



Biotic diversification in the Guayana Highlands: a proposal

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ABSTRACT

Until recently, the high degree of diversity and endemism of the Guayana Highlands was explained within the frame of the refuge theory. Although this hypothesis is unsupported by recent palaeoecological evidence, no new diversification model has been proposed. This paper is a proposal based on the latest palynological findings that indicate a downward biotic migration of *c.* 1100 m altitude during glacials, and the subsequent interglacial upward shift, in response to colder and warmer climates, respectively. Therefore, during glacials, biotic mixing is expected in the lowlands, thus promoting sympatric speciation, hybridization and polyploidy. At the mountaintops, unknown cold-adapted taxa and páramo-like(?) communities are expected to have occurred, and vicariance prevailed. In the interglacials, many taxa have had the opportunity for ascending to the mountains again, allowing genetic interchange among their slopes and summits, while others would have been adapted to lowlands. The interglacial highland communities, where vicariance still predominated, experienced some extinction owing to habitat loss by upland displacement. According to this model, the successive alternation of glacials and interglacials resulted in a net increase of diversity and endemism, favoured by the complex topography and habitat heterogeneity, which allowed high niche diversification. This model has some similarities with the Andean and Amazon modes of diversification, but the special topographical characteristics of the Guayana region made it different in other fundamental aspects. The Guayana Highlands would have acted as a 'biodiversity pump' for the surrounding inner and coastal lowlands, due to the repeated speciation and further spreading events, as a response to climate. Several working hypotheses are suggested in relation to the proposed model. The use of coordinated international multiproxy projects combining palaeoecology and genetic analysis of modern taxa is strongly encouraged for exploring these ideas.

Keywords

Biodiversity, climatic change, diversification, endemism, Guayana Highlands, Neotropics, palaeoclimatology, palaeoecology, South America, speciation.

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INTRODUCTION

This paper discusses the possible causes for the outstanding degree of biodiversity and endemism of the Guayana Highlands, in the light of latest palaeoecological findings that challenge traditional views. The unique biota of the Guayana Highlands had been formerly considered the result of either vicariance after long evolution in isolation (Maguire, 1970) or dispersal, by successive connection and disconnection of summit floras due to Pleistocene climatic changes (Steyermark & Dunsterville, 1980; Huber, 1988). The 'dispersalists' adopted the refuge

hypothesis (Haffer, 1969) as the mechanism for genetic differentiation. This hypothesis proposes the alternation of dry and wet climates because of the recurrence of glacial and interglacial phases, respectively. Glacial aridity would have determined the fragmentation of forests into refugia of wet, stable climates surrounded by a sea of dry savannas and deserts, while interglacials would have been characterized by forest expansion and coalescence through the entire Neotropical lowlands. The associated diversification model suggests allopatric speciation within the forest refugia, which are still recognizable by their higher biodiversity and endemism

patterns (Haffer, 1969, 1982). Elevated areas are among the favourite locations for the assumed refugia and diversification centres. In this way, Mayr & Phelps (1967), to explain the distribution of birds, proposed that the Guayana Highlands constituted a biotic refuge (called Pantepui) during the last glaciation. This proposal was subsequently accepted to account for the biodiversity and endemism patterns of insects (Brown, 1975), terrestrial vertebrates (Müller, 1973) and plants (Steyermark, 1979). Modern botanical and phytogeographical syntheses of Guayana emphasize the potential role of present-day environmental and edaphic conditions for the generation of the high degree of endemism (Berry *et al.*, 1995). The first palaeoecological records, essentially radiocarbon dating of peats from the tepui summits, argued against the existence of the Pantepui refuge (Schubert & Fritz, 1985; Schubert *et al.*, 1986), but the number and distribution of localities examined has been considered insufficient for a definite answer (Rull, 2004c).

So far, besides the criticism of the refugial theory, an alternative model for diversification in the Guyana Highlands has not been proposed, probably because of the lack of appropriate palaeoecological support. In this paper, a tentative diversification model is proposed, based on the following observations from the latest palynological data: (1) vertical shifts and biotic interconnection among tepui summits triggered by glacial/interglacial alternation have indeed occurred (Rull, 2004a); (2) about the half of the summits would have remained isolated, so both vicariance and dispersal are needed to account for the long-term origin and evolution of the Pantepui biota (Rull, 2004b,c); and (3) the Guayana highlands have not been a biotic refuge during the Pleistocene glaciations (Rull, 2004c). The model is compared with similar studies from other Neotropical mountains to search for potential generalizations. An equally important aim of this paper is to raise some keystone hypotheses that can guide future research on the origin of the diversity and endemism patterns of the Guayana region, as well as to suggest the studies to be carried out for their testing.

