

**Establishing a baseline of plant diversity and endemism on a neotropical mountain summit for future comparative studies assessing upward migration: an approach from biogeography and nature conservation**

5 Elisabeth Safont, Valentí Rull, Teresa Vegas-Vilarrúbia, Bruce K. Holst, Otto Huber,  
Shingo Nozawa, Yuribia Vivas & Argelia Silva

**Safont, E.** (corresponding author, +34 934031190, [esafont@ub.edu](mailto:esafont@ub.edu)), **Vegas-**

**Vilarrúbia, T.** (+34 934031376, [tvegas@ub.edu](mailto:tvegas@ub.edu)): Department of Ecology,

10 University of Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain.

**Safont, E. & Rull, V.** ([vrull@ibb.csic.es](mailto:vrull@ibb.csic.es)): Palynology & Paleocology Lab, Botanic

Institute of Barcelona (IBB-CSIC-ICUB), Passeig del Migdia s/n, 08038 Barcelona,  
Spain. Telephone: +34 932890611.

**Holst, B.K.** ([bholst@selby.org](mailto:bholst@selby.org)): Marie Selby Botanical Gardens, 811 South Palm

15 Avenue, Sarasota, Florida 34236, U.S.A. Telephone: +1 9413665731.

**Huber, O.** ([huberotto8@gmail.com](mailto:huberotto8@gmail.com)), **Nozawa, S.** ([s.nozawa@gmail.com](mailto:s.nozawa@gmail.com)), **Vivas, Y.**

([yuriarroyo@gmail.com](mailto:yuriarroyo@gmail.com)) & **Silva, A.** ([argeliasil@gmail.com](mailto:argeliasil@gmail.com)): Botanical Institute of  
Venezuela Dr Tobías Lasser, Av. Salvador Allende, 1053 Caracas, Venezuela.

Telephone: +58 2126053970.

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## Abstract

Climate change is forcing many plant species to shift their range in search of adequate environmental conditions, being localized endemic species particularly at risk on mountain summits. The Pantepui biogeographic province, a set of flat-topped mountain summits (called *tepui*) of northern South America, contains both high plant diversity and high degree of endemism. Previous studies based on warming projections for the area suggested that half of the Pantepui endemic flora would disappear due to habitat loss by 2100. In this study, we selected one of the best-explored tepuis, Roraima-tepui, to establish the baseline of diversity and endemism for comparisons with historical data and future monitoring surveys, aimed at testing the hypothesis of upward migration of plants in response to global warming. We also analysed floristic and physiognomic features of the Eastern Tepui Chain (ETC, the mountain range where Roraima is located), and the phytogeographic patterns of both the ETC and Pantepui. The Roraima summit contains 227 species, including 44 new records, 13 exotic species (some of them with high invasive potential), and at least one species new to science. At the ETC level, Roraima is the tepui with highest species richness and degree of endemism, and shows a relatively high floristic similarity with Kukenán and Ilú. Herbaceous species dominate over shrubs on these tepuis, Tramen and Maringma, whereas on Yuruaní, Karaurín and Uei, they reach similar abundances. At the Pantepui level, endemic species have highly localized distribution patterns (17% local endemics). Conservation opportunities are evaluated in light of these results.

Keywords: Climate change; Floristic survey; Guayana region; Pantepui; Phytogeography; Plant invasion.

## Introduction

Global warming is considered to be a major threat to high-mountain flora worldwide (Grabherr *et al.*, 2010). As a response to climate change, plants may shift their distribution (e.g., Pauli *et al.*, 2007; Kelly & Goulden, 2008; Lenoir *et al.*, 2008; Feeley  
55 *et al.*, 2011; Jump *et al.*, 2012), which can in turn produce the fragmentation or loss of their habitat (Thuiller *et al.*, 2005; Colwell *et al.*, 2008; Engler *et al.*, 2011). Those inhabiting summits could find themselves without suitable substrate; in the case of endemic species, extinctions would result in biodiversity loss on a global scale (Rull & Vegas-Vilarrúbia, 2006; Kreyling *et al.*, 2010; Dirnböck *et al.*, 2011). In addition, as  
60 biotic responses are occurring at species level, changes in diversity and composition of many communities may also occur (Grabherr *et al.*, 2010; Walther, 2010; Sheldon *et al.*, 2011; Gottfried *et al.*, 2012; Pauli *et al.*, 2012). Tropical high-mountain biomes are of particular concern among biomes worldwide because of the high biodiversity and levels of endemism they harbour (Davis *et al.*, 1997; Myers *et al.*, 2000; Malcolm *et al.*,  
65 2006; Rull, 2010; Laurence *et al.*, 2011; Nogué *et al.*, 2013). A way to empirically test predictions of global warming and the corresponding biotic responses is the periodic monitoring of selected plots, in order to verify whether their magnitude and rates square with the expected ones. In this regard, taxonomic research is essential for identifying, mapping, and predicting the biotic impacts of climate change. Standardized floristic  
70 surveys are being increasingly used for that purpose in mountain environments, largely due to the existence of the GLORIA initiative (Global Observation Research Initiative in Alpine environments; <http://www.gloria.ac.at>), a long-term project with large-scale approaches, which has a goal of establishing and maintaining a worldwide network of observatories in order to document changes in high-altitude plant diversity related to  
75 climate change (Grabherr *et al.*, 2000). In order to verify the existence of plant

migrations that may have already occurred in the last decades/century, some studies have used historic floristic surveys (Chou *et al.*, 2011; Stöckli *et al.*, 2011 and literature therein) or herbarium records (Feeley, 2011) to compare current species distribution with those of 40--100 years ago, providing positive results.

80 The neotropical Guayana Highlands constitute a singular high-mountain biogeographic province, located within the Guayana Shield region of northern South America. This discontinuous province, also called Pantepui, is formed by the assemblage of the summits (between 1500 and 3000 m elevation) of ~50 sandstone mountains, mostly table-like, locally referred to as *tepui* (Huber, 1995a). It stands out for its extraordinary

85 biotic differentiation with respect to the surrounding lowlands, especially of vascular plants (Huber, 1987). The difficulty to access the zone, together with the isolation of most tepui summits with respect to the lowlands have enabled the preservation for centuries from anthropogenic impacts of the unique flora of Pantepui. However, recent estimations based on the IPCC temperature projections for the area (Christensen *et al.*,

90 2007) suggest that, by the end of this century, an upward shift of environmental conditions of the order of 500 to 700 m would be expected (Rull & Vegas-Vilarrúbia, 2006), potentially resulting in the loss of >80% of the Pantepui's habitat (Vegas-Vilarrúbia *et al.*, 2012) and the extinction of the 30--50% of its endemic vascular flora (Nogué *et al.*, 2009; Safont *et al.*, 2012). As thoroughly discussed in previous studies

95 (Rull & Vegas-Vilarrúbia, 2006; Nogué *et al.*, 2009; Rull *et al.*, 2009; Safont *et al.*, 2012), the consideration of temperature increases as the only environmental forcing and upward migration as the only biotic response is the main limitation of the analyses of habitat and biodiversity loss in Pantepui. Other factors like geological substrate and edaphic factors may have local importance (Huber, 1995a, 1995c), but the scarce

100 information available is a big handicap. Temperature is generally the main factor

controlling the altitudinal distribution of vascular plant species in Pantepui (Huber, 1995a) and in many other areas (e.g., Guisan & Theurillat, 2000; Thuiller *et al.*, 2005). In addition, precipitation is not expected to be as influential as temperature. Indeed, the 0--5% reduction in mean annual rainfall forecasted by the IPCC scenario by the end of this century (Christensen *et al.*, 2007) is almost negligible, considering the perhumid climate of the tepui summits.

In this study, Roraima-tepui, one of the currently best-explored tepuis with the oldest botanical collections of Pantepui, was selected for the following purposes: 1) to establish the baseline of diversity and endemism of vascular plants for future comparisons, aimed at testing the hypothesis of upward migration of plants in response to global warming; 2) to analyse floristic and physiognomic features of Roraima in the biogeographic context of the mountain range where it is located, the Eastern Tepui Chain (ETC) and Pantepui; 3) to verify the existence and state of exotic species transported by humans; and 4) to evaluate conservation opportunities, especially in light of the large number of ecotourists that visit the mountain summit annually.

Botanical inventories are key elements of monitoring programs aimed at testing the effects of climate change on the distribution and local abundance of plant species (Stöckli *et al.*, 2011). Our study is intended to be used for comparison with past floristic surveys or herbarium records of the Roraima summit, beginning in 1884, and as starting point for future monitoring of migratory phenomenon. Historical data do not provide as high a level of information as that provided by the GLORIA monitoring programs. However, to date it is the only method to document historical vegetation development in places where GLORIA-style monitoring has been absent (Feeley & Silman, 2011). Recently, the use of herbarium specimens combined with historic climatic data is gaining importance, as it also enables the examination of biotic

responses to climate change other than migration, such as those related to phenology (e.g., Calinger *et al.*, 2013). In addition to climatic changes, Roraima offers the possibility of testing the effect of direct anthropogenic impacts. As it is accessible by foot, it provides a ready means for the transportation and introduction of exotic species  
130 from surrounding lowland areas. Therefore, this study represents a baseline state against which changes in distribution and extension of species populations (either native or exotic) and vegetation formations can be assessed through time.

Subsequently, phytodiversity, endemism, and physiognomic patterns are compared among the tepui summits that shape the ETC. Dominant growth forms of  
135 most of the ETC summits were previously described by Huber (1995b). A contribution of this study is the determination of the abundances of the different physiognomic types at each summit of the ETC summits, which may provide important insights into their habitat diversity. Finally, phytogeographic patterns are analysed among the ETC and Pantepui. At the Pantepui level, previous studies used multivariate statistical methods to  
140 classify the tepuis according to their floristic composition, either considering the total set of Pantepui species (Riina, 2003) or only the endemics (Vegas-Vilarrúbia *et al.*, 2012). From these studies it was deduced that there were significant differences in the floristic composition among certain groups of tepuis, which were explained by the geographical distance among them, that is, their connectivity. Here, we use a revised  
145 and validated version of the raw data (Safont *et al.*, 2012) to obtain groups of species (clusters), whose relative abundances are determined for each tepui, and plotted on a map of the whole Pantepui area. Therefore, a graphical measure of floristic similarity is performed, that has implications for the interpretation of the degree of endemism within the Pantepui biome. At the ETC level, no previous studies exist addressing

150 phytogeographic patterns. Here, we calculate the floristic similarity and test the species-  
area relationship among its tepuis.

### Study Area

Pantepui has been defined as a land archipelago (Rull, 2010), occupying an area of  
155 approximately 6000 km<sup>2</sup>. The majority of tepuis are located in southern Venezuela  
(Amazonas and Bolívar states), with some smaller ones in neighbouring areas of Brazil  
and Guyana (Fig. 1). They are the result of progressive erosion since  
Jurassic/Cretaceous periods of the upper sedimentary rocks of the Guayana Shield  
(Precambrian Roraima Group), leaving these remnants isolated from the surrounding  
160 lowlands by spectacular cliffs (Briceño & Schubert, 1990) (Fig. 2). The nutritional  
poverty of the sandstone substrate and the limited drainage conditioned the development  
of nutrient-poor and anoxic soils. Under these conditions, decomposition of organic  
matter is incomplete, thus contributing to the accumulation of acids in the soil (Cuevas,  
1992). Upper montane regions of Pantepui (1500--2400 m) have average annual air  
165 temperature of 12--18 °C and average rainfall high to very high (2500--3500 mm). On  
the highest summits (>2500 m), climate is characterized by average annual air  
temperature around 10 °C or less (Huber, 1995a) and heavy rainfalls. Up to 5000 mm of  
annual rainfall have been estimated in the area of Roraima-Kukenán (Corrales, 2004).  
Other characteristics of the highest tepui summits are dense cloud and mist formation  
170 almost all year, frequent strong winds, and high solar radiation (Huber, 1995a).  
Adiabatic decrease of average air temperature is 0.6 °C per 100 m altitude (Huber,  
1995a). To date, more than 2400 plant species have been documented, of which 30%  
are endemic to Pantepui (Nogué *et al.*, 2009). According to the geographic  
discontinuities of Pantepui and physiognomic differences observed from aerial

175 reconnaissances, Berry *et al.* (1995) divided the province into four districts: East, West,  
Jaua-Duida, and South.

The ETC, one of the most important biogeographic units of Pantepui in terms of  
plant diversity and endemism, is located in the Eastern District, near and along the  
borders of southeastern Venezuela, central-western Guyana, and extreme northern  
180 Brazil (Fig. 3). It is comprised of 11 tepuis, 10 of which stretch in a roughly 70 km long  
arc from northwest to southeast, namely Tramen, Ilú, Karaurín, Wadakapiapué,  
Yuruaní, Kukenán, Roraima, Wei-Assipú, Yakontipú, and Maringma, and one disjunct  
tepuí (Uei), situated 20 km to the southeast of the southern tip of Roraima (Table 1).

Tepui names were obtained from the *Flora of the Venezuelan Guayana* (FVG;  
185 Steyermark *et al.*, 1995--2005) for the Venezuelan tepuis, and the topographic map of  
Guyana (The Survey Department of Guyana, 1975) for the Guyanan tepuis. According  
to these sources, summit elevations and areas range from 2000 m and 0.02 km<sup>2</sup> on  
Wadakapiapué to 2810 m and 34.4 km<sup>2</sup> on Roraima, the largest tepui of the group  
(Table 1). Roraima-tepuí is situated at the triple boundary of Venezuela, Guyana and  
190 Brazil and is the tallest tepui of the Eastern District. Roraima's walls reach up to 700 m  
of vertical drop, and the slopes extend more than 1000 m until reaching the Gran  
Sabana and the lowland rainforests of Guyana and Brazil (Fig. 2). It is one of the icons  
of Canaima National Park, which covers almost 30,000 km<sup>2</sup> and was declared a World  
Heritage Site by UNESCO in 1994.

