

## 11 TEPUI SHRUBLANDS, SOUTHERN VENEZUELA

contributed by María A. Oliveira-Miranda<sup>1</sup>, Jon Paul Rodríguez<sup>1,2</sup> and Sergio Zambrano-Martínez<sup>2</sup>.

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### CLASSIFICATION

Tepui shrublands are included in the Pantepui, a phytogeographical province totaling 6,000 km<sup>2</sup> formed by grouping all table mountain (tepui) summits above 1500 m. Pantepui is part of the Guayana Shield, one of the oldest continental areas in the western hemisphere (Zinck & Huber 2011). They were not recognized as a distinct primary vegetation community until the 1980s, when they were first included as discrete units in vegetation maps (Huber & Alarcon 1988, Huber 1995a, 1995b, Riina & Huber 2003). IUCN Habitats Classification Scheme (Version 3.0): 3. Shrubland / 3.6 Subtropical / Tropical Moist  
Key references: Huber 1995a, 1995b, Oliveira-Miranda et al. 2010.

### ECOSYSTEM DESCRIPTION

#### Characteristic native biota

Tepui shrublands (Fig. 1) are plant communities that occur on tepui summits, characterized by high physiognomic diversity, low species diversity and high degree of endemism. “Tepui” is a native term referred to the table mountains located primarily on the Venezuelan portion of the Guayana Shield (Huber 1995a), mostly above 1500 m. Phytogeographically, Tepui shrublands are one of the main habitats of the Pantepui floristic province (Huber 1987), and can also be called Pantepui scrub (Huber 1995a).

The composition, diversity and distribution of Tepui shrublands (Fig. 1a) are conditioned by edaphic constraints (Huber 1989), with many plant species restricted to particular substrate types such as rock outcrops, sandy soils or peat. Their physiognomy may vary between tepui summits, ranging from 0.5-1 m tall in Guanay-tepui and Auyan-tepui, to 8 m tall on top of Jaua Sarisariñama (Riina & Huber 2003).

Broadly speaking, the shrubs found in Tepui shrublands produce branches that originate at their base. They have coriaceous or sclerophyllous leaves, that are usually densely aggregated at the end of their branches. Typically, they also have conspicuous flowers or inflorescences (Huber 1995a). These shrublands may build up to large formations, such as those found on Huachamacari and Duida (Fig. 1b, c), or appear in small depressions, such as those on top of the tepuis (Riina & Huber 2003). Common plant genera found on tepui shrublands include *Bonnetia* (Theaceae), *Maguireothamnus* and *Pagameopsis* (Rubiaceae), *Tepuianthus* (Tepuianthaceae) and others from Ochnaceae, Ericaceae, Malpighiaceae and Melastomataceae families (Riina & Huber 2003). More than 70 plant taxa are endemic to the Tepui summits, including several endemic genera (Rull & Vegas-Vilarrubia 2006).

