



Biogeography of the ‘Lost World’: a palaeoecological perspective

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Abstract

The uniqueness of the flora from the remote tableaux summits of the Guayana region has been explained either as the result of a long history of evolution in isolation (Lost World hypothesis or LW) or by alternating upward and downward displacements during the glacial–interglacial Quaternary cycles (Vertical Displacement hypothesis or VD). So far, the problem has been addressed solely on the basis of present-day floristic observations. This paper faces the problem from a Quaternary palaeoecology perspective using recent palynological findings in the area, comparisons with palaeoecological records from Neotropical mountains and lowlands of similar latitude, isotopic glacial–interglacial records from marine and ice cores, and different points of view about the response of organisms to Quaternary climatic changes, with emphasis on the LGM and the debate on the existence or not of Neotropical refugia. It is concluded that both LW and VD hypotheses, together with autoecological and synecological considerations, are needed to explain the present-day specialisation and endemism of the flora from the tableaux summits. The case of a highly endemic genus (*Chimantaea*, Asteraceae) is analysed as an example, to illustrate the usefulness and limitations of the different arguments to account for its biogeographical pattern. Some ideas are provided for future research, including a more extensive sampling strategy, the use of molecular phylogenetics, the evaluation of the individualistic versus the community approach, and the use of island biogeography and metapopulation methods on present-day floristic data.

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1. Introduction: vicariance or dispersal

Sir Arthur Conan Doyle coined the expression ‘Lost World’ (Doyle, 1912) to refer to the remote and high plateaux in the middle of the tropical jungle of the Amazon and Orinoco basins, in northern South America (Fig. 1). These mysterious landscapes inspired this author to write a fantastic novel about strange dinosaur-like creatures and forgotten civiliza-

tions living on the top of these table mountains, aside from the rest of the world. The spirit of this novel has carried across into science conducted in this region. The mythology greatly influenced earlier scientific explorations, and to some extent still underlies to some hypotheses explaining the origin of the mountain-top biota (Brewer-Carías, 1978). Nowadays, more than a hundred table mountains are known in the Guayana region, some in Guyana and Brazil, but most of them (around 90%) are in Venezuela (Fig. 2), where they attain their maximum development (Steyermark, 1986), and are called *tepui*, an indige-

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Fig. 1. Aerial view of a typical *tepui* (Cerro Venado), showing its flat summits, the vertical cliffs, the slope area, and the surrounding lowlands at the background.

nous word meaning ‘stone bud’ (Huber, 1987). The *tepuis* are flat-topped, sandstone table mountains between about 200 and 2400 m higher than the surrounding plains, with vertical cliffs up to 1000 m (Fig. 1). The size and maximum elevation of the summits varies, ranging from less than 1 to ca. 1000 km², and from ca. 1000 to ca. 3000 m above sea level (Huber, 1995a). The assemblage of these *tepui* summits, above 1500 m elevation, is a discontinuous biogeographical province called *Pantepui*, with an estimated total area of 5000 km² (Huber, 1995a). The *Pantepui* flora is unique regarding its specialised forms and endemism. The first botanical exploration to one of these summits was conducted by E.F. Im Thurn in 1884 to mount Roraima (Fig. 2), who found many rare plants unknown to science (Huber, 1995b). Subsequent expeditions documented more new taxa, and contributed to the idea of a diverse and peculiar flora with a high degree of endemism. As a result, it was proposed that a total of about 2000 species would exist in *Pantepui*, of which 90–95% would be endemic (Maguire, 1970). To explain this unique flora, it was postulated that this biota was relictual and originated after a long history of evolution in isolation, both among the tableaux themselves, and with the surrounding plains (Maguire, 1970; Brewer-Carías, 1978). This view is called here the ‘Lost World’ (LW) hypothesis, and follows the vicariance approach (Croizat et al., 1974; Nelson and Rosen, 1981), as the

underlying evolutionary mechanism is allopatric speciation from a hypothetical, more or less homogeneous initial flora, in areas progressively isolated by insuperable geographical barriers created by erosion.

Further botanical exploration revealed new facts that challenged the ‘Lost World’ idea. On the one hand, the level of endemism, although high, is not so spectacular. Indeed, of the 2322 species known so far, 766 (33.0%) are endemic to *Pantepui*, 1088 (46.9%) are endemic to the Venezuelan Guayana, and 1517 (65.3%) are endemic to the Guayana Shield (Fig. 2). With regard to genera (630 in total), 23 (3.7%) are endemic to *Pantepui*, 29 (4.6%) are endemic to the Venezuelan Guayana, and 85 (13.5%) are endemic to the Guayana Shield (Berry et al., 1995). On the other

