



Phytogeography of the Kaieteur Falls, Potaro Plateau, Guyana: floral distributions and affinities

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ABSTRACT

Aim The plant diversity of one location on the Guiana Shield, Kaieteur National Park in Guyana, is used to examine the various hypothesized origins of the flora and to evaluate which may best explain the current plant distributions.

Location Kaieteur National Park is located on eastern edge of the Potaro Plateau in central Guyana, South America. The species examined have distributions that vary from local to global.

Methods The distribution patterns of the families, genera and species known from Kaieteur are examined using generalized distribution patterns.

Results Data on distribution patterns, elevation and habitat were gathered from 131 flowering plant families, 517 genera and 1227 species. These plants represent all taxa that are currently known to occur in the area of the original Kaieteur National Park. Families tend to have cosmopolitan or pantropical distribution, genera are mostly neotropical and at the species level, most species are restricted to the Guiana Shield (c. 40%), northern South America (69%) or neotropical (96%) in distribution, each level inclusive of the previous.

Conclusions The flora at the study site in Kaieteur National Park has its strongest affinity with the Guiana Shield; 42.1% of the species have a distribution that corresponds with the Shield or is more restricted within the Shield. There is a distinct flora on the Guiana Shield and its affinities lie with the flora of northern South American and beyond that, the neotropics. The flora is not closely affiliated with the floras of the Brazilian Shield, the Amazon, the Andes, the eastern coastal forests of Brazil, southern South America, or Africa as has been previously suggested.

Keywords

Plant distributions, flora affinities, biogeography, Guyana, Kaieteur, Guiana Shield.

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INTRODUCTION

There are many historical factors that influence the distribution of taxa, ranging from the movements of the tectonic plates which cause significant changes in the terrain and climate of many ancient habitats, to Pleistocene climatic changes which contributed to recent plant diversification. In addition, habitat characteristics, such as hydrology, topography and soil types, as well as ecological factors such as pollinators, competition and hybridization have played important roles in producing present-day phytogeographical patterns (Forero & Gentry, 1988). Dispersal ability plays a crucial role as well, with

well-documented cases such as the flora of the Hawaiian Islands where dispersal agents have travelled thousands of miles to colonize the archipelago (Funk & Wagner, 1995), while other plant offspring disperse no farther than the base of the parent plant (e.g. Brazil nuts). All of these factors must be considered when seeking to understand the distribution patterns of any specific organism. However, when examining an entire flora, one can establish whether or not there are any repeating distribution patterns. In order to do that, we must first understand the history of the area in question.

Geologically, South America was once part of the proto-continent of Gondwana. Geographical matching, involving

structural trends of the rocks and minerals, as well as characteristics of rock belts juxtaposed on both coasts, indicates that South America was once attached to Africa. For instance, pieces of African craton, which are ancient continental blocks 2 billion years old, left stranded on the coast of Brazil, have been matched where the two coasts once joined (Hurley, 1979). On the north-eastern shoulder of South America lies an ancient geological province that underlies the area now known as the Guiana Shield (Fig. 1). The rock basement of the Shield is composed of metamorphic and igneous rock that formed during repeated tectonic-thermal events (Huber, 1995a). Depending on what areas are included the size of the Guiana Shield varies. One estimate is *c.* 1,00,000 km² (Gansser, 1954; Fairbridge, 1975). During the Cretaceous period, this igneous-metamorphic basement was covered with layers of sand that were compressed and fused into what is now known as the Roraima Formation. Current theories suggest that the source of the Roraima sediments originally came from the present basins of the Congo and Niger rivers of Africa (Maguire, 1979) when Africa and South America were still part of Gondwana (Hurley, 1979). Ripple marks frequently found on freshly exposed rock surfaces of the Roraima sandstone indicate that the sediments were laid down as a marine or brackish water deposit (Gibbs & Barron, 1993; Huber, 1995a). Through years of erosion cycles, vast portions of the Roraima sandstones have eroded leaving behind the spectacular tabletop mountains or tepuis found in the Venezuelan Guayana and the Pakaraima Mountains of Guyana.

The Guiana Shield is divided into several political regions: the Venezuelan Guayana (mostly the states of Bolívar and Amazonas), Guyana, Surinam, French Guiana, part of northern Brazil, and the south-eastern corner of Colombia.

Historically, sections of the Shield may have several names (Berry *et al.*, 1995a) depending on the country and geopolitical influences. Most of these names do not include the outlying areas especially in Colombia. The term Guiana Shield is used in this study to reflect the area delimited in Fig. 1. This is the main or core area of the Shield. Small areas of eastern Ecuador and parts of Peru and Bolivia have been proposed as a component of the Guiana Shield because they contain disjuncts, but these areas are not well enough defined to be able to distinguish between what part of the flora was the Shield and what is Andean or Amazonian so they have been excluded from this study. Guayana Highland was a term adopted by Bassett Maguire to refer to the upland area of the Shield characterized by the eroded sandstone of the Roraima sediments (Maguire, 1970). It comprises parts of southern Venezuela, western Guyana, Brazil and Colombia. To the east, where the Roraima area in Guyana is known as the Pakaraima Mountains, the sandstone sediments gently rise westwardly from *c.* 400 m and are studded with flat topped mesas from the Merumé Mountains at 1500 m to Mt Ayanganna (2020 m) and Mt Roraima (2730 m). The Roraima sandstone of Venezuela is mainly discontinuous and forms many mesas over 2000 m in altitude with the highest point, Cerro de la Neblina at 3085 m. Today the term Guayana Highland is commonly applied to the Venezuelan portion of the Roraima sandstone, but in all of the high elevation areas, no matter where they are found, flat topped mountains over 1500 m are often called tepuis (Huber, 1995a).

According to legend, the name Guiana is derived from an Amerindian word for water and the Guiana Shield is true to its designation as the 'land of many waters'. The Shield is divided into several drainage complexes or watersheds that are hydrologically defined and separate areas (Maguire, 1979).

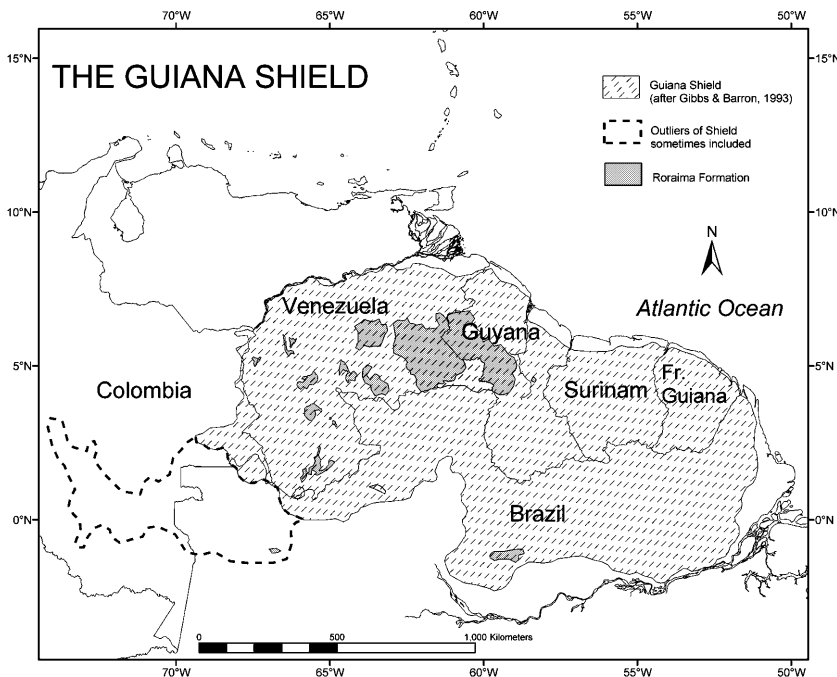


Figure 1 Boundaries of the Guiana Shield (cross-hatched), an ancient geological province of igneous-metamorphic rock located on the north-east shoulder of South America. Overlaying the Shield is the eroded sandstone of the Roraima Formation (shaded). Illustration drawn using ArcMap 8.1 (ESRI, 2001) and follows Gibbs & Barron (1993) and USGS G-topo30 maps.