195 The oldest Pantepui botanical collections were made in 1838 on the southern  
slopes of Roraima by Robert H. Schomburgk, and four years later in the company of his  
brother, Richard M. Schomburgk. After that time several expeditions attempted to find a  
route to the summit, but it was not until 1884 that Everard F. Im Thurn and Harry I.  
Perkins succeeded. Then, during a scant few hours, they made the first collections of the



200 Roraima summit flora. The first significant collections, resulting from extended stays on  
the summit, were made by Frederick V. McConnell and John J. Quelch (1894, 1898).  
Subsequent expeditions that ascended to the ETC summits or high slopes by foot that  
resulted in numerous botanical collections were those of Henry G.H. Tate (Roraima,  
1927), Albert S. Pinkus (Roraima, 1929), Julian A. Steyermark (Roraima, 1944), and  
205 Basset Maguire (Ilú, 1952; Uei, 1954-1955). A total of 31 expeditions were made to  
Roraima through 1960, 12 of which were to the base and slopes and 19 to the summit.  
From that year forward, expeditions with biological exploration purposes rose to 26 (3  
to the slopes and 23 to the summit). Significant contributions were made by more recent  
botanical expeditions via helicopter during 1976-1989 many of which were led by Otto  
210 Huber (Ilú, 1984, 1985; Karaurín, 1987; Kukenán, 1984, 1985; Tramen-tepui, 1985;  
Uei, 1985; Yuruaní, 1984, 1986). Additional explorations were conducted by Charles  
Brewer Carías and the Terramar Foundation. Participating botanists on those trips were  
Julian A. Steyermark (Roraima, 1976), Francisco Delascio C. (Ilú, 1977; Kukenán,  
1977; Roraima, 1977, 1982, 1989; Tramen, 1989), and Ronald L. Liesner (Ilú,  
215 Kukenán, and Roraima, 1988). Other plant collecting work by Venezuelan botanists  
included Aníbal Castillo (Kukenán, 1982), Lionel Hernández (Yuruaní, 1983), Gabriel  
Picón (Roraima, 1986), Hector Rodríguez (Roraima, 1988), and Fabián Michelangeli  
(Roraima, 1992). H. David Clarke of the Smithsonian Institution and collaborators  
climbed to the top of Maringma in 2004, providing the first records of plant species in  
220 the ETC east of Roraima. The most recent botanical expeditions to the Roraima summit  
were conducted as part of this study in 2011 and 2012, the results of which are included  
in this study.

## Methods

225 *Floristic inventory of the Roraima summit*

Field work consisted of exploring routes on foot across the summit, following existing trails but making every effort to traverse areas not previously explored by botanists.

Given the rugged terrain atop Roraima, surveyed areas were limited by accessibility.

230 Despite this, more than 80 linear km were covered, and our routes traversed the greatest possible variety of forest, shrubland, meadow, and epilithic vegetation formations.

Expedition members spent a total of 24 days on the summit, during March 2011 and March 2012. Maximum and minimum elevations reached on the summit were 2770 and 2620 m, respectively.

Individual plants were identified *in situ* when possible (for approximately 50 of  
235 the well-known tepui species). Whenever there was uncertainty of identification, specimens were collected and photographed for subsequent study. A total of 374 collections were prepared, representing approximately 170 species. Collections were pressed in newspaper and preserved in 50% isopropyl alcohol. Subsequently, collected specimens were dried at 40--60 °C for 72 hours. We photographed living specimens of  
240 all the species found, as well as their habitats. In total, nearly 5300 photographs of plants were taken. Geographical coordinates of specimens and landmarks were recorded through a GPS device (Garmin eTrex Vista HCx and WGS84 datum), as well as with GPS-enabled digital cameras. Most taxonomic determinations were made by the authors and with the consultation of several taxonomic specialists (see acknowledgments). The  
245 first set of collections is deposited at VEN, with duplicates to be distributed to GUYN, SEL, BC, and those herbaria where specialists collaborating with the final identifications are based (at present, BRIT: Xyridaceae; CICY: Orchidaceae, F: Eriocaulaceae; MO: Asteraceae, Cyperaceae, Poaceae, Rubiaceae; NY: Ericaceae; UC: Pteridophyta).

250 We also conducted an extensive review of Venezuelan herbarium specimens,  
either directly (GUYN, MY, VEN), or through existing databases (CAR, MYF).  
Specimens deposited at foreign herbaria (F, K, MO, NY, UC and US) were consulted  
through a variety of online sources, especially through the Tropicos database  
(<http://www.tropicos.org>) and Smithsonian Institution's Biodiversity of the Guianas  
255 database. Finally, the inventory was completed through the revision of the  
comprehensive FVG, which was in turn used as the main taxonomic reference (except  
for few taxa that are recognized under a different classification system at the family  
level). For convenience, we recognize the families in three major working groups,  
Pteridophytes (including the Lycophytes), Dicotyledonae in the historical sense, and  
260 Monocotyledonae.

#### *Assessment of exotic species*

The floristic inventory was conducted in part to verify the existence and state of exotic  
species. For the purposes of this study, we applied the definition of exotic species  
265 provided by Richardson *et al.* (2000) and Pyšek *et al.* (2004) that classifies them as  
“those species whose presence in the study area is the result of either intentional or  
accidental human activity”. We also followed the nomenclature and definitions  
suggested by the same authors relating to the stages of the invasion process: casual  
exotic species, naturalized species, and invasive species. We considered the natural  
270 species range as the geographic area and elevations documented in the FVG (based on  
botanical collections from 1884 to 1995--2005, the period of preparation of the FVG).  
*In situ* observations of their habitat and degree of expansion were conducted, and a  
subsequent exhaustive bibliographic research was performed to determine their natural  
range and dispersal method.

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*Floristic composition, physiognomy and phytogeographic patterns of the ETC summits*

Floristic composition is defined as the degree of species diversity and endemism (Huber, 1995b). In our study, species diversity was expressed as species richness for each tepui summit, as well as for the ETC summits as a whole. Slopes were not considered as sufficient botanical information is unavailable at this time. As well, upper slopes (even above 1500 m) may contain species more likely representing the upland flora (Berry & Riina, 2005). The number of endemics was counted for each tepui, distinguishing several categories of endemism: local (single-tepui), ETC summits, ETC, Pantepui, and Guayana Shield. We also determined species of widespread distribution within the Neotropics, and exotic ones. Information on the species geographical and altitudinal ranges was derived from the distribution notes in the FVG, and when endemism was not clear from there, we checked the original specimens, mostly deposited at VEN, or revisions and monographs, which included the particular specimen collection information. As for physiognomy, growth forms were based on the FVG species descriptions (Huber, 1995b). Here, we excluded exotic species in order to compare native floras only. In addition, three tepuis were not included in this analysis as no floristic data are available for their summits, namely Wadakapiapué, Wei-Assipú, and Yakontipú.

To analyse the phytogeographic patterns, we calculated binary Sørensen similarity coefficients (SSC) (Jongman *et al.*, 1995) among tepuis, a commonly used measure to test the floristic similarity between sites, and the species-area relationship (MacArthur & Wilson, 1967) at the scale of the ETC summits. We did not include Karaurín due to insufficient floristic data. The power function was linearized through base-10 logarithm.

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### *Phytogeographic patterns in Pantepui*

To analyse the phytogeographic relationships among tepuis at the Pantepui scale, we ran a Cluster analysis with Pantepui endemic species, as non-endemics may have phytogeographic relationships with other areas, obtaining a number of groups of related species (clusters). Subsequently, we calculated the relative abundances of each cluster in the floristic composition of each tepui, and represented them geographically on a Pantepui map to obtain a new measure of the floristic similarity among tepuis.

Raw data for this analysis were derived from a database based on the FVG, containing all available geographical and elevational information of the species occurring in the Pantepui biogeographic province (Pantepui database; Nogué *et al.*, 2009; Safont *et al.*, 2012). After discarding three endemic species due to the lack of detailed distribution information, a total of 626 endemic species were computed. We considered 43 tepuis that contained endemic species. However, some of them were treated as a single tepui due to its physical connection above 1500 m (the lowermost boundary of Pantepui) or for which had aggregated distributional data in the FVG. These tepuis are: Roraima, Kukenán, and Yuruaní; Karaurín, Ilú, and Tramen; Carrao and Ptari; Kamarkawarai, Tereké-Yurén, Murisipán, and Aparamán (Los Testigos massif); Auyán, Cerro El Sol, and Cerro La Luna (Auyán massif); all tepuis of the Chimantá massif; Yutajé and Coro Coro; and Aracamuni and Avispa. Therefore, the effective number of tepuis used for the analysis was 31. These data were entered into PAST software, version 2.16 (Hammer *et al.*, 2001) to develop the Cluster analysis, in which species were classified according to unweighted pair-group average (UPGMA) algorithm and Raup-Crick similarity measure for presence-absence data, ranging from 0 to 1 (Raup & Crick, 1979). Unlike the Sørensen coefficient (previously used by Vegas-

325 Vilarrúbia *et al.*, 2012), this measure uses a randomization (Monte Carlo) procedure,  
comparing the observed number of species occurring in both associations with the  
distribution of co-occurrences from 1000 random replicates from the pool of samples.  
Clusters of species were defined as groups of species with Raup-Crick similarity  
measure above 0.7.

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## Results

### *Inventory of the vascular flora of the Roraima summit*

The Roraima summit flora includes 51 families, 130 genera, and 227 vascular plant  
species. Of them, 201 (88.5%) were observed during our fieldwork. Among  
335 Pteridophyta, 15 families, 31 genera and 70 species were recorded. In the traditional  
Angiospermae, Dicotyledonae are represented by 26 families, 54 genera and 81 species,  
and Monocotyledonae by 10 families, 45 genera and 76 species. No Gymnospermae  
representatives were found either in the field or in herbaria. At family level,  
Orchidaceae is the most diverse, with 15 genera and 26 species, followed by  
340 Grammitidaceae, Asteraceae, Cyperaceae, Bromeliaceae, Dryopteridaceae, Poaceae,  
Ericaceae, and Pteridaceae (Table 2). These nine families together contain nearly half of  
the species and genera reported for the summit. At the genus level, *Elaphoglossum*,  
*Epidendrum*, *Xyris*, *Octomeria*, *Peperomia*, *Pterozonium*, and *Utricularia* are the most  
species-rich, representing 18.1% of the total. A complete list of the vascular flora of the  
345 Roraima summit is shown in Online Resource 1.

Our collections and extensive herbarium surveys yielded 44 novelties for the  
Roraima summit flora since the publication of the FVG, representing a 24% increase  
with respect to the original compilation of that work (Steyermark *et al.*, 1995--2005).  
These include 15 species that we could not match with historically collected taxa from

350 Roraima and are in further need of study by specialists. They are indicated in Online  
Resource 1 as 'sp.' At least one of these has been identified as a species new for  
science, the orchid *Epidendrum* sp. (G. Carnevali, personal communication). Five  
families of plants were collected for the first time on the summit, Juncaceae,  
Rhamnaceae, Rosaceae, Solanaceae, and Symplocaceae, as well as 15 genera  
355 (Asteraceae: *Gnaphalium*, *Mikania*, *Sonchus*; Ericaceae: *Sphyrospermum*;  
Melastomataceae: *Tibouchina*; Bromeliaceae: *Lindmania*, *Racinaea*; Cyperaceae:  
*Eleocharis*; Orchidaceae: *Elleanthus*, *Eriopsis*, *Gomphicis*; Poaceae: *Avenella*, *Cinna*,  
*Vulpia*; and Dennstaedtiaceae: *Paesia*). Finally, 14 taxa collected represent new  
additions for the Roraima summit flora at the species level (Asteraceae: *Stenopadus*  
360 *sericeus*; Lentibulariaceae: *Genlisea repens*, *Utricularia pubescens*; Piperaceae:  
*Peperomia rotundata*; Rubiaceae: *Psychotria aubletiana*; Cyperaceae: *Rhynchospora*  
*schomburgkiana*; Orchidaceae: *Brachionidium longicaudatum*, *Crocodeilanthe moritzii*,  
*Epidendrum attenuatum*, *Trichosalpinx* sp.; Dryopteridaceae: *Elaphoglossum*  
*paleaceum*; Grammitidaceae: *Cochlidium attenuatum*, *C. furcatum*; Lycopodiaceae:  
365 *Lycopodium clavatum*). Six of the new summit records are from previously collected  
herbarium specimens that were not seen by treatment authors during the preparation of  
the FVG or were collected subsequent to its publication; these are *Elaphoglossum*  
*paleaceum*, *Lycopodium clavatum*, *Mikania lucida* (Delascio Chitty, 1991), *Poa annua*  
and *Polypogon elongatus* (Delascio Chitty & Nozawa, 2010) and *Rhamnus ulei*. We did  
370 not locate 26 species that had been collected during previous expeditions.

