data sets: (1) untransformed data, including all 92 families found in the full collection of 48 plots; (2) truncated data employing only the 43 best represented families; (3) logarithmically transformed data for all 92 families; (4) logarithmically transformed data for the most abundant 43 families; we also employed multidimensional scaling with all of the above variants using both (5–8) Euclidian distance and (9–12) Pearson's correlation coefficient. In all ordinations, the third and higher axes conveyed little additional information beyond that contained in the first two.

In most cases, the patterns generated by the various permutations of the data set and analytical methods were fundamentally similar, differing in minor quantitative detail but not in the basic qualitative outcome. Removing rare familes, for example, had no discernible effect on the ordination (best represented 43 families vs all 92 families); the points of the two versions were essentially superimposable. After reviewing the ordinations, we elected to present those generated by DCA with the full, untransformed data set in which all 92 families are included. We found that, of all variants, this one gave the best spread of the sites within the plane generated by the first two axes, which cumulatively accounted for 16.1 and 23.5% of the variance in family composition. MDS employing Pearson correlation coefficients run on the same variant of the data gave statistically identical results.

After completing the analyses, it came to our attention that the original CANOCO program contains an instability to the order in which species and sites are input, and a bug in the rescaling algorithm (Oksanen & Minchin 1997). To make sure that these defects of CANOCO had not influenced the results, we used a new software package (PC-ORD, McCune & Mefford 1997) which contains a debugged DCA program. We then reran the ordinations, but found no discernible difference in the output from that generated by the original CANOCO program. We presume that no differences emerged because the defects of CANOCO normally appear only in the output for the third and higher axes, which we do not report (Oksanen & Minchin 1997).

Ordinations

The DCA ordination of family-level data for all 48 plots is shown in Figure 2: site designations are decoded in Table 1. Palmae predominated in 15 plots, Leguminosae in 12, Moraceae in seven, Euphorbiaceae in four, Lecythidaceae in two, and eight families in one plot each. All plots in which Palmae was the predominant family were in the right half of the DCA ordination with X-axis values > 125; all but one of the plots in which Leguminosae predominated were in the left half of the ordination. The location of palm-rich plots on the right and legume-rich plots on the left indicates a strong complementarity between the two families. The number of palms varied between plots much more than did the number of legumes, and accounted for 2.5 times as much of the total variance (Table 2). Accordingly, palms were highly correlated with the first DCA axis ($r^2 = 0.69$), while legumes, being more evenly distributed, showed a