Drainage patterns are affected by terrain tilting, uplift, faulting and rifting (Gibbs & Barron, 1993). On a regional scale, tilting is the main influence on the drainage off the Guiana Shield, and as a result nearly all of the rivers of the Shield flow in a north to north-easterly direction to the Atlantic Ocean. The major rivers draining into the Atlantic, beginning in the west, are the Orinoco River and its tributaries which drain the Venezuelan Guayana; the Essequibo and its tributaries which drain a large part of southern Guyana; the Corentyne River which drains eastern Guyana and western Surinam; the Marowijne/Maroni Rivers between Surinam and French Guiana; and the Oyapok/Oiapoque River between French Guiana and the state of Amapá, Brazil. Exceptions to the N or NE flow are along the Guyana–Brazilian boarder where the Takutu–Ireng River system turns south and becomes part of the Amazon River drainage. The water of the Takutu and Ireng Rivers now flow through the Rio Branco, Rio Negro and Amazon Rivers before emptying in the Atlantic Ocean (Berrangé, 1977). This drainage pattern of the Guiana Shield has made it more or less an island on the north-eastern shoulder of South America. To the south it is separated from the Brazilian Shield by the Amazon basin and bounded by the Orinoco River and the Rio Negro, which are connected by the Casiquiare Canal. To the west the Shield stops at the foot of the Andes in the region of the Amazonian Colombia (Gibbs & Barron, 1993). The geomorphology of the Shield along with the drainage system enhances the discreteness of the region and lends support to the concept that it hosts a unique flora of the area.

The Shield is often referred to as a unique biogeographical region (Maguire, 1970; Mori & Prance, 1987) with its vegetation described as 'diverse' and 'abundant' with areas of 'localized restriction of individual species' (Gibbs & Barron, 1993). Berry *et al.* (1995b) has also referred to the flora of the Shield as 'rich and largely unique'. Authors continually stress the high endemism (40–75%) and isolation of the flora (Brown *et al.*, 1901; Maguire, 1970; Brewer-Carias, 1978; Berry *et al.*, 1995b). In addition to the Gondwana or African connection to explain the flora of this region, five other theories have been proposed. Of these theories, one attributes the diversity and uniqueness to refuge forests or refugia (Haffer, 1969a,b; Prance, 1973). According to this theory, the Amazon forest ranged over a large area of central and northern South America. During the late- to post-Pleistocene era, climate in this huge forested area of South America was subjected to long dry periods reducing the forest cover to smaller isolated patches. Species isolated in these forest refugia diversified before the forests reunited during more humid climate conditions, which then allowed the now incompatible species in the refugia to extend their range. Prance (1973) proposed two possible refugia in the Guiana Shield area: *Imataca*, a mountain range in eastern Venezuela just south of the Orinoco delta and *Guiana* (the three Guianas). In contrast to the refugia theory, Colinvaux (1998) proposes that endemics were not a product of forest reduction and isolate but resulted from the effects of lower carbon dioxide and

temperatures. These two climate variables, along with altitude allowed for speciation to occur in elevated areas leaving the lowland forests largely intact. A third theory holds that the Guiana Shield was colonized by plants long before the epicontinental seas receded from the Amazon basin (Lindeman & Mori, 1989) and in this case the forests were not reduced but isolated resulting in a 'high diversity and endemism of plant species' (Huber, 1995b). Maguire (1970) and later Steyermark (1986) proposed a theory that the origin and development of the Guiana Shield was contemporary with the Brazilian Shield (an ancient basement of the South American continent) and that the Guiana Shield had an ancient regional flora with a high incidence of relict species. Huber (1988) proposed that the Guiana Shield was more than a static model where an ancient flora developed under isolation. His analysis suggested that the ecosystems of the tepuis of the Venezuelan Guayana were the result of a dynamic, evolutionary process of speciation with many opportunities for genetic interchange within and outside of the Shield area. The final theory by Kubitzki (1989) states that the core phytogeographical elements of the Guiana Shield developed and differentiated in lowland areas of substrates derived from Roraima sediments. Kubitzki suggested that the flora is relatively recent with an origin in the Andes. These theories are not exclusive of one another and each one is inferred and has not been tested.

Does the Guiana Shield support a unique flora as has been suggested? Is there a connection between the Brazilian Shield and the flora of the Amazon Basin (Takhtajan, 1986) or even to the Andes? Is the flora an ancient one dating back to Gondwana when Africa was connected to South America? Or is it more recent? To investigate these and other questions data were gathered from an area in central Guyana, Kaieteur National Park. The Park sits near the eastern rim of the Pakaraima Mountains on the edge of the Roraima Formation. The Kaieteur area consists of pebble and cobble size quartzite imbedded in pink and white sandstone. It is an idea location as the Park is almost central on the Shield. The elevation of the Park ranges from 400–450 m on the plateau to 50–100 m in the gorge. Kaieteur National Park provides a mixture of both the upland and lowland flora found on the Shield and is composed of a mosaic of different habitats, reliefs, soils (generally nutrient poor), elevations and plant communities. Finally, the flora of the original 19.4 km² of Kaieteur National Park is well known (Kelloff & Funk, 1998 and <http://www.mnh.si.edu/biodiversity/bdg/resource.html>) providing information on a taxon by taxon comparison.

METHODS

In 1999, Kaieteur National Park was expanded from the 1970s boundaries of 19.4 km² (the subject of this study) to 627 km² (Fig. 2). However, only the area within the original park is well sampled. An inventory of a section of the original park, the area near the waterfall, has produced a plant checklist (Kelloff & Funk, 1998). In addition, plot studies in the original park (Kelloff, 2002) have shown that forest composition, once