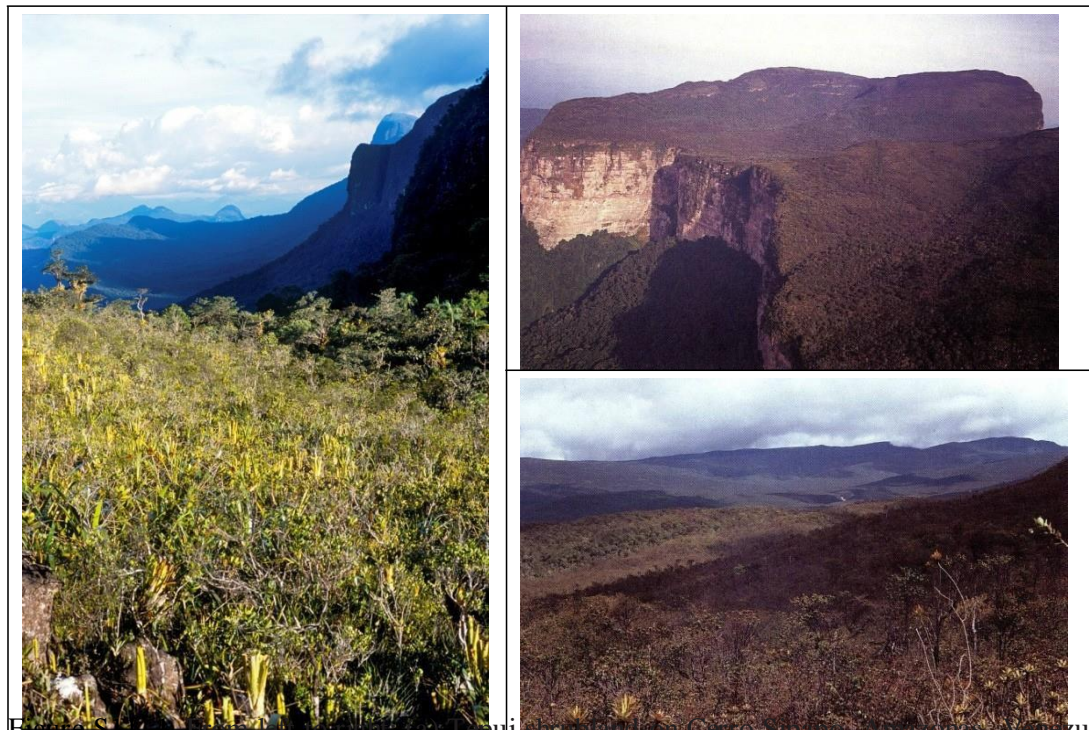


Figure S11. 1. From left to right: (a) Tepui shrubland on Cerro Sipapo, Amazonas, Venezuela. Photo: Gustavo Romero. (b) (top) Tepui shrubland on Cerro Huaramacachi, Amazonas, Venezuela. Photo: Otto Huber. Photo 3. (c). Tepui shrubland on Cerro Duída, Amazonas, Venezuela. Photo: Otto Huber.

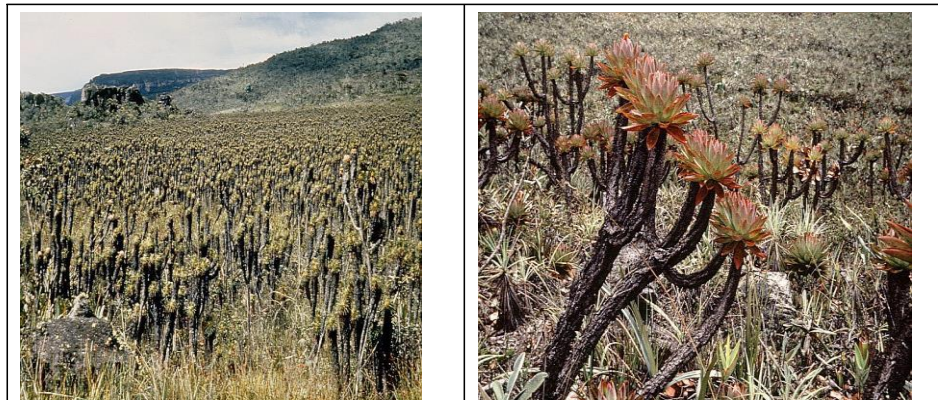


Figure S11. 2. (a) Left. Tepui shrubland on Chimanta massif, showing a paramoid shrubland (*Chimantaeamirabilis*), photo: Otto Huber. (b) Right. Caulirosulate shrubland on Serranía La Neblina (*Bonnetia maguireorum*), photo: Susanne Renner.

