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Using checklists and collections data to investigate plant diversity: II. An analysis of five florulas from northeastern South America

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ABSTRACT—Five plant checklists from areas on and adjacent to the Guiana Shield were analyzed and used to test hypotheses of the salient properties of the flora of northeastern South America. Newly available checklists of Iwokrama, Mabura Hill, and Kaieteur Falls (all three in Guyana), Central French Guiana, and Reserva Ducke near Manaus, Brazil were compiled and their nomenclatural synonymies standardized. Data from checklists provide an attractive alternative to transect or plot data because they are based on rigorously determined plants of all habit types rather than the sterile vouchers of tree species often used in plot or transect studies. Descriptive data were compiled from the checklists regarding diversity, overlap, and endemism. Ranking of diversity at the family level was subjected to Kendall's coefficient of concordance of ranks test and Spearman rank correlation coefficients to evaluate similarities among the five sites. A UPGMA dendrogram was created from data for the presence or absence of species shared by two or more sites. The results indicate strong similarity among the three sites in Guyana and between Central French Guiana and Reserva Ducke, supporting a model of plant distributions determined by the presence or absence of sandstone or white sands rather than disjunct between the Roraima sandstone formation ("Guiana Highland") and other areas of the Guiana Shield. Relatively little overlap was found even between adjacent areas with ostensibly very similar abiotic environments, indicating that plant diversity will not necessarily be protected by conserving representative areas selected on the basis of general characteristics.

INTRODUCTION

How may the abundant data available from plant collections in herbaria be used to refine concepts of regional patterns of floristic diversity in northern South America? This question has obvious implications for biogeography in general and conservation in particular. However, synthesis of data from plant collections has been hampered by the lack of comprehensive and uniform data. The paucity of information regarding the diversity and distribution of plant species in this region has frustrated attempts to make a historical and ecological synthesis that accounts for observed floristic patterns. Concepts such as the Pleistocene refugia hypothesis (Haffer 1969; Whitmore & Prance 1987) have been criticized because centers of plant diversity and endemism may, in fact, be artifacts of uneven collecting activity (Nelson et al. 1990). Therefore, any attempt to apply collections data to rigorous analyses of patterns of plant diversity must overcome limitations arising from the qualitative and incomplete nature of these data. Data taken from transects, for instance, are popular because transects may be sampled in locations selected to provide the most applicable data, essentially all of the plant diversity along a transect may be sampled, and quantitative data may be collected such as basal area, relative density and dominance, and importance values (Balslev & Renner 1989; Balslev et al. 1987; Gentry 1988a, b). Data from transects, however, have limitations because of the difficulty of determining the identity of the mostly sterile plants encountered on any given transect. Tuomisto (1998) attempted to overcome this limitation by sampling only pteridophytes and Melastomataceae, which could be unambiguously and thoroughly sampled along transects in the upper Amazon and used as an indicator of general floristic patterns. This approach, however, although more rigorous and repeatable than those relying on determinations of sterile vouchers, is limited by being a fragmentary view of only a very small subset of the total diversity in any given area. Terborgh & Andresen (1998) used data from 48 one-hectare plots across Amazonia to study floristic patterns; their study is limited because, like most others using plots or transects, only trees above a certain size class ($\geq$ 10 cm dbh) were used. Further, their analyses were limited by being largely based on family-level determinations of individual trees in the plots. General plant collections made as part of flora and monographic projects have been underutilized