#### *Exotic species' richness*

Among the 227 species recorded, we consider 13 to be exotics, representing 5.7% of the  
summit flora of Roraima. They are: *Gnaphalium elegans* and *Sonchus oleraceus*

375 (Asteraceae), *Rhynchospora schomburgkiana* and *Eleocharis filiculmis* (Cyperaceae),  
*Juncus effusus* (Juncaceae), *Avenella flexuosa*, *Cinna poiformis*, *Poa annua*, *Polypogon*  
*elongatus* and *Vulpia myuros* (Poaceae), *Rubus urticifolius* (Rosaceae), and  
*Lycopersicum esculentum* and *Solanum tuberosum* (Solanaceae). With the exception of  
380 *Poa annua* and *Polypogon elongatus*, which were recently reported at the Roraima  
summit (Delascio Chitty & Nozawa, 2010), the rest of exotic species are here reported  
as new records for the ETC summits. All of them have broad geographical distributions  
outside of the Guayana Shield, with the exception of *Rhynchospora schomburgkiana*,  
which heretofore was considered a lowland species (0--200 m elevation) from the upper  
Rio Negro in Brazil, Venezuela and Colombia, and in Guyana. As shown in Figure 4,  
385 the exotic species found atop the Roraima are distributed around camping areas, called  
“hotels”.

*Floristic composition, physiognomy, and phytogeography of the ETC summits*

Based on current data, the richest summits of the ETC in terms of vascular plant  
390 diversity are Roraima (227 species), Kukenán (137), and Ilú (128), followed by Yuruaní  
(46), Maringma (40), Tramen (34), and Uei (33). Based on the number of new records  
found on Roraima through intensive fieldwork, we expect the summit flora of all other  
tepuis to increase with further exploration. In particular, the flora of Karaurín may be  
comprised of well over one hundred species, but it has only visited by botanists once  
395 during a brief expedition in 1987, which yielded 14 species. To our knowledge no  
botanical collections have been made on Wadakapiapué, Wei-Assipú, or Yakontipú.  
However, photographs taken by herpetologists on the summit of Wei-Assipú (P. Kok,  
personal communication) show a mosaic of exposed sandstone rock, mixed low  
shrubby/herbaceous vegetation with at least the following species: *Bonnetia roraimae*,



400 *Brocchinia reducta*, *B. tatei*, *Epidendrum* sp., *Everardia* sp., *Microlicia benthamiana*,  
*Nietneria* sp., *Orectanthe sceptrum*, *Connellia augustae*, *Heliamphora nutans*, *Racinaea*  
*spiculosa*, *Stegolepis guianensis*, *Utricularia humboldtii*, and *Xyris* sp. Some taller  
shrublands can be seen in more protected areas and are likely dominated by *Bonnetia*  
(possibly *B. sessilis*).

405 Species richness on the ETC summits follows the same pattern as above within  
the major vascular plant groups, Dicotyledonae, Monocotyledonae, and Pteridophyta  
(Tables 3--5). Altogether, the ETC summits harbour at least 289 species (Online  
Resource 1). As regards to Dicotyledonae, the summits of the ETC contain 31 families,  
68 genera, and 122 species (Table 3). The richest families are Asteraceae (12 genera, 17  
410 species), Ericaceae (8, 12), Melastomataceae (6, 11), and Rubiaceae (5, 10).

Monocotyledonae are represented by only 10 families, though these include large  
numbers of genera and species (51, 93), especially Orchidaceae (17, 32) (Table 4).  
Other rich families of monocots are Poaceae (12, 12), Cyperaceae (5, 12), Bromeliaceae  
(5, 11), and Eriocaulaceae (5, 9). Finally, Pteridophyta are represented by 15 families,  
415 32 genera, and 74 species (Table 5). Among the ETC summits, Pteridophyta are almost  
exclusively known from only three tepuis, Roraima, Kukenán, and Ilú. Here, two  
families stand out because of their high number of species: Grammitidaceae (7, 16) and  
Dryopteridaceae (2, 10). Gymnospermae have not been found on any ETC summit.  
However, we expect Podocarpaceae, particularly *Podocarpus roraimae* Pilg. to be  
420 found on the lower, forested tepuis (e.g., Karaurín) as it has been collected at the base of  
the wall on Roraima-tepui (*Steysmark 58949*, VEN) at approximately 2000--2350 m  
elevation.

Endemic species richness and abundance of species of wide distribution among  
the Neotropics increases as does total species richness in all biogeographic areas

425 considered for degree of endemism (Table 6). More than half of the species of the ETC  
summits are endemic to the Guayana Shield (155, 53.6%), 100 to Pantepui (34.6%), 37  
to the ETC (12.8%) and 10 to a single tepui (3.5%). The taxa with highest number of  
Pantepui endemic species in the ETC are, for families: Orchidaceae (16), Asteraceae  
(8), Ericaceae (6), and Rubiaceae (5), and for genera: *Epidendrum* (6), *Connellia* (3),  
430 *Cyathea* (3, formerly *Hymenophyllopsis*, see Christenhusz, 2009), *Cybianthus* (3),  
*Paepalanthus* (3), *Stegolepis* (3) and *Xyris* (3). There are no genera endemic to the ETC,  
though *Connellia* (Bromeliaceae) appears to have a centre of diversity in the ETC with  
three of its five species commonly found on most of the ETC summits. Both the number  
of endemic species and degree of endemism is higher on Roraima than on other of the  
435 ETC summits. The Roraima flora also has the highest percentage of exotic and the  
highest percentage of widely distributed neotropical species, representing 5.7% and  
44.9% of its summit vascular flora, respectively.

Three categories of growth forms were recognized among the ETC flora, namely  
trees, shrubs, and herbs. Their corresponding physiognomic plant communities are low-  
440 growing forests, shrublands, and meadows, with the latter divided into gramineous and  
non-gramineous meadows. The ETC contains a total of 276 native species, distributed  
in 183 herbaceous (66.3%), 82 shrubby (29.7%), and 11 forest species (4.0%).  
Abundance of herbaceous and shrubby species is unequally distributed among the ETC  
summits, as shown in Figure 5. Significant differences ( $\chi^2 = 4.137$ ;  $p = 0.042$ ) of the  
445 abundance of herbs were found between Roraima, Kukenán, Ilú, Maringma, and  
Tramen (average of 63.3% herbaceous species), and Yuruaní, Uei, and Karaurín  
(42.9%). The latter three tepuis have similar percentages of herbaceous and shrubby  
species. Relatively few species of trees are present on the ETC summits, with similar  
abundances among tepuis, except for Karaurín, where no trees have been recorded.

450 We found a positive relationship between species richness and summit area at  
the scale of the ETC summits. Determination coefficients and significance of the  
relationship are given for log-log transformation of data:  $r^2 = 0.640$ ;  $p = 0.031$  with the  
total set of ETC species, and  $r^2 = 0.516$ ;  $p = 0.069$  using Pantepui endemics (Fig. 6).  
Finally, the analysis of floristic similarity based on Sørensen coefficients indicates a  
455 relatively high floristic affinity between the summits of Roraima and Kukenán (SSC =  
0.69), Roraima and Ilú (SSC = 0.60), and Ilú and Kukenán (SSC = 0.62). Floristic  
similarity was relatively low for the remainder of tepui combinations.

#### *Phytogeographic patterns in Pantepui*

460 As depicted in Figure 7, 24 clusters of Pantepui endemic species were obtained. Their  
abundance and distribution indicate that the Pantepui endemic flora has very marked  
local distribution patterns. Districts are not grouped by endemic floras, rather the  
opposite; they have almost no endemic species in common. Despite that, some tepui  
clusters have been established based on their values of Raup-Crick floristic similarity.  
465 In the Eastern district, these groups are: 1) Roraima-Kukenán-Yuruaní, Karaurín-Ilú-  
Tramen, Uei, and Sierra de Lema; 2) Carrao-Ptarí, Los Testigos massif, Auyán massif,  
Uaipán, and Aprada; and 3) Chimantá massif and Angasima. In the Western district: 4)  
Guanay, Yaví, and Yutajé-Coro Coro; and 5) Cuao and Sipapo. In the Jaua-Duida  
district: 6) Jaua and Sarisariñama; and 7) Huachamacari, Duida, and Marahuaka.  
470 Noticeably, the updating and validation of the Pantepui database indicate that 17% of  
the Pantepui flora and 65% of the Pantepui endemic species are local endemics, that is,  
distributed over a single tepui or tepui massif.

## **Discussion**

475 *Comparison of past-present-future botanical data*

Roraima is the tepui with the oldest botanical collections from its summit. In addition, it is probably the best known botanically due to the high number of expeditions (more than 50 since 1884), relative to the rest of tepuis. However, despite the abundant floristic information available on Roraima summit, an updated compilation has not been  
480 prepared since 1966 and that was based on field work carried out only through 1944 (Steyermark, 1966), long before any of the central or northern portions of the summit had been explored. Thus, we initiated a study of baseline diversity and endemism for future comparisons which included field and herbarium activities.

The Roraima summit is relatively small (34.4 km<sup>2</sup>) in comparison with other  
485 summit areas of Pantepui, which range from 200 to 500 km<sup>2</sup> (Huber, 1995a). This gives to the summit of Roraima certain advantages for repeated surveys for comparison with historical data, as it can serve, in a sense, as a permanent plot for vegetation monitoring, until homologated permanent plots can be installed (for example, 1 x 1 m quadrats required by GLORIA). However, some authors have questioned the applicability of  
490 historical plant records for comparative studies, due to uncertainties of their completeness and reproducibility (e.g., Vittoz *et al.*, 2008). According to Stöckli *et al.* (2011), historical data must meet two basic requirements. First, it must be reliable to be treated as presence/absence data (species not listed must be absent and not just unrecorded), and second, exact collection sites must be traceable. The second  
495 requirement may not be a major problem with the collections of Roraima. Although the oldest ones were not accompanied by geographical coordinates, collection areas may be delimited with certain confidence, thanks to the site descriptions made by collectors themselves in the labels of herbarium specimens or in expedition reports, and the difficulty in traversing the plateau by foot south to north.

500            Nevertheless, the first requirement may represent a limitation in the use of  
historical data. In mountain ranges of temperate zones, the lower floristic diversity  
(Nagy *et al.*, 2003), together with a longer and prolific botanical tradition (e.g., Stöckli  
*et al.*, 2011, in the Alps), suggest that many early twentieth century inventories are  
reliable, therefore, that any new species subsequently found will not be the product of  
505 incomplete previous inventories. This is neither the case of Pantepui nor of Roraima.  
Indeed, the exploration of Pantepui still enables the discovery of species hitherto  
unknown to specific places, as shown by the current 24% increase in species richness at  
the Roraima summit through our surveys. This does not detract from historical data,  
though. Comparative studies may use a representative sample of known species, for  
510 example based on their ecological function, abundance, distribution, or biological  
characteristics. Another possibility would be to use the total set of species, but then new  
species records must be individually studied, identifying the processes that may have  
led them to the summit, raising the corresponding hypothesis and seeking ways to test  
them. Undoubtedly, this process involves more work and time, but is required to make  
515 the most of such valuable data.

In the case of Roraima, four reasons emerge that can potentially explain the new  
records: 1) upward climate-induced migration from lower altitudinal levels, 2) natural  
migration processes, 3) intentional or unintentional translocation by humans and 4)  
omissions in previous explorations. Except for hypothesis 4, where species would have  
520 not moved at all (they were already present, but we did not know), the rest of  
hypotheses involve range displacements. In hypotheses 1 and 2, species would have  
arrived by their own means, whereas in hypothesis 3 they would have been transported  
by humans. All three hypotheses may be tested by comparing past botanical collections  
with the baseline of diversity and endemism established for the Roraima summit. For

525 example, some species were seen many times on southern slopes and base of walls, but  
not on the summit during historic expeditions, and have been repeatedly observed in the  
southern part of the summit during modern expeditions, indicating that they could have  
migrated from lower elevations (hypotheses 1 or 2). Specific knowledge of dispersal  
method and rates, local abundance and distance from the natural (previously known)  
530 range may be helpful to further differentiate each hypothetical case. Specifically, to  
disentangle hypotheses 1 and 2 a long-term monitoring of the species along an  
altitudinal transect, spanning from the base to the summit of Roraima, and establishing a  
record of the local climatic conditions, would provide the most accurate information to  
evaluate if there is an upward migration.

535 On Roraima, exotic species are found largely growing around camping sites (Fig. 4),  
which would suggest that humans have been the main vector. On the time scale of  
decades (the focus of invasive plant ecology), examples of exotic taxa introduced  
without associated human activities have been rare (but see Whittaker *et al.*, 1989).  
However, the high rates at which many plant taxa are being forced to move uphill due to  
540 ongoing global warming (1 to 5 m elev./yr) (Beckage *et al.*, 2008; Kelly & Goulden,  
2008; Lenoir *et al.*, 2008) shows that, changes of geographical and/or elevational ranges  
due to non-direct human action may also occur at short time scales, thus suggesting the  
need for a case-by-case study of their characteristics in order to evaluate whether human  
actions or natural migration have been the effective cause of introduction. The  
545 following section describes our knowledge of the invasiveness characteristics and status  
in the tepui ecosystems (casual, naturalized, invasive) of each of the exotic species that  
we found on the Roraima summit, and hypothesizes their potential causes of  
introduction.