Several peculiar types of shrubs grow in the Venezuelan tepui shrublands, such as the paramoid and caulirosulate (which hold the shape of an artichoke). The paramoid (Fig. 2a) and caulirosulate scrublands are found on the Chimantá massif. The paramoid receive their name from their physiognomic and floristic similarity with Andean shrublands (known as “páramos”) (Huber 1992). The shrubs with caulirosulate growth form (Fig. 2b) are also found on the summit of Serranía La Neblina, at the southernmost tip of Venezuela. Both shrubland types develop dense communities formed by thousands of individuals of the *Chimantaea* genus, on the Chimantá massif, and by the species *Bonnetia maguireorum* on Serranía La Neblina (Huber 1992, 1995a, Steyermark pers. comm.) The vertebrate fauna is also highly distinctive, with numerous amphibians, reptiles, birds and mammals exclusive or almost restricted to the tepuis (Señaris et al. 2009). For example, the sira poison

frog (*Allobates rufulus*; Amphibia: Aromobatidae), *Stefania ginesi* (Amphibia: Hemiphractidae) and *Thamnodynastes chimanta* (Reptilia: Colubridae), have only been found on the summit of the Chimantá massif (Gorzula 1992). Likewise, over 30 bird species are endemic to Pantepui, primarily from the order Passeriformes, but also Apodiformes, Psittaciformes, Caprimulgiformes, and Tinamiformes (Molina & Salcedo 2009).

Tepui shrublands, as well as other tepui communities, were considered biologically isolated units for a long time (Maguire 1970; Brewer-Carías 1978; George 1988). However, in many tepuis, especially on the larger massifs of Venezuelan Guayana, the summits are not completely isolated from the surrounding lower vegetation belts by vertical walls (Huber 1995a). Total physical isolation of tepui summits occurs only in a few tower-like mountains, such as Roraima-tepui, Ilú-tepui, and Los Testigos massif, where impoverished plant communities prevail.

## Abiotic environment

Tepui shrublands are mostly associated with the slopes and summits of the tepuis, on granite and pink sandstone formations, dating back to the Precambrian period (Huber 1995 veg). Although the Tepui shrubland ecosystem appears sporadically at altitudes of 800-1,500 m, with a mesothermic climate (12-24°C), the best developed and densest communities are found on higher grounds (1,500-3,000 m), with submicrothermic climate (6-12°C). At all elevations, Tepui shrublands are exposed to high air humidity and precipitation, greater than 2000 mm (Huber 1989; Riina & Huber 2003). With the exception of soils with high organic content, these communities develop on rocky soils (sandstone or granite), where in spite of high precipitation, moisture conditions are limited due to the low water-retention capacity of the substrate and excessive draining (Riina & Huber 2003), as a consequence of strong winds and high solar radiation periods (Huber 1995a, Zinck & Huber 2011).

## Distribution

Typical montane tepui shrublands are only found on higher elevations of the Guayana Shield, mainly in the States of Bolívar and Amazonas in southern Venezuela (Figure 3), on two tepui summits in adjacent Guyana and, to a very small extent, on the Brazilian section of Cerro de la Neblina (Huber 2012, pers. comm.). At lower elevations (800-1500 m), other peculiar scrub types are growing with different floristic composition and growth forms, such as in the Gran Sabana, Cerro Guaiquinima, or Cerro Sarisariñama, where they could be considered as "subtepuian" vegetation (Huber 1995a), but they are not yet sufficiently well explored.



