FERNS AND THE MELASTOMATACEAE AS INDICATORS OF PHYTOGEOGRAPHIC PATTERNS IN AMAZONIA

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Résumé : Les modèles de distribution des plantes de la forêt pluvieuse de l'Amazonie sont peu connus à cause d'une recherche botanique inadéquate et géographiquement inégale. Si les espèces végétales forment de manière récurrente des communautés écologiquement restreintes, il devrait y avoir des modèles de distribution récurrents qui pourraient être découverts en étudiant seulement une partie de la flore. Les comparaisons de la flore de douze terrains d'étude différents dans l'Amazonie péruvienne sur la base d'arbres supérieurs à 2,5 cm diamètre à la hauteur de la poitrine, fougères terrestres et Melastomataceae, indiquent qu'il existe des communautés de plantes récurrentes et que les fougères et Melastomataceae sont de très bons indicateurs de plusieurs modèles phytégéographiques généraux en Amazonie.

Mots-clés : forêt pluvieuse de l'Amazonie, Melastomataceae, fougères, indicateurs phytogéographiques.

Abstract: The distribution patterns of Amazonian rain forest plants are poorly known as a result of inadequate and geographically uneven botanical exploration. If the plant species form ecologically restricted recurring communities there should also be some repeating patterns of distribution that can be found by studying only a part of the flora. Floristical comparisons of twelve different study plots in Peruvian Amazonia on the basis of trees over 2.5 cm diameter at breast height, terrestrial ferns and the Melastomataceae suggest that there are recurring plant communities and that ferns and Melastomataceae are promising candidates for serving as indicators of more general phytogeographical patterns in Amazonia.

Keywords: Amazonian rain forest, Melastomataceae, ferns, phytogeographical indicators.

Introduction

In the considerations of Amazonian biogeography the central point has been the recognition of separate areas where species richness and endemism is observed to be higher than in the surroundings. These so-called centers of endemism are variously thought to be caused by allopatric speciation in distinct rain forest patches during drier episodes of Pleistocene (HAFFER, 1969), by Holocene dispersal of species to previously water-covered Amazonia (FRAILEY *et al.*, 1988), fluvial dispersal barriers (HAFFER, 1978; HERSHKOVITZ 1977), or by present-day ecological factors that may be induced by climatic differences (ENDLER, 1982) or geologically induced habitat differentiation (ENDLER, 1982; RÄSÄNEN *et al.*, 1987). Despite the essential role that biogeography has played in the development of these theories about the evolution and structure of Amazonian ecosystems, our knowledge of the distribution of species in the area is still quite inadequate. The general collection activity in Amazonia has been very low (CAMPBELL & HAMMOND, 1989) in spite of recently increasing effort and, more importantly, collections are very unevenly distributed so that even the very idea of centers of endemism remains unsupported under a closer scrutiny (NELSON *et al.*, 1990).

Evidently, one of the central tasks in Amazonian phytogeographical studies has to be the revealing of true patterns in the distribution of plant species. To achieve this goal collection intensity and geographical coverage must be considerably increased. It is especially important to gather observations that are quantitatively comparable among separate sites so that site to site floristic differences and similarities can be revealed in an unbiased way. The standard method is to use sampling units within which all the plant species are recorded and the size of the sampling unit is defined so that nearly all species present in the community are met (BRAUN-BLANQUET, 1932). However, in tropical rain forests this approach is in practice nearly impossible because of the great species richness and the inability in most cases to distinguish any clear limits for plant communities (MANGENOT, 1955).

An obvious way to avoid the special difficulties of rain forests is to sample only a part of the flora and to use it as an indicator of the rest. Such an indicator group should 1) be easy to recognize in the field, 2) be easy to sample, 3) be species-rich enough to reflect different kinds of distribution patterns and ecological responses, 4) be species-poor enough to enable rapid field and laboratory work, 5) be present in all parts of the study area, and 6) reproduce as accurately as possible the general distribution patterns of the total flora. A group of species that fits with the first five requirements can be considered a potential indicator and the sixth condition is a test for real applicability. The sixth condition necessarily includes the idea that in rain forests there should be distinct plant communities that are determined by some environmental constraints like precipitation, temperature and soil quality largely in the same manner as in the temperate part of the world. So, a good indicator group should be able to present equally unique species combinations for given ecological conditions as are observable among the rest of the flora. The assumption of separable and in a predictable manner recurring plant communities in unflooded Amazonian forests is, however, not approved neither much studied and there are also several theories supposing that different kinds of stochastic phenomena (HUBBELL & FOSTER, 1986) largely define the species composition of any given site.

The idea of a certain kind of indicator group has been applied in Amazonian phytogeographical studies by eg. KAHN & GRANVILLE (1992) and PRANCE (1973) but these authors have not tried to estimate if their indicator groups can really reproduce a pattern common to the rest of the flora. To my knowledge, the only such attempt in rain forests has been made by WEBB *et al.* (1967) in Australia where it was found that big trees work best. It is also intuitively appealing to think that trees could be good phytogeographical indicators. The biomass of trees is biggest of different life forms in tropical rain forests and trees are the main component in determining the structure of the forest. Furthermore, they have a major contribution to the species richness of the forest (BALSLEV & RENNER, 1989). However, trees are not a very practical indicator group because of the high number of species involved and the laborious sampling of especially big individuals. Potentially better indicator groups can be found among smaller plants, such as ferns and the family Melastomataceae. Both taxa fulfil all the first five conditions described above. In this paper I shall explore how well these two plant groups fulfil the requirement of reproducing a floristic pattern that is common to other parts of the flora. For practical reasons not the whole flora but only trees are compared to ferns and Melastomataceae.

Data collecting and analysis

Twelve plots of 25 m per 25 m (0.0625 ha) were established in two separate localities (fig. 1) close to the city of Iquitos in primary unflooded rain forest avoiding recent tree falls as far as possible. The average annual rainfall of the area is ca. 2600 mm and mean annual temperature 25.9°C (PEÑAHERRERA, 1986). The study area along Río Momón was a remnant rain forest patch on clay soil belonging to the tourist enterprise "Amazon Selva Tours" that was surrounded by cultivations. Two plots (n° 1 and 2) were set on an old flat terrace of Río Momón and two other (3 and 4) on a somewhat undulating terrain (relative height differences ca. 5-10 m) beside the terrace.