550 *Assessment of exotic species*

We consider the potato (*Solanum tuberosum*) and tomato (*Lycopersicon esculentum*), both Solanaceae, to be casual exotics. Cultivated plants are generally highly dependent on humans for their survival in wild conditions (Crawley *et al.*, 2001; Gepts & Papa, 2002). Therefore, we consider it unlikely that these two species will be able to further  
555 propagate, except possibly for vegetative propagation of *Solanum tuberosum*. Additionally, the cultivated plants, especially those genetically modified, entail hybridization or introgression concerns with their wild relatives, conferring them characteristics such as resistance to herbivory by insects, fungi, etc. (Stewart *et al.*, 2003). However, the absence of native taxa of the Solanaceae family at the Roraima  
560 summit discards this possibility.

*Sonchus oleraceus* (Asteraceae) is of European origin, though now widely considered as cosmopolitan (Aristeguieta, 1964). This is the first report of the genus for the Venezuelan Guayana, however, its presence was expected due to its widespread distribution and weedy nature (Pruski, 1997; Badillo *et al.*, 2008). The species is wind  
565 dispersed by means of the feathery pappus on the fruit (achene), and reportedly the maximum dispersal distance of an individual plant is up to 7 m in controlled conditions (Sheldon & Burrows, 1973). According to Bullock & Clarke (2000), the maximum dispersal distance measured for a non-tree anemochoric plant is 80 m. Given that there were no previous reports of the species in the Guayana Shield, natural dispersal from  
570 the nearest population seems unlikely so its introduction is probably due to human causes. It cannot be considered yet as naturalized because of the lack of previous reports and further its incipient colonies.

*Gnaphalium elegans* (Asteraceae) has a wide distribution among the Neotropics. In Venezuela, it mostly grows at the Coastal Range and the Andes (Pruski, 1997). As in

575 the case of *Sonchus oleraceus*, introduction by long-distance dispersal events may be  
uncommon given the large distance between the source populations and Pantepui. It is  
also found at high elevations on Sororopán-tepui, and Auyán-tepui, where it is reported  
to be abundant, but we consider these populations exotic as well, due to the limited  
wind dispersal capacity. In the Roraima summit, we documented it from a small  
580 population at a single hotel, which suggests human introduction and non-naturalized  
state.

*Rhynchospora schomburgkiana* (Cyperaceae) is naturally distributed in the  
lowlands of the Amazonas State of Venezuela, adjacent Colombia, Guyana, and  
northern Brazil (Thomas, 1998). Our collection from the summit of Roraima represents  
585 a significant change in the upper elevational range limit, from 200 to around 2700 m.  
We found it growing exclusively around the Roraima summit hotels, and suspect  
humans are the most probable cause of introduction. Pyšek *et al.* (2004) considered that,  
for exotic species to be considered naturalized, a 10-year period of persistence at a site  
may be required, which would reflect possible negative effects of short-term  
590 ‘catastrophic events’ (e.g., climatic extremes, outbreak of pests and pathogens). Despite  
the lack of previous reports, we believe that, for conservation purposes, this viviparous  
species found growing around numerous hotels on the Venezuelan side, should be  
considered as naturalized on Roraima.

*Eleocharis filiculmis* (Cyperaceae) is the most widespread species of the genus  
595 in the Venezuelan Guayana. However, prior to our surveys it was not known to exceed  
1400 m elevation (González-Elizondo & Reznicek, 1998). Its presence on the Roraima  
summit is likely due to human causes, as it was only found growing in the vicinity of a  
hotel. It cannot be considered naturalized.



*Juncus effusus* (Juncaceae) is a cosmopolitan species, common in northern  
600 temperate regions and found at high elevation of the tropics (Balslev, 1996). In  
Venezuela, it is known to be a species of the cool highlands of the Andes and the  
Coastal Range. On Roraima, it was observed forming small colonies at disturbed camp  
areas and their surroundings; as such, we postulate its presence is due to human  
activities. Its status in the ecosystem is not easy to establish, given the lack of previous  
605 reports. However, its presence in two hotels (being the population of Hotel Basilio  
particularly vigorous), together with its rhizomatous nature and its consequent potential  
for vegetative reproduction, suggest it to be treated, at least for conservation purposes,  
as naturalized.

*Rubus urticifolius* (Rosaceae) was widely reported on the slopes of Roraima by  
610 many collectors (e.g., Im Thurn, 1885), but never on the summit. Though our collection  
is the first known record of the species on the summit, we consider it fully naturalized  
given the presence of spiny thickets many meters in diameter at several hotels. In  
addition, the records from the slopes suggest that the species will be able to survive and  
reproduce consistently on the summit. This species produces drupelet-like fruits which  
615 are eaten and dispersed by birds (Rincón, 2005), while other species of the genus  
showing similar fruits are dispersed by mammals as well (Brunner *et al.*, 1976; Fedriani  
& Delibes, 2009). The populations of the Roraima summit may have been transported  
either by the mammals (coatis) or birds reported for the zone. However, it is worth  
noting that many of them were located around hotels, thus suggesting that the species  
620 was carried to the summit by humans from populations on the slopes.

We found five species of Poaceae in as many genera growing widely around the  
hotels, all of which are considered exotic to the Venezuelan Guayana. *Avenella*  
(*Deschampsia*) is a new genus record for Venezuela and *Cinna* and *Vulpia* are new

genus records for the Venezuelan Guayana. *Poa annua* and *Polypogon elongatus* were  
625 previously reported to occur on the Roraima summit by Delascio Chitty & Nozawa  
(2010). The first three mentioned were found only around hotels and were possibly  
introduced by humans. They cannot yet be considered naturalized due to the lack of  
historic records from the area and the small number of individuals seen. However,  
*Avenella flexuosa* is of concern because of its pseudo-viviparous reproduction, a  
630 mechanism that allows the generation of progeny without crossing. To our knowledge  
this is the first report of pseudo-vivipary in this species.

In its natural range, *Avenella flexuosa* commonly grows below 1000 m elevation  
in all continents, including Argentina and Chile in South America (Cialdella & Zuloaga,  
2010). However, we found it around 2700 m elevation, which coincides with a similar  
635 report from Costa Rica at nearly 3000 m elevation (Davidse & Pohl, 1994). In the case  
of *Cinna poiformis*, it is distributed from Mexico to Bolivia (Brandenburg *et al.*, 1991).  
In Venezuela, it is known from cool regions of the Andes and the Coastal Range. On  
Roraima, we found several clumps in different spaces of the same hotel. Finally, *Vulpia*  
*myuros* is native to Europe and Northern Africa (Lonard, 2007).

640 Both *Poa annua* and *Polypogon elongatus* are distributed naturally in cool  
regions of the Andes and the Coastal Range. *Poa annua* is an introduced and naturalized  
species in the New World (Soreng *et al.*, 2003), whereas *Polypogon elongatus* has an  
American origin, growing from southern U.S.A. to Argentina. *Poa annua* was first  
reported as possibly occurring on the summit in 2002 (Davidse *et al.*, 2004) and the first  
645 herbarium vouchers for both species were reported in 2008 (Delascio Chitty & Nozawa,  
2010). At present, both species have relatively extensive populations and are present  
around almost all hotels. *Polypogon elongatus* has exceeded the dispersion rate  
suggested by Richardson *et al.* (2000) and Pyšek *et al.* (2004) to be considered invasive

( $>100$  m from parent plants in  $<50$  years) and *Poa annua* will likely do the same in the  
650 next few years if no management actions are undertaken. Both are well-known invasive  
plants (Schroeder *et al.*, 1993; Holm *et al.*, 1997), with *Poa annua* already recognized  
as such in Venezuela (Ojasti, 2001). Therefore, we consider them to be invasive or  
potentially invasive on Roraima, following the Precautionary Principle (Cooney, 2004).  
Fortunately, neither has been found in undisturbed areas of the summit.

655 In summary, as almost all of the exotic species are new reports for the ETC, the  
nearest populations, which are found hundreds of kilometres away, should have suffered  
long-distance dispersal events to reach the Roraima summit in a natural way. According  
to Cain *et al.* (2000), these can be achieved through wind (anemochory), water  
(hydrochory) or vertebrates (zoochory) dispersal. Hydrochory would not seem to be an  
660 option given the  $>2700$  m elevation at which the Roraima summit is found, and long-  
distance dispersal by wind would not seem to be as common as previously thought  
(Bullock & Clarke, 2000; Renner, 2004). In depth studies would be required to reach  
sound conclusions about dispersal agent, and population genetics may help to establish  
the relationships between the populations of the Roraima summit and the neighbouring  
665 ones. At the moment, all the available data points towards a human-mediated  
introduction of these species.

#### *Floristic and physiognomic patterns of the ETC summits*

Table 7 summarizes the taxonomic richness by traditional major groups (gymnosperms,  
670 angiosperms, and pteridophytes) in different biogeographic units, namely the Roraima  
summit, the ETC summits, Pantepui, and the Venezuelan Guayana. All of them exhibit  
a higher diversity of angiosperms (A) than of pteridophytes (P). The ratio A/P increases  
as does the area of the biogeographic units considered, which suggests that the tepui

summits, and especially the ones with patches of vegetation and rocky habitats like  
675 Roraima, are comparatively more prone to harbour higher diversity of pteridophyte  
species. As for gymnosperms, the Venezuelan Guayana has relatively little diversity  
overall, with only three native families, each one represented by a single genus:  
Gnetaceae (*Gnetum*: 7 spp.), Podocarpaceae (*Podocarpus*: 10 spp.), and Zamiaceae,  
(*Zamia*: 4 spp.) (Hokche *et al.*, 2008). Together they account for just 21 species. This  
680 level of diversity is similar to that of Peru and the Guianas, with 17 species in four  
families native to Peru (Brako & Zarucchi, 1993), and only four species in two families  
native to the Guianas (Boggan *et al.*, 1992). However, both *Gnetum* and *Podocarpus* are  
known widely from other tepuis and tepui slopes ranging up to 1800 m and 2700 m  
respectively, and quite possible will be found in the ETC.

685 At the ETC level, the available information points towards a higher species  
richness on Roraima, Kukenán, and Ilú. Nogué *et al.* (2009), applying the species-area  
relationship to the area of Pantepui at 100 m elevation intervals, and Riina (2003), using  
tepui summit areas, proved that a significant positive relationship existed between area  
and species richness in Pantepui. Our data also support this relationship at the scale of  
690 the ETC summits (Fig. 6), on the understanding that a wider botanical knowledge of the  
ETC summits as a whole may introduce some variation in the patterns of species  
richness and endemism derived from the currently available data. In addition, local  
endemism at species level on the summit of Roraima (2 species, 0.9%) (Table 6) is  
much lower than that previously proposed by Gleason (68--90%; Gleason, 1929) or  
695 Steyermark (54%; Steyermark, 1966). These high estimates were the result of  
incomplete knowledge of tepui species distribution at the time, and we expect further  
exploration on summits and slopes to yield lower levels of endemism than currently  
believed for other tepuis as well.

Distribution and abundance of the three growth forms (herbs, shrubs, and trees) show differences among the ETC tepuis, which may be explained by the tepui morphology and the ecological requirements of each vegetation type. The dwarf, evergreen, high-tepui forests and shrublands grow commonly in organic soils (histosols) of black peat overlying sandstone, which are generally restricted to wind-protected sites or depressions (Huber, 1995b). Soil availability, its nutrient content, wind, and solar radiation are thus the main factors limiting the distribution of these plant formations atop the rocky summits of the ETC. Herbaceous vegetation types dominated by grasses and/or sedges (Poaceae and Cyperaceae) occur sporadically in upper montane localities of Pantepui (Huber, 1995b). On the ETC, they clearly play a secondary role in most of the herbaceous plant communities, although they can be successful under some particular site conditions, for example, in periodically water-logged areas of peat located in wide valley bottoms, as in the case of *Cladium costatum* (Cyperaceae) and of *Cortaderia roraimensis* (Poaceae) on Roraima. Non-gramineous meadows are very characteristic of the vegetation of the Venezuelan Guayana. In the highlands, species of Rapateaceae, an entirely herbaceous monocot family, have reached a great degree of differentiation and predominate in the herb layer (Huber, 1995b, 2006). On the rocky, open, and windswept plateaus of Roraima, Kukenán, Yuruaní, Ilú, and Tramen, meadows are distributed in small patches of herbaceous and subshrubby species growing preferably on shallow to deep, extremely acidic and water-saturated organic soils, although in some cases they may be found growing on rocky substrates, performing as pioneer species (Huber, 2006). The herbaceous vegetation on Uei is notably different from that of the rest of tepuis of the ETC, as it contains different floristic composition and soil characteristics; its summit is covered by a relatively thick brown soil which is absent in the other tepuis (Huber, 2006). In addition, Uei is

separated from the remaining tepui chain by a distance 20 km, whereas the remaining  
725 tepuis are separated from one another by distances of 1--9 km.

Based on the vegetation descriptions of Huber (1995*b*, 2006), six tepuis  
(Tramen, Ilú, Yuruaní, Kukenán, Roraima, and Wei-Assipú) have rocky summits with  
herbaceous vegetation along with patches of shrub or elfin forest in protected places,  
whereas the rest (Karaurín, Wadakapiapué, Yakontipú, Maringma, and Uei) are  
730 completely covered with a combination of shrublands and tepui meadows. This pattern  
is well reflected in the analysis of growth forms depicted in Figure 5. The only  
discrepancies in our results with respect to the patterns described above are the  
relatively low abundance of shrubs on Maringma, showing a distribution of growth  
forms similar to the rocky plateaus, and the predominance of shrubs over meadows in  
735 Yuruaní, a tepui with a rocky summit that shares most features with Roraima and  
Kukenán. For the moment, these facts may not be resolved with the available data.  
Potential changes in the composition of the mentioned tepui communities atop the ETC  
summits, associated to individual responses to climate change, may be detected by  
comparing present and future relative abundances of species with different growth  
740 forms, or alternatively by measuring the cover of each physiognomic type on a regular  
basis, either directly on the ground or through the analysis of aerial photographs.