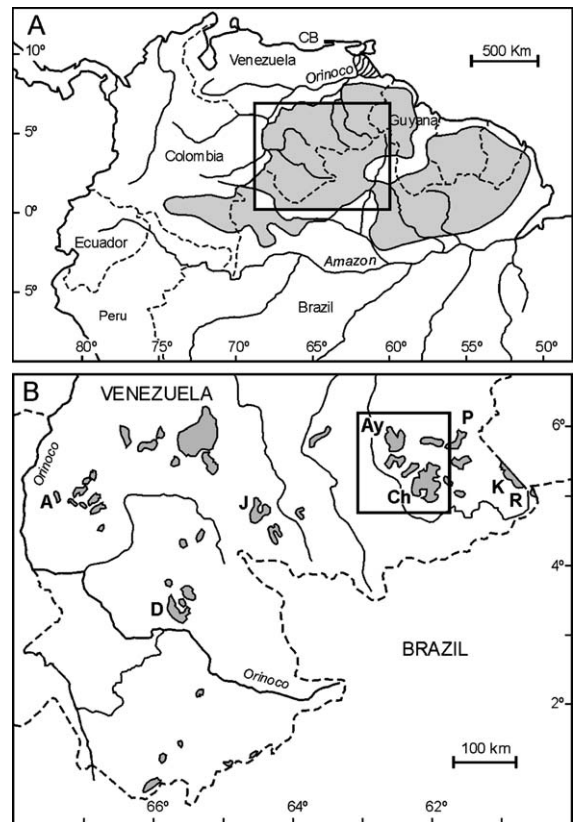


Fig. 2. (A) Map showing the Guayana Shield (shaded area), CB = Cariaco Basin. (B) Map of the *Pantepui* region (shaded areas), with indication of the *tepuis* mentioned in the text and in Fig. 4, as well as the area corresponding to Fig. 6. A = Autana, Ay = Auyán, Ch = Chimantá, D = Duida, J = Jaua, K = Kukenán, P = Ptari, R = Roraima.

hand, the assumed total geographical isolation of the *tepui* summits by the vertical cliffs is not real for many of them, because of the existence of extensive valleys and gentle slopes physically communicating lowlands and highlands, thus providing possible migrational pathways (Huber, 1988). In addition, it was realised that the altitudinal range of many assumed high-altitude species was wider than previously known, and that several patches of *tepuian*-like vegetation (both physiognomically and taxonomically) occurred in the plains surrounding a number of *tepuis* summits (Steyermark and Dunsterville, 1980; Huber, 1995c). All these factors led to a new hypothesis, in which it was proposed that the *Pantepui* flora would have been interconnected in the past by two mechanisms: (a) vertical migration through river valleys, and (b) vertical shifts of vegetation during the Pleistocene glacial–interglacial cycles (Steyermark and Dunsterville, 1980). This is called here the ‘Vertical Displacement’ (VD) hypothesis, that was further developed under the dispersal approach, defining several ‘centres of origin’ (Briggs, 1984, 1987). In this hypothesis, the speciation follows migration from these centres and subsequent local differentiation (Steyermark, 1979, 1986).

The controversy about the origin of the *tepuian* flora reproduces once more the classical biogeographical debate between the defenders of the vicariance and the dispersal approaches (Croizat et al., 1974; Nelson and Rosen, 1981; Briggs, 1984, 1987). All the evidence used so far, however, comes from present-day botanical and phytogeographical studies. To be properly tested, biogeographical and evolutionary hypotheses need evidence from the past. Palaeoecological testing of the LW hypothesis has not been possible due to an absence of sedimentary rocks between the Precambrian and the Holocene in *Pantepui* (Briceño and Schubert, 1990, 1992). However, the two components of the VD hypothesis, i.e. vertical migration along river valleys and vertical displacement of vegetation, can be approached through the analysis of recent sediments. This paper discusses the problem in the light of new palaeoecological and phytogeographical data gathered during the last decade. The answer seems more complex than the adherence to either the LW or the VD hypothesis, and probably needs elements from both, as well as from other proposals.

The debate about the earliest origin of the *Pantepui* flora is beyond the scope of this review. Some authors think that most of the components derive from ancient lineages that evolved in *in situ*, while others postulate that endemics evolved from Andean ancestors that migrated to the Guayana region. These propositions, however, are solely based on present-day floristic relationships; there is no any palaeoecological evidence to support either one or another proposition. The reader is referred to Berry et al. (1995) for a discussion.

2. Palaeoecological evidence and biogeographical implications

2.1. Vertical migration versus isolation

The assumption of vertical displacement as a response to climate had been not demonstrated in the Guayana region since its proposal, and remained as a possibility. However, recent palynological studies on peats from a *tepui* summit of the Chimantá massif (Fig. 2), above 2000 m elevation, showed that dominant and subdominant taxa of the main vegetation types of the *tepui* summits, notably *Chimantaea* (Asteraceae) and *Stegolepis* (Rapateaceae), actually moved up and down, responding to temperature shifts, in the last 5000 years before present (5 ky BP) (Rull, 2004a,b). It is important to note that these vertical movements correspond to the Holocene, when climatic changes have been comparatively small. The magnitude of these movements is expected to be notably higher during the Pleistocene glacial–interglacial cycles. Therefore, the VD hypothesis is supported by these results. The next question is if these vertical displacements have been frequent and intense enough to be determinant in the evolution of the *Pantepui* flora. The first evidence of widespread glaciation in the Northern Hemisphere, or the onset of glacial–interglacial cycles, is at ~ 2.5 million years (My) BP. Between that time and 800 ky BP, about 30 glacial–interglacial cycles had occurred with a periodicity of 41 ky. During the last 800 ky, the eight glacial cycles documented have been not only longer (100 ky periodicity) but also more intense (Raymo, 1994). Another interesting fact is that glacial phases have been notably larger than interglacials, so glacial con-

ditions have been the rule. Therefore, in theory, they have been roughly 40 opportunities for biotic interchange between the *tepui* summits during the last 2.5 My.