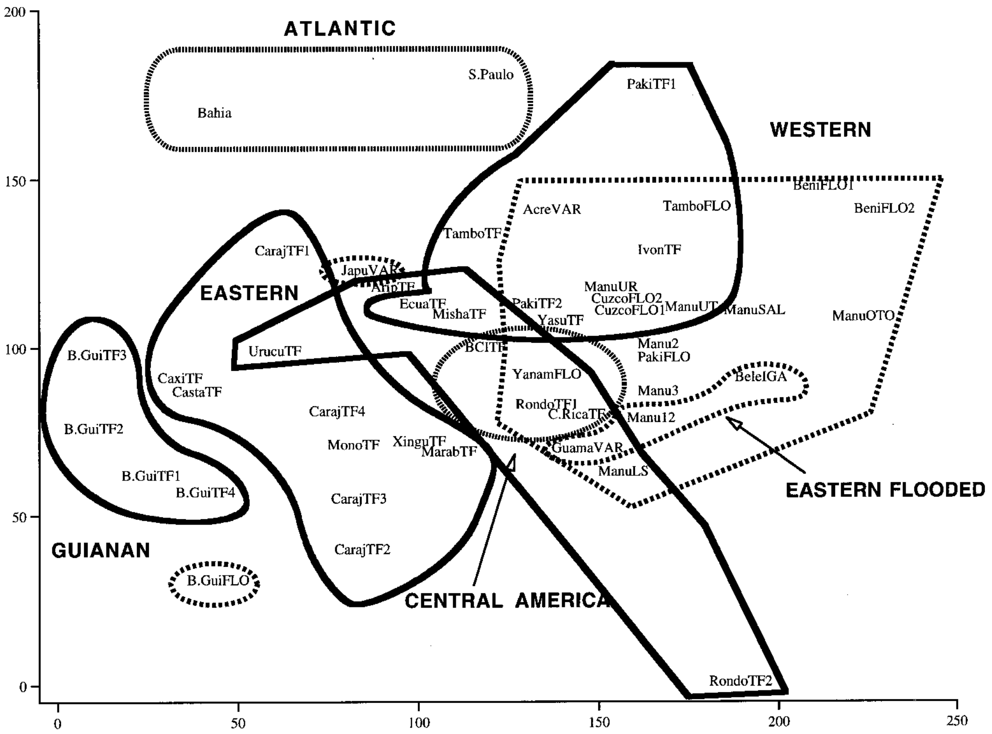

Figure 2. Family-level DCA ordination of 450-tree samples of Neotropical forests. The lines encompass plots from the regions described in the text. Solid lines enclose Amazonian and Guianan terra firme plots; dashed lines enclose plots from flooded forests and extra-limital localities: Central America and Atlantic Coastal Forest. Euclidian distances in the 2-D ordination space represent dissimilarities in family composition. See Table 1 for information about the sites.

lower level of correlation ($r^2 = 0.32$). Almost as highly, but negatively, correlated with the first DCA axis as palms, was the family Lecythidaceae ($r^2 = -0.59$). Moraceae was moderately correlated with the first DCA axis ($r^2 = 0.27$), whereas Euphorbiaceae was weakly correlated with the Y-axis ($r^2 = 0.10$), but not the X-axis ($r^2 = 0.01$). Plots forming the outliers in the ordination tended to be dominated by minor plant families (e.g., British Guiana TF2 – Chrysobalanaceae, Bahia – Myrtaceae, São Paulo – Euphorbiaceae, Pakitza TF1 – Violaceae, Rondonia TF2 – Sterculiaceae).

If important plant families, instead of plots, are subject to DCA ordination, the proximity of pairs of families in the two-dimensional space is a measure of positive co-occurrence between them within the plots comprising the data set (Figure 3). Moraceae and Myristicaceae are thus closely associated, covarying less closely with Palmae, Meliaceae, Bombacaceae and Annonaceae. Most negatively associated with palms are the Chrysobalanaceae and Lecythidaceae, families characteristic of the Guianan region, where palms are scarce to absent (Table 2). Lauraceae and Sapotaceae also tend to be well-represented in palm-poor forests, while several other families – Anacardiaceae, Burseraceae, Rubiaceae, Tiliaceae and Euphorbiaceae – do not strongly covary, either positively