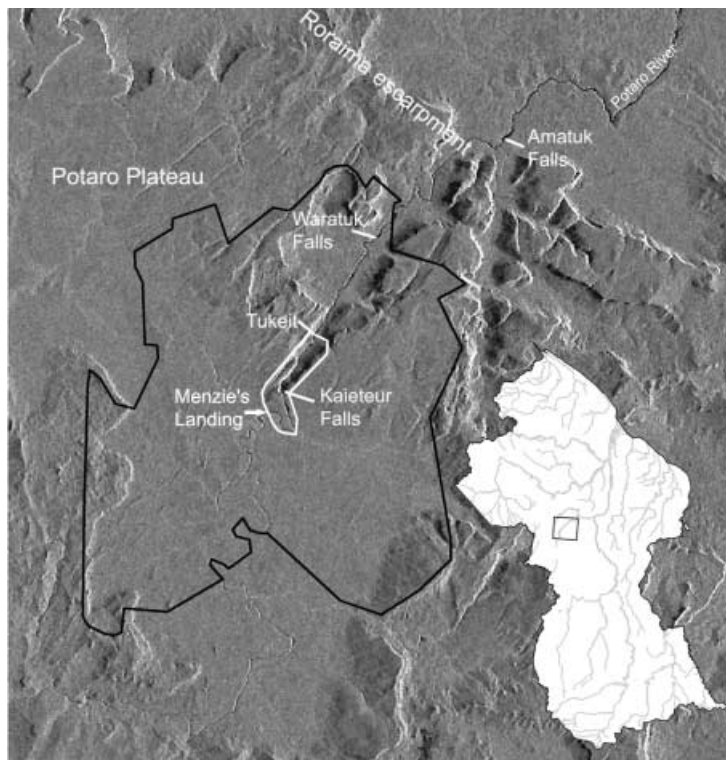


Figure 2 Kaieteur National Park, Guyana is located on the eastern edge of the Roraima Formation known as the Potaro Plateau region. The radar image provides an aerial view of the topography of the area. The 1973 (19.4 km²) boundary of Kaieteur National Park is indicated by the white line and the present area of 627 km² by black. The image was produced from a mosaic of two 1995 JERS-1 SAR images downloaded from the NASA website (http://trfic.jpl.nasa.gov/GRFM/samerica_frame.html).

thought to be fairly homogeneous over large areas, can vary over relatively short distances. There are numerous revisions of individual taxonomic groups, usually genera that map the distribution of each species. However, no one has examined all of the species in an area to determine the sum of the affinities of the flora.

Plant distribution information for Kaieteur National Park was gathered from specimens, primarily from the following herbaria: Missouri Botanical Garden (MO), New York Botanical Garden (NY), Royal Botanic Gardens (K), US National Herbarium (US), and the University of Utrecht (U), and from the literature (Pulle *et al.*, 1932–1984; Schnee, 1943; Foldats, 1969–1970; Steyermark, 1974; Prance & Mori, 1979; Cronquist, 1981; Rizzini, 1982; Görts-van Rijn, 1985–1997; Werkhoven, 1986; Burns-Balogh, 1989; Mori & Prance, 1990; Pennington, 1990; Kvist & Skog, 1992; Simpson, 1992; Mori & Lepsch-Cunha, 1995; Steyermark *et al.*, 1995–2003; Boggan *et al.*, 1997; Mabberley, 1998; R. Barneby and J. Grimes, unpublished data) as well as numerous recent collecting expeditions. Based on a brief survey of several monographs and floras and personal experience, a set of 13 typical distributions were proposed, beginning with the very restricted distribution of 'endemic' to Kaieteur National Park and moving to wider patterns such as the 'Guiana Shield' and 'neotropical'.

Individual worksheets were used to record the distribution of each species at Kaieteur for the ranks of family, genus and species (including infraspecific taxa). The study included 131 families, 517 genera and 1227 species. Only 21 species had more than one infraspecific taxon and these were treated as separate species. When available, additional data were

Table 1 Distribution patterns and their numbers

Area no.	Distribution patterns
1	Endemic to Kaieteur National Park (original park)
2	Pakaraima Mountains of Guyana
3	Guyana (lowland)
4	Roraima Formation (Pakaraima Mountains and adjacent Venezuela)
5	Guyana, Surinam and French Guiana (the Guianas)
6	Guiana Shield
7	Northern South America (east of the Andes)
8	Neotropics (8a) Excluding the Caribbean (8b) The Caribbean
9	South America
10	Western Hemisphere
11	Tropical Africa and South America
12	Pantropical
13	Cosmopolitan

recorded including elevation, habitat, altitude and endemism. During the data gathering phase, each species was assigned a distribution number that matched one of the 13 distribution patterns. The areas and their corresponding number are listed in Table 1. The map of north-eastern South America (Fig. 3) depicts the distribution patterns of 'Kaieteur National Park' (1); 'upland Guyana as represented by the Pakaraima Mountains' (2); 'lowland Guyana' (3); 'the three Guianas' (5); and the area of the 'Roraima Formation' (4). These five patterns cover the Venezuelan Guayana, Pakaraima Mountains and the

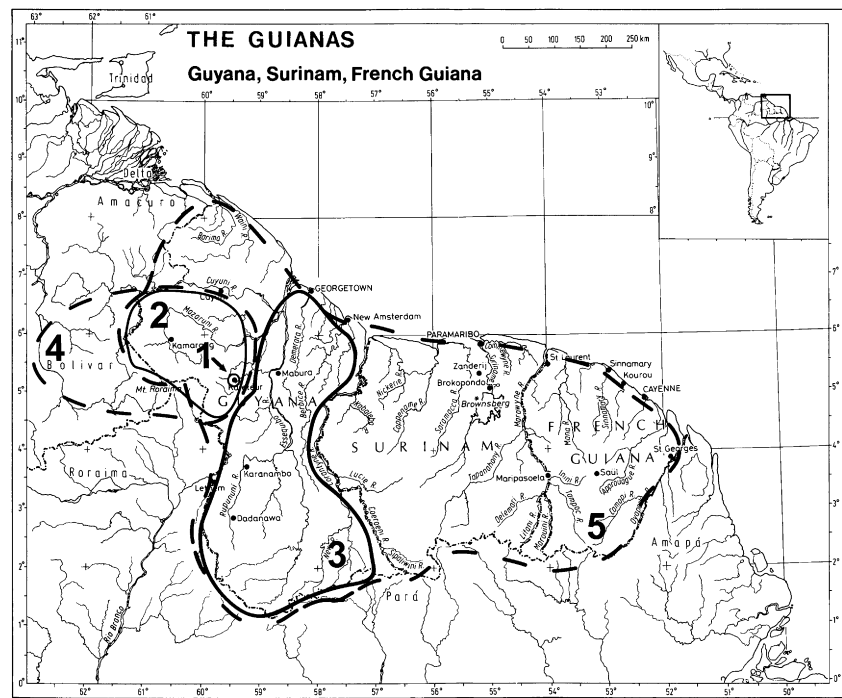


Figure 3 Restricted distribution patterns of north-eastern South America: (1) Kaieteur National Park, endemics; (2) Pakaraima Mountains only; (3) lowland Guyana; (4) Guyana and adjacent Venezuelan Highlands; and (5) the three Guianas. Basemap modified from Gorts-van Rijn (1985–1997).

lowlands of the Guianas. Distribution patterns of the New World Tropics (basemap, Rypkema, 1979) are illustrated in Fig. 4: the 'Guiana Shield' (6); the area of non-Andean 'northern South America' (7); and the neotropics, illustrating the distribution from 'Mexico to northern Argentina' (8a), 8b adds the Caribbean to area 8. Figure 5 shows all of the remaining distribution patterns except 'cosmopolitan' (13). Two areas that were originally included in the analysis had only a few species and they were removed as distribution patterns. These areas, 'eastern coastal forest of Brazil' and the 'Andes', will be discussed later.