In order to assess the intensity of both climatic and altitudinal oscillations, the Last Glacial Maximum (LGM), occurred at about 21 ky BP, will be used as a reference for further comparisons. This has been the coldest phase of the Last Glaciation. In the Neotropics, average temperatures were about 8 °C lower than today in the Andes, and around 5 °C below the present ones in the Amazon lowlands (Van der Hammen and Hooghiemstra, 2000; Bush et al., 2001). The treeline was inferred to be 1300–1500 m lower than today in the Colombian Andes (Van der Hammen and Cleef, 1986), situated at the same latitude as the *Pantepui* region. In the Venezuelan Andes, between about 8 and 9°Lat. N, a similar shift of 1200 m was recorded (Rull, 1998a). Considering all the available literature, Farrera et al. (1999) estimated an average shift of 1100 m for the Neotropics. Hence, a shift of similar intensity seems reasonable for the Guayana highlands. Is this enough to allow the plants of the *tepui* summits reaching lowlands thus favouring biotic interchange among them? To answer this question, it is necessary to know the altitudinal range of the *tepuis*, or the difference between their bases—the surrounding lowlands—and summits. Fig. 3 shows the distribution of the altitudinal range for the most important table mountains of the Venezuelan Guayana. First of all, it can be seen that a very

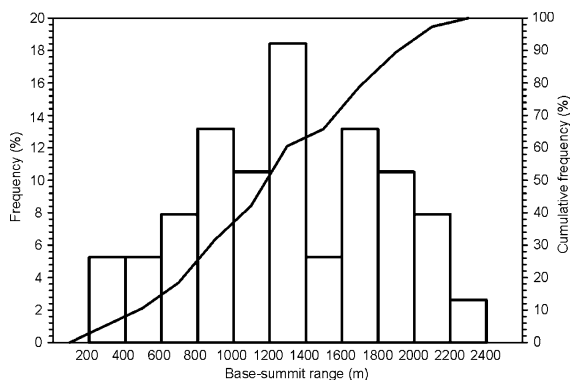


Fig. 3. Frequency distribution of the base–summit altitudinal difference for the most important tepuis of the Venezuelan Guayana (raw data from Huber, 1987). Bars correspond to simple frequency (left scale) and solid line to cumulative frequency (right scale).

unlikely lowering of 2400 m is needed for the plants of all these *tepui* summits to reach the base level and thus be interconnected. A most probable lowering of 1100 m (Farrera et al., 1999) would have determined the biogeographical connection of about the half of the *tepuis* considered, while the remaining 50% would have remain isolated during the LGM. Since temperature shifts of former glaciations have been equally or even less pronounced, especially before 800 ky BP, a higher degree of biogeographical connection is not likely to be expected in previous glaciations. This means that a significant proportion of the *tepui* summits would have been never connected biogeographically, except for hypothetical mechanisms such as seed dispersal or migration through river valleys connecting lowlands and highlands. It is important to emphasise that 1100 m is the maximum descent expected for the last glaciation, the average being notably lower. Isotopic records from Greenland ice cores show that, in the North Atlantic region, the LGM and similar stadials that occurred during the full glacial conditions were short and intercalated with warming events (Dansgaard et al., 1993); hence, the temperature decrease for the whole glaciation was of 2–3 °C in average. The same pattern has been found recently in marine cores from the near Caribbean Cariaco Basin (Fig. 1), showing that the climate of the region considered here has been under the North Atlantic influence during the last 90 ky (Peterson et al., 2000). A mean lowering of 2–3 °C would have produced a downward displacement of 600 m or less in the *tepuis*, which involves that only ~ 15% of the *tepui* summits in average, would have been connected floristically (Fig. 3).

Therefore, isolation seems to be as real as vertical displacement. As a consequence, both LW and VD hypothesis seem to be required to explain the origin of the *Pantepui* flora as a whole, in the light of palaeoecological data. Direct evidence of the assumed LGM floral interchange, however, is still lacking because no Pleistocene sediments have been found so far. Molecular phylogenetics also supports a mixed origin for the *Pantepui* flora. Indeed, the analysis of DNA sequence variations in chloroplast genes indicated that the endemic genus *Stegolepis*, which species are commonly restricted to one or few *tepuis*, emerged between 6 and 12 My BP—long after the isolation of the *tepui* summits by erosion—and the

speciated. As a consequence, not only vicariance but also long-distance dispersal are required to account for speciation of this genus in the *tepui* summits (Givnish et al., 2000). Two implications of a combined LW–VD hypothesis are that (a) endemism should be indirectly related to the possibility of connection during glacial times, hence the percentage of endemic species should increase with the altitudinal range (base–summit difference) of the *tepuis* and (b) the higher percentage of endemism should be found in the more high-altitude taxa, since those with their lower altitudinal limit of distribution around 1100 m above the base of the *tepuis* would have reached lowlands during glacial coolings and migrated to neighbouring *tepui* summits in the interglacial warmings, whereas those restricted to higher altitudes would not. The first prediction is strongly supported by the data available so far in a wide range of table mountains (Fig. 4). The second one is supported by the patterns of generic endemism. Indeed, considering the 23 genera endemic to *Pantepui*, the vertical distance between the base of the *tepuis* and their lower limit ranges from 900 to 2300 m (raw data from Berry et al., 1995). As a

consequence, a significant part of the summit flora would actually remained isolated, even during glacial times. This involves the apparently trivial, but still undemonstrated, assumption that the *tepui* summits were vegetated during the LGM and former glacial phases.

