

Valentí Rull

Is the ‘Lost World’ really lost? Palaeoecological insights into the origin of the peculiar flora of the Guayana Highlands

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Abstract The peculiar biogeography of the so-called ‘Lost World’, i.e. the summits of sandstone tableaux (*tepui*) in the Neotropical Guyana region of Venezuela, has generated a debate regarding the factors that are thought to account for modern vegetation patterns in the region. Some argue that plant communities on these high-elevation summits reflect a long history of evolution in isolation, while others surmise that there has been substantial biotic interchange with the surrounding lowlands during glacial times. Until now, these apparently competing hypotheses have not been tested using palaeoecological methods. I used pollen analysis of Quaternary sediments and documented past vertical migrations of vegetation in response to climate changes, which supports the second hypothesis. Physiographical analysis, however, shows that about half the tableaux summits are too high for their flora to have reached the lowlands during the last glaciation, suggesting that a portion of the tableaux vegetation has always experienced some degree of biotic isolation. Thus, a component of the summit vegetation evolved in isolation, whereas other taxa experienced interchange, as reflected in endemism patterns among the tableaux summits. Biogeographical patterns on the summits are the result of complex evolutionary processes. The two hypotheses invoked to explain the vegetation patterns are not mutually exclusive, but instead complement one another.

the spectacular sandstone plateaux that emerge from the lowlands between the Orinoco and the Amazon basins (Fig. 1). The indigenous name for these plateaux is *tepui*, and the biogeographical province comprising the ensemble of all the *tepui* summits is called Pantepui (Berry et al. 1995). The summits are more or less flat surfaces extending up to 1,000 km² and 3,000 m elevation, most of them situated in the Venezuelan Guayana region. This inspired A.C. Doyle’s fantasy story in which the *tepui* summits were inhabited by dinosaurs and forgotten civilisations, isolated from the rest of the world for millions of years (Doyle 1912). Early botanical researchers assumed that 90–95% of Pantepui plant species were endemic, and thus adopted Doyle’s idea of a long history of evolution in isolation (Maguire 1970; Brewer-Carías 1978). Later, it was realised that not all the *tepui* summits were topographically isolated from the adjacent lowlands, and it was postulated that plants could have been dispersed through them, after vertical shifts during glaciations (Steyermark and Dunsterville 1980; Huber 1988). This idea was further supported by the realisation that the degree of endemism was notably lower (33%) than previously estimated (Berry et al. 1995). Until now, no conclusive palaeoecological evidence has been available to evaluate these hypotheses. This paper addresses the problem from a palaeoecological perspective, using a combination of pollen analysis of radiocarbon-dated sediments, and an analysis of plant endemism patterns.

Introduction

The ‘Lost World’ (Doyle 1912) is a remote, uninhabited region of the Guayana shield, made up of the summits of

Materials and methods

The study was conducted on a *tepui* summit from the Chimantá massif (Fig. 1). The climate is mild (average temperature 14.1°C) and humid (average precipitation 3,351 mm/year) (Huber 1992). The main vegetation types are *tepuian* meadows, paramoid shrublands and gallery forests. The meadows are dominated by *Stegolepis ligulata* (Rapateaceae), with an upper altitude limit of 2,300 m (Huber 1992). The paramoid shrublands reach the highest elevations, up to 2,600 m, and are dominated by several species of *Chimantaea* (Compositae). The gallery forests grow along water courses, and are dominated by *Bonnetia roraimae* (Theaceae). Rull (2004) provides a more detailed description of the vegetation. The

V. Rull (✉)
Departament de Biologia Animal, Vegetal i Ecologia,
Universitat de Barcelona,
Bellaterra, 08193 Barcelona, Spain
e-mail: valenti.rull@uab.es
Tel.: +34-93-5812279
Fax: +34-93-5811321