The locality along Río Nanay was close to the village of Mishana and the plots were established in a more or less linear south-north orientation in the same area where GENTRY (1988) has reported one of the most species-rich hectare-plots of the world. Plots n° 5 to 7 were established on an essentially flat terrace of Río Nanay about 1.5 km south from the village of Mishana. Four plots (9 to 12) were put ca. 2-3 km south from Mishana on white sand forest on a hilly terrain (relative height diffe-

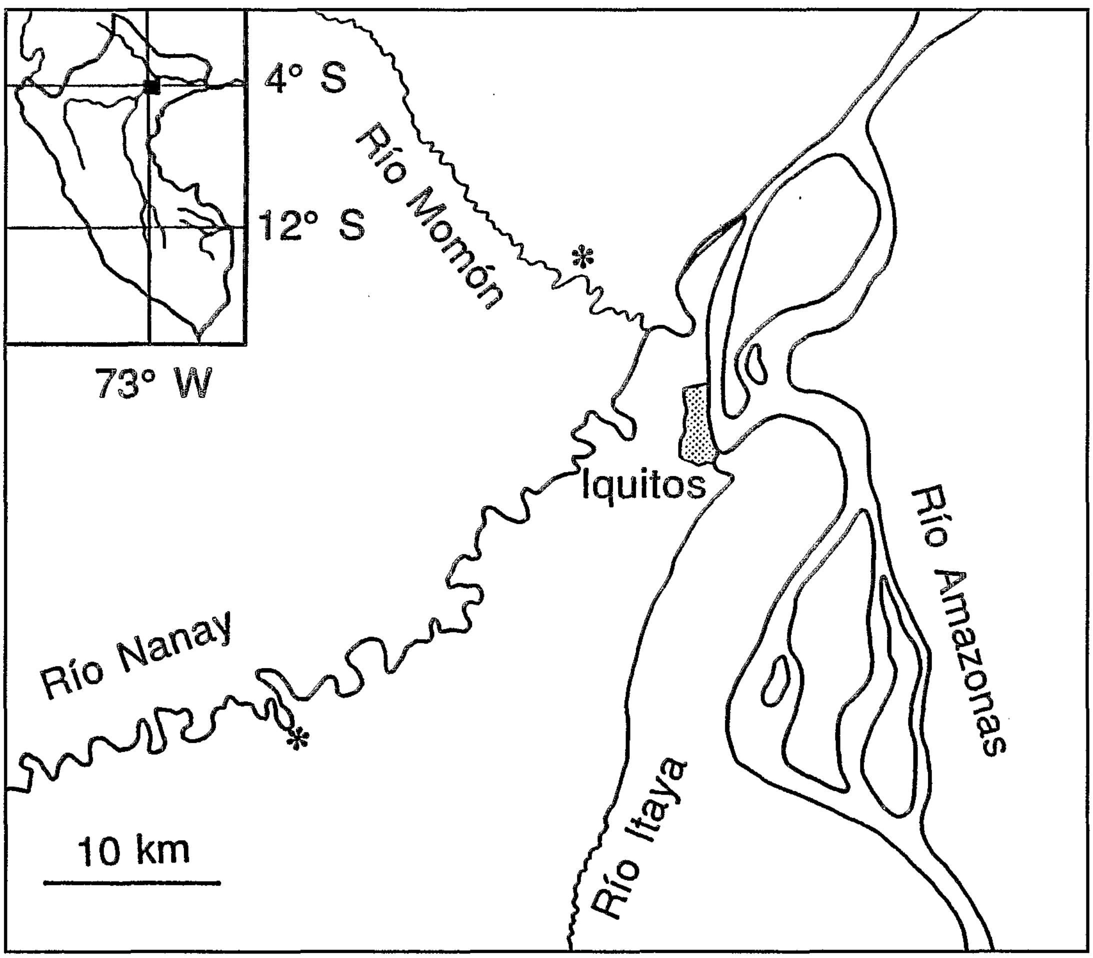

Figure 1
The study area in Peruvian Amazonia. Collecting localities are indicated with stars.

rences ca. 10 m) bordered by the terrace. Plot n° 8 was set exactly in the limit between the white sand area and the clayey terrace.

Within the plots, all the terrestrial and low epiphytic (below the height of 2 m) species of ferns, the height and number of individuals of all Melastomataceae species, and the circumference and number of individuals of all tree species having more than 2.5 cm diameter at breast height (DBH) were recorded.

Two different methods, correspondence analysis (CA), HILL (1973) and Mantel's test (MANTEL 1967) were used to investigate the similarity of the floristic relationships that are produced independently with ferns, the Melastomataceae and trees. In CA ordination, presence-absence data was used. Because the number of tree species exceeded the capacity of the computer program CANOCO (TER BRAAK, 1987), those species that were represented by only one individual were excluded from the analysis. This arrangement does not affect the resulting ordination. For Mantel's test, floristic similarity matrices of the plots were computed using each plant group separately. The Jaccard coefficient of community (JACCARD, 1901) was used for ferns, and the percentage similarity (BRAY & CURTIS, 1957) based on the importance value index (IVI, CURTIS & MCINTOSH, 1950) for Melastomataceae and trees. Because most species of the Melastomataceae are small, the IVI values were calculated using the height of each individual instead of basal area. The use of height gives relatively more importance for vines and instead of biomass probably reflects more of the capability of capturing light.

In Mantel's test, a test criterion (Z) is calculated as the sum of the cross products of the corresponding values in the two similarity matrices. Then one of the matrices is kept constant while the other has its cells randomly permutated. After each permutation the test criterion is calculated again (Z'). When all permutations are made, the statistical significance of the original test criterion is computed: the commonness of Z' values that exceed Z gives the probability of getting a value at least as extreme as the original test criterion by chance only. The Mantel's test was calculated with the computer program "R-package" (LEGENDRE and VAUDOR 1991) using 2000 permutations and a standardized form of the test criterion (equivalent to the Pearson correlation coefficient (SMOUSE *et al.*, 1986).

Results

The study included 2114 individuals and 505 species of trees over 2.5 cm DBH, 457 individuals and 29 species of Melastomataceae, and 53 species of ferns. The floristical list of trees is presented in the appendix and Melastomataceae and ferns are found in RUOKOLAINEN *et al.* (in press).

The CA ordination gave almost identical results in trees and ferns but in the Melastomataceae the result was somewhat different (fig. 2). In all three ordinations it was possible to distinguish the plots on clayey soil and respectively on white sand soil along Río Nanay. Plots 5, 6 and 7 formed a distinct group as well as plots 10, 11 and 12. Trees and ferns located plot n° 9 among other plots on white sand and n° 8 that situated in the transition zone between clayey and white sand soil was found in between the corresponding plots in the ordination, too. In the Melastomataceae, however, plot 8 clustered together with clayey soil plots and the first plot (n° 9) on white sand took an intermediate position in the ordination.

The plots along Río Momón do not separate as a very tight group but in all the three ordinations plots 1 and 2 and, respectively 3 and 4 formed fairly clear pairs. In ferns and trees the former pair has a more or less central position in the ordination whereas the latter pair is relatively far from all the other plots. In the Melastomataceae this pattern is rather the opposite.