2.2. The *Pantepui* refuge

The refuge hypothesis was originally proposed to explain the survival of rainforest species of the Amazon lowlands during the assumed general aridity occurred in the LGM (Haffer, 1969; Prance, 1982). According to it, these species remained isolated in some lowland areas with special microhabitat characteristics, in the middle of a ‘sea’ of deserts and savannas that dominated most of northern South America. After glaciation, rainforest species would have spread over, thus forming the present-day rainforests that cover most of the Amazon basin. The *Pantepui* province was considered one of these refugia, based on the present-day distribution of birds (Mayr and Phelps, 1967), and was further adopted by some botanists to explain the diversity and endemism patterns of the flora (Steyermark, 1979). This seems to be contradictory with the VD hypothesis because, according to the refuge theory, the contraction of the ‘refugee’ species took place during glaciations and their expansion in the interglacials; while the VD defenders (curiously the same that defined the *Pantepui* plant refuge) proposed that the spreading and interconnection of the flora from *tepui* summits should have occurred during glacial phases. This is not an insoluble controversy as we will see later, but now we will concentrate on the existence or not of the *Pantepui* refuge.

The first palaeoecological data gathered seemed to deny the reality of *Pantepui* as a glacial refuge. Indeed, the oldest peats encountered in the *tepui* summits were early to mid-Holocene in age. It is known that peat accumulation is largely controlled by climate (Clymo, 1978; Barber, 1981). In the tropics, the suitable environmental conditions for peat accumulation are high humidity, low pH, and a high production/decomposition ratio, which is favoured by cold climates (Meadows, 1988). Therefore, arid or semi-arid climates, unfavourable for peat accumulation, have been proposed for the *tepui* summits

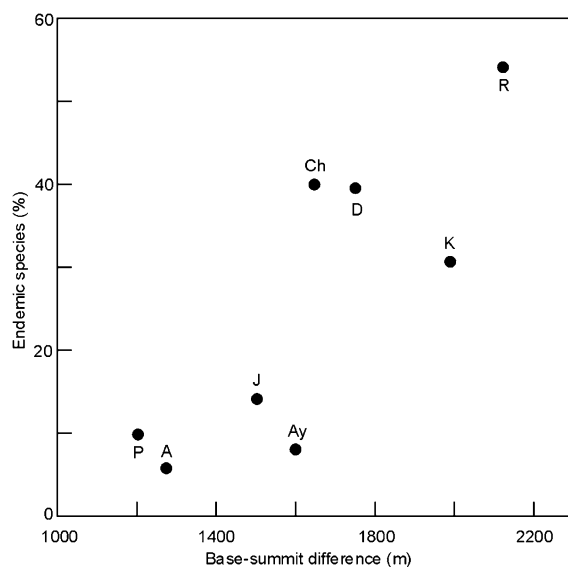


Fig. 4. Relationship between the base–summit altitudinal difference (raw data from Huber, 1987), and the percentage of endemism for the *tepuis* with reliable data (raw data from Steyermark, 1986). See the geographical location of the *tepuis* in Fig. 2. A=Autana, Ay=Auyán, Ch=Chimantá, D=Duida, J=Jaua, K=Kukenán, P=Ptari, R=Roraima.

during the LGM and the Pleistocene–Holocene transition (Scubert and Fritz, 1985; Schubert et al., 1986). Under these conditions, summit vegetation would have been very scarce or absent. In this context, the survival of highland plants during glaciations were explained by the existence of scattered and small plant stands in restricted summit areas with special microclimatic conditions, called microrefugia (Rull, 1991; Rull et al., 1988). Other microrefugia were proposed at lower elevations (600–1500 m), depending on the ecological requirements of species involved (Marcano, 1999). The existence of similar glacial microrefugia have been postulated also for the African tropics, covered today by extensive rain forests (Leal, 2001). Anyway, the subsistence of extensive summit communities during the LGM and, consequently, of the *Pantepui* refuge, was considered very unlikely (Scubert and Fritz, 1985; Schubert et al., 1986). However, the number and distribution of sites analysed palaeoecologically are not enough to reject the existence of extensive peats during the Pleistocene. Due to severe constraints derived from the remoteness of the *tepui* summits, less than 10 sites have been bored in the about 5000 km² *Pantepui* area (Rull, 1991), with accessibility as the main sampling criterion. Moreover, from a climatic point of view, peat formation during the LGM is fairly possible, since the summits should have not been necessarily dry. A general reduction of around 40% with respect to the present-day precipitation has been estimated for the LGM in northern South America (Hooghiemstra and Van der Hammen, 1998; Van der Hammen and Hooghiemstra, 2000). The average annual precipitation of the *tepui* summits is so high (2500–3500 mm, Huber, 1995a), that such a reduction would have maintained their climate still humid (1500–2100 mm). This, together with the estimated reduction in average temperatures of 5 to 8 °C (Van der Hammen and Cleef, 1986; Van der Hammen and Hooghiemstra, 2000; Bush et al., 2001), suggests that during the LGM the *tepui* summits were under a cool and humid climate, favourable for peat formation. Thus, the finding or not of Pleistocene peats would be actually a matter of chance, due to insufficient and inadequate, though understandable, sampling strategies. In this sense, it should be stressed that the refuge hypothesis is falsifiable using pollen analysis. For example, the existence of a glacial refuge area for temperate forests