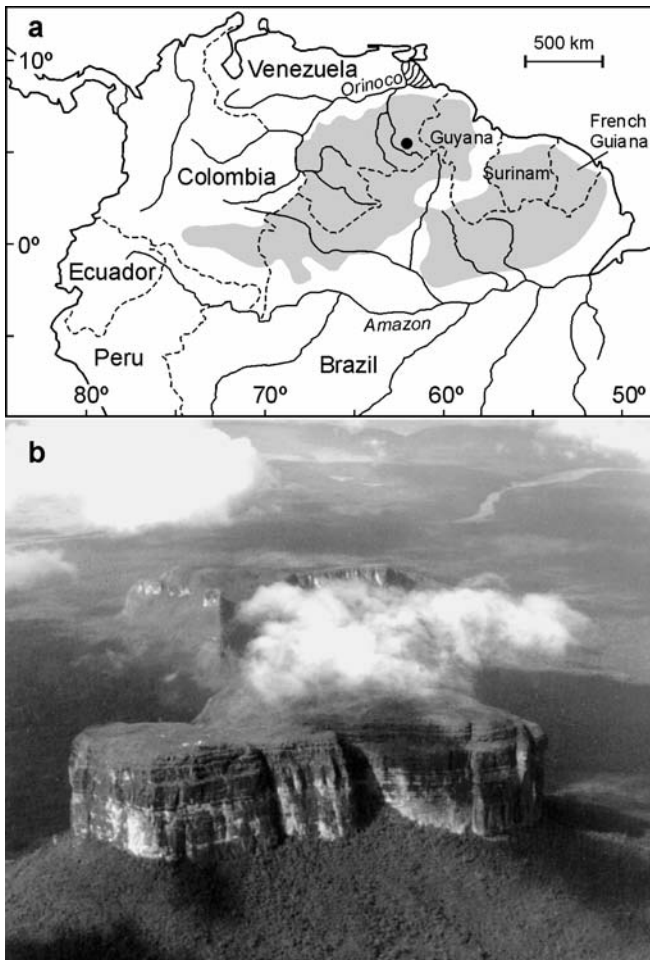


Fig. 1a, b Map of northern South America and typical *tepuian* landscape. **a** Location map showing the situation of the Chimantá massif (black dot). The shaded area is the Precambrian Guayana Shield. The scale bar is approximately 500 km. **b** Aerial view of the *tepuí* called 'Cerro Venado', with a summit at about 1,300 m elevation. Note the spectacular vertical cliffs separating the summit from the adjacent lowlands, at about 400 m altitude

locality studied is on the Churí-*tepuí*, at 5°19' N, 62°10' W and 2,250 m elevation, close to the upper altitudinal limit of *Stegolepis*. The dominant vegetation is a paramoid shrubland. Two peat outcrops situated few hundreds of metres apart, CHIM-1 and CHIM-2, were sampled at 5-cm intervals for pollen analysis. Samples were processed by common palynological methods (Faegri et al. 1989), after the addition of exotic markers by weight (Salgado-Labouriau and Rull 1986). Pollen identification and counting methods followed Rull (1987, 2003). Radiocarbon dating for CHIM-2 was taken from former workers (Schubert and Fritz 1985), and calibrated according to Stuiver et al (1998). The physiographical analysis as related to endemism is based on raw floristic and topographical data available in the literature and from maps.

Results

The sampled outcrops record the vegetation dynamics for the past 6,500 years before present (y BP) (Fig. 2). The detailed pollen percentage diagrams, their description and