Table 2. Abundance of the 16 most important families in the 450-tree samples.*

Site	Location	Palm	Legu	Mora	Euph	Myri	Sapo	Meli	Lecy	Bomb	Laur	Anno	Burs	Chry	Ster	Viol	Rubi	Total
S1	Castanhal, Para, BrazilTF	1	56	17	12	5	76	14	62	1	6	5	54	19	13	18	1	360
S2	Rio Guama, Para, Brazil, Varz	136	109	4	40	6	7	37	12	38	0	0	26	7	9	0	0	431
S3	Belem, Para, Brazil, Iga	231	53	9	1	3	4	29	10	10	0	1	29	1	14	0	0	395
S4	Alto Ivon, Bolivia, TF	94	26	110	6	95	5	0	1	1	8	8	5	13	1	0	7	380
S5	Brit. Gui, Morabukea, TF	13	153	0	10	2	28	4	66	24	19	3	7	30	5	3	0	367
S6	Brit. Gui. Mixed, TF	9	75	1	11	6	15	1	61	7	27	20	3	108	15	1	1	361
S7	Brit. Gui. Greenheart, TF	0	57	0	36	1	18	0	68	19	64	3	8	61	12	11	0	358
S8	Brit. Gui, Wallaba, TF	0	163	0	2	0	26	0	13	72	14	2	0	65	0	0	6	363
S9	Brit. Gui, Mora, Flooded	0	220	0	11	2	2	48	52	1	12	4	10	1	4	0	0	367
S10	Japura, Brazil, Varz	3	59	16	63	13	24	8	27	11	22	56	0	9	1	6	6	324
S11	BCI, Panama, TF	15	44	54	23	24	3	7	15	19	6	4	12	3	0	0	63	292
S12	Urucu, Amaz. Brazil, TF	24	42	40	18	32	61	0	84	10	15	12	19	31	7	4	5	404
S13	Yasuni, Ecuador, TF	78	52	48	24	19	6	22	23	20	12	10	12	7	10	23	11	377
S14	Xingu, Brazil, TF	52	125	20	6	4	14	26	24	16	9	19	11	15	19	18	1	379
S15	Manu, late succ. Peru, Flood	43	63	41	16	27	2	60	0	11	13	41	3	7	16	3	1	347
S16	Manu, trail3, Peru, Flood	65	17	26	22	62	18	37	0	35	2	38	2	6	18	4	2	354
S17	Manu, trail2, Peru, Flood	121	32	27	12	17	28	16	0	27	10	42	5	9	8	7	3	364
S18	Manu, trail12, Peru, Flood	55	29	32	17	53	22	29	0	47	5	50	4	2	18	0	3	366
S19	Manu, Otorongo, Peru, Flood	216	19	26	8	46	4	17	0	41	5	14	1	0	11	0	0	408
S20	Manu, Salvador, Peru, Flood	131	18	29	4	36	13	24	1	48	7	21	1	2	18	18	1	372
S21	Manu, terrace, Peru, TF	99	44	60	27	18	15	13	3	19	2	8	0	4	18	13	11	354
S22	Manu, ravine, Peru, TF	84	43	51	49	15	20	11	10	14	8	14	5	5	9	21	7	366
S23	Pakitza, Peru, dissected TF	74	27	61	32	13	9	1	2	3	7	9	4	2	3	119	11	377
S24	Pakitza, Peru, alluvial terrace	97	33	26	33	37	16	33	1	33	6	15	2	7	14	7	2	362
S25	Pakitza, Peru, TF	59	69	75	18	24	12	2	2	3	5	3	12	3	4	15	9	315
S26	Beni, Bolivia, inund. forest	195	14	104	1	0	42	7	0	0	0	2	0	0	0	0	22	387
S27	Beni, Bolivia, non-flooded“	255	24	40	30	1	0	3	0	2	1	0	0	0	0	0	8	364
S28	Serra Norte, Para, Brazil, TF	7	62	5	34	15	24 (19	17	6	34	9	7	5	0	3	4	251	

Table 2. (*contd.*)

Site	Location	Palm	Legu	Mora	Euph	Myri	Sapo	Meli	Lecy	Bomb	Laur	Anno	Burs	Chry	Ster	Viol	Rubi	Total
S29	Rio Gelado, Para, Brazil, TF	22	160	28	3	0	25	27	20	5	6	9	37	2	35	2	2	383
S30	Carajas, Para, Brazil, TF	2	80	27	16	14	13	26	12	6	30	26	66	0	22	8	3	351
S31	Carajas airport, Para, Braz. TF	8	101	26	41	10	24	29	17	4	15	14	21	1	1	1	2	315
S32	Maraba, Para, TF	11	62	32	92	3	5	43	8	15	10	21	61	2	17	9	0	391
S33	Rondonia 1, Brazil, TF	66	64	85	3	13	24	11	2	2	9	9	51	2	10	3	2	356
S34	Rondonia 2, Brazil, TF	64	19	30	1	6	11	66	4	8	5	9	4	4	121	4	1	357
S35	Ubatuba, S.Paulo, Brazil, TF	53	23	12	72	5	8	3	5	15	29	9	0	4	3	0	68	309
S36	Yanmono, Loreto, Peru, floodplain	41	44	30	13	67	16	22	23	10	11	15	10	2	22	1	24	351
S37	Cabeza de Mono, Pasco, Peru, TF	1	61	5	42	40	47	48	22	3	29	7	31	15	12	1	1	365
S38	Mishana, Loreto, Peru, TF	46	59	27	29	52	28	6	2	11	22	12	15	22	4	1	7	343
S39	Cuz.Amaz.1, Peru, floodplain	62	36	76	9	6	23	15	5	33	6	23	0	9	9	6	11	329
S40	Cuz.Amaz.2, Peru, floodplain	64	37	66	10	4	26	14	2	30	10	26	7	4	9	29	3	341
S41	Tambopata-TF, Peru	12	41	64	26	47	14	0	6	13	28	13	7	15	3	9	12	310
S42	Tambopata-floodplain, Peru	122	30	36	22	17	17	15	2	5	28	16	4	1	7	42	0	364
S43	Aripuana, M.Gros.Braz. TF	25	46	43	19	39	9	13	18	0	61	19	15	5	10	3	21	346
S44	Caxiuana, Para, Brazil, TF	3	58	11	5	11	39	2	56	0	12	21	34	24	6	25	4	311
S45	La Selva, C.Rica, TF	104	83	33	10	8	8	15	1	4	10	29	42	1	2	0	9	359
S46	Bahia, Brazil, TF	0	65	16	18	6	63	1	13	12	32	4	9	17	3	19	13	291
S47	NE Amaz. Ecuador, TF	25	43	62	29	23	28	5	29	17	28	10	23	11	8	1	15	357
S48	Jurua, Acre, Brazil, Var	52	39	44	86	46	2	2	3	1	15	7	4	0	3	1	31	336
TOTAL		2879	1675	1112	993	944	831	804	732	715	712	683	563	554	459	414	170	10