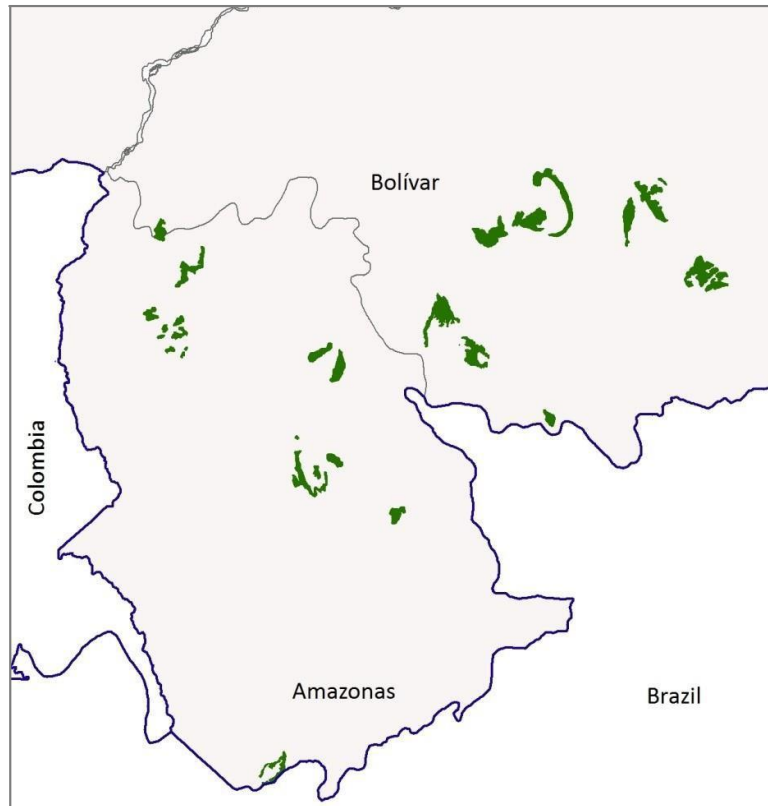


Figure S11. 3. Geographic distribution of Venezuelan tepui shrublands. They are restricted to the States of Amazonas and Bolívar.

### Key processes and interactions

Venezuelan Tepui shrublands (> 1,500 m) correspond to the montane life zone, which is present in all tropical and extra-tropical mountains above the tree line, such as the páramos in the Andes and the alpine meadows of the Alps and the Rocky Mountains (Huber 1995a). Furthermore, as mentioned above, tepuis are not actually isolated from lowland landscapes (Huber 1989; 1995a). Extremely adverse environmental conditions such as lack of soil, nutrient deficiency, strong winds, and high radiation appear as the main cause of these relatively depauperate communities (Huber 1995a) and play key roles in the evolution and ecology of the ecosystem. For example, sclerophyllous foliage and diversity of carnivorous plants are likely evolutionary responses to nutrient deficient soils that characterize the old stable landscapes in which these shrublands occur (Hopper 2009). Like other sclerophyllous shrublands, the tepui are prone to recurring fires (e.g. Givnish et al. 1986), although these appear to be infrequent and their role in ecosystem dynamics is poorly understood.

### Threatening processes

The Tepui shrublands have few known processes that threaten their persistence. Human effects are limited to localized impacts in the tepuis more visited by tourists, or to damage caused by the arrival of groups (tourists or scientists) in helicopters or small planes. Among the most common adverse effects are the disposal of garbage, fuel cans and other items left by visitors in their temporary camps (Huber 1995c). Nevertheless, in many tepuis there are clear signs of deterioration of the vegetation due to trampling, helicopter landing, rock-climbing and rappelling, paragliding, introduction of exotic species and accumulation of rubbish. This damage, although limited to relatively small areas, is almost irreversible, as it has been shown that the affected vegetation recovers very slowly (Gorzula & Huber 1992; MARN 2000; Riina & Huber 2003).

The second process currently considered a threat to the persistence tepui shrubland is global climate change. A small range of tolerance of the component species to changes in humidity and temperature could be a clear weakness of the system (Huber 1995c; Rull et al. 2005; Rull et al. 2009), but additional research is necessary to support this assumption. On the other hand, it is estimated that an increase of 2-4°C in average temperatures could cause the extinction of 10% to 30% of the plants endemic to the tepuis before the end of the century (Rull & Vegas-Vilarrubia 2006). For eight species of Chimantaea, it is predicted that two will completely lose their habitat and six would be very close to the critical limit. Although their habitat would not disappear completely, it would be reduced to a few tiny isolated areas in the highest summits (Rull et al. 2005). However, there are no data available either on the resistance nor the resilience capacity of any tepui plant or animal species to climatic change, so such assumptions must be considered carefully (Huber 2012, pers. comm.).