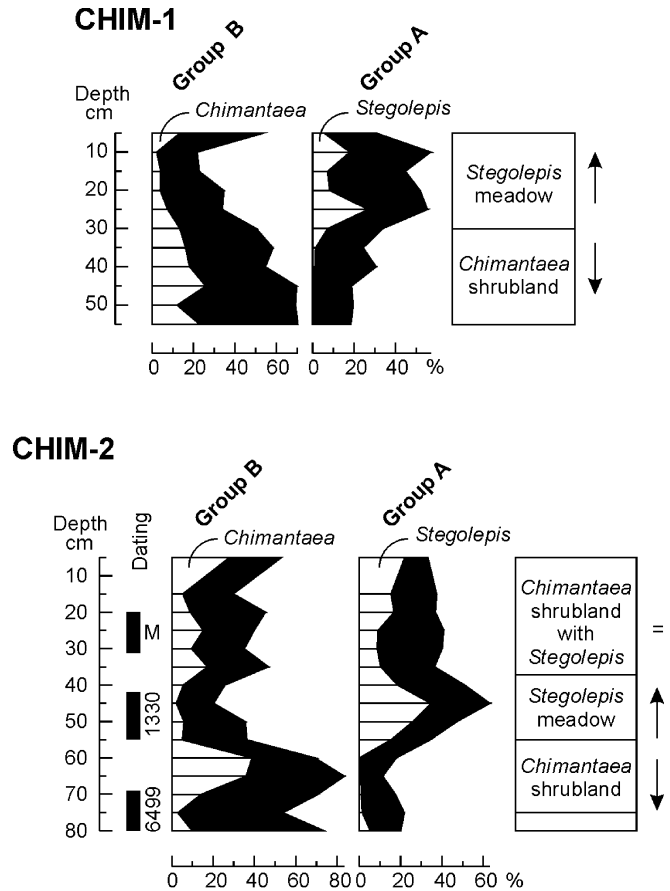


Fig. 2 Synthetic pollen diagrams of the two peat outcrops studied. The curves of the two assemblages found by cluster analysis (Pearson correlation coefficient and the unweighted centroid agglomerative method) are in *black*, and those of *Chimantaea* and *Stegolepis* (indicators for paramoid shrublands and meadows, respectively) in *white*. The vegetation corresponding to each pollen zone is indicated at the right side of each diagram. Arrows indicate the altitudinal position of the vegetation for each pollen zone with respect to present-day conditions. An upward displacement indicates conditions warmer than at present, while a downward displacement is linked to climates cooler than the present ones (= means equal). Dates are in calibrated ^{14}C years BP (cal ^{14}C -y BP); the confidence interval for 1,330 (1 σ) is 1,294–1,406, and for 6,499 is 6,409–6,663 cal. ^{14}C -y BP. *M* = modern

palaeoecological interpretation are published elsewhere (Rull 2004). Here, the patterns of change were examined using an assemblage approach. Two pollen assemblages were obtained in each locality by cluster analysis. These groups are the same in both localities. Assemblage A is characterised by *Stegolepis*, Poaceae, *Ilex* (Aquifoliaceae) and *Cyrilla* (Cyrillaceae), whereas assemblage B is formed by *Chimantaea*, *Xyris* (Xyridaceae) and Ericaceae. Group A is characteristic of *Stegolepis* meadows and group B represents the *Chimantaea* shrublands. These assemblages show consistent stratigraphic patterns in both sequences (Fig. 2). The pollen diagrams have been subdivided into pollen zones that represent different vegetation types. The lowermost zone (55–30 cm in CHIM-1 and 75–60 cm in CHIM-2) represents a *Chi-*

mantaea shrubland with practically no *Stegolepis*, similar to the present-day paramoid shrublands of the uppermost altitudinal levels in the Chimantá massif (Huber 1992). Therefore, the sampling site, which nowadays is around the altitudinal boundary between the paramoid shrublands and the *Stegolepis* meadows, was occupied by paramoid shrublands characteristic of the uppermost *tepuian* elevations at that time. Hence, between about 6,500 and 2,550 y BP (interpolated age), the vegetation was displaced downward with respect to its present-day position, due to colder conditions at that time. In the overlying zone (30–0 cm in CHIM-1, and 55–40 cm in CHIM-2), the percentages of *Stegolepis* pollen are similar to those of modern *Stegolepis* meadows, typically from lower elevations. Therefore, after 2,550 y BP the site was occupied by a *Stegolepis* meadow, suggesting that the vegetation had migrated upward. The present-day situation, a paramoid shrubland with *Stegolepis*, is represented by the uppermost zone of CHIM-2 (40–0 cm), and indicates that another downward displacement, although less pronounced, took place after 1,330 y BP (AD 620). The altitudinal arrangement of these vegetation types depends mainly on annual average temperatures; hence these altitudinal shifts reflect primarily temperature changes (Huber 1992). Unfortunately, the scarcity of modern pollen analogues for the *tepu* summits (Rull 1991) prevents quantification of the vertical displacement of vegetation, which could have been used to estimate the temperature changes. Nevertheless, maximum shifts of several hundreds of metres are likely to have occurred. Climatically, a phase colder than today occurred before 2,550 y BP, followed by a phase warmer than today after this date, and a return to present-like, intermediate conditions since 1,330 y BP (AD 620) to the present.

Discussion

Pollen results indicate that vertical displacement of the Pantepui vegetation occurred in response to climate, i.e. temperature change. Coeval and similar climatic trends have been recorded on other Neotropical areas (Chepstow-Lusty et al. 1998; Curtis et al. 1996; Rull 1992; Salgado-Labouriau et al. 1988; Thompson et al. 1988, 1995). However, given the vertical difference between the *tepu* summits and the surrounding lowlands (Huber 1987), a downward moving like that recorded here would not have been enough for the *tepuian* highland vegetation to reach the lowlands. Nevertheless, Holocene temperature variations were small relative to the temperature changes that occurred during glacial times. In the Neotropical Andes, at the same latitude range as the Venezuelan Guayana region, the vertical displacements of the vegetation have been hundreds of metres in the Holocene, whereas during the Last Glacial Maximum (LGM), about 21,000 y BP, the shift had been in the order of 1,200–1,500 m (Van der Hammen and Cleef 1986; Rull 1998). The situation must have been the same in the Guayana Highlands. Using all the available literature, Farrera et al.