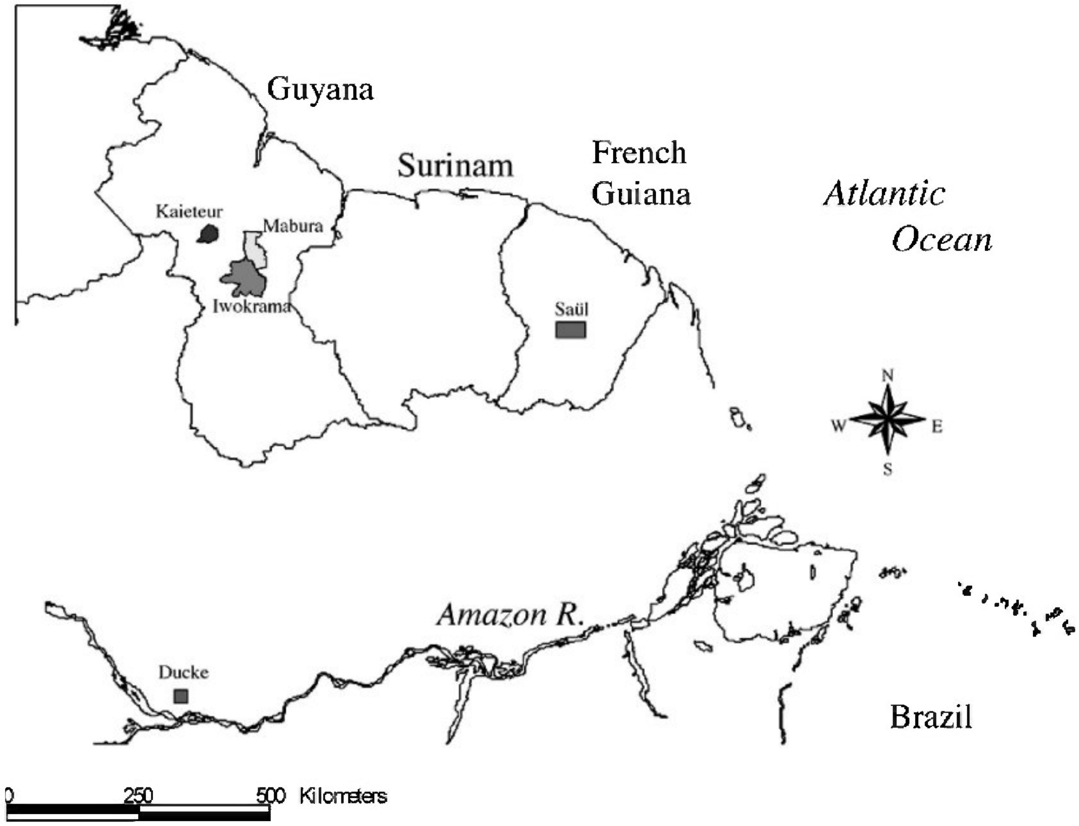

Fig. 1. Map of northeastern South America showing the location of the five florulas.

in studies analyzing patterns of plant diversity. While the regional and continental floras and monographs that will be the full fruition of these projects may be decades away, sufficient progress has been made on a number of local florulas (a plant inventory of a limited geographic area) in northeastern South America to allow for the development of hypotheses concerning floristic gradients and their ecological and historical correlates.

Thus, although a complete flora of the Guianas or Brazil cannot be expected in the near- or medium-term and the *Flora Neotropica* has an estimated completion time of 300 years (Mori 1992), five checklists of floras of restricted areas on and proximate to the Guiana Shield have recently been made available. They may be used as proxies for regional floras to answer questions concerning the composition and dynamics of the flora of a significant portion of the Guiana Shield in its ecological, geographical, and historical context (Fig. 1). Three of these five areas are in Guyana: the Iwokrama International Centre for Rain Forest Conservation and Development (hereafter Iwokrama Forest; Clarke & Funk 1998; Clarke et al. 2001), Mabura Hill (Ek & ter Steege 1997), and Kaieteur Falls National Park (Kelloff & Funk 1998). A comprehensive checklist is also available for Central French Guiana (Mori et al. 1997, 2002) and a checklist has been produced for Reserva Ducke near Manaus, Brazil (Ribeiro & Hopkins 1999). A complete, synonymized checklist of all five areas is found in Clarke et al. (2001). Iwokrama Forest and Mabura Hill are characterized by low elevation (generally less than 100 meters above sea level (m asl), but Iwokrama has an isolated mountain range rising to 1000 m asl) and both sandstone- and granite-derived soils. Central French Guiana is very similar except that sandstone and white sands are absent. Reserva Ducke is also characterized by low elevation, but is in Amazonia proper and is not part of the Guiana Shield. Kaieteur Falls National Park is located at mid-elevation (500 m asl) on the edge of the Pakaraima escarpment and is dominated by sand substrates associated with the Roraima sandstone formation. These areas and their associated checklists have features that make them appropriate for floristic comparisons on a regional scale: 1) the area of coverage of each flora is discrete, ranging from 10,000 to 360,000 hectares (ha); 2) they occupy positions and contain habitats that span significant geographic and ecological gradients of the

Guiana Shield and immediate environs; 3) the level of collecting intensity in each area is documented and can be compared with a view toward assessing the relative completeness of each of the checklists; 4) the areas are relatively well characterized regarding environmental variables of precipitation, soils, climate, and topography (Kelloff & Funk 2004); 5) human disturbance in the areas is low or absent, allowing for inferences to be drawn from an essentially pristine flora; and 6) these five areas are fairly uniform regarding all but two of their environmental parameters (soils and topography), allowing for the exclusion of differences in factors such as climate and precipitation as possible confounding factors when attempting to explain observed differences.