Each of the three plant groups gave a relatively similar indication of the floristic distances among the study plots as shown by the highly significant positive correlations in the Mantel's test (table 1). Between ferns and trees the correlation is very high, and even though the correlation coefficients involving the Melastomataceae have lower values, they are still statistically significant.

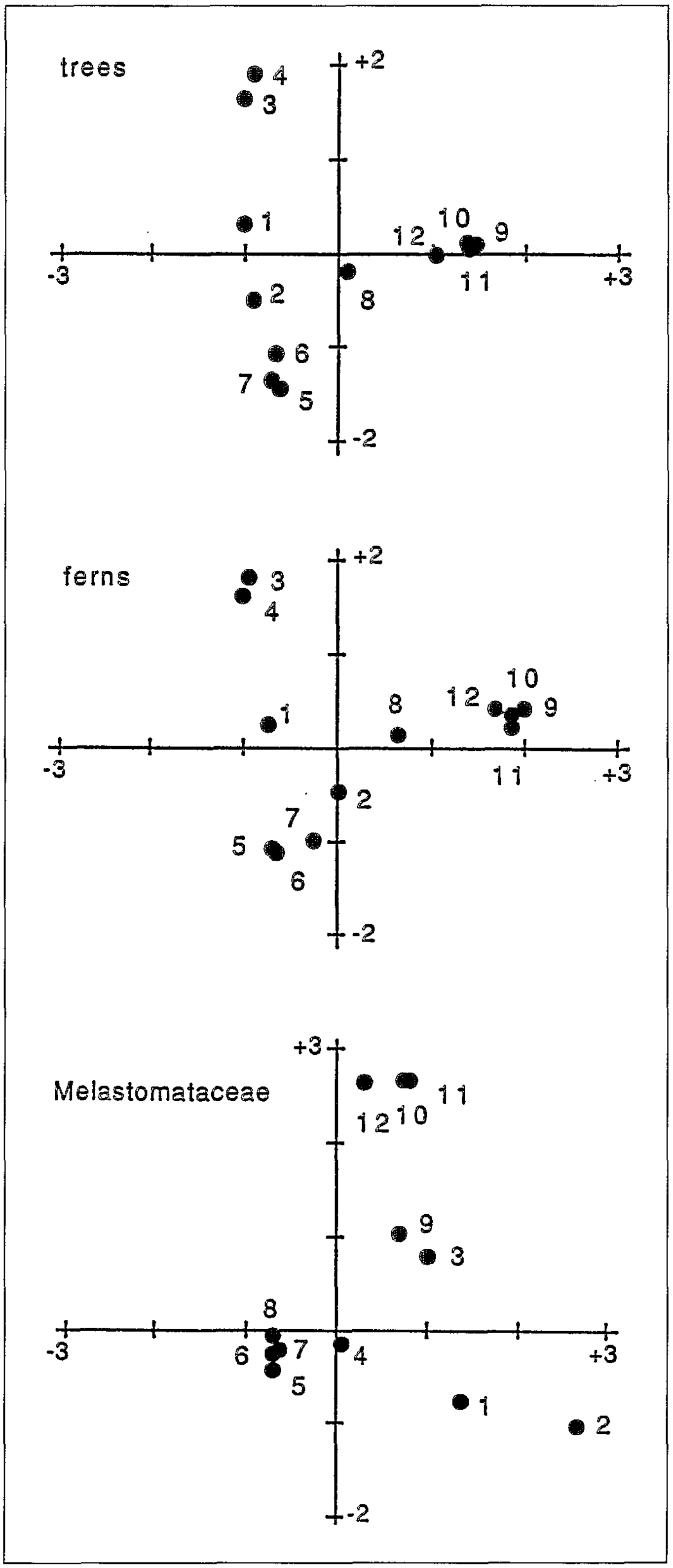

Figure 2
CA ordinations of the twelve study plots using independently presence-absence data of trees, ferns and the Melastomataceae.

	Melastomataceae	Trees
Ferns	0.396 **	0.823 ***
Melastomataceae		0.553 ***

Table 1
Standardized correlations among three different plant groups according to Mantel's test. The probability (P) to observe equal or better correlation by chance is indicated by stars:
** = P<0.01, *** = P<0.001.

Discussion

The ordination result given by ferns was almost identical to the one given by trees, which was also reflected in the high correlation coefficient between these groups. The same overall pattern was also produced by the Melastomataceae, but in this case the details of the ordination differed more, and the correlation coefficients with the other plant groups were lower. Hence, it is possible that ferns and trees bear more resemblance to each other than to the Melastomataceae in their phytogeographical behaviour. However, it is also possible that the result is partly a sampling artifact. The Melastomataceae had notably fewer individuals and species than the other groups, and therefore random variation may have played a greater role. In a more detailed scrutiny of the same data set (RUOKOLAINEN *et al.* in press), it was found that also another small group, the Myristicaceae, differed somewhat from the general pattern of ferns and trees. It must be noted that the total flora was not inventoried, but trees were taken as a representative sample of it. Trees certainly form an important part of the total floristical diversity, but their correlation with the rest of the flora is unknown. However, in any case the positive geographical correlations between all the three plant groups studied here suggest that there were really non-random plant species assemblages and therefore the very possibility for defining relevant phytogeographical indicators is supported.

An important part of the surveyed plots were situated in white sand forest that is known to be floristically distinct (ANDERSON 1981) and therefore there was probably a tendency to get better correlations in Mantel's test than would have been the case without the white sand plots. On the other hand, the CA ordination indicated that especially between ferns and trees there was almost exact one to one correspondence in the floristic distances among the plots, and therefore the positive result in Mantel's test can be considered fairly reliable.

Despite differences in details, two relatively species-poor groups have produced generally the same floristical overview of the plots as the species-rich group of trees. This means that both ferns and the Melastomataceae are promising as indicator groups in the search of phytogeographical patterns in Amazonia. Faced with the huge size of Amazonia, phytogeographers need methods that can be learned and practiced rapidly by as many people as possible during the limited time left to study the rain forests in a relatively undisturbed state. Even though ferns and the Melastomataceae are species-poor groups only in relation to the rest of Amazonian flora, it is still feasible or at least more rapid to make workable field guides for them than for the whole flora. Therefore, it might even be possible to train relatively modestly educated people to collect the urgently needed field data of these potential indicator groups, in the same way as the parataxonimists work in Costa Rica (TANGLEY 1990).

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APPENDIX

Observed species of trees, followed by a number of a representative voucher (K. Ruokolainen *et al.*) and number(s) of study plot(s) that include the species.