was documented in southern Europe (Tzedakis, 1993; Tzedakis et al., 2002). Furthermore, the subsequent northward postglacial expansion of these forests was reconstructed, using extensive pollen databases (Tzedakis and Bennett, 1995; Bennett, 1997; Brewer et al., 2002).

The refuge hypothesis has been rejected arguing that significant lowering in temperatures and not extended aridity was the decisive environmental factor, in the northern South American lowlands, during the LGM (Colinvaux et al., 1996). According to these workers, the lowlands were not occupied by savannas with patches of rainforest (refugia), but by a continuous forest cover with different composition than nowadays. Their arguments are based on palaeoecological studies, and have two main challenging foundations. On the one hand, underlying most of the propositions analysed so far is the idea that present-day conditions are the ‘normal’ conditions, and glaciations are exceptional cold phases that plants have to endure until the climate becomes normal again. Palaeoecological evidence, however, has shown that the situation is the reverse. Indeed, glacial conditions have been the dominant, whereas interglacials are short warming peaks (Fig. 5). A logical consequence is that plant species would be adapted to normal glacial conditions and, in the interglacial peaks, they escape from lowlands to more elevated terrains until normality establishes again (Bush et al., 2001; Bush, 2002). On the other hand, the unit that responds to environmental changes is considered to be the species population and not the community, hence, this vertical upward migration was experienced by the most stenothermic and less warm-tolerant taxa only. It thus involves that community composition would not be stable, and transient communities with no modern analogues would have existed in the past (Bush et al., 2001; Colinvaux et al., 2000). According to the defenders of this alternative approach, the situation is the reverse of that initially stated by the lowland refugia hypothesis. In the Neotropical lowlands, the origin of most endemic species would not have occurred by vicariant speciation in the assumed lowland refugia surrounded by a sea of dry vegetation, but in elevated isolated areas, within a ‘sea’ of intact rain forests (Colinvaux, 1998). *Pantepui* is a good candidate for such a proposal, what would solve the apparent contradiction mentioned before. Regarding

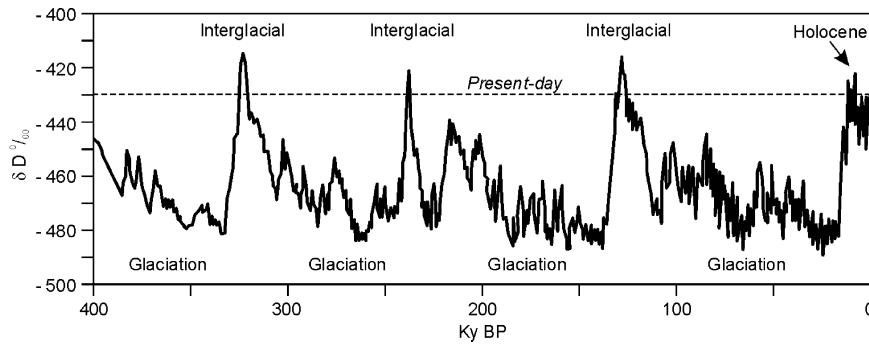


Fig. 5. The last four glacial cycles as expressed by Deuterium isotopic composition (a proxy for temperature) from the Vostok ice core, in Antarctica. The dashed line is the present-day temperature. Glacials and interglacials (including the present, the Holocene) are indicated. Redrawn from Petit et al. (1999).

the endemism of the *Pantepui* flora, this later view could have some additional, interesting consequences. On the one hand, present-day, interglacial plant communities of *Pantepui* could be transitional as the product of mixing of warm-intolerant taxa from lower elevations with those more adapted to highlands. Another interesting element is the possibility of different community composition in time, which is necessary to explain why some taxa are endemic while others are not, although they coexist nowadays in the same community. Finally, if geographical isolation of taxa were concentrated in interglacials, opportunities for allopatric speciation would have been restricted to periods of about 10-ky duration (Fig. 5). This seems not enough to produce the high levels of diversification and endemism recorded in *Pantepui*, and favours the existence of geographical isolation, even during glacial times, for most of the endemic taxa.