Comparisons made here among the five checklists have the goal of testing a number of salient and, in some cases, competing hypotheses that have been proposed for the flora of the Guiana Shield: 1) the Guiana Shield overall represents a center of endemism of the neotropical flora (Berry et al. 1995); 2) there exists a Guiana Lowland center of endemism that complements the better-known Guiana Highland center of endemism (Mori 1991); 3) that endemic elements of the flora of the Guiana Shield should more properly be considered to be those associated with sand and sandstone substrates ("psammophilous") rather than high elevation per se (Kubitzki 1989, 1990); 4) that certain plant families should be over-represented in each of the florula areas in comparison to the regional flora (Boggan et al. 1997) because of their emergent ecological properties, e.g. Fabaceae in lowland forests and Bonnetiaceae in the Guiana Highlands (Ek & ter Steege 1997).

Predictions based on these hypotheses for the data from the checklists include:

If there is a Guiana Lowland floristic province, the three florulas on the Guiana Shield, but not those associated with the escarpment of the Roraima Formation (Mabura Hill, Iwokrama, and Central French Guiana) should share a greater number of species than, for example, Kaieteur, Mabura, and Iwokrama or Iwokrama, Mabura, and Reserva Ducke. As a corollary, the three Guyanan florulas (Iwokrama, Mabura, and Kaieteur), though in close geographic proximity, should not share a greater number of species than other sets of three florulas;

-the existence of an endemic psammophilous flora would predict a high number of species shared among the three areas that have extensive white sand and sandstone habitats, viz., Kaieteur at mid-elevation and Mabura and Iwokrama at low elevation. The competing hypothesis of an endemic Guiana Highland flora, i.e., one centered on the upland tepui habitats of the Roraima sandstone formation, predicts that the flora of Kaieteur would share very little of its diversity with these two, or other, areas;

-the existence of a flora that is endemic to the Guiana Shield overall predicts that the florula of Reserva Ducke would share the least number of species with any other of the five florulas.

MATERIALS AND METHODS

Checklists of the floras were obtained for Kaieteur Falls National Park (Kelloff & Funk 1998), the Iwokrama Forest (Clarke & Funk 1998), Mabura Hill (Ek & ter Steege 1997), and Reserva Ducke (Ribeiro & Hopkins 1999). The checklist of the flora of Central French Guiana was taken from the website maintained by S. Mori (www.nybg.org/bsci/french_guiana/Families.html). To make the data from these five checklists more comparable, only native, vascular plants have been used in this analysis and only determined species were used in the combined checklist, i.e. varieties or subspecies were pooled into a combined record of the species. Species recognized as distinct but indeterminate (e.g. *Pouteria* sp. "A" or *Licania* sp. "1,2,3") were excluded except where that record constituted the only record of that genus for a given site. In that case, the record was maintained as an undetermined, unique species of that genus. These checklists were reconciled with respect to their synonymies and authorities and compiled into a combined checklist covering all five flora areas. The combined checklist is presented as a separate publication (Clarke et al. 2001). Data for the five flora areas was compiled to detail the physical characteristics and habitat diversity in each area; they are presented below for each area in succession.

Iwokrama Forest

Iwokrama Forest is located in central Guyana between 04°–05°N and 58.5° and 59.5°W, occupying a total of 360,000 ha. The elevation ranges from 65 to 1000 m asl, but is for the most part low with the exception of the isolated granitic massif of the Iwokrama Mountains (1000 m) and doleritic intrusions in the Pakutau Hills and Turtle Mountain (400 and 300 m asl, respectively). Aside from these three upland areas, the topography is relatively flat although very limited local relief associated with incised streambeds may shift the balance between terra firme and seasonally or permanently flooded forest. Levees associated with the three major rivers (Essequibo, Siparuni, and Burro Burro) are responsible for seasonally flooded forests occurring up to several kilometers from rivers. Although meteorological data are lacking, rainfall in Iwokrama Forest probably averages between 2500 and 3000 mm per year based on interpolation from surrounding areas. Soils are predominantly brown and white sands and laterite and are well-drained except in areas near streambeds or rivers and in a few limited areas where a clay hardpan occurs near the surface.