### *Phytogeographic patterns*

According to our results, Pantepui shows a high degree of endemism, with many plant  
745 species being local endemics. This characteristic of the Pantepui flora has attracted the  
attention of many researchers, though most of them formed their hypotheses using  
present-day botanical and phytogeographical studies (see Rull, 2004*a*). To date the only  
model using evidence of the past that attempted to explain the biogeographic patterns of

Pantepui and the origin of its high endemism of vascular plants was based on  
750 Quaternary glacial/interglacial cycles, assuming that species shifted proportionally to  
temperature changes. One-hundred and three cold and warm stages have alternated  
since the beginning of the Quaternary 2.588 Ma, with a frequency of 41,000 years until  
1 Ma, and 100,000 years after that (Lisiecki & Raymo, 2005). On the top of the tepuis,  
it is likely that open ground predominated even during glaciations, as no geologic or  
755 geomorphologic feature demonstrating the presence of past ice sheets has ever been  
documented. According to the above-mentioned model, downward migration of species  
during glacial phases promoted sympatric speciation, hybridization, and polyploidy,  
whereas vicariance occurred during interglacials, when species moved upwards. This  
would have resulted in a net increase of diversity and endemism favoured by the  
760 complex topography and habitat heterogeneity of Pantepui (Rull, 2004a, 2004b, 2004c,  
2005). It is worth noting that the role of Quaternary climatic cycles in neotropical  
diversification has been already stated in several phylogeographic studies (e.g.,  
Richardson *et al.*, 2001; Givnish *et al.*, 2004, 2011; Noonan & Gaucher, 2005, 2006).  
On this basis, Rull & Nogué (2007) conducted a detailed physiographical study to  
765 reconstruct the potential migration routes and barriers of the Quaternary in Pantepui and  
found that a significant 40% (164 species) of present high-altitude local endemics were  
unable to migrate, even during glaciations when temperatures in the Neotropics were  
about 5--6 °C lower than today (Farrera *et al.*, 1999, for the last glacial maximum,  
21,000 years BP). In other words, 81% of the isolated flora (unable to migrate even  
770 during glacial maxima) is comprised of local endemics. Indeed, our results show a high  
percentage of agreement with the hypothesis of migratory routes and barriers suggested  
by these authors.

For example, the disappearance of temperature-induced barriers to migration for vascular plants among the four districts occurred when species moved down 900 m  
775 below their current ranges, so that only the species with current lower altitudinal distribution level below 1700 m could take advantage of the migration pathways for gene flow among districts. Therefore, the magnitude of the potential genetic interchange between highland and lowland species throughout the different districts of Pantepui must have been quite limited, thus explaining their high present-day floristic  
780 differentiation, especially concerning Pantepui endemics (Fig. 7). As regards to the ETC, the tepuis that comprise it kept their migratory routes opened during most of the Quaternary (Nogué & Rull, 2007); a barrier between Roraima-Kukenán-Yuruaní and Karaurín-Ilú-Tramen only appeared when temperature increased such that the difference with respect to the present one was lower than 1.6 °C. The maintenance of migratory  
785 routes between these two groups of tepuis, together with their geographic proximity, may have defined their present-day similar composition of endemics. Uei-tepui, for its part, has gradual slopes for the most part that connect the summit to the surrounding lowlands, and as mentioned is relatively isolated from the rest of the tepuis of the ETC. This may explain the low number of Pantepui endemics on its summit (4) and the  
790 floristic differentiation with respect to the neighbouring tepuis. The Guaiquinima massif, a large massif of 1096 km<sup>2</sup> and 1650 m elevation, is one of the most dissimilar tepuis in terms of floristic composition. This may be due to its geographic isolation from the rest of tepuis, with marked valleys in between (Vegas-Vilarrúbia *et al.*, 2012), and the fact that its summit is connected to the Gran Sabana lowlands, and is mainly  
795 covered by upland forest species; only a portion of 50 m<sup>2</sup> of its summit belongs to the high-tepui biome.



Overall, local endemism in Pantepui have more weight than endemism at Pantepui level. The percentage of local endemism obtained for Pantepui (17%) strongly supports the vision of Pantepui as a continental archipelago (Rull, 2010). Indeed, the island/archipelago pattern of endemism in Pantepui is similar to those of oceanic islands, as supported by its proportion of endemic species (30% Pantepui endemics) in comparison with other islands such as the Galápagos (40%), Cape Verde (30%), Jamaica (27%), or Seychelles (15%) (Whittaker & Fernández-Palacios, 2007). We suggest that patterns of vascular plant diversity and endemism in Pantepui should be ideally studied using island biogeography techniques. Recently, species-area relationships were applied to the Pantepui flora to estimate biodiversity loss through potential habitat loss by global warming (Nogué *et al.*, 2009). Another possibility would be to analyse nestedness patterns (Patterson & Atmar, 1986), which has been mostly applied to studies on insular archipelagos (Wright *et al.*, 1998 and literature therein) and which could have implications on the conservation of the Pantepui biome. For example, nestedness indexes may inform the decision of whether single large conservation areas are more effective in preserving biodiversity than several small areas. A strong degree of richness-ordered nestedness (where data matrix is ordered by the size of the flora or fauna) would imply that most species could be represented by conserving the richest (largest) patch. Conversely, a low degree of nestedness would mean that particular habitat patches contain different species sets and that several reserves of differing size and richness may be required to maximize regional diversity (Whittaker & Fernández-Palacios, 2007). In this regard, Vegas-Vilarrúbia *et al.* (2012) suggested the Chimantá massif as a potential refugium for the Pantepui flora, due to the possible large remaining habitat (43%) after the 4 °C temperature increase forecast for the area by the end of this century by the A2 IPCC scenario. The analysis of distributional patterns of the Pantepui

endemic flora may provide additional criteria to support or readjust the recommendations derived from the study of Vegas-Vilarrúbia *et al.* (2012).

As regards to the ETC, summit area explains quite well the differences in  
825 species richness on the ETC summits (Fig. 6). However, the study of the  
phytogeographical patterns of the ETC, as well as of Pantepui, would greatly benefit  
from a multivariate direct gradient analysis, which deal simultaneously with species and  
many environmental variables (Jongman *et al.*, 1995; Quinn & Keough, 2002). For the  
moment, elevation and summit area are the only ones readily available. We carried out a  
830 preliminary Detrended Canonical Correspondence Analysis (DCCA) with these two  
variables and the ETC summit species but it did not provide much novel information.  
Therefore, a better understanding may be developed by analysing additional factors,  
such as soil and microclimate. Additionally, information about dispersal mechanisms is  
still largely unknown for the native Pantepui plant species, thus preventing the  
835 estimation of a more realistic dispersal capacity and migration rates. DNA-based  
phylogeographical studies are also lacking, which would significantly improve our  
understanding of the present-day biogeographic, richness, and endemism patterns of the  
Pantepui flora.

#### 840 *Conservation opportunities*

Tourism activities throughout Pantepui have increased in recent decades, in parallel  
with the decrease of scientific expeditions (Rull, 2010). Unfortunately, the effects of  
tourism were markedly evident on the Roraima summit during our visits, increasing  
noticeably even from 2011 to 2012, especially the trampling of vegetation. Effects of  
845 such trampling on tepuis, even without recurrence may take longer than several decades  
to recover (Gorzula & Huber, 1992). As well, we noticed the presence of garbage, food

scraps, toilet paper, human excrement, graffiti, and abundant exotic species around camping areas, as well as mining equipment found sequestered away from the camps. Invasive plants may have the potential to reduce fitness of native species by reducing  
850 their populations, while overcoming the environmental barriers imposed by acidic and poorly developed soils, limited nutrient availability and high solar radiation. Therefore, given the remarkable diversity, endemism, and uniqueness of the tepui flora (Berry *et al.*, 1995; Huber, 1995*b*), the tourism impacts discovered during this study on the Roraima summit have major implications for tourism management and conservation of  
855 the Pantepui flora as a whole.

In accordance with the Venezuelan National Strategy 2010-2020 for the Conservation of Biodiversity (MINAMB, 2010), we recommend that management of exotic species on Roraima be based on four strategies: 1) prevention of new introductions, 2) early detection of new populations, 3) monitoring of existing  
860 populations, and 4) containment or eradication of the most aggressive species. To prevent the arrival of new propagules, vectors and introduction pathways need to be evaluated to determine their level of introduction potential. In this regard, proximity of the exotic species to hotels (Fig. 4) suggests that propagules are transported by humans. Unlike lowland areas where arrival/departure points may be numerous, tepui summits  
865 have very few points of access, which means that preventive actions could be focused. In the case of Roraima, ascent to the summit is largely by foot. Lesser visitation is by helicopter, though with typically lesser levels of oversight. Cooperation of park managers and tourist guides at an early stage is essential in raising awareness among tourists. Surveys to detect new populations and the monitoring of the existing ones  
870 should be conducted on a regular basis, especially of the camp surroundings. Any control action upon exotic populations should be subjected to an environmental impact

assessment (Erickson, 1994), and to a prioritization of the significance of their potential impact and feasibility of controlling or managing their populations (e.g., Hiebert & Stubbendieck, 1993; Brunel *et al.*, 2010).

875           The majority of the Roraima exotics may be easy to eradicate because of the low number of individuals and the restricted areas of distribution. However, eradication of *Rhynchospora schomburgkiana* and *Polypogon elongatus* may be more difficult. *Rhynchospora schomburgkiana* is an herb of short stature which can be easily pulled from the soil. Yet, the same short stature makes it inconspicuous and small clumps may  
880           escape the human eye. The goal for *Polypogon elongatus* should also be the containment of its population. Nevertheless, there are two incipient populations for which we recommend eradication. The first one is at Hotel Coatí, represented by a few sparse clumps, and the second is located far from the camps along the pathway to the ‘Jacuzzis’. Populations at the remaining hotels should be contained or eliminated,  
885           particularly those at the Hotel Indio, which appear to be especially vigorous. Based on our observations and using the framework proposed by Hiebert & Stubbendieck (1993), we provide a preliminary prioritization of control actions in Figure 8.

          Overall, existing knowledge of these species and their invasiveness, although limited, should be enough to start controlling proactively their populations, for various  
890           reasons. Firstly, prompt implementation of eradication actions, that is, when number of individuals is low and the species is still in the naturalized phase, normally leads to better outcomes (McNeely *et al.*, 2001). In this regard, time lag for tropical plant invasions may be much shorter than previously thought (5 and 14 years for herbaceous and woody plants, respectively) (Daehler, 2009). Secondly, the rugged terrain and  
895           remoteness of Roraima summit may make containment and eradication especially costly and difficult; and finally, the autochthonous flora of the Roraima summit is composed

of many endemic species, which are in turn threatened by potential climate-induced habitat fragmentation and/or loss, and the possible migration to higher elevations of competitors and pathogens. Indeed, potential synergies between human-mediated  
900 invasions and climate change could produce non-linear, mutually reinforcing ecological responses (Brook *et al.*, 2008; Walther *et al.*, 2009 and literature therein), which in our case may radically change the diversity and endemism patterns on the tepui summits, as well as the composition of their unique communities. In view of these forecasts, a permanent monitoring site assessing the response of native and non-native tepui flora to  
905 climate change could be implemented since, to our knowledge, very few studies have addressed this issue in flat-topped and vegetated mountain summits (but see Kreyling *et al.*, 2010). In this context, the Roraima summit should be conceived as a pilot study to assess the possibility of adhesion to GLORIA. At the moment, the option of monitoring plots is being considered for all Pantepui. An equally interesting and desirable option  
910 would be to establish and monitor the upper and lower limits of distribution in Roraima of some of its keystone species, but the incomplete floristic knowledge of vegetation growing on its slopes represents a significant limitation. Finally, in order to investigate the tolerance thresholds and estimate the time lag to the forecasted climatic changes, it would be recommendable to establish an envelope of tolerance to combined variations  
915 of abiotic factors in laboratory experiments for the keystone or most endangered species, according to the priority categories previously established by Safont *et al.* (2012). Hence, Roraima has great potential as a natural laboratory where the hypothesis of upward migration and local extinctions may be tested (Rull, 2010), and also offers to scientists and land-managers the opportunity to respond in time to preserve its unique  
920 flora from both climate change and human impacts.

## Conclusions

The only information currently available for Pantepui concerning plant responses to climate change comes from models based on IPCC projections, which predict high  
925 habitat loss by the end of this century associated with significant plant diversity declines on many tepuis (Rull & Vegas-Vilarrúbia, 2006; Nogué *et al.*, 2009; Safont *et al.*, 2012; Vegas-Vilarrúbia *et al.*, 2012). Our inventory establishes a baseline of diversity and endemism on the Roraima summit, which can be compared with past historical plant surveys and herbarium records (dating back to 1884). This, along with future surveys  
930 can help verify whether or not species migrate or become extinct due to climate change. Roraima-tepui is especially suited for comparative studies on the effect of climate change on plant diversity as it harbours a good representation of the flora of Pantepui and because of its long history of botanical collections.