3. A case study: the genus *Chimantaea*

In this section, the case of the endemic genus *Chimantaea* is analysed, in order to test the ability of the different arguments stated previously to explain its present-day geographical patterns. *Chimantaea* is a highland genus restricted to a small *Pantepui* area around the Chimantá massif, and with little geographical differentiation. Its altitudinal range is 1600–2600 m (Berry et al., 1995), and is present only in four neighbouring *tepui*s: Chimantá, Auyán, Aprada and Murisipán (Fig. 6) (Huber, 1992a). Nine of the ten

species of this genus are in the Chimantá massif. The species of the Auyán-*tepui* (*Ch. cinerea*), is endemic to it, while those of the Aprada (*Ch. eriocephala*) and Murisipán (*Ch. cf. lanocaulis*) also occur in the

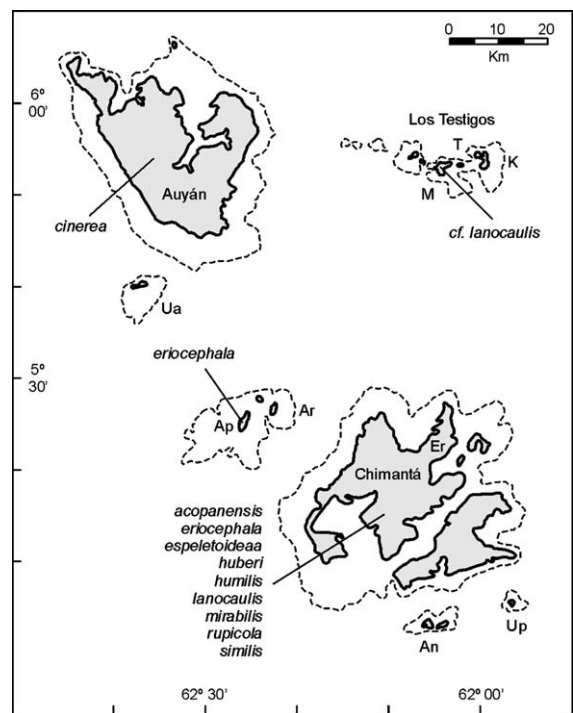


Fig. 6. Distribution of *Chimantaea* species in the Chimantá massif and neighbouring tepuis. Solid lines with shaded areas are the summits and dashed contour the slopes. An=Anasigma, Ar=Arapán, Er=Eruoda, K=Kanarkawarai, M=Murisipán, T=Teréké-yurén, Ua=Uaipán, Up=Upuigma. Map composed after Huber (1995a) and data on *Chimantaea* from Huber (1992a).

Chimantá. However *Ch. cf. lanocaulis* of the Murisipán shows some degree of phenotypic differentiation from the species of the other peaks. The Chimantá has been considered as the centre of origin for the genus, from which it would have dispersed to the other summits. As in many Asteraceae, *Chimantaea* seeds are dispersed mainly by wind (anemochory). At present, however, the dominant winds are from the north, northeast and northwest (Galán, 1992), blowing in the opposite direction to favour seed dispersal from the Chimantá to the other summits holding *Chimantaea* species. On the other hand, the Chimantá, the Aprada, and the Auyán are interconnected by a series of erosion surfaces with variable altitudes between 1000- and 1400-m elevation. These observations have led to the suggestion that *Chimantaea* species in the Aprada and the Auyán dispersed via vertical migration and subsequent expansion during glacial phases, whereas the occurrence of *Ch. cf. lanocaulis* in the Murisipán has been tentatively attributed to chance dispersal by birds (Huber, 1992a). However, according to Huber (1992a), important questions remain unexplained: Why should only 3 of the 10 *Chimantaea* species successfully dispersed from their centre of diversity? Why the numerous, flying seeds of *Chimantaea* have reached and colonised only one of the three available and almost identical summits of the Los Testigos massif (the Murisipán)? Why is the genus present on only one of the nearest summits to Chimantá (the Aprada)? And why the contrasting diversity between the Chimantá (with nine species) and the Auyán (with only one), if both have comparable summit areas and microhabitat variability to promote speciation?

Before continuing, some important concepts should be clarified, thereby avoiding a simplistic view of dispersal, migration and speciation. Taxa do not stand alone. Evolution takes place within a context of ecological succession and is modulated by both biotic and abiotic interactions, thus determining the biogeographical patterns for any given time slice (Margalef, 1986). The basic ideas to be discussed here are that: (a) the ability of a taxon to reach a place by dispersal does not guarantee its successful establishment and survival; (b) dispersal does not necessarily involve migration; and (c) the absence of a taxon from a given place is not necessarily an expression of its inability to reach the site. Concerning the first point, a propagule

must fall onto a suitable habitat for it to establish a population. The more specialised taxa, often belonging to more mature successional stages (*sensu* Margalef, 1968) are less adapted to successfully colonise new areas than the more generalist ones, typical of the earlier phases of ecological succession. For example, species with a very specialised pollination system cannot establish unless their pollinators are present, whereas anemophilous species are not limited in this way. Similarly, the successional stage of the ecosystem into which they are dispersing is also important. Mature ecosystems, with complex and well-established ecological interactions are more difficult to invade than communities in early successional stages, in which both diversity and complexity is lower, and more opportunities to find a suitable or vacant niche exist. Furthermore, it is important to distinguish between different forms of dispersal. According to Pielou (1979), the movement of individual organisms across great distances, followed by the successful establishment of a population of the original dispersers' descendants at the destination is called 'jump dispersal'. This involves only the successful dissemination of seeds or individual organisms, including the eventual successful establishment of a population, and is accomplished in a short period of time (comparable to the life span of an individual). Jump dispersal usually takes place through inhospitable terrains. A second type is the 'diffusion' or the gradual movement of populations across hospitable terrains for a period of many generations. The result is the steadily expansion of the range of the involved species. If the diffusion takes place so slowly that the species undergoes appreciable evolutionary change in the process, then the term 'secular migration' is used (Pielou, 1979). Finally, the range expansion of a group of species due to the elimination of some topographic or climatic barrier by continental drift has been designated as 'geo-dispersal' (Lieberman and Eldredge, 1996). Not only the meaning, but also the biogeographical consequences of these processes are very different and should always be bear in mind.