*Anno = Annonaceae; Bomb = Bombacaceae; Burs = Burseraceae; Chry = Chrysobalanaceae; Euph = Euphorbiaceae; Laur = Lauraceae; Lecy = Lecythidaceae; Legu = Leguminosae, Meli = Meliaceae; Myri = Myristicaceae; Mora = Moraceae; Palm = Palmae; Rubi = Rubiaceae; Sapo = Sapotaceae; Ster = Sterculiaceae; Viol = Violaceae.

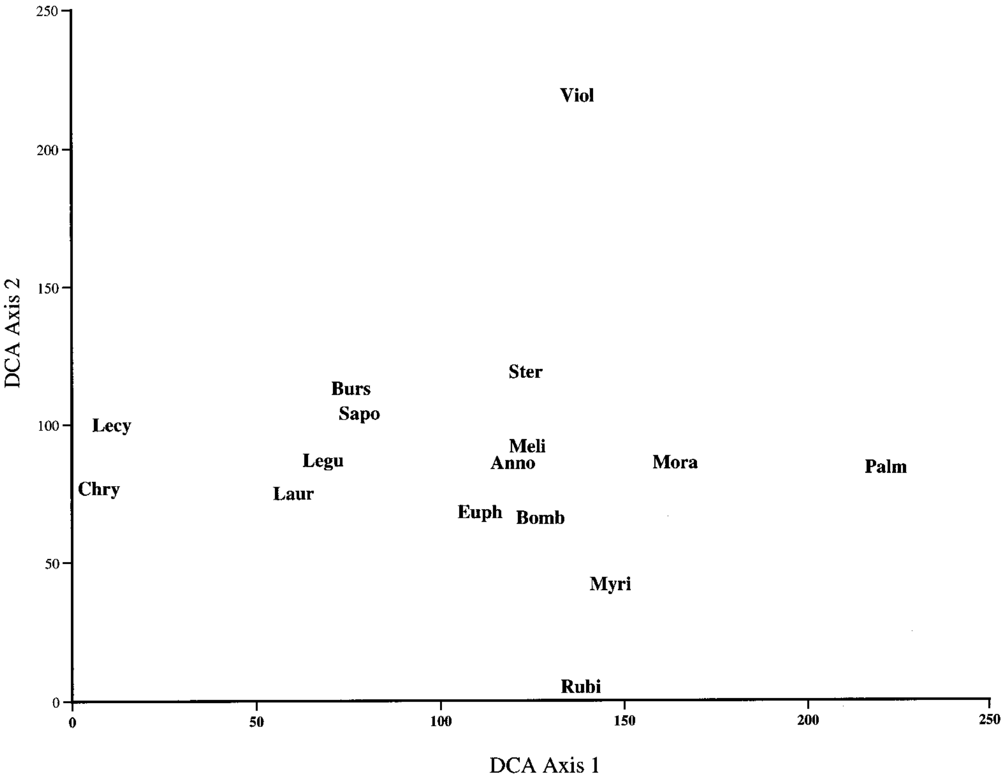

Figure 3. DCA ordination of forty-eight 450-tree samples from 29 Neotropical localities: relationships among the 16 most prominent families (see Table 2).

or negatively, with any of the more prominent families. Violaceae and Rubiaceae stand as outliers due to their anomalously strong representation in just one or two plots.