## Ecosystem collapse

For assessment of criteria A and B, Tepui shrublands were assumed to collapse if their mapped distribution declines to zero. Species composition and richness of Tepui shrubland vegetation were selected as suitable variables for assessing biotic processes and interactions under criterion D. As no trends were evident, collapse thresholds were not specified.

## ASSESSMENT

### Summary

Criterion	A	B	C	D	E	Overall
subcriterion 1	LC	LC	NE	LC	DD	LC
subcriterion 2	LC	LC	NE	DD		
subcriterion 3	LC	LC	NE	LC		

### Criterion A

Current and future decline: There is no evidence of measurable reductions in the distribution of Tepui shrublands over the last 50 years, considering botanical, faunal and geological expeditions carried out since the 1950s. Studies performed comparing recent and historical maps based on Landsat and radar images (currents and from the early eighties) did not detect any appreciable reduction of spatial occurrence of the Venezuelan tepui shrublands in the past ~25 years (Huber & Oliveira-Miranda 2010; Oliveira-Miranda et al. 2010). The current knowledge of the spatial distribution of this ecosystem in Venezuela, however, is better than previous estimates which were calculated very roughly (Huber & Alarcon 1988; Huber 1995), so some degree of uncertainty regarding their exact past extent still remains. Despite this uncertainty, the available data strongly support a classification of Least Concern under A1.

We do not expect any major change in the next 25 years, as all Tepui shrublands are included in National Parks and Natural Monuments, and they are fairly remote, located relatively far away from major human settlements. Changes in distribution due to landuse or exploitation are therefore unlikely in the short to medium term. Within a 50-year period that represents 25 years into the past and 25 years into the future, the distribution of tepui scrublands is expected to remain stable and well below the threshold for Vulnerable under criterion A2b, and therefore they are considered Least Concern. Global climate change, is a possible threat for the future persistence of Venezuelan Tepui shrublands, given their temperature and humidity constraints (Huber 1995; Rull et al. 2005; Rull & Vegas-Vilarrubia 2006; Rull et al. 2009). Some individual species are projected to decline under future climates, but these estimates are for the end of the century, a period longer than 50 years into the future (Rull et al. 2005). However, there are no models or projections of change in extent at the community level. In terms of criterion A2a, therefore, these data are not adequate for performing an assessment, leading to a listing as Data Deficient. Despite the lack of information for assessing criterion A2a, sufficient data on recent and future decline of this

ecosystem exist to support a classification of Least Concern under criteria A1 and A2b.

**Historic decline:** To the best of our knowledge, the distributions of the ecosystems associated with summits of tepuis have not significantly declined since 1750. There is no evidence that tepui shrublands once occupied significant areas of land that are now dominated by human land use (Huber 1995c). Although indigenous peoples have lived in the area for centuries, tepuis have been considered sacred and therefore object of minimal intervention. The status of the ecosystem is therefore Least Concern under criterion A3.

## Criterion B

The current mapped area of Venezuelan Tepui shrublands, estimated from Landsat satellite images, is approximately 5,170 km<sup>2</sup> (Figure 3). They naturally occur in ~35 locations (patch size range: 4-456 km<sup>2</sup>) associated with table-mountains and massifs in the Venezuelan Guayana Shield.

**Extent of occurrence:** A minimum convex polygon enclosing all mapped occurrences of Venezuelan Tepui shrublands (Figure 4a) has an area of 196,148 km<sup>2</sup>, well above the threshold for Vulnerable under criterion B1. The ecosystem is therefore listed under this criterion as Least Concern.

**Area of occurrence:** Superimposing a 10 km grid over the mapped polygons of Venezuelan Tepui shrublands (Figure 4b) indicates that 210 grid cells contain more than 1 km<sup>2</sup> of the ecosystem. Since this is well above the threshold for Vulnerable, they are listed as Least Concern under criterion B2.