ANACARDIACEAE

Astronium leicontei Ducke, 528 ..... 1, 2
Astronium sp.1, 1510 9
Tapirira retusa Ducke, 1929 12
Tapirira guianensis Aubl., 1298 ..... 1, 5, 7
Tetragastris panamensis (Engl.) O.K., 2653 3
Thyrsodium spruceanum Benth., 2571 2

ANNONACEAE

Anaxagorea cf. *dolichocarpa* Sprag. & Sandw., 2206 12
Anaxagorea brevipes Benth., 1349 ..... 8, 10, 12
Annona sp.1, 1001 ..... 6, 9, 10, 11
Bocageopsis mattogrossensis (R.E. Fr.) R.E. Fries, 414 ..... 2, 6, 7
Cremastosperma cauliflorum R.E. Fries, 756 4
Cymbopetalum sanchezii N.A. Murray, 679 4
Cymbopetalum aequale N.A. Murray, 647 3
Diclinanona tessmannii Diels, 953 ..... 5, 6, 7, 8, 9, 10, 11, 12
Duguetia cauliflora R.E. Fries, 1571 ..... 8, 9, 10, 12
Duguetia macrophylla R.E. Fries, 843 5
Duguetia latifolia R.E. Fries, 467 2
Ephedranthus guianensis R.E. Fries, 277 1
Froesiodendron amazonicum R.E. Fries, 2500 ..... 1, 7
Guatteria decurrens R.E. Fries, 2178 ..... 4, 8, 10
Guatteria cf. *elata* R.E. Fries, 1085 6
Guatteria megalophylla Diels, 1729 ..... 1, 2, 3, 5, 8, 10, 12
Guatteria multivenia Diels, 631 3
Guatteria schomburgkiana Mart s.l., 2537 ..... 1, 2
Guatteria sp.1, 1311 7
Oxandra xylopioides Diels, 711 4
Oxandra macrophylla R.E. Fries, 682 ..... 3, 4
Rollinia sp.1, 2675 4
Tetrameranthus pachycarpus Westra, 1875 ..... 9, 10, 11, 12
Trigynea sp.1, 2133 8
Unonopsis guatterioides (DC.) R.E. Fries, 1457 8
Unonopsis spectabilis Diels, 569 ..... 3, 4
Unonopsis stipitata Diels, 330 ..... 1, 2 3, 6, 7
Xylopia benthamii R.E. Fries, 2217 11
Xylopia cuspidata Diels, 2081 6
Xylopia parviflora Spruce, 1279 ..... 5, 6, 7
Annonaceae sp.1, 2115 7

APOCYNACEAE

Aspidosperma exelsum Benth., 1392 ..... 8, 9, 10, 11, 12
Aspidosperma rigidum Rusby, 1211 7
Aspidosperma schultesii Woodson, 1830 11
Aspidosperma spruceanum Benth. ex Muell.Arg., 1526 ..... 9, 10, 12
Aspidosperma sp.1, 1208 7
Couma macrocarpa Barbosa Rodrigues, 1491 8

Himatanthus sucuuba (Spruce) Woods., 2659 .... 3, 4
Lacmellea cf. *klugii* Monach., 1530 .... 9, 10, 11
Lacmellea cf. *floribunda* (Poepp.) Benth., 945 5
Macoubea guianensis Aubl., 1319 7
Macoubea cf. *sprucei* (M.Arg.) Mgrf., 1216 .... 7, 8
Malouetia quadrecasarum Woodson, 741 4
Rauvolfia sprucei Muell.Arg. in Mart., 316 1
Tabernaemontana macrocalyx Muell.Arg., 2564 2

AQUIFOLIACEAE
Ilex sp.1, 1808 .... 9, 11

ARALIACEAE
Dendropanax macropodus (Harms) Harms, 561 .... 1, 3
Dendropanax umbellatus (R. & P.) Dcne. & Planch., 1765 .... 8, 10
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin, 1288 .... 9, 7

ARECACEAE
Bactris sp.1, 650 3
Bactris sp.2, 833 5
Euterpe precatoria Mart., 1006 .... 6, 8
Geonoma juruana Damm., 2674 4
Geonoma sp.1, 2708 4
Jessenia bataua (Mart.) Burret, 368 .... 1, 5, 6, 7, 8
Mauritia flexuosa L.f., 1358 8
Socratea exorrhiza (Mart.) Wendl., 427 .... 1, 2

BIGNONIACEAE
Jacaranda macrocarpa Bur. & K. Schum., 920 .... 5, 6, 8, 9, 10, 11, 12
Tabebuia obscura (Bur. & Schum.) Sandw., 1773 10

BOMBACACEAE
Matisia malacocalyx (Robyns & Nilsson) Alverson, 580 3
Rhodognaphalopsis brevipes Robyns, 1558 .... 9, 10

BORAGINACEAE
Cordia nodosa Lam., 638 .... 1, 3, 5, 6, 8
Cordia toqueve Aubl., 1408 8
Cordia ucayaliensis Johnst., 817 5

BURSERACEAE
Crepidospermum prancei Daly, 1917 .... 5, 7, 12
Dacryodes chimantensis Steyerm. & Maguire, 490 .... 2, 5, 7
Dacryodes cf. *peruviana* (Loes.) Lam., 531 .... 2, 3, 6, 7, 9
Dacryodes sp.1, 1062 2
Protium alstonii Sandw., 698 4
Protium cf. *apiculatum* Swart, 866 .... 5, 6, 7
Protium cf. *carnosum* A.C. Smith, 2129 .... 5, 7
Protium decandrum (Aubl.) Marchand, 2125 7
Protium divaricatum Engl., 517 2
Protium ferrugineum (Engl.) Engl., 1563 9
Protium fimbriatum Swart, 276 .... 1, 2, 3, 6, 7
Protium grandifolium Engl., 2055 .... 2, 5, 7, 8
Protium cf. *klugii* Macbr., 322 .... 1, 3, 4, 7, 8
Protium nitidifolium (Cuatr.) Daly, 921 .... 5, 6
Protium nodulosum Swart, 338 .... 1, 4
Protium paniculatum Engl., 1869 .... 2, 9, 12

Protium strumosum Daly, 290 .... 1, 3, 4
Protium subserratum (Engl.) Engl., 634 3
Protium tenuifolium (Engl.) Engl., 662 .... 1, 4
Protium sp.1, 2533 .... 1, 3, 4
Trattinickia aspera (Standl.) Swart., 1067 .... 6, 7
Burseraceae sp.1, 725 4

CARYOCARACEAE
Caryocar glabrum (Aubl.) Pers., 733 .... 1, 4

CECROPIACEAE
Cecropia cf. *membranacea* Trécul, 1010 6
Pourouma bicolor Mart., 358 1
Pourouma cf. *cecropiifolia* Mart., 687 4
Pourouma cuspidata Warb. ex Ule in Engl., 2706 4
Pourouma guianensis Aubl., 894 .... 5, 6
Pourouma minor Benoist, 502 .... 2, 3, 4, 6
Pourouma ovata Trecul, 1542 .... 9, 11, 12
Pourouma tomentosa Miq., 390 .... 1, 6, 7, 8