Mabura Hill

The checklist of the flora of Mabura Hill lists plants collected near the town of Mabura Hill in Central Guyana (5°13′N, 58°48′W) about 15 km N of a 900 ha ecological reserve maintained by the Tropenbos Foundation (Wageningen, The Netherlands). Although Ek & ter Steege (1997) list the flora area as 10,000 ha, specimens were collected throughout the 220,000 ha Demerara Timbers Ltd. concession which is centered around the town of Mabura Hill. Mabura Hill is the only one of the five sites that has experienced human disturbance of any significant magnitude. This disturbance, resulting from wide-scale, selective, commercial logging, certainly altered the flora quantitatively (for the most part after the plant collecting activities associated with producing the checklist took place) but, has had no qualitative effect on the flora since probably neither extinction nor invasion of exotic species has occurred with increased frequency. Elevations in this area are uniformly low, ranging from 50–425 m asl and rainfall is estimated at 2700 mm per year (Brouwer 1996). Soils are of white and brown sands with some laterite and are for the most part well-drained except in low areas or in association with the two major rivers, the Demerara and Essequibo (Kekem et al. 1996).

Kaieteur National Park

The Park is located at 5°10′N, 59°29′W in north-central Guyana where the Potaro River descends from the escarpment of the Pakaraima Mountains to the lowlands, forming Kaieteur Falls which, at 226 m, is the highest sheer drop waterfall in the world. Kelloff & Funk (1998) state that historically the Park had an area of 58,000 ha. Although its size has recently been expanded, the coverage area of the flora does not extend beyond 58,000 ha. Although elevations within the Park range from 150 m in the gorge below the falls to 500 m around the falls, most collections were made above the falls because access to the gorge is difficult. The topography is dominated by features of the Roraima sandstone formation, which is relatively flat and forms numerous sandstone outcroppings. Soils, where they develop, are white sands and drainage varies depending on slope and proximity of the relatively impervious sandstone layers. Annual precipitation is approximately 3000 mm.

Central French Guiana

Coverage area of this flora is 140,000 ha bounded by 3°30′–3°45′N and 53°00′–53°28′W in the headwaters of the Mana, Approuague and Lawa/Maroni Rivers and centered on the village of Saül. The topography of this area is varied, but mostly dominated by granite of the Guiana Shield, and elevations are mostly low, about 200 m asl with a maximum of 760 m asl. Rainfall is approximately 2500 mm per year. Soils in the area are brown sands and laterite; white sands are absent.

Reserva Ducke

The reserve is located on the outskirts of Manaus, Brazil at 2°53′S, 59°58′W and occupies 10,000 hectares. The topography is relatively flat and the elevation is low (ca. 60 m). Sand terraces associated with the ancient Amazon riverbed provide limited local relief. Rainfall averages 2000 mm per year and soils are either white or brown sands and are for the most part well drained.

Descriptive data were extracted from the combined checklist regarding the species diversity of individual sites, overall diversity, and overlap of this diversity between sites. Further, the five sites and the Guianas overall (Boggan et al. 1997) were compared with regard to the rank of the twenty most diverse families at the species level and the percentage of the total flora of each site contained in the twenty most diverse families from the regional checklist. Data from the regional checklist (Boggan et al. 1997) were included to show deviation in floristic composition at the family level for the five sites from the more comprehensive, regional flora.

A Kendall's coefficient of concordance of ranks test (Sokal & Rohlf 1995) was performed on the rank of species diversity for the five sites plus the Guianas overall to test agreement among the six rankings of family diversity. Spearman rank correlation coefficient tests (Sokal & Rohlf 1995) were performed between all fifteen combinations of the five sites as well as the Guianas overall to test for significance of correlations in rankings between the sites. Clustering by the unweighted pairgroup method, arithmetic average (UPGMA; Rohlf 1994) was used to create a phenogram indicating the relative similarities of the florulas. To correct for biases introduced by disparities in the sizes of the florulas, only the 1691 species present at two or more of the five sites were input into a matrix listing each of these species as present (1) or absent (0) at each site. These binary data were then used to create a similarity matrix with simple matching coefficients which was subsequently used to create the dendrogram.

Table 1. Species diversity of the five florulas. Diagonal: Number of unique species/total number of species. Above diagonal: Number of uniquely shared species/number of shared species.