The Roraima summit flora is comprised of 227 known vascular plant species, 42  
935 of which are added to the summit flora as a result of this study, and two others from works published after the completion of the FVG. One of the species, belonging to the genus *Epidendrum* (Orchidaceae), has been confirmed to be new for science. The inventory also confirmed the existence of 13 exotic species, most likely transported by humans, among which *Poa annua* and *Polypogon elongatus* (Poaceae) are noteworthy  
940 due to their invasive potential.

At the present state of botanical exploration, Roraima appears to be the tepui of the ETC with the highest species richness and degree of endemism. The tepuis showing the highest floristic similarity are Roraima, Kukenán, and Ilú. These tepuis, together with Tramen and Maringma, show a dominance of herbaceous species over shrubs,  
945 whereas Yuruaní, Karaurín, and Uei reach similar abundances. The only discrepancies in our results with respect to vegetation descriptions of Huber (1995*b*, 2006) are the

relatively low abundance of shrubs on Maringma, and the predominance of shrubs over meadows in Yuruaní. For the moment, these facts may not be resolved with the available data. Furthermore, we found a significant positive relationship between total species richness and summit area at the scale of the ETC, a result which agrees with the pattern found in Pantepui by Riina (2003) and Nogué *et al.* (2009).

The endemic flora of Pantepui shows very marked local distribution patterns. These patterns are in accordance with hypothesized location and timing of appearance and disappearance of migratory routes in Pantepui during the climatic cycles of the Quaternary (Rull & Nogué, 2007). Our results show that 17% of the Pantepui species and 65% of the Pantepui endemic species are local endemics. Given the archipelago-like pattern of endemism prevailing in Pantepui, the use of island biogeography techniques are recommended to further study floristic patterns.

As for future research, both species and community-level changes taking place at the Roraima summit in the coming decades may be evaluated through the implementation of an integrated monitoring program, including measures of local climate, soil, and vegetation. Although our work focused on a single tepui, results of long-term monitoring on the Roraima summit would be relevant to the whole Pantepui province, and also to the Neotropics, as Pantepui is one of its most diverse and endemic biomes (Berry *et al.*, 1995).

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1325 **Tables**

**Table 1.** Tepuis of the ETC, indicating the countries to which they belong, the elevation and the summit area. Sources: The Survey Department of Guyana (1975); Huber (1995a); Kok (2009); B. Holst (unpublished data derived from Google Earth Pro).

Tepui	Country	Elevation (m)	Summit area (km <sup>2</sup> )
Uei – Ue	Venezuela, Brazil	2250	2.5
Maringma – Mr	Brazil, Guyana	2150	1.3 <sup>a</sup>
Yakontipú – Yk	Brazil, Guyana	2320 <sup>a</sup>	0.5 <sup>a</sup>
Wei-Assipú – We	Brazil, Guyana	2280	1.5 <sup>a</sup>
Roraima – Ro	Venezuela, Brazil, Guyana	2810	34.4
Kukenán – Kn	Venezuela	2650	20.6
Yuruaní – Yu	Venezuela	2300	4.4
Wadakapiapué – Wp	Venezuela	2000	<0.01
Karaurín – Kr	Venezuela	2450	1.9
Ilú – Il	Venezuela	2700	4.7 <sup>a</sup>
Tramen – Tr	Venezuela	2700	0.1 <sup>a</sup>
Total ETC			71.9

1330 <sup>a</sup> Estimated from Google Earth Pro.

**Table 2.** Most diverse families and genera of the Roraima summit.

Family	Genera	Species	Genus	Species
Orchidaceae	15	26	<i>Elaphoglossum</i> (Dryopteridaceae)	8
Grammitidaceae	7	16	<i>Epidendrum</i> (Orchidaceae)	7
Asteraceae	10	13	<i>Xyris</i> (Xyridaceae)	6
Cyperaceae	5	11	<i>Octomeria</i> (Orchidaceae)	5
Bromeliaceae	5	10	<i>Peperomia</i> (Piperaceae)	5
Dryopteridaceae	2	10	<i>Pterozonium</i> (Pteridaceae)	5
Poaceae	9	9	<i>Utricularia</i> (Lentibulariaceae)	5
Ericaceae	7	9	Total	41
Pteridaceae	2	8		
Total	62	112		

**Table 3.** Richness of Dicotyledonae on the ETC summits (number of genera/number of species). Tepuis are grouped according to species

1335 richness.

Dicotyledonae (here including Magnoliids and Eudicots)

	Apocynaceae	Aquifoliaceae	Araliaceae	Asteraceae	Bonnetiaceae	Clusiaceae	Cunoniaceae	Cyrillaceae	Droseraceae	Ericaceae	Gentianaceae	Hypericaceae	Lentibulariaceae	Melastomataceae	Myrsinaceae	Myrtaceae	Ochnaceae	Passifloraceae	Phyllanthaceae	Piperaceae	Polygalaceae	Polygonaceae	Rhamnaceae	Rosaceae	Rubiaceae	Santalaceae	Sarraceniaceae	Scrophulariaceae	Solanaceae	Symplocaceae	Winteraceae	Total
Roraima	1/2	1/3	1/2	10/13	1/1	-	1/4	1/1	1/2	7/9	3/3	1/1	2/7	5/7	2/2	1/1	1/1	-	-	1/5	1/1	-	1/1	2/2	4/6	1/2	1/1	-	2/2	1/1	1/1	54/81
Kukenán	1/1	1/2	1/2	7/8	1/1	1/1	1/3	1/1	1/1	8/10	3/3	1/1	2/8	2/3	2/3	1/1	1/1	-	-	1/1	-	-	-	4/4	1/2	1/1	-	-	-	1/1	43/58	
Ilú	1/1	1/2	1/2	6/8	1/1	1/1	1/4	1/1	1/1	7/9	3/3	-	2/4	4/6	2/4	2/2	2/2	-	-	1/4	-	1/1	-	1/1	4/6	1/2	1/4	1/1	-	-	1/1	47/71
Yuruaní	-	1/1	1/2	4/4	1/2	-	1/1	1/1	1/1	4/4	-	-	1/2	2/2	1/2	1/1	2/2	-	-	-	-	-	-	3/4	-	1/2	-	-	-	-	25/31	
Maringma	-	1/1	1/1	2/2	1/1	1/1	-	1/1	1/3	1/1	-	-	1/1	2/2	1/1	1/1	2/2	-	-	-	-	-	-	3/3	-	1/1	-	-	-	-	20/22	
Tramen	-	-	-	1/1	1/1	-	1/1	1/1	1/1	2/3	1/1	-	1/1	3/3	-	1/1	1/1	-	-	-	-	-	-	-	-	1/2	-	-	-	-	15/17	
Uei	-	-	-	4/4	1/1	2/2	-	1/1	-	2/2	-	-	1/1	4/4	1/1	-	-	1/1	1/1	-	1/1	1/1	-	-	-	1/1	-	-	-	-	21/21	
Karaurín	-	-	-	2/2	-	-	-	1/1	1/1	1/1	-	-	-	-	1/1	2/2	-	-	-	-	-	-	-	1/1	-	1/1	-	-	-	-	10/10	
Total ETC	1/2	1/3	1/2	12/17	1/2	2/2	1/6	1/1	1/4	8/12	3/4	1/1	2/10	6/11	2/7	2/2	3/3	1/1	1/1	1/5	1/1	1/1	1/1	2/2	5/10	1/2	1/4	1/1	2/2	1/1	1/1	68/122

1336 **Table 4.** Richness of Monocotyledonae on the ETC summits (number of genera/number  
 1337 of species). Tepuis are grouped according to species richness.

Monocotyledonae											
	Bromeliaceae	Cyperaceae	Eriocaulaceae	Juncaceae	Nartheciaceae	Orchidaceae	Poaceae	Rapateaceae	Tofieldiaceae	Xyridaceae	Total
Roraima	5/10	5/11	5/7	1/1	1/2	15/26	9/9	1/2	1/1	2/7	45/76
Kukenán	5/7	2/3	5/5	-	1/1	14/21	2/2	1/2	1/1	2/7	33/49
Ilú	2/3	3/5	4/6	-	-	8/12	3/3	1/1	-	2/4	23/34
Yuruaní	1/2	-	3/3	-	1/1	2/2	1/1	1/1	1/1	1/2	11/13
Maringma	4/4	2/2	1/1	-	-	-	1/1	1/2	1/1	3/4	13/15
Tramen	2/2	2/3	1/1	-	-	2/3	1/1	1/1	1/1	1/1	11/13
Uei	1/1	1/1	3/3	-	-	1/1	2/2	1/1	-	2/2	11/11
Karaurín	-	1/1	1/1	-	-	-	1/1	1/1	-	-	4/4
Total ETC	5/11	5/12	5/9	1/1	1/2	17/32	12/12	1/3	1/1	3/10	51/93

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1340 **Table 5.** Richness of Pteridophyta on the ETC summits (number of genera/number of  
 1341 species). Tepuis are grouped according to species richness.

		Pteridophyta															
		Aspleniaceae	Blechnaceae	Cyatheaceae	Dennstaedtiaceae	Dicksoniaceae	Dryopteridaceae	Gleicheniaceae	Grammitidaceae	Hymenophyllaceae	Isoetaceae	Lycopodiaceae	Polypodiaceae	Pteridaceae	Selaginellaceae	Thelypteridaceae	Total
Roraima		1/2	1/3	1/4	5/5	1/1	2/10	2/3	7/16	2/6	1/1	3/5	1/1	2/8	1/3	1/2	31/70
Kukenán		1/1	1/1	1/3	1/1	-	2/3	1/1	6/8	1/2	-	2/4	-	2/4	1/2	-	19/30
Ilú		1/1	1/1	1/3	1/1	-	1/1	1/1	4/5	1/1	1/1	2/2	-	2/4	1/1	1/1	18/23
Yuruaní		-	-	-	-	-	-	-	-	-	-	1/1	-	1/1	-	-	2/2
Maringma		-	-	-	1/1	-	-	-	-	-	-	1/1	1/1	-	-	-	3/3
Tramen		1/1	-	1/1	-	-	1/1	-	-	-	-	-	-	1/1	-	-	4/4
Uei		-	-	-	-	-	-	-	-	-	-	1/1	-	-	-	-	1/1
Karaurín		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0/0
Total ETC		1/2	1/3	1/4	5/5	1/1	2/10	2/3	7/16	2/7	1/1	3/7	2/2	2/8	1/3	1/2	32/74

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1345 **Table 6.** Plant species richness and degree of endemism of the ETC summits. Numbers  
 1346 of widely distributed Neotropical species and exotic species are provided. Tepuis are  
 1347 grouped according to species richness.

	Sp. richness	Endemics				Widespread		Exotics
		Local	Summits ETC	ETC	Pantepui	Guayana Shield	Neotropics	
Roraima	227	2	21	26	79	112	102	13
Kukenán	137	1	17	21	66	86	48	-
Ilú	128	4	18	23	60	81	46	-
Yuruaní	46	-	6	8	25	36	10	-
Maringma	40	1	2	4	15	30	8	-
Tramen	34	-	7	9	17	21	13	-
Uei	33	2	4	6	10	24	9	-
Kaurín	14	-	2	4	6	10	4	-
Total ETC	289	10	31	37	100	155	117	13

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1351 **Table 7.** Number of taxa by major plant group in the Venezuelan Guayana (VG),  
 1352 Pantepui, the ETC summits and the Roraima summit. A: angiosperms, P: pteridophytes.

	VG <sup>a</sup>		Pantepui <sup>b</sup>		ETC summits		Roraima summit	
	Genera	Species	Genera	Species	Genera	Species	Genera	Species
Gymnosperms	3	21 <sup>c</sup>	2	12	-	-	-	-
Angiosperms	1694	8740	1485	2097	119	215	99	157
Pteridophytes	92	671	155	324	32	74	31	70
Ratio A/P	18.41	13.03	9.58	6.47	3.72	2.91	3.19	2.24

1353 <sup>a</sup> From Berry et al. (1995).

1354 <sup>b</sup> From the Pantepui database (Nogué et al. 2009; Safont et al. 2012).