Regarding the third point in discussion, even in the case of a successful initial establishment by jump dispersal, unpredictable biotic and abiotic interactions will eventually operate further, and determine the survival or not of the incipient populations. For a given taxon, jump dispersal is not site-selective, since

it operates always in the same way. No matter the size of its distribution area, the probability of jump dispersal of a taxon is expected to be the same along it. Hence, its absence in certain places would be explained, not by dispersal or migration inability, but by failure in the establishment for ecological reasons stated before, and/or by local extinction. So far, differential extinction has not been considered in *Pantepui*, although it has been recognised as a fundamental trait for the understanding of present-day biogeographical patterns elsewhere (Lieberman, 2003). The local disappearance of a taxon in a given place can be produced by destructive environmental events (glaciation, dryness, flooding, fires), biotic interactions such as predation, competition, parasitism, pathogens, etc., or purely by stochastic demographic processes if their populations are small remnants (Leigh, 1981). Extinction rates are particularly high in isolated areas, where a more or less continuous supply of new individuals is prevented, as it occurs on islands and fragmented metapopulations (MacArthur and Wilson, 1963, 1967; Levins, 1970; Opdam, 1991; Rull, 1998b). From a biogeographical point of view, the *tepui* summits can be considered as ‘islands’ and many of their summit taxa form metapopulations, or assemblages of monospecific populations (Levins, 1970). Therefore, the *tepui* summits are more vulnerable to biotic extinction than the lowland environments.

Coming back to *Chimantaea*, it seems reasonable to assume that it originates in the Chimantá, where some initial speciation occurred. The assumed glacial migration is supported by palaeoecological data, because the vertical distance between its lower distribution limit and the surrounding plains is of 200–600 m, thus falling within the range of vertical displacement estimated for the last glaciation (see above). The absence of *Chimantaea* species in summits theoretically able to hold them could be explained in terms of differential survival by local extinction, rather than inability to disperse to those sites. There is no reason to think that the *tepuis* in which the genus does not occur have never received their seeds via jump dispersal, or even plants by diffusion or secular migration, after glacial spreading. Given the present state of knowledge, it is not possible to know which of the species present nowadays in the Chimantá had more extensive populations in the past, but it is clear

that only two are found outside of this area: *Ch. lanocaulis* and *Ch. eriocephala*, the first showing some degree of phenotypic differentiation. On the other hand, *Ch. cinerea*, endemic to the Auyán, is very similar both taxonomically and ecologically to *Ch. similis* (Huber, 1992a) which, together with *Ch. eriocephala*, are among the most widespread *Chimantaea* species in the Chimantá (Fig. 6). It is possible that *Ch. similis* or a common ancestor reached the Auyán, where *Ch. cinerea* emerged later by allopatric speciation. Due to the stated resemblance between these two species, it is hypothesised that their differentiation occurred in relatively recent times. This could explain why the Auyán has only one species, while the Chimanta (from which *Chimantaea* seems to have originated in earlier times) holds nine of them. The case of Murisipán and *Ch. cf. lanocaulis* could be similar, but here the differentiation is even smaller. It is important to note that Murisipán is only 50 km north of the Eruoda summit (Fig. 6), the northernmost end of the Chimantá massif, where the largest and denser populations of *Ch. lanocaulis* occur (Huber, 1992a). The Chimantá and the Los Testigos massifs are also connected by midlands of 1000 m elevation or more (Huber and Berry, 1995). Perhaps the most recent migration has been that of *Ch. eriocephala* to the Aprada, since no taxonomic differentiation has been observed. A detailed study of the altitudinal range of each species and the possible topographic pathways should be done to examine the possibility of diffusion during glacial times. The case of *Chimantaea* fits well with several principles of the metapopulation theory, at a long-term scale. According to this theory, the driving forces of population dynamics are local extinction and recolonisation of vacant patches. As in island biogeography, extinction is directly related to the area of the habitat fragment (patch) occupied by the involved population, whereas the possibility of a successful recolonisation depends on the size of the patch and its distance from the source area for dispersers. Large areas, with populations large enough to stay out of risk of extinction due to demographic stochasticity, are a source of dispersers, acting as a stable distribution centre (Levins, 1970; Harrison, 1991; Opdam, 1991). As noted above, the large source for the dispersal of *Chimantaea* is the Chimantá massif. The presence of the genus on few small *tepui* summits and its absence from the others

might be explained by differential extinction due possibly to stochastic demographic processes. The varying degree of taxonomic differentiation observed outside the Chimantá massif could be due to differences in the dispersal/migration timing, which derived in contrasting isolation histories and, hence, different levels of genetic differentiation.