Total = 4659	Iwokrama	Mabura	Kaieteur	Central French Guiana	Ducke
Iwokrama	312/1251	116/545	71/383	135/589	40/370
Mabura		255/1240	63/405	132/627	51/422
Kaieteur			438/1134	73/416	41/275
Central French Guiana				835/2069	227/658
Ducke					1047/1922

RESULTS

The combined checklist contains 4790 species: 1175 at Iwokrama, 1245 at Mabura Hill, 1060 at Kaieteur, 2073 in Central French Guiana, and 2085 in Reserva Ducke. These totals along with figures of endemism and overlap of the species are presented in Table 1.

The twenty most diverse families from Boggan et al. (1997) account for approximately 75% of the total species diversity in the combined checklist, so conclusions drawn from data from these families may be expected to reflect properties of the entire flora. The Kendall's coefficient of concordance of ranks test was highly significant ($\chi^2_r = 82.6801$, p < 0.001) indicating strong disagreement among the rank order of the twenty most diverse families across the five sites and the Guianas. Table 2 shows these twenty most diverse families with the total number and rank order of number of species in each of these families. Spearman rank correlation coefficients for all pairwise comparisons of rankings of the twenty most diverse families at the five sites and the Guianas overall are listed in Table 3. Lower, non-significant correlation coefficients were found in comparisons of Kaieteur with Mabura Hill (0.3093), Reserva Ducke (0.0685), and Central French Guiana (0.2425) as well as the Guianas overall with Mabura Hill (0.2794), Central French Guiana (0.2889), and Reserva Ducke (0.1918).

The UPGMA dendrogram (Fig. 2) shows that, in relative terms, Central French Guiana and Reserva Ducke are most similar floristically, Iwokrama and Mabura Hill next most similar, that the flora of Kaieteur Falls is related to those of Mabura Hill and Iwokrama, and that these three florulas are more

Table 2. Kendall's coefficient of concordance of ranks test of the 20 most diverse families from Boggan et al. (1997) for the five florulas and the Guianas.

	Iwokrama	Mabura	Central French Guiana	Kaieteur	Ducke	Guianas
Fabaceae	103 (1)	114 (1)	136 (2)	66 (3.5)	192 (1)	742 (1)
Rubiaceae	81 (2)	60 (3)	127 (3)	72 (2)	85 (5)	506 (3)
Orchidaceae	51 (3)	110 (2)	150 (1)	111 (1)	92 (3)	701 (2)
Cyperaceae	42 (4)	22 (15)	27 (19)	43 (6)	22 (17)	303 (6)
Myrtaceae	36 (5)	35 (5.5)	76 (4)	66 (3.5)	80 (6)	324 (5)
Poaceae	34 (7)	20 (17)	38 (12)	52 (5)	21 (18)	374 (4)
Araceae	32 (8.5)	23 (13.5)	57 (5)	18 (12)	50 (10.5)	139 (10)
Lauraceae	32 (8.5)	28 (9.5)	51 (7)	8 (17)	96 (2)	129 (16)
Annonaceae	30 (10)	30 (7)	29 (17)	7 (18)	62 (7)	126 (17)
Chrysobalanaceae	29 (11)	35 (5.5)	35 (13.5)	20 (10.5)	50 (10.5)	134 (13)
Euphorbiaceae	25 (12)	25 (11)	46 (8.5)	15 (14)	46 (12)	191 (7)
Sapindaceae	23 (13)	24 (12)	42 (11)	6 (19.5)	40 (15)	122 (18)
Apocynaceae	20 (14)	29 (8)	35 (13)	23 (9)	41 (14)	134 (13)
Piperaceae	18 (15.5)	17 (19.5)	46 (8.5)	9 (16)	34 (16)	108 (20)
Bignoniaceae	18 (15.5)	37 (4)	43 (10)	17 (13)	45 (13)	132 (15)
Asteraceae	16 (17.5)	17 (19.5)	26 (20)	20 (10.5)	11(20)	159 (9)
Sapotaceae	16 (17.5)	28 (9.5)	55 (6)	6 (19.5)	87 (4)	115 (19)
Clusiaceae	15 (19)	23 (13.5)	28 (18)	25 (8)	53(9)	138 (11)
Bromeliaceae	7 (41)	20 (17)	33 (15)	33 (7)	17 (19)	134 (13)

Table 3. Spearman rank correlation coefficients test of the rank of the twenty most diverse families in the five florulas and the Guianas overall. H_0: $\rho_s = 0$; H_1: $\rho_s \neq 0$, r_s indicated for each comparison. Nonsignificant r_s values underlined.