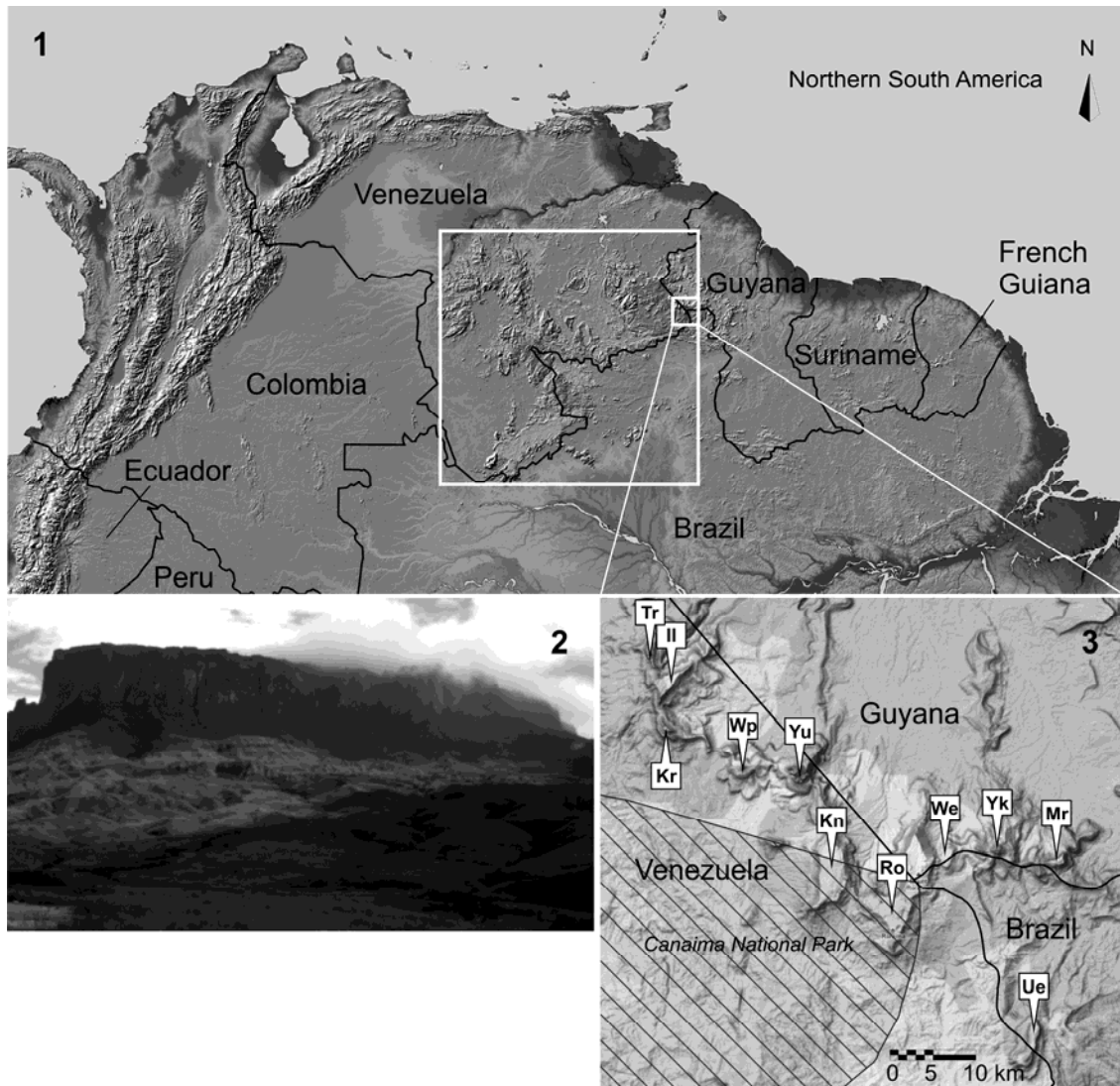
1355 <sup>c</sup> From Hokche et al. (2008).

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1357

1358 **Figures**

1359

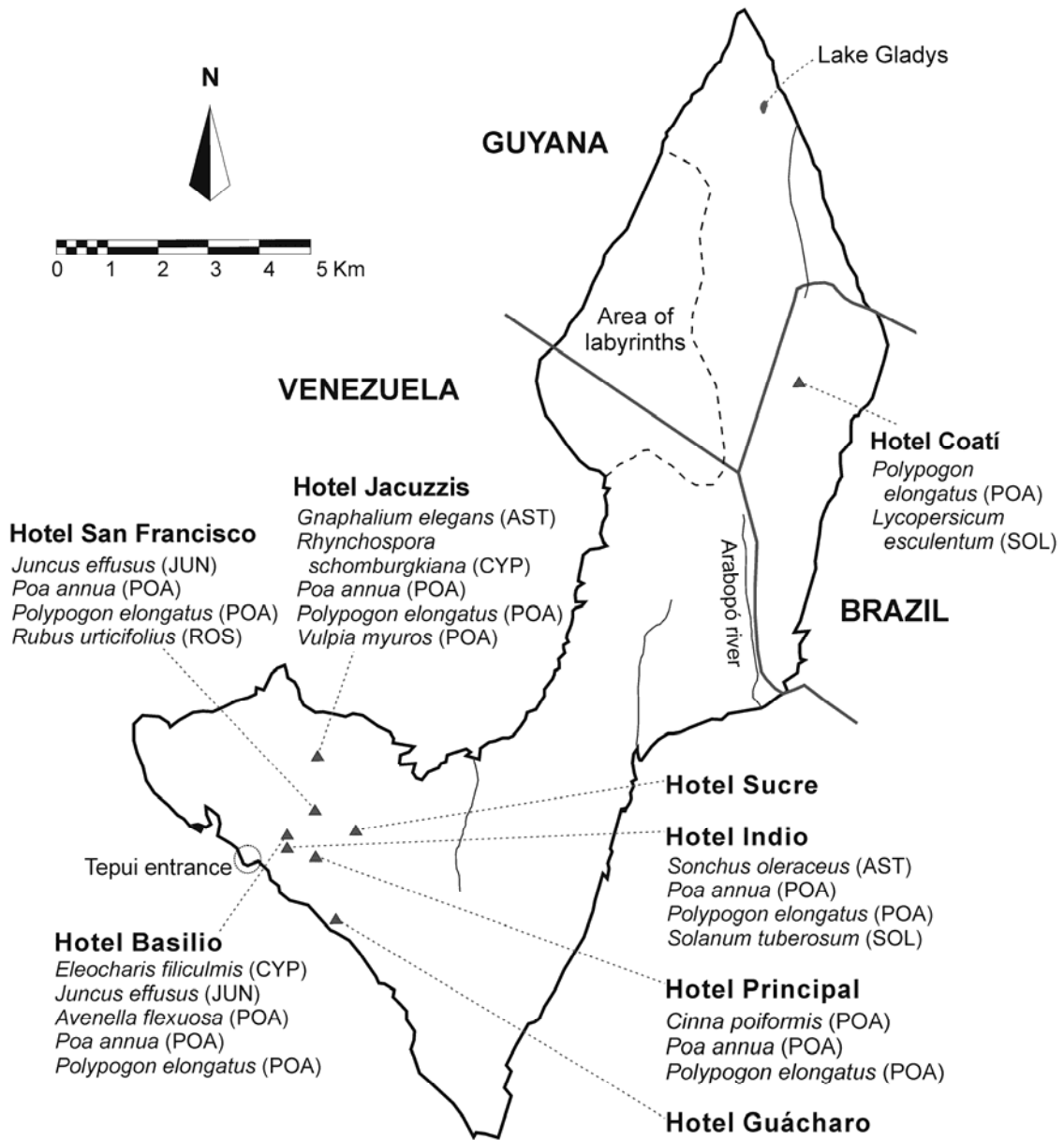


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1362 **Figs 1-3.** Location of the study area. **1.** Map of northern South America showing the  
1363 Pantepui province (larger white box) and location of the Eastern Tepui Chain (ETC) and  
1364 Roraima-tepui (smaller white box). Radar image courtesy of NASA/JPL-Caltech. **2.**  
1365 View of the Roraima-tepui from the Gran Sabana. Photograph: Yuribia Vivas. **3.**  
1366 Extension of the ETC. Abbreviations of tepuis as in Table 1. Hash-mark area  
1367 corresponds to Canaima National Park. Modified from Google Maps 2013.

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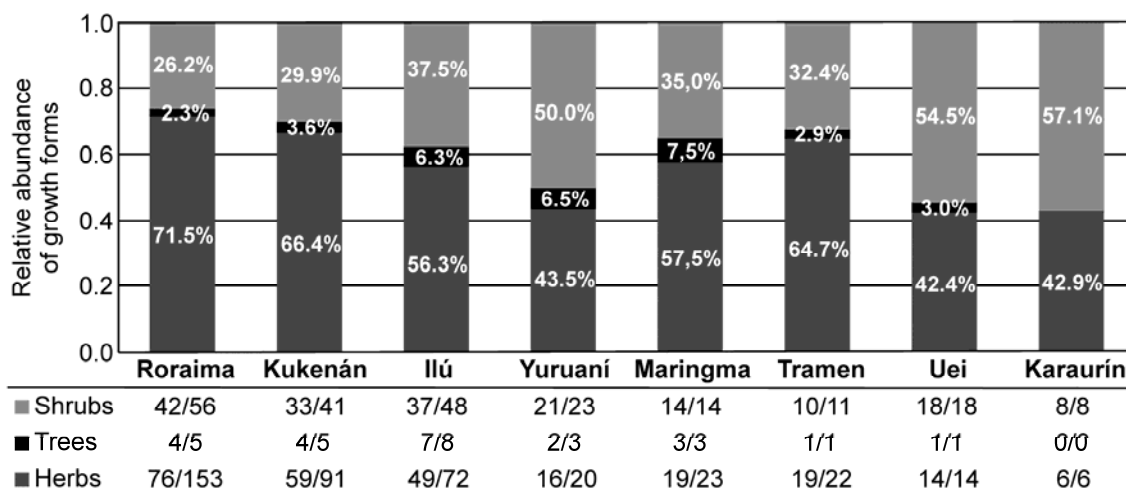
1370

1371 **Fig. 4.** Location of exotic species found on the summit of Roraima-tepui, coinciding

1372 with hotels and their surroundings. AST: Asteraceae, CYP: Cyperaceae, JUN:

1373 Juncaceae, POA: Poaceae, ROS: Rosaceae, SOL: Solanaceae.

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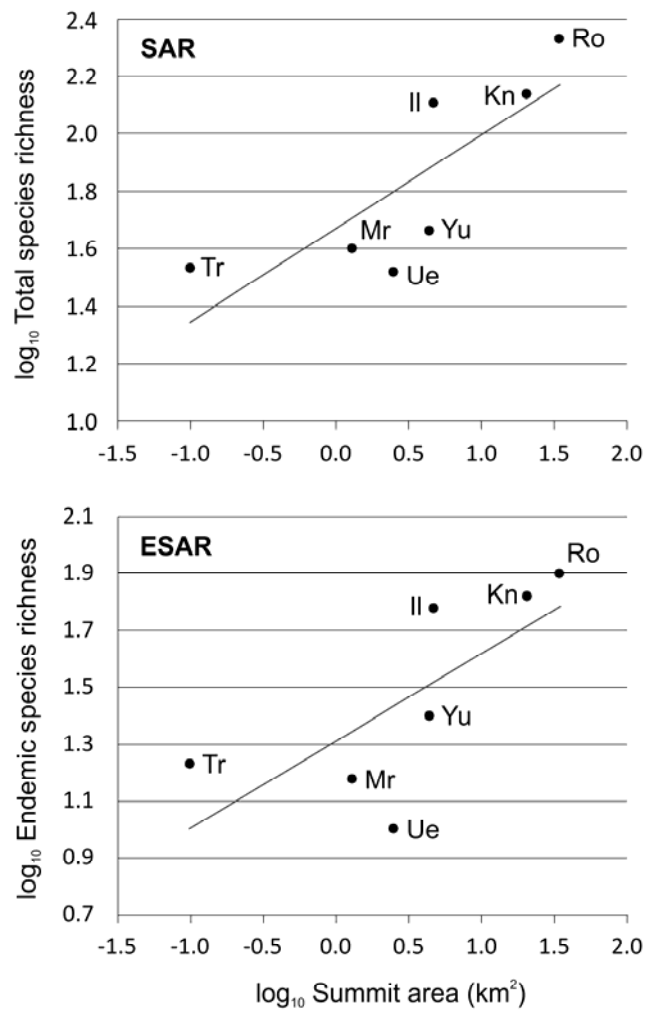


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1377 **Fig. 5.** Relative abundance of native species of herbaceous (dark gray), shrubby (light  
 1378 gray) and tree (black) growth forms in the tepui summits of the ETC. Diversity of  
 1379 genera and species are indicated before and after the slash, respectively.

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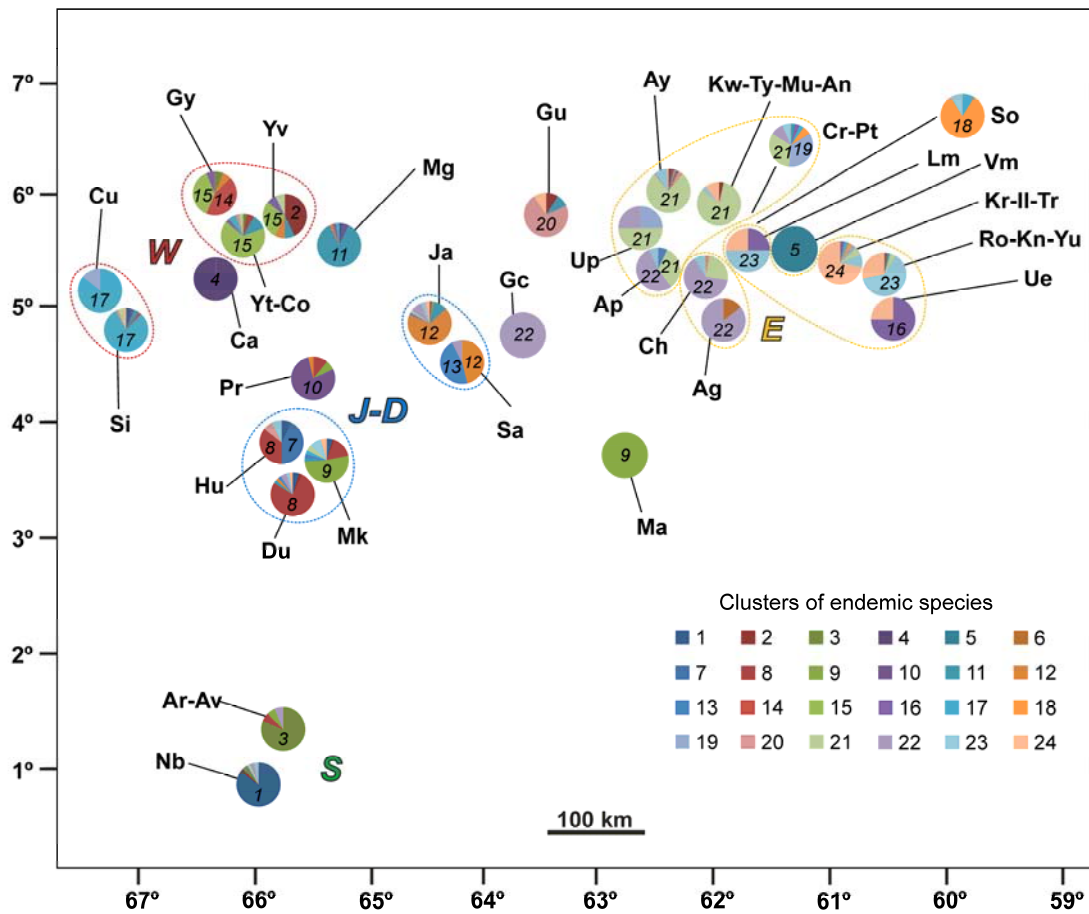
1382

1383 **Fig. 6.** Species-Area Relationship (SAR:  $r^2 = 0.640$ ,  $p = 0.031$ ) and Endemic Species-

1384 Area Relationship (ESAR:  $r^2 = 0.516$ ,  $p = 0.069$ ) for the ETC summits, with log-

1385 transformed data. Abbreviations of tepuis as in Table 1.