CHRYSOBALANACEAE
Couepia bernardii Prance, 891 5
Couepia dolichopoda Prance, 323 1
Couepia guianensis Aubl., 345 1
Couepia parillo DC., 1651 .... 9, 10
Couepia williamsii Macbr., 1277 .... 7, 11, 12
Licania harlingii Prance, 929 5
Licania heteromorpha Benth., 1952 .... 2, 6, 7, 12
Licania hypoleuca Benth., 1314 7
Licania intrapetiolaris Spr. ex. Hook.f., 1350 .... 8, 12
Licania lata Macbr., 809 .... 5, 8
Licania cf. *macrocarpa* Cuatr., 677 4
Licania oblongifolia Standl., 2072 6
Hirtella cf. *guainiae* Spr. ex Hook., 1980 5
Hirtella racemosa Lam., 2677 .... 3, 4
Chrysobalanaceae sp.1, 586 3

COMBRETACEAE
Buchenavia macrophylla Spruce ex Eichl., 380 1
Buchenavia cf. *pallidovirens* Cuatr., 1804 .... 1, 11
Buchenavia parvifolia Ducke, 1536 9
Buchenavia cf. *seriocarpa* Ducke, 1092 .... 4, 6, 8
Terminalia amazonica (J.F. Gmell) Exell, 457 2

CONNARACEAE
Connarus fasciculatus (DC.) Planch., 2531 1
Rourea amazonica (DC.) Planch., 286 1

DICHAPETALACEAE
Tapura juruana (Ule) Rizzini, 753 4
Tapura juliana Macbr., 309 1
Tapura amazonica P. & E., 289 1

EBENACEAE
Diospyros cf. *tessmannii* Mildbr., 1905 .... 9, 12
Diospyros sp.1, 1483 8
Lissocarpa stenophylla Steyerm., 1389 .... 8, 9, 10, 11, 12

ELAEOCARPACEAE

Sloanea durissima Spruce ex Benth., 287 1
Sloanea cf. *gracilis* Uittien, 1304 7
Sloanea guianensis (Aubl.) Benth., 305 .... 1, 2, 11
Sloanea latifolia (Rich.) Schum., 498 2
Sloanea meianthera Donn.Sm., 351 1
Sloanea pubescens (P. & E.) Benth., 495 .... 2, 4, 8
Sloanea cf. *sinemarensis* Aubl., 283 .... 1, 5, 7
Sloanea spathulata C.E. Smith, 344 1
Sloanea sp.1, 2538 2
Sloanea sp.2, 2053 .... 5, 8
Sloanea sp.3, 374 1
Sloanea sp.4, 1287 7

ERYTHROXYLACEAE

Erythroxylum macrophyllum Cav., 841 5

EUPHORBIACEAE

Aparisthmium cordatum (A.Juss.) Baill., 1545 .... 9, 10, 11
Conceveiba martiana Baill., 950 .... 5, 6, 7
Conceveiba rhytidocarpa Muell.Arg., 744 .... 3, 4, 7
Gavarrettia terminalis Baill., 1681 .... 9, 10
Hevea guianensis Aubl., 377 .... 1, 4, 8
Hieronyma oblonga (Tul.) M.Arg., 970 6
Mabea cf. *maynensis* M.Arg., 2655 3
Mabea cf. *occidentalis* Benth., 775 .... 3, 4
Mabea cf. *pulcherrima* Muell.Arg., 416 2
Mabea cf. *speciosa* M.Arg., 795 .... 5, 6, 7, 8
Mabea subsessilis Pax & Hoffman, 1501 .... 9, 10, 11, 12
Micrandra elata (Diedr.) Muell.Arg., 1504 .... 9, 11, 12
Micrandra spruceana (Baill.) R.E. Schultes, 1412 .... 8, 10
Nealchornea yapurensis Huber, 628 .... 3, 4
Pausandra trianae (M.Arg.) Baill., 301 .... 1, 9, 10, 11, 12
Senefeldera inclinata M.Arg., 1430 8

FLACOURTIACEAE

Carpotroche longifolia (P. & E.) Benth., 612 .... 3, 4
Casearia javitensis H.B.K., 550 .... 1, 3, 4, 8, 9, 10, 12
Casearia pitumba Sleum., 1747 .... 8, 10
Casearia sp.1, 699 .... 3, 4
Laetia procera (P. & E.) Eichl., 773 4
Lindackeria paludosa Benth., 572 .... 3, 4
Ryania speciosa Vahl., 1918 .... 2, 9, 10, 12
Tetrathylacium macrophyllum P. & E., 710 4

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Calophyllum brasiliense Camb., 2562 .... 2, 8
Caraipa tereticaulis Tul., 1468 8
Garcinia macrophylla C. Mart., 928 .... 5, 6, 7
Haploclathra paniculata (Mart.) Benth., 1544 .... 9, 10, 11, 12
Tovomita cf. calophyllophylla Hammel, 1385 .... 8, 10, 11, 12
Tovomita cf. *krukovii* A.C. Smith, 1042 6
Tovomita cf. *laurina* Pl. & Tr., 2503 1
Tovomita cf. *umbellata* Benth., 1648 .... 7, 9, 10
Tovomita sp.1, 422 .... 2, 4, 5, 6
Tovomita sp.2, 1096 .... 6, 8
Tovomita sp.3, 1714 .... 9, 10

Tovomita sp.4, 2652 ... 2, 3, 7
Vismia cf. *sprucei* Sprague, 1973 ... 12
Vismia cf. *tomentosa* R. & P., 1075 ... 6

HIPPOCRATEACEAE

Hylenaea praecelsa (Miers) A.C. Smith, 333 ... 1
Salacia macrantha A.C. Smith, 472 ... 2

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Humiriastrum cuspidatum (Benth.) Cuatr., 1274 ... 7
Saccoglottis guianensis Benth., 2182 ... 7, 9, 10
Saccoglottis sp.1, 688 ... 4
Vantanea sp.1, 522 ... 2

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Discophora guianensis Miers, 2197 ... 7, 9, 12
Emmotum acuminatum (Benth.) Miers, 1503 ... 9, 10

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Lacistema nena Macbr., 1043 ... 6
Lacistema sp.1, 2575 ... 2