**Number of locations:** There are ~35 locations of Venezuelan tepui shrublands, where human pressures are minimal. The status of the ecosystem is therefore Least Concern under criterion B3.

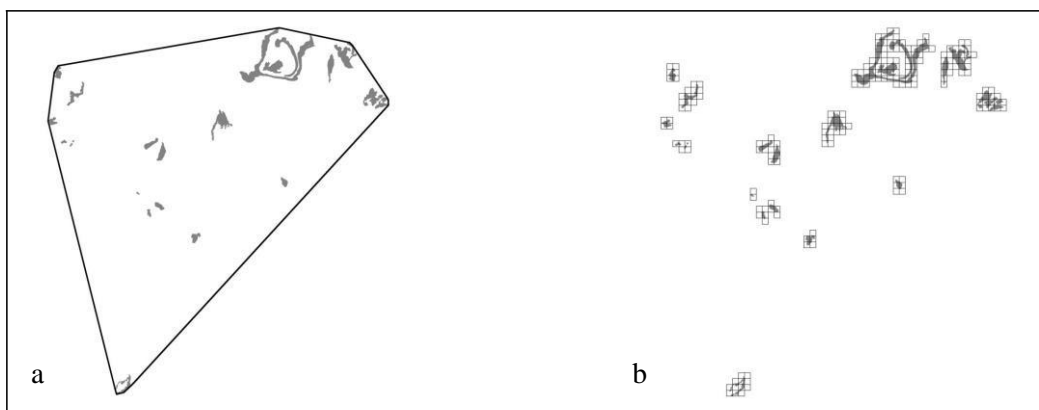


Figure S11. 4. Estimates of the geographic distribution of Tepui shrublands in Venezuela: a) extent of occurrence (EOO) considering one minimum convex polygon encompassing all known patches of the ecosystem, b) area of occupancy estimated by the number of occupied 10 x 10 km cells that include at least 1 km<sup>2</sup> of the ecosystem.

## Criterion C

We have no evidence of major degradation or biotic disruption in ecological function. Global climate change could be the main process to threaten the ecosystem in the future, but the time scale of this process is uncertain and could be longer than the 50 year period considered by the criteria. Vega et al. (2012) project that the area of the climatic envelope currently occupied by the Tepui summits will contract by 57-85% based on projected rises in mean annual temperature of 2-4°C to year 2100, and that the number of Tepuis within this envelope will decline by 21-37%. However, it is unclear how this will affect the persistence of the characteristic native biota. The status of the ecosystem is therefore Not

## Criterion D

Climate change is the most salient threat to Tepui shrublands, as warming potentially makes the plateau summits unsuitable for persistence of the characteristic native biota. Changes in plant species composition and richness are potentially suitable for assessing disruption to biotic processes and interactions in the ecosystem, although the availability of data is limited.

Current decline: There are no records of any extinctions in the Tepui shrublands over the last 50 years. Although there are insufficient data to support more quantitative assessment of changes in plant species composition over this period, the lack of evidence of species loss or disturbances that might result in losses tentatively suggests a status of Least Concern under criterion D1.

Future decline: Several recent studies have projected the persistence of climatically suitable habitat for plant species of the Tepui shrublands under future climate change (Rull & Vegas-Vilarrubia 2006, Nogue et al. 2009a, Vega et al. 2012). An initial Altitudinal Range Displacement analysis of endemic flora suggests that temperatures will move outside the current range by the end of the twenty-first century for 9-27 of the 76 species assessed (9-35%), potentially threatening them with extinction unless they can persist under the new temperature regime (Rull & Vegas-Vilarrubia 2006). Further analysis combining species-area relationships with projected available areas derived from present-day temperatures at low altitude limits, suggests that 28-90% of the total Tepui flora, depending on the model used, will be outside its present-day temperature envelope by year 2100 (Nogue et al. 2009a). For individual Tepuis, the projected loss of climatically suitable potential habitat varies from 50 to 100%, while the potential loss of endemic species varies from 2 to 100% (Vega et al. 2012). These projections are based on limited survey data and spatial climatic data, as well as indirect modelling methods that exclude consideration of species life histories, potential lagged responses and micro-refugia, and will be revised as improved data become available to support use of more advanced methods (Nogue et al. 2009a).