Each taxon worksheet was assigned a distribution pattern number (Table 1) and these numbers were entered into a data base. The data base contained 1876 records and has one entry for each family (131), genus (517) and species (1227), with the latter including subspecific taxa. The list was taken from the updated version of Kelloff & Funk's (1998) plant checklist of Kaieteur National Park, which can be found online (<http://www.mnh.si.edu/biodiversity/bdg>). The data base was sorted and percentages of each of these ranks were tabulated (Table 2). There were some problems distinguishing two sets of patterns. First, the 'Pakaraima Mountains' (2) and 'Lowland Guyana' (3) tended to overlap. Taxon descriptions in the literature did not always distinguish the 'Pakaraima Mountains' separate from 'Guyana'. If details were provided such as habitat, location or elevations at the genus and species level, the species were assigned to the correct distribution pattern. If no further details were provided in the literature, the species were scored as 'lowland Guyana' for this analysis. Secondly, distributions that included Brazil often did not distinguish between Amazonian Brazil and southern Brazil, which made separating these two categories difficult. These species were

generally scored as 'northern South America' if no other information was available.

No scientific study arises *de novo* and this one has its roots in J.D. Hooker and L. Croizat. Hooker sought to know and understand the origins of the floras from around the world. In his treatments of the floras of lands of the southern hemisphere he evaluated the affinities of floras. Hooker's (1853–1855) treatment of the 'Botany of the Antarctic voyage' provides an example of his work. His method was to place species into groups with similar distribution. After examining the species in common among the floras of Australia, New Zealand, Tasmania, the Antarctic islands, South America and South Africa, he came to the conclusion that the 'bands of affinity' (species shared among areas) demonstrated a previous connection among the floras in question. Croizat used distributions in a method that he called Panbiogeography. He believed that geography and life evolved together. Croizat's (1964) book, 'Space, time, form: the biological synthesis' is one of his better efforts, however, it is still difficult to understand, and one can read Nelson (1973) for a concise explanation. Croizat's method involved examining hundreds of 'tracks' (distribution patterns) mostly for genera or families and grouping them into 'generalized tracks', which he believed provided an estimate of the ancestral biota. Our analysis differs from both of these in that we are evaluating a specific area and we use family, genus and species distributions for all taxa found in those areas. In addition, we use some percentages, Venn diagrams and other methods of examining the data. There are several books that explore the phylogenetic approach of biogeography (Brooks & McLennan, 2002; Crisci *et al.*, 1991 & 2003) but for the vast majority of species in this study there is little data so a phylogenetic approach was not feasible at this time.

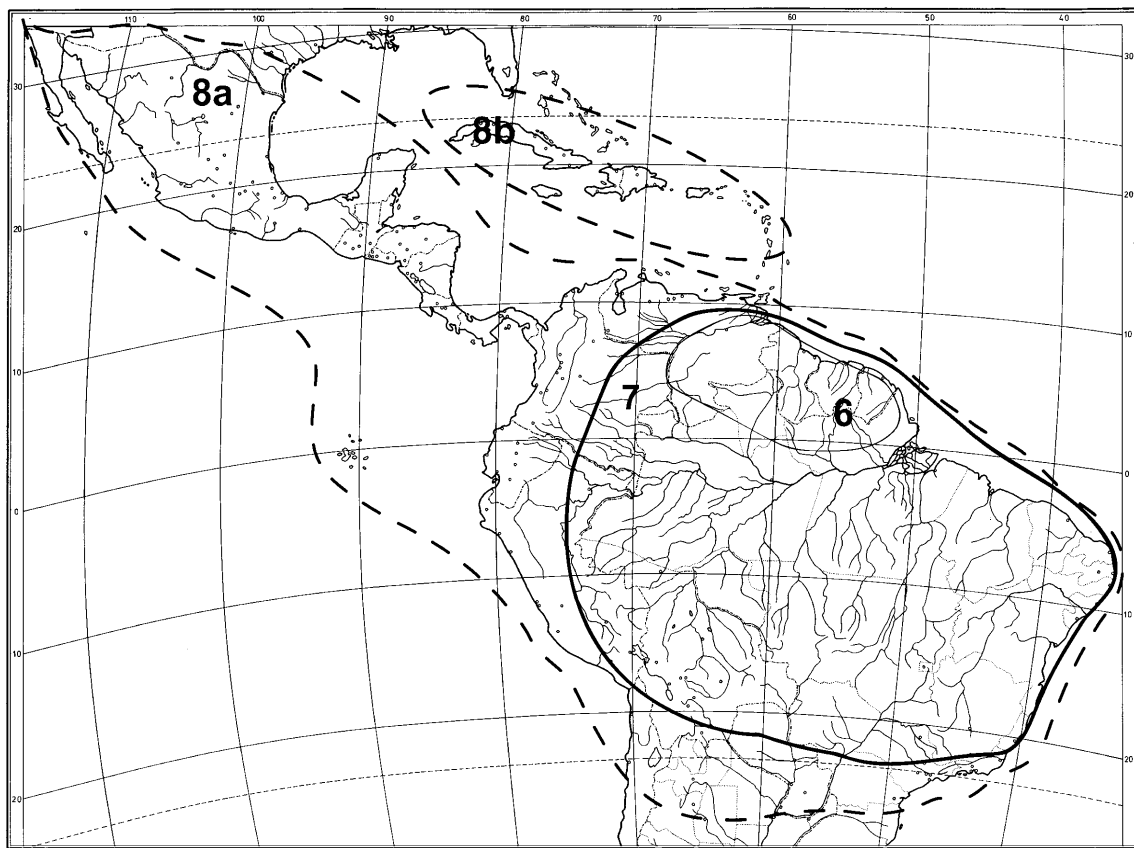


Figure 4 Floristic units of the New World Tropics: (6) Guiana Shield, (7) northern South America, (8) the Neotropics (8a) as defined by the areas of Mexico to northern Argentina and (8b) the Caribbean. Basemap modified from Rypkema (1979).

RESULTS AND DISCUSSION

Most of the plant species of Kaieteur National Park fall into four categories: 1) taxa that have a more global distribution, 2) taxa that are distributed in the new world, 3) taxa that are restricted to the Guiana Shield with an element on the Roraima Formation, and finally, and 4) taxa that have a distribution wholly within Guyana, Surinam and French Guiana, with the latter two overlapping somewhat. The results are different for different taxonomic levels.

Distribution patterns

Family

Of the 131 plant families at Kaieteur, 40.5% belonged to the 'cosmopolitan' (13) distribution pattern and 51.1% were 'pantropical' (12). The percentage of families in the 'neotropical' (8) distribution was 4.6% and that of 'northern South America' (7) was 0.8%. Four families, 3.0% of the total, were represented by species in both Africa and South America (11). There were no plant families in the flora that were restricted to the 'Guiana Shield' (6), although Thurniaceae came close with a distribution endemic to 'Guyana' (3) and parts of the Amazon basin (Heywood, 1993).