Edaphic vs regional differentiation of forests

We distinguished two main classes of sites: seasonally flooded (16 sites) and unflooded forests (terra firme: 32 sites). The distinction is basic, because it recognizes a primary division of the landscape into depositional vs erosional surfaces. The corresponding soil types tend to fall into different orders of the several systems of soil taxonomy in current use (Richter & Babbar 1991). Floristic responses to variation in local edaphic conditions should therefore be expected to reflect the same fundamental division, as indeed does the parsimonious terminology used by Amazon residents to refer to different forest types: igapó and várzea for flooded forests; terra firme for unflooded forests (i.e., nearly everything else).

We may thus ask whether compositional variation at the family level in Amazonian forests is related more to locally varying factors, such as soil and exposure to inundation, or to geographical influences, most simply represented by distance. We have addressed this question by grouping the plots into four sets representing western, central and eastern Amazonia, and the Guianas. We then ask, separately, for terra firme and seasonally inundated plots, whether compositional variation within regions is greater or less than between regions. These questions were answered using bootstrap methods (internal resampling) to generate expected distributions of distances (=dissimilarity) within groups of plots, along with associated confidence limits, and then comparing the distributions between groups of plots (Efron & Tibshirani 1991). Between-group comparisons are presented in Table 3, along with the corresponding levels of statistical significance.

Table 3. Euclidian distances between groups of sites, taken from the DCA ordination (Figure 2), and levels of significance of comparisons.

	GTF	GFL	EATF	EAFL	CATF	CAFL	WATF	WAFL
GTF[1]	0	48**	53*	149**	98**	82**	122**	157**
GFL		0	56	136**	88	102**	127**	153**
EATF			0	96**	46	47	73*	105**
EAFL				0	51	94**	52	30
CATF					0	58	47	65*
CAFL						0	48	89**
WATF							0	41*
WAFL								0

1. G = Guianan region; EA = Eastern Amazon; CA = Central Amazon; WA = Western Amazon; TF = terra firme; FL = flooded forest
2. * P ≤ 0.1, ** P ≤ 0.05, *** P ≤ 0.01.

The procedure clearly reveals a predominant influence of geographical distance on forest composition in Amazonia and the Guianas. Among terra firme forests, there is a consistent trend for the mean dissimilarity of plots to increase with geographical distance from west to east. Guianan forests are distinct from all Amazonian forests, most closely resembling those of eastern Amazonia, and least closely those of western Amazonia. The terra firme forests of central and eastern Amazonia are more alike than those of any other two regions, but from the perspective of western Amazonia, the forests of eastern Amazonia are more distinct than those of central Amazonia.

Similar geographical relationships emerge among the seasonally inundated forests, but with one exception. The two plots representing inundated forests in eastern Amazonia, Rio Guama várzea and Rio Guama igapó, are both strongly dominated by palms, and therefore cluster in the DCA plot with the palm-rich sites of western Amazonia. Otherwise, the flooded forests of different regions consistently show decreasing compositional similarity with distance and, in general, exhibit less mutual resemblance than terra firme forests.

A surprising result emerges when terra firme and inundated forests are compared. Mean dissimilarity between the terra firme and flooded forests within each region is hardly greater than the mean dissimilarity in pairwise cross comparisons between terra firme and flooded forests within regions. The exception is again in eastern Amazonia, where the palm-rich Rio Guama várzea and igapó plots contrast sharply with the palm-poor terra firme forests of the same region.

DISCUSSION

Four major results emerge from our analysis. (1) Palms or legumes constitute the predominate family of trees in a large majority of Amazonian and Guianan forests, followed by Moraceae and Euphorbiaceae. (2) There are strong patterns of positive and negative association between plant families that extend across the entire South American continent. (3) There is a general trend of increasing compositional dissimilarity with distance in the tree communities of both terra firme and inundated sites. (4) The tree communities of inundated forests tend to resemble more closely those of terra firme forests within the same geographical region than they do the inundated forests of adjacent regions. We shall comment on these results in turn, and then offer some speculations about how the respective patterns might have arisen.