The broad bounds of the estimates and limited modelling methods suggest substantial uncertainty in future projections. In addition, the projections are based on a time frame extending to year 2100, beyond that required for Red List assessment. Consequently, further work is needed to assess the functional significance of these projections and to assess changes over the relevant time frames, and the Tepui shrublands are currently assigned to Data Deficient status under criterion D2.

Historic decline: Limited historical data are available on the composition of the Tepui flora. However, Rull (2005) and Nogue et al. (2009b) carried out paleo-ecological studies of peat sediments from the summits of several Tepuis, and found that the vegetation had been stable over the past 4,300 - 6,000 years, with representation of pollen types consistent with contemporary vegetation and minor temporal variations in pollen abundance apparently reflecting local dynamics of meadow-forest ecotones. The long-term stability of Tepui vegetation composition suggests a status of Least Concern under criterion D3.

## Criterion E

No quantitative assessment is available for this ecosystem, so under criterion E its status is Data Deficient.

## REFERENCES

- Brewer-Carías C. 1978. La Vegetación del Mundo Perdido. Caracas: Fundación Eugenio Mendoza.
- George U. 1988. Inseln in der Zeit. Venezuela-Expeditionen zu den letzten weissen Flecken der Erde. Hamburg: GEO.
- Givnish TJ, McDiarmid RW, Buck WR. 1986. Fire adaptation in *Neblinaria celiae* (Theaceae), a high-elevation rosette shrub endemic to a wet equatorial tepui. *Oecologia* 70: 481–485.
- Gorzula S. 1992. La herpetofauna del macizo del Chimantá. Chapter 15. Pp. 267-280. In: O. Huber (ed.) Chimantá, Escudo de Guayana, Venezuela. Oscar Todtmann Editores, Caracas.
- Gorzula S. & Huber O. 1992. Consideraciones finales. Chapter 18. Pp. 325-330. In: O. Huber (ed.) Chimantá, Escudo de Guayana, Venezuela. Oscar Todtmann Editores, Caracas.
- Hopper SD. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant Soil* 322:49–86.
- Huber O. 1987. Consideraciones sobre el concepto de Pantepui. *Pantepui* 2: 2-10.
- Huber O. 1989. Shrublands of the Venezuelan Guayana. Pp. 271-285. In: LB Holm-Nielsen, IC Nielsen, H Balslev (eds.). *Tropical forest: Botanical dynamics, speciation and diversity*. Academic Press: London & N.Y.
- Huber O. 1992. El macizo de Chimantá, Escudo de Guayana, Venezuela. Un ensayo ecológico tepuyano. Oscar Todtmann Editores: Caracas. 343 pp.
- Huber O. 1995a. Vegetation. Pp. 97-160. In: PE Berry, BK Holst, K Yatskievych (eds.). *Flora of the Venezuelan Guayana*. Vol. 1: Introduction. Missouri Botanical Garden: St. Louis, Missouri & Timber Press: Portland, Oregon.
- Huber O. 1995b. Mapa de vegetación de la Guayana Venezolana. Escala 1:2.000.000. CVG EDELCA, Missouri Botanical Garden. Ediciones Tamandúa: Caracas.
- Huber O. 1995c. Conservation of the Venezuelan Guayana. Pp. 193-218. En: PE Berry, BK Holst, K Yatskievych (eds.). *Flora of the Venezuelan Guayana*. Vol. 1: Introduction. Missouri Botanical Garden: St. Louis, Missouri & Timber Press: Portland, Oregon.
- Huber O, Alarcón C. 1988. Mapa de vegetación de Venezuela 1:2.000.000. The Nature Conservancy, MARNR. Oscar Todtmann Editores: Caracas.
- Huber O, Oliveira-Miranda MA. 2010. Ambientes terrestres. Pp: 29-89. In: JP Rodríguez, F Rojas- Suárez, D Giraldo Hernández (eds.). *Libro Rojo de los Ecosistemas Terrestres de Venezuela*. Provita, Shell Venezuela, Lenovo (Venezuela). Caracas: Venezuela.
- Maguire B. 1970. On the flora of the Guayana Highland. *Biotropica* 2: 85-100.
- MARN. 2000. Primer informe de Venezuela sobre Diversidad Biológica. Ministerio del Ambiente y de los Recursos Naturales: Caracas.
- Molina C, Salcedo M. 2009. Aves del Parque Nacional Canaima. Pages 133-149 In: J. C. Señaris, D. Lew and C. Lasso, editors. *Biodiversidad del Parque Nacional Canaima: bases técnicas para la conservación de la Guayana venezolana*. Fundación La Salle de Ciencias Naturales and The Nature Conservancy, Caracas.
- Nogué S, Rull V, Vegas-Vilarrúbia, T. 2009a. Modeling biodiversity loss by global warming on Pantepui, northern South America: projected upward migration and potential habitat loss. *Climate Change* 96: 77–85.
- Nogué S, Rull V, Montoya E, Huber O, Vegas-Vilarrúbia T. 2009b. Paleoecology of the Guayana Highlands (northern South America): Holocene pollen record from the Eruoda-tepui, in the Chimantá massif. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281: 165-173.
- Oliveira-Miranda MA, Huber O, Rodríguez JP, Rojas-Suárez F, De Oliveira-Miranda R, Hernández- Montilla M, Zambrano-Martínez S, Giraldo-Hernández D. 2010. Riesgo de eliminación de los ecosistemas terrestres de Venezuela. Pp: 106-236. In: JP Rodríguez, F Rojas-Suárez, D Giraldo- Hernández (eds.). *Libro Rojo de los Ecosistemas Terrestres de Venezuela*. Provita, Shell Venezuela, Lenovo (Venezuela). Caracas: Venezuela.