The 'cosmopolitan' (13) and 'pantropical' (12) distribution patterns account for 91.6% of the families. Four families: Bromeliaceae (59 genera/±2400 species total), Humiriaceae (8/50), Mayacaceae (1/10), and Rapateaceae (16/84) have distributions that are centred in tropical South America, yet have one or two species somewhere in Africa. Rapateaceae, a family with a distribution centred in the Pantepui area, has a monotypic genus, *Maschalocephalus*, in Liberia and Sierra Leone. Mayacaceae, a monogeneric family of small aquatic herbs, and Bromeliaceae, a moderate sized family, each have one species in Africa: *Mayaca baumii* Guerin (Mayacaceae) in Angola and *Pitcairnia feliciana* (A. Cheval.) Harms & Mildr. in Gabon. Humiriaceae, also predominantly a neotropical family, has two species of *Sacoglottis* Mart. in Gabon. There were no reverse patterns with distributions centred in Africa and one or two species in the 'Guiana Shield' area. Using molecular data Givnish *et al.* (2000) has shown that *Maschalocephalus* in Africa was the product of an infrequent long-distance dispersal event and not the result of an ancient continental connection. Given the few species in Africa and their separate locations it is most likely that all of these species are the result of long-distance dispersal. Certainly, long-distance dispersal has been recorded in several areas including the Hawaiian archipelago (Wagner & Funk, 1995) where geological activity and dispersal has given rise to local endemism.

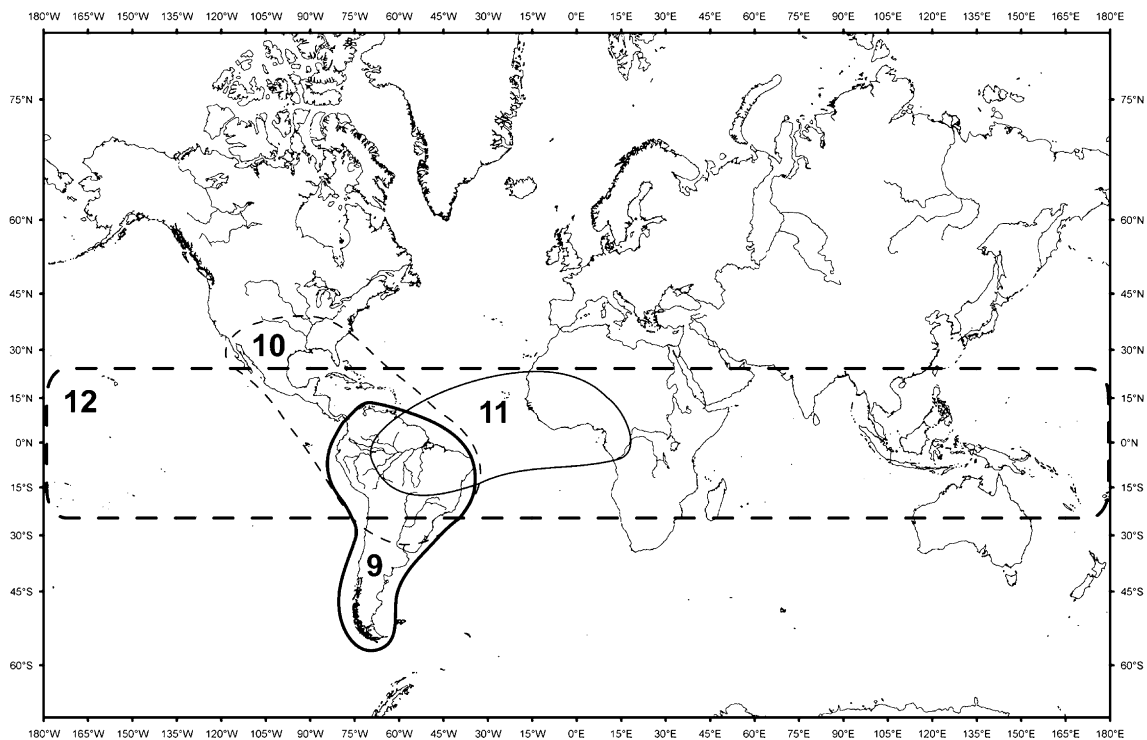


Figure 5 Distribution patterns as represented by the floristic units of (9) South America, (10) the Western Hemisphere, tropical Africa and (11) northern South America, and (12) pantropical. Cosmopolitan not illustrated as it is understood to represent worldwide. Map drawn using ArcMap 8.1.

Table 2 Percentage of taxa found in each distributional area within each rank of family, genus and species. The distribution pattern of Guyana, Surinam and French Guiana (5) also contained data for Guyana (3). These two units were used to calculate percentages for 'the Guianas' in the table

Distribution pattern	Area no.	Families (no./%)	Genera (no./%)	Species (no./%)
Kaieteur National Park	1	1/0.2	23/1.9	
Pakaraima Mountains	2			12/1.0
Guyana	3		1/0.2	74/6.3
Roraima Formation	4		3/0.6	89/7.5
Guyana, Surinam, French Guiana	5		2/0.4	87/7.8
Guiana Shield	6		28/5.4	204/17.6
Northern South America	7	1/0.8	53/10.3	322/27.3
Neotropics (w/o Caribbean)	8a	1/0.8	96/18.6	145/12.3
Neotropics (Caribbean only)	8b	5/3.8	135/26.1	171/14.5
South America	9		7/1.3	2/0.2
Western Hemisphere	10		17/3.3	6/0.5
Tropical Africa and South America	11	4/3.0	27/5.2	17/1.4
Pantropical	12	67/51.1	108/20.9	22/1.8
Cosmopolitan	13	53/40.5	34/6.6	4/0.3
Weeds/cultivars	Weeds/cultivars		5/0.9	9*
Distribution unknown	Unknown			40*
Total		131/100%	517/100%	1227/100%

*Not added in the calculation of percentages.

Six families from the Kaieteur flora have a 'neotropical' (8) distribution pattern. Members of Caryocaraceae (two genera/ 25 species) are found from 'Mexico to tropical Argentina' (8a)

but they are not in the 'Caribbean' (8b). The remaining families have a similar distribution but also extend into the Caribbean: Cyclanthaceae, Lacistemataceae, Marcgraviaceae,

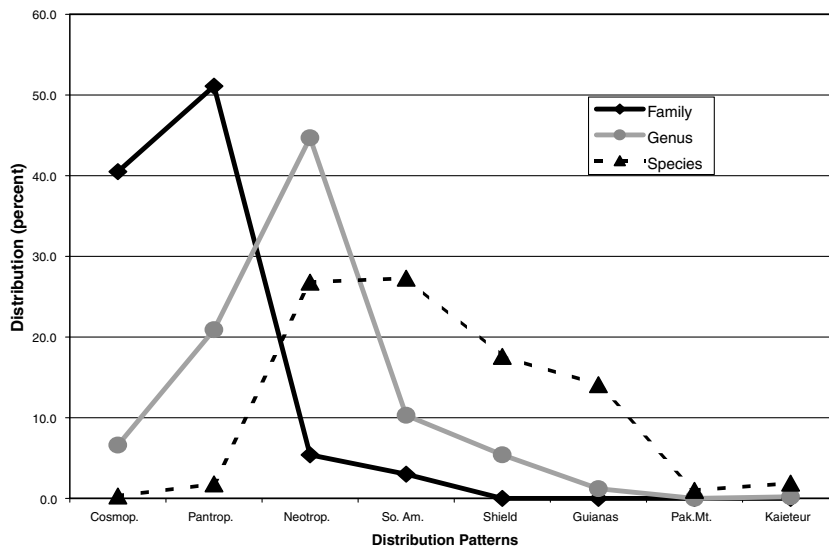


Figure 6 The distributional patterns at the family, genus and species level (including infraspecific taxa) of the Kaieteur National Park flora (Guyana) are examined. At the family level the highest percentages of the flora showed a cosmopolitan/pantropical distribution. At the generic level the highest percentage was in the neotropical/South America area. At the species level shift in percentage is towards northern South America and the Guiana Shield region.