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Anaueria brasiliensis Kosterm., 469 ... 2, 3, 4, 6
Aniba megaphylla Mez, 1456 ... 2, 8
Aniba rosaeodora Ducke, 1361 ... 8
Endlicheria citriodora v.d. Werff, 1381 ... 8
Endlicheria formosa A.C. Smith, 2627 ... 3
Endlicheria gracilis Kosterm., 611 ... 3
Endlicheria mishuyacensis A.C. Smith, 1108 ... 6
Endlicheria sprucei (Meissn.) Mez, 1961 ... 5, 12
Endlicheria cf. *tessmannii* O.C. Schmidt, 332 ... 1
Endlicheria cf. *verticillata* Mez, 750 ... 4
Licaria aurea (Huber) Kosterm., 2031 ... 5, 7
Licaria brasiliensis (Nees) Kosterm., 1451 ... 8
Licaria canella (Meissn.) Kosterm., 352 ... 1
Licaria macrophylla (A.C. Smith) Kosterm., 1227 ... 7
Mezilaurus opaca Kubitzki & v.d. Werff, 1213 ... 3, 7
Nectandra cf. *globosa* (Aubl.) Mez, 1153 ... 7
Ocotea aciphylla (Nees) Mez, 2214 ... 2, 5, 6, 7, 12
Ocotea argyrophylla Ducke, 670 ... 4, 12
Ocotea bofo H.B.K., 410 ... 2
Ocotea cernua (Nees) Mez s.l., 748 ... 4
Ocotea costulata (Nees) Mez, 1864 ... 10, 11
Ocotea gracilis (Meissn.) Mez, 331 ... 1, 3, 4
Ocotea leucoxylon (Sw.) de Laness, 1766 ... 9, 10
Ocotea cf. *myriantha* (Meissn.) Mez, 1312 ... 7
Ocotea oblonga (Meissn.) Mez, 302 ... 1
Ocotea olivacea A.C. Smith, 2148 ... 9
Ocotea teleiandra (Meissn.) Mez, 1560 ... 9
Ocotea venenosa Kosterm. & Pinkley, 2734 ... 1, 2, 3, 4
Ocotea sp.1, 777 ... 4
Ocotea sp.2, 555 ... 1, 3
Ocotea sp.3, 1077 ... 6
Ocotea sp.4, 511 ... 2, 5, 12
Ocotea sp.5, 1464 ... 8, 9, 12
Ocotea sp.6, 1207 ... 7

Ocotea sp.7, 1419	8
Pleurothyrium acuminatum v.d. Werff, 822	2, 5
Pleurothyrium brochidodromum v.d. Werff, 1490	8
Rhodostemonodaphne cf. grandis (Mez) Rohwer, 578	3
Lauraceae sp.1, 994	6
Lauraceae sp.2, 1461	8
Lauraceae sp.3, 1914	12
Lauraceae sp.4, 657	4
Lauraceae sp.5, 1234	7
Lauraceae sp.6, 1291	7
Lauraceae sp.7, 2108	6, 7
Lauraceae sp.8, 1948	12
Lauraceae sp.9, 2142	9
Lauraceae sp.10, 1427	8

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Couratari cf. *guianensis* Aubl., 667	4
Eschweilera andina (Rusby) Macbride, 2033	2, 3, 5, 6, 7
Eschweilera cf. *chartaceifolia* Mori, 1276	2, 7
Eschweilera coriacea (DC.) Mori, 464	2, 5
Eschweilera gigantea (Knuth) Macbr., 785	4
Eschweilera cf. *itayensis* Knuth, 846	5, 6
Eschweilera micrantha (Berg) Miers, 754	4
Eschweilera rufifolia Mori, 548	3, 4
Eschweilera tessmannii Knuth, 2604	2, 5, 7
Eschweilera wachenheimii (R. Ben.) Sandw., 295	1, 2
Eschweilera sp.1, 799	5
Eschweilera sp.2, 317	1

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Brownea sp.1, 1579	9
Cedrelinga catenaeformis Ducke, 1127	6
Dialium guianense (Aubl.) Sandw., 2118	3, 7
Dipteryx micrantha Harms, 691	3, 4
Hymenaea oblongifolia Huber, 1293	2, 7
Inga alba (Sw.) Willd., 2711	3, 4
Inga brachyrhachis Harms, 659	3, 4
Inga cf. *coruscans* Humb. & Bonpl. ex Willd., 830	5, 6
Inga lopadadenia Harms, 1080	6, 12
Inga cf. *macrophylla* Humb. & Bonpl. ex Willd., 1081	6
Inga cf. *nobilis* Willd., 404	2
Inga pruriens Poeppig, 2703	4
Inga semialata (Vell. Conc.) Mart., 1896	12
Inga tenuistipula Ducke, 776	2, 4
Inga tessmannii Harms, 627	3
Inga vismiifolia Poeppig, 669	4
Inga yacoana Macbr., 2609	3
Inga sp.1, 1070	6
Inga sp.2, 2128	7
Inga sp.3, 771	4
Macrolobium angustifolium (Benth.) Cowan, 1566	9, 10, 11, 12
Macrolobium cf. *discolor,* 1278	7
Macrolobium limbatum Spruce ex Benth., 930	5, 8, 9, 10, 11, 12
Macrolobium microcalyx Ducke, 658	4, 9, 10, 11
Ormosia coccinea (Aubl.) Jacks., 1616	9
Parkia igneiflora Ducke, 1511	9
Parkia panurensis Benth. ex Hopkins, 1152	7, 10, 12

Pithecellobium basijugum Ducke, 1163 7
Pithecellobium macbridii Barbosa, 2656 3
Pithecellobium nuriensis Irwin, 1506 9
Pithecellobium unifoliolatum Benth., 709 4
Sclerolobium cf. *bracteosum* Huber, 1347 .... 8, 11, 12
Swartzia benthamiana Miq., 1435 .... 8, 10, 12
Swartzia cardiosperma Spr. ex Benth., 1708 .... 5, 10
Swartzia cuspidata Spr. ex Benth., 1270 7
Swartzia pendula Spr. ex Benth., 306 .... 1, 9, 10, 11
Swartzia polyphylla DC., 2563 .... 2, 3, 5, 6, 12
Swartzia racemosa Cowan, 808 .... 5, 6, 8, 12
Swartzia cf. *tessmannii* Harms, 913 5
Swartzia sp.1, 896 5
Swartzia sp.2, 915 5
Swartzia sp.3, 278 1
Swartzia sp.4, 1679 .... 10, 11, 12
Tachigalia multijuga Benth., 1313 .... 5, 6, 7
Tachigalia paniculata Aubl., 1341 .... 8, 9, 10, 11, 12
Tachigalia ptychophysca Spruce ex Benth., 1617 .... 9, 10
Tachigalia sp.1, 2135 .... 4, 8
Taralea oppositifolia Aubl., 1667 .... 10, 11
Vatairea erythrocarpa (Ducke) Ducke, 304 1
Caesalpinioidae sp.1, 1577 .... 9, 12
Caesalpinioidae sp.2, 1768 10
Papilionoidae sp.1, 1594 9