Riina R, Huber O. 2003. Ecosistemas exclusivos de la Guayana. Pp. 828-861. In: M Aguilera, A Azócar, E González Jiménez (eds.). Biodiversidad de Venezuela. Tomo II. Fundación Polar,

Ministerio de Ciencia y Tecnología, Fondo Nacional para la Ciencia, Tecnología e Innovación (FONACIT). Editorial ExLibris: Caracas.

Rull V. 2005. Vegetation and environmental constancy in the Neotropical Guayana Highlands during the last 6000 years? Review of palaeobotany and palynology 135: 205 -222.

Rull V, Vegas-Vilarrúbia T. 2006. Unexpected biodiversity loss under global warming in the neotropical Guayana Highlands: a preliminary appraisal. Global Change Biology 12: 1-9.

Rull V, Vegas-Vilarrúbia T, Nogué S. 2005. Cambio climático y diversidad de la flora vascular en las montañas tabulares de Guayana. Orsis 20: 61-71.

Rull V, Vegas-Vilarrubia T, Nogué S, Huber O. 2009. Conservation of the unique Neotropical vascular flora of the Guayana Highlands in the face of global warming. Conservation Biology 23(5): 1323-1327.

Señaris J C, Lew D, Lasso C, editors. 2009 Biodiversidad del Parque Nacional Canaima: bases técnicas para la conservación de la Guayana venezolana. Fundación La Salle de Ciencias Naturales and The Nature Conservancy, Caracas. 256 pp.

Vegas-Vilarrúbia T, Sandra Nogué S, Rull V. 2012. Global warming, habitat shifts and potential refugia for biodiversity conservation in the neotropical Guayana Highlands. Biological Conservation 152: 159–168.

Zinck JA, Huber O, editors. 2011. Peatlands of the western Guayana Highlands, Venezuela: properties and paleogeographic significance of peats. Springer-Verlag, Berlin. 295 pp.