Metaxyaceae and Quiinaceae. These families have little in common with one another. Metaxyaceae, a fern family, is monotypic and weedy. Lacistemataceae, a group of small trees or shrubs, is a segregate of Flacourtiaceae (two genera/14 species). Members of the Cyclanthaceae (11 genera/200 species) are herbs to erect shrubs and sometimes lianas. Quiinaceae, a family of trees and shrubs (four genera/45 species), is centred in the state of Amazonas, Venezuela of the Shield area, but it is also found in the tropical forests of the Caribbean and northern South America.

The Thurniaceae (one genus/three species), herbaceous monocots that grow in standing or slow moving water, is found only in the 'northern South America' (7) region. There are no families at Kaieteur that are restricted to the 'Guiana Shield' (6) area, although the three come close: Rapateaceae, Thurniaceae and Quiinaceae. The percentages of each distribution pattern for the families are illustrated in Fig. 6.

Genus

Of the 517 genera in this study a 'cosmopolitan' (13) distribution was found in 6.6% of them and 20.9% were 'pantropical' (12). By far the largest percentage of genera was found in the 'neotropics' (8) (44.7%) and only 10.3% in 'northern South America' (7). The 'Guiana Shield' (6) held 5.4% of the genera, two of which have recently been found in the Andes (*Digomphia* and *Pagamea*), and the 'Guianas' (5) held only 0.4%. One genus (*Potarophytum*) was found to be endemic to 'Kaieteur National Park' (1). Of the remaining genera, 5.2% had a 'tropical South America-Africa' (11) distribution, 3.3% were in the 'Western Hemisphere' (10), 1.3% were only in 'South America' (9) and 0.6% in the 'Roraima Formation' (4). Several genera (0.9%) were recorded as weeds (e.g. the grass, *Eleusine*) or may have been imported for cultivation (*Cucurbita*) or as ornamentals (*Zingiber*).

At the genus level, the percentage of distribution show a shift away from the wide distribution pattern seen at the

Table 3 Genera within the Kaieteur flora that have a distribution of 'tropical South America and Africa'. Family level distribution for these genera range from 'pantropical' to 'cosmopolitan'

Family	Genera
Annonaceae	<i>Annona</i>
Bromeliaceae	<i>Pitcairnia</i>
Chrysobalanaceae	<i>Hirtella</i>
Clusiaceae	<i>Symphonia</i>
Eriocaulaceae	<i>Paepalanthus</i> <i>Syngonanthus</i>
Euphorbiaceae	<i>Conceveiba</i> <i>Maprounea</i>
Fabaceae – Caesalpinioideae	<i>Copaifera</i> <i>Pentaclethra</i>
Fabaceae – Papilionoideae	<i>Andira</i>
Gentianaceae	<i>Neurotheca</i>
Grammitidaceae	<i>Cochlidium</i>
Lentibulariaceae	<i>Genlisea</i>
Marantaceae	<i>Thalia</i>
Mayacaceae	<i>Mayaca</i>
Meliaceae	<i>Carapa</i> <i>Guarea</i>
Olacaceae	<i>Heisteria</i>
Polypodiaceae	<i>Microgramma</i>
Rubiaceae	<i>Diodia</i> <i>Sabicea</i>
Sapindaceae	<i>Paullinia</i>
Simaroubaceae	<i>Simaba</i>
Solanaceae	<i>Physalis</i>
Tectariaceae	<i>Triplophyllum</i>
Zingiberaceae	<i>Renalmia</i>

family level of mostly 'cosmopolitan' and 'pantropical' distribution (now only 27.3%) to a more 'neotropical-northern South America' flora (60.0%; Fig. 6). Within the Kaieteur flora, there are 27 genera (Table 3) that are found in both 'tropical South America and Africa' (11; 5.2%). The

families of these genera have either a 'cosmopolitan' or 'pantropical' distribution.

Seventeen genera have a 'Western Hemisphere' (10) distribution (3.3%) ranging from North America to southern Argentina: *Blepharodon* (Asclepiadaceae), *Acanthospermum*, *Calea* and *Erechtites* (Asteraceae), *Arrabidaea* (Bignoniaceae), *Clusia* (Clusiaceae), *Pithecellobium* and *Zygia* (Fabaceae–Mimosoideae), *Myrciaria* (Myrtaceae), *Nymphaea* (Nymphaeaceae), *Aspidogyne*, *Encyclia* and *Epidendrum* (Orchidaceae), *Cupania*, *Matayba* and *Serjania* (Sapindaceae) and *Phoradendron* (Viscaceae). Restricted to the 'South America' (9) region are *Aechmea* and *Ananas* (Bromeliaceae), *Macrosamanea* (Fabaceae–Mimosoideae), *Sextonia* (Lauraceae), *Retiniphyllum* and *Sipanea* (Rubiaceae) and *Pradosia* (Sapotaceae).

The 'neotropical' (8) distribution is subdivided to show the Caribbean element. Of the 231 neotropical genera, 135 genera (nearly 60% of this category) are found in the Caribbean (8b).

It is interesting to note that there are at least 26 genera (5.4%) confined to the 'Guiana Shield' (6) area, excluding the two genera recently found in the Andes (Table 4). Two genera: *Rheedia* (Clusiaceae) and *Phlebodium* (Polypodiaceae), are restricted to the 'Guianas' (5), and three genera recorded for the 'Venezuelan Guayana and the Pakaraima Mountains' (4)

Table 4 Genera from the Kaieteur National Park flora that have a distribution within the Guiana Shield area (6) of South America

Family	Genera
Bonnetiaceae	<i>Archytaea</i>
Bromeliaceae	<i>Lindmania</i>
Bromeliaceae	<i>Navia</i>
Bignoniaceae	<i>Digomphia</i> *
Cyclanthaceae	<i>Stelestylis</i>
Cyperaceae	<i>Cephalocarpus</i>
Cyperaceae	<i>Didymiandrum</i>
Cyperaceae	<i>Exochogyne</i>
Eriocaulaceae	<i>Rondonanthus</i>
Fabaceae – Caesalpinioideae	<i>Aldina</i>
Fabaceae – Caesalpinioideae	<i>Dicymbe</i>
Fabaceae – Caesalpinioideae	<i>Elizabetha</i>
Fabaceae – Caesalpinioideae	<i>Recordoxylon</i>
Fabaceae – Papilionoideae	<i>Alexa</i>
Gesneriaceae	<i>Rhoogeton</i>
Gesneriaceae	<i>Tylopsacas</i>
Ochnaceae	<i>Elvasia</i>
Ochnaceae	<i>Poecilandra</i>
Podostemaceae	<i>Jenmaniella</i>
Podostemaceae	<i>Rhyncholacis</i>
Rapateaceae	<i>Saxofridericia</i>
Rapateaceae	<i>Spathanthus</i>
Rubiaceae	<i>Didymochlamys</i>
Rubiaceae	<i>Duroia</i>
Rubiaceae	<i>Pagamea</i> *
Thurniaceae	<i>Thurnia</i>
Trigoniaceae	<i>Trigonia</i>
Viscaceae	<i>Dendrophthora</i>

*Shield endemic recently discovered in the Andes.

area of the Roraima Formation: *Calophyllum* (Clusiaceae), *Notopora* (Ericaceae) and *Stegolepis* (Rapateaceae). One genus, *Windsorina*, is endemic to Guyana. This member of the Rapateaceae is found only along the Potaro River between Pamela Landing and Kaieteur. Also in the Rapateaceae and endemic to 'Kaieteur National Park' (1) is the genus *Potaro-phytum*.