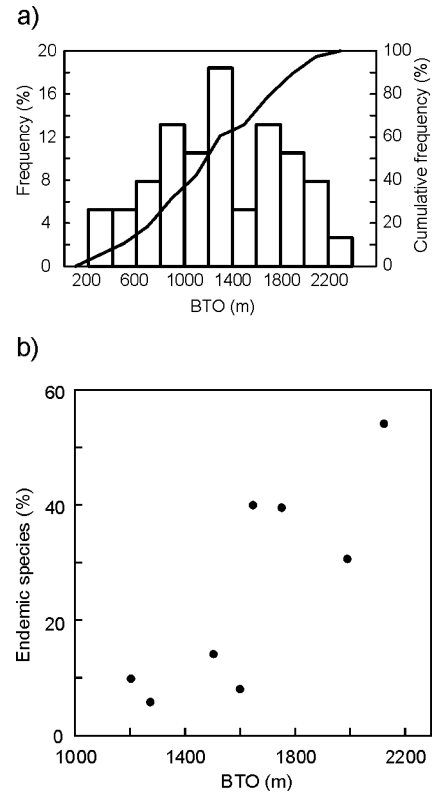


Fig. 3 **a** Distribution of *BTO* (base-top offset) for the 48 most important *tepuis* of the Venezuelan Guayana. Bars indicate the relative frequency for each category, and solid line is the cumulative frequency. Raw data are from Huber (1987) and Berry et al. (1995). **b** Relationship between *BTO* (base-top offset) and species endemism. Only the *tepuis* of the Venezuelan Guayana with a *BTO* above 1,100 m, having reliable and updated data on endemism, are depicted. Raw data are from Steyermark (1986)

(1999) estimated a shift of 1,100 m for the Neotropical region during the LGM. Such a shift would have permitted about 40% of the flora on the Venezuelan Guayana *tepu* summits to descend and mix with that at lower elevations (Fig. 3). Isotopic studies of long marine cores have shown that the LGM has been one of the coldest glacial episodes of the last 2.5 million years, where around 40 glacial cycles have occurred (Raymo 1994). Hence, a greater downward shift probably did not occur in previous glaciations. As a consequence, *tepu* summits that lie more than 1,100 m above the surrounding terrain, or about 60% of them, would have possessed vegetation that remained isolated from the surrounding lowland forests, even during glacial times. Figure 3 shows that the proportion of endemism on *tepuis* increases with the *BTO*, suggesting that vegetation isolation was a function of altitude. In *tepuis* with *BTO*s between 1,200 and 1,600 m, <15% of the species are endemic. This is most probably due to differences in the altitudinal range of the taxa, and to the fact that each taxon can have its particular response to climatic forcing (Bush 2002; Bush et al. 2001). Especially important is the lower altitudinal limit (LAL) of distribution. Taxa with a narrow altitudinal

ranges and a high LAL as compared to the BTO of the *tepuis* where they live, have the maximum probability of being endemic; while those with wider ranges and lower LAL in relation to the BTO would have reached the lowlands in the past. In support of this, of the 23 genera endemic to Pantepui (Berry et al. 1995), only three have a LAL lower than the BTO of their *tepuis*. During interglacial warmings, the vegetation reacted to climate again and moved upward. In this way, taxa formerly restricted to one or few *tepuis* have the possibility of colonising new summits, thus reducing the degree of endemism. As a result, the percentage of present-day endemic taxa is lower (33%) than that formerly estimated under assumed isolation conditions (90–95%).

In conclusion, the present-day biogeographical patterns of the Pantepui flora are the result of a complex evolutionary process in which both isolation and vertical displacement due to glacial/interglacial alternation have played a role, depending on the taxa and the *tepuis* considered. For the complete understanding of the endemism patterns in the region, much work is still needed. Accurate estimates of the vertical shifts occurred during the LGM are needed in order to know exactly the degree of connection of each particular *tepuis* with the lowlands. In this way, the most probable pathways and topographical barriers for taxa migration would be identified, and the biogeographical history of particular taxa reconstructed. As has been shown in this paper, pollen data and radiocarbon dating contribute to eliminate speculation, as they provide direct evidence to test the hypotheses dealing with historical biogeography and evolution of plants. Therefore, these techniques should be encouraged in future studies.

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