If one were to conduct such an analysis of North American forests, similar patterns of regional complementarity would be found, for example, between oaks and hickories in the south and maples and birches in the north, or between oaks, hickories, beeches and other deciduous species in the East and pines and other conifers in the West (Barbour & Billings 1988). At such a rough level, there are parallels in the compositional patterns shown by North and South American forests. In other respects, to be discussed below, there are major differences.

On an even larger geographical scale, Gentry (1988, 1992) showed that humid tropical lowland forests around the world are consistently dominated by a small group of plant families, foremost among them Leguminosae (*sensu latu*), followed variously by Moraceae, Euphorbiaceae, Annonaceae and others. At middle elevations, Leguminosae are replaced by Lauraceae as the leading family, followed by Rubiaceae in a pattern found in such widely scattered localities as the Neotropics, Madagascar and tropical Australia (Gentry 1988, Lieberman *et al*. 1996). Global consistency in the representation of plant families in tropical lowland and montane forests has been attributed to historical factors, namely, the origination of many modern plant families prior to the breakup of Pangea in the Mesozoic. By a parallel argument, the observed patterns of positive and negative association between plant families within tropical South America could result from the interaction of historical and evolutionary circumstances. However, complementarity between plant families could also result from contemporary ecological conditions, if the members of families tended to specialize on limited ranges of environmental conditions.

Both evolutionary and ecological interpretations of the observed patterns are plausible. An evolutionary interpretation could rest upon the separate geological histories of eastern and western Amazonia (Bigarella & Ferreira 1985). Eastern Amazonia (including the Guianas) contains two ancient, Precambrian shields, the Guiana Shield north of the Amazon, and the Brazilian Shield to the south. Both are characterized by highly weathered, nutrient-poor soils (Richter & Babbar 1991). The soils of central Amazonia are also nutrient-poor, but of different origin, being derived from Tertiary marine deposits, now strongly weathered (Bigarella & Ferreira 1985; Räsänen *et al*. 1992, 1995). In contrast, the landscape of western Amazonia consists mostly of comparatively young and relatively fertile sediment deposited subsequent to the initiation of the Andean orogeny in the Miocene (Räsänen *et al*. 1987, Kalliola *et al*. 1993a, Linna 1993). The flora of western Amazonia is therefore of more recent origin than that of eastern Amazonia, and may in part have been derived from Central America, as is consistent with our finding that the plots representing BCI (Panama) and La Selva (Costa Rica) cluster in the ordinations near those of western Amazonia (Gentry 1990, Figure 2).

Do Amazonian tree communities conservatively reflect ancient geological relationships or do they represent dynamic responses to contemporary ecological conditions? A tight correlation between soils and geology makes the question difficult to resolve. The dilemma of confounding variables could potentially be circumvented by seeking situations that represent exceptions to regional generalities. For example, the landscape around Iquitos, Peru is largely constructed of recent sediments of Andean origin (Räsänen 1993). Neverthelesss, deeply weathered Miocene marine sediments and white sand soils of extreme infertility are exposed at the surface in some areas. These white sands are derived from the Guiana Shield, from which they were transported to western South America prior to the Andean orogeny when continental drainage flowed from east to west (Kalliola *et al*. 1993b, Räsänen 1993). To date there has been no effort to sample regionally anomalous situations of this kind, so even a preliminary conclusion is not possible.

It is probable that the patterns we document here are of ancient origin, and, if so, would be independent of any contractions and expansions of the Amazonian forest that may have taken place during the Pleistocene (Haffer 1969). In any case, we would not expect Pleistocene speciation events to strongly influence the family-level analysis we conduct here (Prance 1982).

Our third finding, that the compositional differences between plots increase with distance in both terra firme and inundated forests suggests both historical-evolutionary and ecological explanations. Alternative possibilities cannot be separated with the available information (Schluter & Ricklefs 1993).

Finally, it was found that the familial composition of seasonally inundated forests tends to resemble that of terra firme forests of the same region more closely than that of inundated forests in adjacent regions and vice versa. This was an entirely unexpected result, because the pattern in North America is diametrically the opposite.