	Mabura	Kaieteur	Central French Guiana	Ducke	Guianas
Iwokrama	0.4531	0.4772	0.4644	0.5004	0.7054
Mabura		0.3093	0.6081	0.7171	0.2794
Kaieteur			0.2425	0.0685	0.8371
Central French Guiana				0.6417	0.2889
Ducke					0.1918

similar to each other than they are to the floras of Central French Guiana and Reserva Ducke.

DISCUSSION

Sources of Error

Bias may have been introduced in this study at any of three points: 1) selection of sites for comparison, 2) during plant collecting at each site, and 3) in the identification of plant specimens. Therefore, conclusions drawn from this study rest on the following assumptions: 1) that the five florulas are equally well sampled and that collecting methods at each site were equally successful in sampling plant diversity, 2) that all of the florulas are equivalent in size, 3) that differences in the sizes of coverage areas of the florulas do not result in significant differences in the sizes of the florulas, and 4) that determinations and synonymies have equal accuracy and precision for all five florulas.

The number of plant collections providing the basis for the florulas vary from 3,887 collections of 1,075 species from Iwokrama to 12,847 collections of 2,073 species from Central French Guiana. That Central French Guiana, at 140,000 hectares, is less than half the size of Iwokrama's 360,000 hectares leads us to believe that plant collecting at Iwokrama has been insufficient to thoroughly sample the flora. In the absence of more objective criteria, this conclusion must be drawn on the assumption that alpha diversity does not vary greatly between the two sites. Oliveira and Mori (1999) and Oliveira & Daly (1999) however, indicate a mechanism by which Reserva Ducke and the Manaus area may have enriched alpha diversity resulting from being in the contact zone among putative Tertiary and Quaternary refugia, the Guiana Shield among them. Thus, the high diversity of Reserva Ducke in proportion to its size (2,085 species in 10,000 hectares) compared with the other four sites, in addition to being an artifact of greater collecting intensity, may also

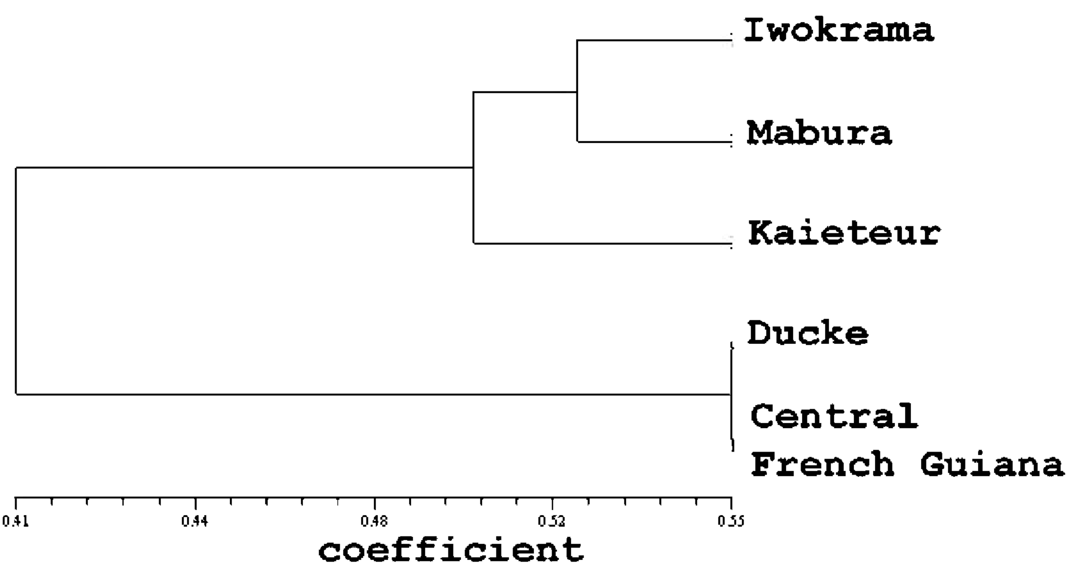

Fig. 2. UPGMA dendrogram showing relative similarity of the five florulas.

be an indication of higher actual diversity per unit area.