Species

Of the 1227 species known from Kaieteur National Park, nine species were recorded as weeds or cultivars, 21 had unresolved taxonomy or were undescribed new species and 19 had confusing or missing distribution data. These groups were excluded from the calculations as they provided no information on the distributional history of the area. A total of 1178 species were used to calculate the percentages.

Examining the distributional aspect of the Kaieteur flora at the species level provided a more accurate insight into the theories of the origin of the Guiana Shield flora. From the 1178 species examined 26.8% (316 species) were recorded as having a 'neotropical' (8) distribution with 171 of them extending into the Caribbean (8b). The highest percentage of the flora (27.3%, 322 species) was centred in the 'northern South America' (7) region with another 204 species or 17.6% recorded as just 'Guiana Shield' (6). As the distributional descriptions become more defined for each species, 161 species or 13.7% are reported for areas in the categories of 'Guyana' (3) and 'Guyana, Surinam and French Guiana' (5) with two disjunct species: *Dioclea coriacea* Benth (Fabaceae – Papilionoideae) and *Fimbristylis aspera* (Schrader) Boeckeler (Cyperaceae) reported in the Andes and in the east coast forests of Brazil (respectively). The region of the Venezuelan Highlands and the Pakaraima Mountains of the 'Roraima Formation' (4) had 88 species (7.5%) recorded for this area. Species restricted to just the 'Pakaraima Mountains' (2) are believed to be an underestimation as the written descriptions tended to generalize this area as 'Guyana' but for those with detailed elevation and/or locality information, 12 species (1.0%) were noted for this area: *Gymnosiphon recurvatus* Snelders & Maas (Burmanniaceae), *Andira grandistipula* Amshoff (Fabaceae – Papilionoideae), *Neurotheca loeselioides* (Spruce ex Progel) Baillon subsp. *loeselioides* (Gentianaceae), *Tococa desiliens* Gleason (Melastomataceae), *Ouratea mazaruniensis* A.C. Smith & Dwyer (Ochnaceae), *Dulacia crassa* (Monach.) Sleumer (Olacaceae), *Epistephium subrepens* Hoehne, *Maxillaria pterocarpa* Barbosa Rodrigues and *Myoxanthus simplicicaulis* (C. Schweinfurth) Luer (Orchidaceae), *Peperomia elongata* Kunth var. *guyanensis* Yuncker (Piperaceae), *Rhyncholacis jenmanii* Engler forma *laciniata* R. Royen (Podostemaceae), and *Rudgea ayangannensis* Steyermark (Rubiaceae). It is worth noting that one species, *Neurotheca loeselioides* subsp. *loeselioides*, has also been found on Tafelburg. Although a granitic outcrop (Gibbs & Barron, 1993), Tafelburg is believed to be a remnant of the Roraima Formation in Surinam. Finally, 23 species (1.9%) have been

Table 5 Plants taxa endemic within the original 19.4 km² of Kaieteur National Park, Guyana

Family	Species
Aquifoliaceae	<i>Ilex soderstroomii</i> Edwin var. <i>soderstromii</i> <i>Ilex soderstroomii</i> Edwin var. <i>ovata</i> Edwin
Bromeliaceae	<i>Aechmea brassicoides</i> Baker
Chrysobalanaceae	<i>Couepia cognata</i> Fritsch var. <i>minor</i> Prance <i>Licania microphylla</i> Fanshawe & Maguirec
Fabaceae – Caesalpinioideae	<i>Dicymbe jenmanii</i> Sandwith <i>Macrobolium huberianum</i> Ducke var. <i>pubirachis</i> Amshoff <i>Swartzia eriocarpa</i> Bentham <i>Swartzia lamellata</i> Ducke var. <i>kaieteurensis</i> Cowan <i>Tachigali pubiflora</i> Bentham <i>Clitoria kaieteurensis</i> Fantz
Melastomataceae	<i>Graffenrieda irwinii</i> Wurdack <i>Miconia maguirei</i> Gleason
Myrtaceae	<i>Marlierea buxifolia</i> Amshoff <i>Myrcia extranea</i> R. McVaugh
Poaceae	<i>Thrasya achlysophila</i> Soderstrom <i>Paspalum bifidifolium</i> Soderstrom
Podostemaceae	<i>Jenmaniella guianensis</i> Engler <i>Jenmaniella isoetifolia</i> van Royen
Rapateaceae	<i>Potarophytum riparium</i> Sandwith <i>Stegolepis ferruginea</i> Baker
Rubiaceae	<i>Psychotria kaieteurensis</i> Sandwith
Sapotaceae	<i>Pouteria kaieteurensis</i> T.D. Pennington

found to be endemic to the 19.4 km² portion of Kaieteur National Park (Table 5).

The Kaieteur National Park flora has a very low percentage of species distributed in the broader categories (Table 2). The distributional aspect of the flora tends towards the ‘Guiana Shield’. When the distributional percentages from categories 1–6 were added 42.1% of the species were restricted to the Guiana Shield.

The species distributions continue the trend established with families and genera becoming increasingly more restricted (Fig. 6) to the ‘northern South America’ region with a large percentage of the species centred on the ‘Guiana Shield’ (Fig. 7).

Flora affinities

A Venn diagram (Fig. 8) is used to illustrate the eastern and western affinities that species of the Kaieteur National Park flora have with other distributional areas. Moving easterly away from the Roraima Formation towards the lowlands of the Guianas, Kaieteur shares c. 8.2% of its species with only ‘Guyana’ (3) and 16.0% (including the 9.2% found only in Guyana) among the lowlands of ‘Guyana, Surinam and French Guiana’ (5). As one moves west from Kaieteur towards the tepuis (tabletop mountains) of the Pakaraima Mountains and the Venezuelan Guayana (Highlands), Kaieteur shares 2.9% with the ‘Pakaraima Mountains’ (2) and 10.4% with the ‘Roraima sandstone formation’ (4). These two groups are nested within the ‘Guiana Shield’ (6) region that hosts 42.1% of the species from Kaieteur. Approximately 69% of the flora is confined to the ‘north-eastern South America’ (7) area and 96% can be found in the ‘neotropics’ (8). The remaining flora falls in the broader categories (‘pan-tropical’ or ‘cosmopolitan’).