In North America, floodplain and upland forests have a consistent, continent-wide generic and familial composition. In floodplains, the following genera, among others, are found from New Jersey to California: *Acer*, *Fraxinus*, *Juglans*, *Platanus*, *Populus*, *Salix* and *Ulmus*. In contrast, on well-drained upland soils, *Juniperus*, *Pinus* and *Quercus* are ubiquitous, complemented by *Carya* in the eastern half of the continent (Barbour & Billings 1988, Latham & Ricklefs 1993). In short, there is pronounced continent-wide consistency at higher taxonomic levels in the composition of both floodplain and upland forests throughout North America. Moreover, the floodplain forests of any region (e.g., east, central and west) are far more similar at the generic and familial levels than any floodplain forest is to forests in the adjacent uplands. But in South America this pattern is turned on its head. Why?

We can offer only speculations. One possibility is that the environment of Amazonian floodplains is more heterogeneous than that of North American floodplains. In the Amazonian headwaters region, mature floodplain forests are emergent nearly all year (Terborgh *et al*. 1996). Heavy flooding can occur, but the episodes are infrequent and brief, normally lasting only a few days. The root systems of trees therefore do not have to be adapted to anaerobic conditions. In central Amazonia, the flood regime of major rivers follows an annual cycle in which much of the floodplain remains under many metres of water for months at a time (Ayres 1986, Sioli 1984). Some species endure continuous immersion for as long as 9 mo, yet retain functional foliage throughout the year (Junk 1989). It seems doubtful that such severe ecological stresses could be tolerated by any species that lacked special adaptations to prolonged immersion. Further downstream, near the mouth of the Amazon, the main channel broadens and enters a tidal zone. In this region, submergence and emergence occur twice daily, imposing other, not well investigated, adaptive challenges.

Nevertheless, one could imagine that certain adaptations to periodic immersion would be common to all three major hydrological regimes, e.g., seed dispersal by fish and water, seed germination at the end of the flood season, tolerance of waterlogged and anaerobic soils. The existence of such adaptive common denominators could reasonably lead to a pattern of downstream diffusion of floodplain species via water transport of seeds. Yet, paradoxically, this apparently does not occur on a large scale, because the tree floras of flooded forests are even more strongly differentiated by region than those of upland (terra firme) forests.

Contrary to the pattern for North America described above, our family-level results suggest that the flooded forests of each major region in tropical South America are more closely allied taxonomically to the adjacent upland forests, than to other floodplain forests, either upstream or downstream. If confirmed by further investigation, the pattern overrides what must be a strong adaptive gradient between the leached, acidic, and drought-prone soils of the uplands, and the young, fertile, moist and neutral soils of floodplains (Lieberman *et al*. 1985, Tuomisto & Ruokolainen 1994, Tuomisto *et al*. 1995, Terborgh *et al*. 1996). The paradox of the regional affinity of upland and floodplain forests may have an historical explanation; certainly it is hard to argue for the pattern on ecological grounds.

Finally, the special status of swamp forests merits a comment. Swamp forests were excluded from the analysis because they tended to appear in the ordinations as extreme outliers. As the term is used here, floodplain forests are distinct from swamp forests on the criterion of drainage. Floodplains tend to be flat, elevated above mean river level, and relatively well-drained. In contrast, swamps occur in depressions or low-lying areas with poor drainage, so that flooding is generally prolonged relative to floodplains. Swamp forests of many kinds occur in Amazonia (Junk 1989, Kalliola *et al.* 1991). They are characterized by low tree diversity and high dominance by one or a small number of species (Richards 1952).

For a North American analogy, one can point to the *Taxodium-Nyssa* swamps of the southeastern U.S. Two small families dominate the tree flora, and neither family is prominent in normal floodplain forests. It is commonly assumed that swamps represent edaphically extreme conditions, and consequently support only a few species with special adaptations, such as the pneumatophores of *Taxodium* and the swollen trunk bases of *Nyssa*. The tropical swamp forests we have examined conform to the pattern of low species diversity and high dominance noted by Richards (1952). However, the várzea of central Amazonia appears to be an exception, in that high diversity forests occur in sites that are regularly flooded for *c.* 6 mo a year. The distinction may be that water actively circulates in the várzea, while swamps tend to lie under stagnant water prone to anoxia. Clearly, more research on the exceptional status of várzea is in order.

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