Endemism and Overlap of the Florulas

The results of this study indicate remarkably little overlap of the combined flora of the five areas. Between 25 percent (at Mabura Hill) and 59 percent (at Reserva Ducke) of the species are found at only a single site in the combined checklist. Further, even Iwokrama and Mabura Hill, which share a common boundary, share only 513 species or less than half of each of their plant diversities. This may be a conservative estimate of the proportion of the flora shared by the two sites, given that the two areas are undersampled and that widespread and common taxa have almost certainly been oversampled compared with the uncommon, endemic, or patchily distributed species that, when sampled, would decrease our estimate of the percentage of the flora shared by Iwokrama and Mabura Hill. This strong indication of floristic heterogeneity occurs in the virtual absence of environmental gradients (soils, topography, temperature, precipitation, elevation). It has important implications for conservation efforts in the region, because we cannot assume that conservation efforts in Iwokrama, which is protected at present, also preserves the plant diversity of even very similar adjacent areas such as Mabura Hill, which is now very seriously threatened by widescale logging. Additional collecting and soils and habitat mapping are needed in both Mabura and Iwokrama to obtain a more refined understanding of species overlap.

Models of Elevational and Edaphic Endemism

The inclusion of Kaieteur Falls, which is a classic example of the escarpment forming the border of the Roraima sandstone formation, with the other largely low elevation areas from the Guiana Shield (Iwokrama, Mabura Hill, and Central French Guiana) in this study allows for testing of competing hypotheses of elevational or landform ("Guiana Highland," Maguire 1979) and edaphic ("psammophilous," Kubitzki 1989 and 1990) models of endemism for the Guiana Shield. Our study indicates that Kaieteur Falls shares approximately one third of its flora with the two nearby low elevation areas in Guyana, Iwokrama and Mabura Hill (318 and 349, respectively, of its 1065 species). Further, the UPGMA dendrogram indicates a similarity coefficient greater than 0.5 among these three areas and a high similarity in the composition of their floras. Also, the Central French Guiana and Reserva Ducke florulas were not found to be very similar to that of Kaieteur. That these two areas lack sandstone substrates but have elevations similar to Iwokrama and Mabura Hill indicates that the endemic flora of the Guiana Highland should more properly be considered as an endemic flora of white sand and sandstone substrates rather than one determined by elevation or landform per se. It is important to note that elevations in the Guiana Highland, particularly in Guyana, are often relatively low (500 m asl, for instance, in the example of Kaieteur) and that lowland areas in the Guiana Shield are frequently punctuated by massifs of moderate elevation (1000 m asl in the case of the Iwokrama mountains). It is therefore not surprising that elevation turns out to be a confounding factor in explaining the distribution and endemism of the flora in this region.

Geographic Endemism, Centripetal and Centrifugal Models of Dispersal of Plants of the Guiana Shield

Mori (1991) argues for the existence of an endemic Guiana Lowland flora to complement that of the Guiana Highland. The basis of the argument is abundant evidence for the existence of a rainforest refugium across the entire Guiana Shield rather than just in the Guiana Highland throughout the Tertiary and Quaternary. This refugium would have resisted both marine and savanna incursions resulting from global climatic fluctuations. This hypothesis predicts strong similarities among the floras of the three low elevation areas of the Guiana Shield, (Iwokrama, Mabura, and Central French Guiana), and strong dissimilarities between both Reserva Ducke and Kaieteur on the one hand and any of the other florulas on the other. That the UPGMA dendrogram of our study indicates a strong similarity between the floras of Central French Guiana and Reserva Ducke and relatively little similarity between those of Reserva Ducke and the other two low elevation Guiana Shield areas, Iwokrama and Mabura Hill, is an indication that Central French Guiana has been relatively porous to centripetal migration of floristic elements from Amazonia proper onto the Guiana Shield. That the floras of Iwokrama and Mabura Hill, though geographically closer to Reserva Ducke than Central French Guiana, have resisted this centripetal dispersal may possibly be attributed to the existence of white sand soils in these areas and the importance of competitive exclusion by those taxa adapted to sterile substrates of invading species with more general edaphic and nutrient requirements. Further testing of these ideas will be accomplished by integrating data from other collections into the existing data set. In particular, the 8000 collections made by the senior author in southern Guyana south of Iwokrama and Mabura Hill, an area that, like Central French Guiana, lacks white sand soils, may help to document the transition between areas with a fundamentally Hylaean or Amazonian flora, such as Reserva Ducke, to that of a genuinely Guianan flora, such as Iwokrama, Mabura, and Kaieteur.

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