Endemicity

For Kaieteur National Park, 68% of the families have at least one species endemic to the ‘Guiana Shield’ (6). Thirty-eight families (30% of the total number of families) have more than 50% of their species endemic to the Shield area. Those families that have more than one to three species and 80% or more of their species endemic to the Guiana Shield include the following: Rapateaceae (100%; 10 species/10 endemic to the Guiana Shield), Podostemaceae (88%; 8/7),

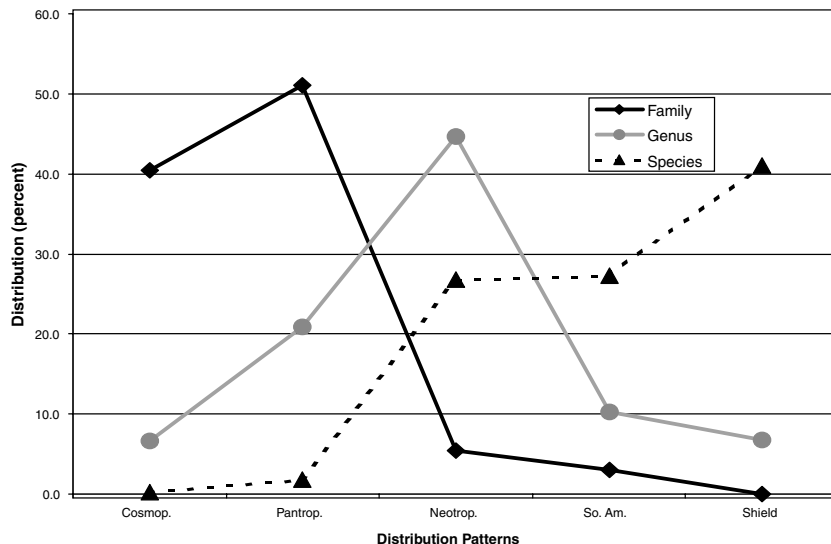


Figure 7 Comparison of the distributional patterns for the family, genus and species levels of the flora of Kaieteur National Park, Guyana. There are no plant families and only 35 genera (6.8%) in the Kaieteur flora restricted to the Guiana Shield. At the species level, the percentage increased to 42.1% of the Kaieteur flora endemic to the Guiana Shield.

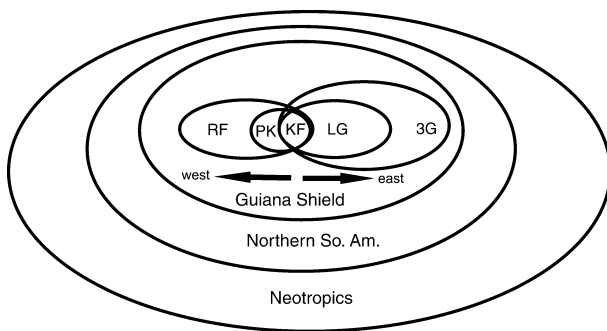


Figure 8 A Venn diagram illustrating the species level affinities the flora of Kaieteur National Park, Guyana has with other distributional areas: Kaieteur no. 1 (KF: 1.9%), lowland Guyana no. 3 (LG: 6.3%), the three Guianas no. 5 (3G: 16.0%), Pakaraima Mountains no. 2 (PK: 1.0%), Roraima Formation no. 4 (RF: 10.4%), the Guiana Shield no. 6 (42.1%), northern South America no. 7 (69.4%), and the neotropics including the Caribbean no. 8a/b (96.2%).

Aquifoliaceae (83%; 6/5), and the Loranthaceae (80%; 5/4). The larger families with over 50% of species endemic are the Myrtaceae (71%; 21/15), Xyridaceae (65%; 17/11), Apocynaceae (62%; 26/16), Fabaceae – Papilionoideae (56%; 34/19), Araceae (56%; 18/10), Fabaceae – Caesalpinoideae (54%; 41/22), Lecythidaceae (53%, 15/8) and the Rubiaceae (50%, 88/44). The total for all legume subfamilies are 55% (75/41). These figures are interesting when the list is compared with the list of the families that have the largest number of species at Kaieteur National Park: Rubiaceae (88), Melastomataceae (81), Poaceae (56), Orchidaceae (56) and Cyperaceae (47). Of the aforementioned families, only the Rubiaceae are on the list of families with 50% or more endemic species. So the number of endemics do not appear to be the result of the taxa belonging to families with the largest number of species.

CONCLUSIONS

In the past, most attempts to examine the distribution and composition of tropical floras were generalizations at the genus or family level (Maguire, 1970; Forero & Gentry, 1988). This has led to many broad statements in the literature about the composition and affinities of various tropical floras at a regional level. For instance, there are many theories in the literature that attempt to explain the flora in the region of the Guiana Shield. There are some that believe the flora developed from a refugium forest and had a close affinity with either the Amazon basin (Prance, 1973; Takhtajan, 1986; Lindeman & Mori, 1989) or the Brazilian Shield (Maguire, 1970; Steyermark, 1986). Some theorized that it was an ancient flora developed under isolation resulting in a region with high diversity and endemism (Huber, 1988, 1995b), while others hypothesize that the flora developed in the lowland area on substrates derived from the Roraima sandstone and has an element of the Andean flora showing

that its flora is not strictly an ancient one (Kubitzki, 1989). In Guyana, Kaieteur National Park presented an excellent site for examining the various hypothesis on the origin and affinity of the Guiana Shield. Situated on the eastern extent of the Roraima Formation on the edge of the Pakaraima Mountains, Kaieteur National Park forms a spectacular backdrop for an interesting flora. Its location is almost centred on the shield and has a diversity of habitats that include both lowland and upland plants. Although Kaieteur National Park is now much larger (624 km²), the flora of the original 19.4 km² park is better known (Kelloff & Funk, 1998). From an examination of the distributions of 131 families, 517 genera and 1227 species at Kaieteur, the family distributions were found to be mostly cosmopolitan or pantropical, while the genera centred on a more neotropical distribution. However, it is at the species level that the distributions provide a detailed view of the composition of the flora at Kaieteur National Park. The flora at Kaieteur contains both an element from the Roraima sandstone formations, (including the tepuis) and an element of lowland Guyana, Surinam, and French Guiana. It is more directly related to the Guiana Shield (42.1%) than any other area. This is in line with the 40% estimated for the Guiana Shield by Berry *et al.* (1995b) for the Venezuelan Guayana. Also, the Kaieteur flora is largely northern South American (69%). It is neither closely related to the floras of the Brazilian Shield, the Amazon, the Andes, the eastern coastal forests of Brazil, southern South America, or Africa but rather deserves status as a unique flora. It certainly is not the result of ancient connections to either Africa or the Brazilian Shield and has no historical relationship to the break-up of Gondwana.

What is interesting to note is while there are many theories about origin of the flora of the Guiana Shield, none took into account the affinities with Mexico–Central America or the Caribbean of which is expressed at the species level in 25% of the Kaieteur flora. This study also recognized that 25% of the northern South American distribution were plants also from the Brazilian Shield and the Amazon basin. It is possible that there is an indication that a sizable component of the neotropical flora actually radiated from the Guiana Shield. Only a more detailed study of the Brazilian distribution will be able to answer this question.

Increased exploration of the tropical regions of the world has led to a better understanding of the floristic composition of plant communities. However, the work is far from complete. More inventories are needed in remote or unexplored areas. Through inventories, new populations and species are discovered and our information on plant distributions is expanded. One cannot overemphasize the importance of surveys, inventories, checklists and floras in our attempts to understand the distribution of life on earth. Finally, because the tepui areas, in general are poorly known we feel that as knowledge of the flora of Kaieteur National Park increases, the tepui element will show a much stronger influence, thus further defining the knowledge of the origin, distribution and diversity of the plants in this region.

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