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Hebepetalum humiriifolium (Planch.) Benth., 350 1
Roucheria punctata Ducke, 1666 .... 9, 10
Roucheria schomburgkii Planchon, 1775 10

LOGANIACEAE

Potalia amara Aubl., 1683 .... 9, 10, 11, 12

MAGNOLIACEAE

Talauma sp.1, 590 .... 3, 8

MALPIGHIACEAE

Byrsonima poeppigiana A. Juss., 356 1
Byrsonima stipulina Macbr., 1898 .... 9, 12
Byrsonima sp.1, 1535 .... 9, 12

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Cedrela odorata L., 716 4
Guarea cinnamomea Harms, 645 .... 3, 4, 5, 6
Guarea cristata Penn., 2167 .... 9, 10, 12
Guarea grandifolia DC., 644 .... 1, 3, 4, 8
Guarea juglandiformis Penn., 1126 .... 6, 7
Guarea kunthiana A. Juss., 764 4
Guarea pubescens (Rich.) A. Juss., 1018 .... 4, 6, 7
Guarea trunciflora DC., 868 .... 5, 7
Guarea sp.1, 848 .... 2, 5
Guarea sp.2, 452 .... 2, 9, 12
Guarea sp.3, 2700 4
Trichilia cf. *maynasiana* DC., 1981 5
Trichilia micrantha Benth., 800 .... 5, 6
Trichilia rubra DC., 423 .... 2, 5, 6, 7

Trichilia septentrionalis DC., 361 .... 1, 5, 6, 7
Trichilia sp.1, 740 4

MONIMIACEAE
Mollinedia krukovii A.C. Smith, 680 4
Mollinedia sp.1, 2104 6
Siparuna cristata (P. & E.) DC., 693 .... 3, 4, 6
Siparuna cf. *cuspidata* (Tul.) DC, 2678 .... 3, 4
Siparuna decipiens (Tul.) DC., 1439 8
Siparuna guianensis Aubl., 329 .... 1, 2, 3, 4
Siparuna cf. *micrantha* DC., 2132 8

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Brosimum lactescens (S. Moore) C. Berg, 583 3
Brosimum parinarioides Ducke, 432 2
Brosimum rubescens Taubert, 990 .... 6, 8, 9, 12
Brosimum utile H.B.K., 451 2
Helicostylis cf. *elegans* (Macbr.) C.C. Berg, 2539 2
Helicostylis scabra (Macbr.) C. Berg, 1066 .... 6, 8
Helicostylis tomentosa (P. & E.) Rusby, 608 .... 2, 3
Naucleopsis amara Ducke, 549 .... 3, 4
Naucleopsis imitans (Ducke) C.C.Berg, 433 .... 1, 2, 4, 6, 8
Naucleopsis mello-barretoi (Standl.) C. Berg, 981 .... 6, 7
Naucleopsis ulei Warb., 1459 .... 5, 8
Perebea cf. *mollis* (P.& E.) Huber, 2560 2
Perebea xanthochyma Karst., 765 4
Pseudolmedia laevigata Trecul, 318 .... 1, 2, 4, 5, 7, 8
Pseudolmedia laevis (R.& P.) Macbr., 2103 .... 4, 6
Sorocea muriculata Miq., 382 1
Sorocea pubivera Hemsley, 319 1

MYRISTICACEAE
Compsoneura capitellata (DC.) Warb., 523 .... 1, 2
Iryanthera elliptica Ducke, 1266 .... 1, 5, 7
Iryanthera cf. *juruensis* Warb., 2629 .... 3, 4, 7, 8
Iryanthera lancifolia Ducke, 1399 .... 6, 7, 8
Iryanthera macrophylla (Benth.) Warb., 347 .... 1, 2, 3, 4, 6, 8
Iryanthera cf. *paraensis* Hub., 291 .... 1, 2, 4, 6, 8
Iryanthera polyneura Ducke, 820 .... 5, 6, 11, 12
Iryanthera tricornis Ducke, 485 .... 2, 5, 6, 7
Iryanthera ulei Warb., 832 .... 5, 8, 10, 11, 12
Osteophloem platyspermum (DC.) Warb., 1240 .... 5, 7
Otoba glycycarpa (Ducke) Rodr., 642 3
Virola calophylla Warb., 342 .... 1, 3, 4, 5, 6, 7, 8, 11
Virola decorticans Ducke, 381 1
Virola elongata (Benth.) Warb., 816 .... 5, 6, 7
Virola cf. *flexuosa* A.C. Smith, 606 3
Virola marlenei Rodr., 1272 .... 5, 7
Virola mollissima (DC.) Warb., 2071 6
Virola obovata Ducke, 297 .... 1, 2, 7
Virola pavonis (DC.) Smith, 339 .... 1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12
Virola peruviana (DC.) Warb., 730 4
Virola sebifera Aubl., 853 5
Virola sp.1, 308 1
Virola sp.2, 2621 .... 1, 3

MYRSINACEAE

Cybianthus cf. *peruvianus* (DC.) Miq., 1299 .... 7, 9, 12
Cybianthus resinosus Mez, 1722 .... 10, 12
Cybianthus sp.1, 1239 7
Myrsinaceae sp.1, 1636 9
Myrsinaceae sp.2, 1758 10

MYRTACEAE

Calyptranthes crebra McVaugh, 1943 12
Calyptranthes cf. *longifolia* O. Berg, 734 4
Calyptranthes cf. *speciosa* Sagot., 349 1
Eugenia florida DC., 751 .... 4, 8, 9, 11, 12
Eugenia cf. *macrocalyx* (Rusby) McVaugh, 719 .... 3, 4
Eugenia sp.1, 676 .... 4, 12
Eugenia sp.2, 435 .... 2, 7
Eugenia sp.3, 1873 12
Marlierea caudata McVaugh, 1537 .... 9, 10, 11, 12
Marlierea imperfecta McVaugh, 1692 .... 8, 10
Marlierea cf. *umbraticola* (HBK.) DC., 2109 6
Myrcia cf. *guianensis* (Aubl.) DC., 738 4
Myrcia sylvatica (G. Meyer) DC., 1844 11
Myrcia sp.1, 1776 10
Myrcia sp.2, 1881 .... 5, 12

NYCTAGINACEAE

Neea cf. *divaricata* P. & E., 1589 .... 9, 10, 11, 12
Neea parviflora P. & E., 639 .... 3, 4
Neea cf. *verticillata* R. & P., 668 .... 4, 8, 9, 10, 11, 12
Neea sp.1, 757 4
Neea sp.2, 1580 9
Neea sp.3, 1557 .... 9, 10, 11, 12
Neea sp.4, 1807 .... 9, 11, 12