At a regional scale, the very reduced range of *Chimantaea* within the *Pantepui* province may be explained by a long evolutionary process in isolation, favoured by a topographical barrier, i.e. the vertical distance with respect the surrounding lowlands, which is higher than 1100 m, the approximate threshold for a hypothetical glacial connection (see above). In summary, to understand the present biogeographical patterns of the *Chimantaea* and its species, several lines of reasoning are necessary, including long evolution in isolation, downward and upward migration during glacial–interglacial phases, as well as complex ecological processes and chance, leading to differential survival and local extinction patterns.

4. Concluding remarks and some proposals

Palaeoecology is still in its infancy in *Pantepui*, but with the data available so far, we are not so lost in this world. The two main contributions so far are the real occurrence of vertical displacements of taxa, and the estimation of frequency and intensity of these vertical movements during the Pleistocene glacial–interglacial cycles. There is still a lot of palaeoecological work to be done, and the search for Pleistocene sediments, especially those corresponding to the LGM, is critical. Only by finding and analysing sediments of an appropriate age can we eliminate speculation and establish empirical data for the history of this region. Indeed, the amount of vertical displacement used in this paper is a first-order estimation of its magnitude, since it is based on submodern analogs from mountains situated at about the same latitude. However, pollen analyses of Pleistocene sediments would provide a more precise quantification of the altitudinal movement, allowing a detailed topographic reconstruction of glacial conditions using Geographic Information System (GIS) tools. Such a physiographical framework would allow endemism patterns of *Pantepui* taxa to be studied, using the combined LW–VD

approach. Molecular phylogenetics is also a promising technique to derive evolutionary and biogeographical information. So far, only several genera from two families (Bromeliaceae and Rapateaceae) have been studied in *Pantepui* using this methodology (Givnish et al., 1997, 2000). These types of studies could be very enlightening, especially in the key taxa and lineages previously identified by palaeoecological studies. The combination of genetic and palaeoecological analyses is strongly encouraged.

As a working framework to be tested with these studies, a number of hypotheses and ideas have been stated in this paper. Some are more speculative than others, but it is evident that in considering the origin of the *Pantepui* flora and its degree of endemism, a single general approach is not possible. Both vicariance and dispersal approaches are necessary, together with synecological and autoecological factors, and their corresponding interactions. Furthermore, the view that considers that biota responds to environmental changes at a species and not at community level, provides arguments that fit well with the main features of the *Pantepui* flora. In the view of the palaeoecological data collected so far, it is difficult to escape the idea that a part of the *Pantepui* biota could have been ‘lost’ for a long time, whereas the rest have been actually interconnected at times. This individualistic perspective should be considered in the interpretation of future palaeoecological records from the Guayana region.

On the other hand, under the appropriate ecological and biogeographical perspective, present-day observations can still provide a great amount of information. For example, as an assemblage of isolated summits, *Pantepui* could be a suitable region to be studied using the island biogeography approach (MacArthur and Wilson, 1963, 1967). According to this theory, the species richness of an island is a balance between immigration and local extinction, and is directly related to the island size (Connor and McCoy, 1979). A recent study has shown that a significant positive correlation exists between species richness and area, in one of the highest *tepuian* massifs, the Roraima (Fig. 1), thus suggesting that island biogeography mechanisms could have played a role in the evolution of their biota (Michelangeli, 2000). This potential has not been yet fully realized, but with the large amount of floristic information gathered so far

(Steyermark et al., 1995), a survey of this type is already possible and is encouraged. A successful analysis of this type was carried out to explain the distribution of birds in the north Andean highlands, called *páramos*, situated above 3000 elevation, and isolated as patches in the middle of a ‘sea’ of montane cloud forests (Luteyn, 1999). According to this interpretation, the altitudinal lowering of the páramos during the glaciations determined their connection and promoted migration among them, whereas the interglacials favoured their isolation and the consequent speciation and extinction patterns, due to ecological interactions (Vuilleumier, 1979). The same reasoning could be used to interpret the geographical differentiation of the subgenera of *Espeletia* (Asteraceae), one of the most characteristic páramo plants (Cuatrecasas, 1979), which is taxonomically and physiognomically related to *Chimantaea* (Huber, 1992b). The metapopulation approach, strongly related to the island biogeography principles (Farina, 1998), could be also useful to analyse and explain the present-day distribution of particular taxa and lineages, as it has been shown in the case of *Chimantaea*. Many *tepuian* taxa can be considered to form metapopulations, since they occur in several isolated summits which constitute a naturally fragmented habitat.

Finally, *Pantepui* is still a remote region with minimal direct impact from humans. Indigenous communities living in the lower plains do not climb to the *tepuí* summits, which are practically unknown for them (Huber, 1987). Scientific exploration carried out over more than one century has produced a great amount of data with negligible disturbance and, fortunately, commercial exploitation has not transformed these landscapes so far. However, this pattern is not true for the surrounding lowlands, where fires, road building, mining, tourism and other activities are severely damaging the biota (Huber, 1995a,b,c,d). In this sense, it is desirable that the *Pantepui* region will remain a ‘Lost World’ to certain humans.

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