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1389 **Fig. 7.** Schematic map of Pantepui, showing the relative abundance of species clusters  
 1390 for each tepui/tepui massif (pie charts). Clusters were defined as groups of species with  
 1391 Raup-Crick similarity measure above 0.7. Dashed circles group the tepuis with highest  
 1392 floristic similarity within each district, based on Raup-Crick measure on the endemic  
 1393 species data matrix. **Eastern district (E):** Ag – Angasima, An – Aparamán, Ap –  
 1394 Aprada, Ay – Auyán, Ch – Chimantá, Cr – Carrao, Il – Ilú, Kn – Kukenán, Kr –  
 1395 Karaurín, Kw – Kamarkawarai, Lm – Lema, Mu – Murisipán, Pt – Ptarií, Ro – Roraima,  
 1396 So – Sororopán, Tr – Tramen, Ty – Tereké-yurén, Ue – Uei, Ug – Upuigma, Up –  
 1397 Uaipán, Vm – Venamo, Yu – Yuruaní; **Western district (W):** Ca – Camani, Co – Coro  
 1398 Coro, Cu – Cuaó, Gy – Guanay, Mg – Maigualida, Si – Sipapo, Yv – Yaví, Yt – Yutajé;

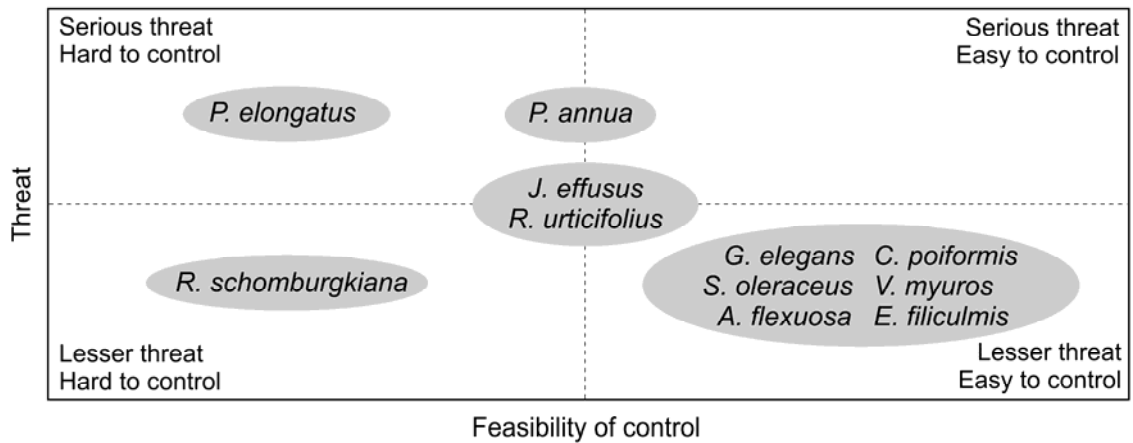


1399 **Jaua-Duida (J-D):** Du – Duida, Hu – Huachamacari, Ja – Jaua, Mk – Marahuaka, Pr –  
1400 Parú, Sa – Sarisariñama; **Southern district (S):** Ar – Aracamuni, Av – Avispa, Nb –  
1401 Neblina. **Others:** Gc – Guanacoco, Gu – Guaiquinima, Ma – Marutaní.

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1407 **Fig. 8.** Plot of level of potential impact vs. feasibility for control of exotic plant species  
1408 on the Roraima summit (excluding casual exotics).

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Major group	Family	Species	Infraspecifics on Roraima	Roraima	Kukenán	Ilú	Yuruaní	Maringma	Tramen	Uei	Karaurín	Exotic species	New records for Roraima summit since FVG	New species for ETC summits	New genus for Roraima summit	New genus for ETC summits	New family for Roraima summit	New family for ETC summits
	Araliaceae	<i>Schefflera chimantensis</i>	ssp. <i>rugosifolia</i>	++	+	+	+	+										
		<i>Schefflera umbellata</i>		++	+	+	+											
	Asteraceae	<i>Ageratina roraimensis</i>		++	+													
		<i>Baccharis brachylaenoides</i>		++	+	+	+		+	+								
		<i>Baccharis densa</i>		++	+	+												
		<i>Baccharis schomburgkii</i>		++														
		<i>Calea lucida</i>				+					+							
		<i>Calea lucidivenia</i>	var. <i>cardonae</i>			+		+										
		<i>Gnaphalium elegans</i>		++								+	+	+	+	+		
		<i>Gongylolepis benthamiana</i>				+												
		<i>Guayania roupalifolia</i>		++	+	+	+			+								
		<i>Koanophyllon fuscum</i>		++	+					+								
		<i>Mikania boomii</i>						+						+				
		<i>Mikania lucida</i>		++									+					
		<i>Quelchia conferta</i>		++	+	+	+											
		<i>Sonchus oleraceus</i>		++								+	+	+	+	+		
		<i>Stenopadus connellii</i>		++	+													
		<i>Stenopadus sericeus</i>		++									+	+				
		<i>Stomatochaeta condensata</i>		++	+	+	+			+	+							
	Bonnetiaceae	<i>Bonnetia roraimae</i>		++	+	+	+	+	+	+								
		<i>Bonnetia tepuiensis</i>				?	+			?	?							

Major group	Family	Species	Infraspecifics on Roraima	Roraima	Kukenán	Ilú	Yuruaní	Maringma	Tramen	Uei	Karaurín	Exotic species	New records for Roraima summit since FVG	New species for ETC summits	New genus for Roraima summit	New genus for ETC summits	New family for Roraima summit	New family for ETC summits
	Clusiaceae	<i>Clusia amabilis</i>						+		+								
		<i>Moronobea intermedia</i>				+				+								
	Cunoniaceae	<i>Weinmannia brachystachya</i>			+	+												
		<i>Weinmannia fagaroides</i>		++		+												
		<i>Weinmannia glabra</i>		++	+													
		<i>Weinmannia guyanensis</i>	var. <i>guyanensis</i>	++		+	+		+									
		<i>Weinmannia ilutepuiensis</i>				+												
		<i>Weinmannia laxiramea</i>		++	+													
	Cyrtillaceae	<i>Cyrtilla racemiflora</i>		++	+	+	+	+	+	+	+							
	Droseraceae	<i>Drosera hirticalyx</i>		+														
		<i>Drosera kaieteurensis</i>						+						+				
		<i>Drosera roraimae</i>		++	+	+	+	+	+		+							
		<i>Drosera solaris</i>						+										
	Ericaceae	<i>Bejaria imthurnii</i>		++	+	+	+		+	+								
		<i>Bejaria sprucei</i>			+	+												
		<i>Gaultheria erecta</i>		++	+	+												
		<i>Gaultheria setulosa</i>		++	+	+												
		<i>Ledothamnus guyanensis</i>							+	+								
		<i>Ledothamnus sessiliflorus</i>		++	+	+		+	+		+							
		<i>Pernettya marginata</i>		++	+	+	+											
		<i>Sphyrospermum cordifolium</i>		++	+	+							+		+			

Major group	Family	Species	Infraspecifics on Roraima	Roraima	Kukenán	Ilú	Yuruaní	Maringma	Tramen	Uei	Karaurín	Exotic species	New records for Roraima summit since FVG	New species for ETC summits	New genus for Roraima summit	New genus for ETC summits	New family for Roraima summit	New family for ETC summits
		<i>Tepuia tatei</i>			+		+											
		<i>Thibaudia nutans</i>		++	+	+	+											
		<i>Vaccinium corymbodendron</i>		++														
		<i>Vaccinium roraimense</i>		++	+	+												
	Gentianaceae	<i>Celiantha imthurniana</i>		++	+	+			+									
		<i>Rogersonanthus quelchii</i>		++	+	+												
		<i>Symbolanthus aureus</i>				+												
		<i>Symbolanthus elisabethae</i>		++	+													
	Hypericaceae	<i>Hypericum roraimense</i>		++	+													
	Lentibulariaceae	<i>Genlisea pygmaea</i>			+	+												
		<i>Genlisea repens</i>		++	+								+					
		<i>Genlisea roraimensis</i>		++	+	+												
		<i>Utricularia amethystina</i>		++			+		+									
		<i>Utricularia aureomaculata</i>			+	+												
		<i>Utricularia campbelliana</i>		++	+													
		<i>Utricularia humboldtii</i>						+						+				
		<i>Utricularia pubescens</i>		++	+					+			+					
		<i>Utricularia quelchii</i>		++	+		+											
		<i>Utricularia subulata</i>		++	+	+												
	Melastomataceae	<i>Marcetia taxifolia</i>		++		+	+	+	+	+								
		<i>Meriania crassiramis</i>						+						+		+		



Major group	Family	Species	Infraspecifics on Roraima	Roraima	Kukenán	Ilú	Yuruaní	Maringma	Tramen	Uei	Karaurín	Exotic species	New records for Roraima summit since FVG	New species for ETC summits	New genus for Roraima summit	New genus for ETC summits	New family for Roraima summit	New family for ETC summits
	Passifloraceae	<i>Passiflora sclerophylla</i>								+								
	Phyllanthaceae	<i>Phyllanthus pycnophyllus</i>								+								
	Piperaceae	<i>Peperomia acuminata</i>		++														
		<i>Peperomia delascioi</i>		++		+												
		<i>Peperomia galioides</i>		++		+												
		<i>Peperomia rotundata</i>	var. <i>rotundata</i>	++		+								+				
		<i>Peperomia tenella</i>	var. <i>tenella</i>	++	+	+												
	Polygalaceae	<i>Monnina cacumina</i>		++						+								
	Polygonaceae	<i>Coccoloba schomburgkii</i>				+				+								
	Rhamnaceae	<i>Rhamnus ulei</i>		++									+	+	+	+	+	+
	Rosaceae	<i>Hesperomeles obtusifolia</i>	var. <i>obtusifolia</i>	++		+							+	+	+		+	
		<i>Rubus urticifolius</i>		++									+	+	+	+	+	+
	Rubiaceae	<i>Maguireothamnus speciosus</i>	ssp. <i>speciosus</i>	++	+		+	+										
		<i>Notopleura crassa</i>		++	+	+	+											
		<i>Notopleura tapajozensis</i>							+						+			
		<i>Pagamea magniflora</i>				+												
		<i>Palicourea obtusata</i>		++	+	+												
		<i>Psychotria aubletiana</i>		++		+								+				
		<i>Psychotria concinna</i>		++	+	+												
		<i>Psychotria everardii</i>					+	+										
		<i>Psychotria glandulicalyx</i>									+							









Major group	Family	Species	Infraspecifics on Roraima	Roraima	Kukenán	Ilú	Yuruaní	Maringma	Tramen	Uei	Karaurín	Exotic species	New records for Roraima summit since FVG	New species for ETC summits	New genus for Roraima summit	New genus for ETC summits	New family for Roraima summit	New family for ETC summits	
		<i>Habenaria roraimensis</i>		++	+	+													
		<i>Helonoma bifida</i>		+	+		+												
		<i>Lepanthes unitrinervis</i>		++		+													
		<i>Maxillaria mapiriensis</i>			+														
		<i>Maxillaria meridensis</i>			+														
		<i>Maxillaria quelchii</i>		++		+													
		<i>Octomeria connellii</i>		++	+	+			+										
		<i>Octomeria flaviflora</i>		+	+														
		<i>Octomeria monticola</i>		++	+														
		<i>Octomeria parvifolia</i>		++	+	+													
		<i>Octomeria</i> sp.		++															
		<i>Prescottia carnosa</i>		++	+	+													
		<i>Stelis</i> sp.			+														
		<i>Trichosalpinx roraimensis</i>		++	+														
		<i>Trichosalpinx</i> sp.		++									+	+					
		<i>Zygosepalum angustilabium</i>			+														
	Poaceae	<i>Aulonemia deflexa</i>		++		+													
		<i>Avenella flexuosa</i>		++								+	+	+	+	+			
		<i>Axonopus caulescens</i>								+									
		<i>Chusquea linearis</i>		++	+														
		<i>Cinna poiiformis</i>		++								+	+	+	+	+			