OCHNACEAE

Ouratea cf. *aromatica* Macbr., 1727 10
Ouratea amplifolia Sleum., 1494 8

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Dulacia candida (Poepp.) Ktze., 1797 .... 3, 7, 9, 11
Heisteria duckei Sleum., 919 5
Heisteria insculpta Sleum., 2625 .... 3, 4
Heisteria nitida Engl., 641 3
Tetrastylidium peruvianum Sleum., 294 .... 1, 3, 5, 6, 7, 10

OLEACEAE

Chionanthus cf. *implicatus* (Rusby) P.S. Green, 2150 9

PIPERACEAE

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Quiina obovata Tul., 303 1

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Anisophyllea guianensis Sandw., 963 5
Sterigmapetalum obovatum Kahlm., 1940 .... 7, 12

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Alibertia hispida Ducke, 1508 .... 9, 10, 11, 12
Amaioua corymbosa H.B.K., 1386 8
Borojoa clariflora (Schumann) Cuatrec., 1955 12
Borojoa patinoi Cuatr., 588 3
Botryarrhena pendula Ducke, 1089 .... 6, 8
Calycophyllum megistocaulon (Krause) Taylor, 782 4
Capirona decorticans Spruce, 565 3
Elaegia cf. *mariae* Wedd., 2037 5
Faramea anisocalyx P. & E., 547 3
Faramea sp.1, 2705 4
Ferdinandusa clorantha (Wedd.) Standl., 1652 .... 9, 10, 11, 12
Ferdinandusa loretensis Standl., 373 .... 1, 2
Hoffmannia sp.1, 1079 6
Ixora panurensis Muell.Arg., 835 5
Kotchubaea sericantha Standl., 1972 12
Ladenbergia amazonensis Ducke, 411 2
Pagamea guianensis Aubl., 1825 11
Palicourea nigricans K. Krause, 2707 .... 3, 4, 7
Pentagonia parvifolia Steyerm., 2710 4
Posoqueria cf. *panamensis* (Walp. & Duchass.) Walp., 1497 .... 1, 6, 8
Remijia ulei Krause, 1273 7
Remijia peruviana Standl., 917 5
Rudgea fissistipula M.Arg., 1724 .... 8, 10
Rudgea cf. *loretensis* Standl., 546 3
Simira cf. *pisoniiformis* (Baill.) Steyerm., 2676 4
Simira sp.1, 704 4
Warscewiczia coccinea (Vahl) Kl., 629 3

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Adiscanthus fusciflorus Ducke, 1543 .... 9, 10, 11, 12
Galipea sp.1, 610 .... 3, 4
Ravenia biramosa Ducke, 1576 .... 9, 10, 11

SABIACEAE

Ophiocaryon heterophyllum (Benth.) Urban, 937 .... 5, 6, 7, 8, 9
Ophiocaryon klugii Barneby, 654 .... 3, 4

SAPINDACEAE

Cupania sp.1, 1470 8
Matayba inelegans Spr. ex Radlk., 1362 .... 8, 9, 10, 11, 12
Matayba macrocarpa Gereau, 1284 .... 5, 7
Matayba sp.1, 1612 .... 9, 12
Talisia sp.1, 2603 2

SAPOTACEAE

Chrysophyllum bombycinum Penn., 823 .... 5, 6, 8, 11, 12
Chrysophyllum cf. *colombianum* (Aubl.) Penn., 310 1
Chrysophyllum manaosense (Aubl.) Penn., 1620 .... 9, 10, 11
Chrysophyllum cf. *prieurii* DC., 1828 .... 9, 11, 12
Chrysophyllum sanguinolentum (Pierre) Baehni, 852 .... 5, 8, 9, 10, 11, 12
Chrysophyllum sp.1, 1562 .... 9, 10
Ecclinusa guianensis Eyma, 805 5
Ecclinusa lanceolata (M. & E.) Pierre, 951 .... 4, 5
Micropholis egensis (DC.) Pierre, 1739 10
Micropholis guyanensis (DC.) Pierre, 341 .... 1, 5, 6, 7, 10, 11
Micropholis madeirensis (Baehni) Aubr., 1963 12

Micropholis cf. *obscura* Penn., 1635	9, 10, 11, 12
Micropholis porphyrocarpa (Baehni) Monachino, 1120	6
Micropholis sanctae-rosae (Baehni) Penn., 620	3
Micropholis venulosa (M. & E.) Pierre, 1533	9, 10, 11, 12
Pouteria caimito (R. & P.) Radlk., 837	5, 6
Pouteria cuspidata (DC.) Baehni, 646	3, 4, 5, 6, 9, 10, 11, 12
Pouteria cf. *deliciosa* Penn., 1302	7
Pouteria durlandii (Standl.) Baehni, 321	1
Pouteria filipes Eyma, 724	4
Pouteria cf. *hispida* Fynn., 798	5, 9, 11, 12
Pouteria lucumifolia (Reisseck ex Max) Penn., 1551	9, 10, 11, 12
Pouteria oblanceolata Pires, 1588	9, 11
Pouteria putamen-ovi Penn., 505	2, 3, 7, 12
Pouteria reticulata (Hub.) Baehni, 1170	7
Pouteria torta (Mart.) Radlk., 478	2, 4, 5, 7
Pouteria trilocularis Cronq., 2671	4
Pouteria sp.1, 2578	2
Pouteria sp.2, 703	4
Pouteria sp.3, 2146	9
Pouteria sp.4, 1772	10
Pradosia cf. *cochlearia* (Lecomte) Penn., 1755	8, 10
Sapotaceae sp.1, 1326	8
Sapotaceae sp.2, 1641	9
Sapotaceae sp.3, 475	2
Sapotaceae sp.4, 1858	9, 11
Sapotaceae sp.5, 2106	6
Sapotaceae sp.6, 2638	3

SIMAROUBACEAE

Simaba sp.1, 399	1
Simaba sp.2, 2509	1
Simaba sp.3, 1682	10

STERCULIACEAE

Sterculia frondosa Rich., 1069	4, 6
Sterculia killipiana E. Taylor, 2577	2, 7
Sterculia peruviana (Simpson) Taylor, 714	4
Sterculia sp.1, 633	3
Theobroma obovatum Kl. ex Bern, 2630	3
Theobroma subincanum Mart., 441	2, 6

THEACEAE

Ternstroemia klugiana Kobuski, 1749	10, 11, 12

TILIACEAE

Luehea sp.1, 2112	6

ULMACEAE

Ampelocera edentula Kuhlm., 690	3, 4

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Leonia crassa Smith & Fernandez, 652	3, 4
Leonia glycicarpa R. & P., 280	1, 2, 4, 6
Rinorea flavescens (Aubl.) Ktze., 312	1, 2
Rinorea lindeniana (Tul.) Ktze., 736	4
Rinorea racemosa (Mart.) Ktze., 825	5, 7

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sp.1, 2222	11, 12