BIODIVERSITY AND ENDEMISM IN THE GUAYANA HIGHLANDS

The Guayana region, situated between the Amazon and the Orinoco basins (Fig. 1), is one of the largest biodiversity and endemism reserves in the world, and a priority subject for conservation purposes, whatever the criteria employed. Geographically, this region lies on the north-western part of the Precambrian Guayana Shield, which extends over a large part of Venezuela and the Guayanas (Guyana, Suriname and French Guiana), the north of Brazil, and a small part of south-east Colombia. Physiographically, it is characterized by several erosion surfaces developed on the Precambrian sandstones/quartzites of the Roraima Formation (Briceño & Schubert, 1990). This determines a characteristic landscape with typical table mountains or tepuis, of flat and extensive summits, separated from the surrounding lowlands by vertical escarpments up to 1000 m high and basal slopes (Fig. 1). These

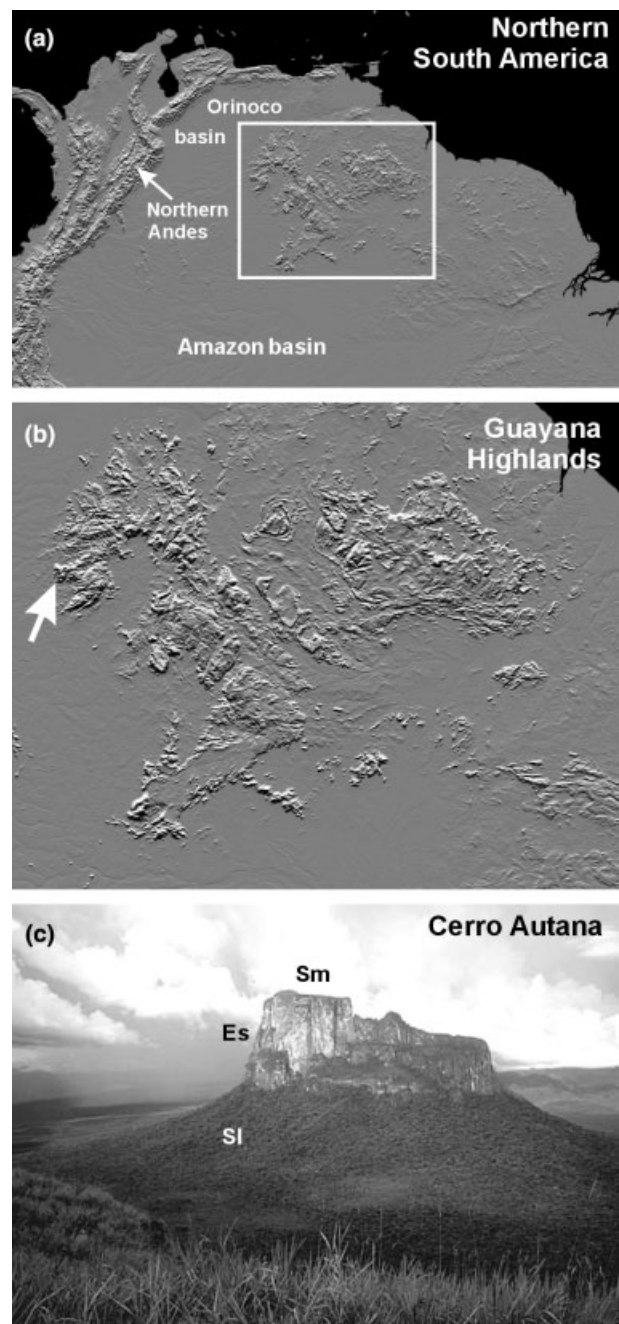


Figure 1 Location map and typical landscape of the Guayana Highlands. (a) Map of northern South America showing the location of the Guayana highlands (white rectangle) and other regions referred in the text, as the northern Andes and the Amazon basin. (b) Close up of the Guayana Highlands showing their complex topography. (c) The tepui called *Cerro Autana*, indicated by an arrow in b. Sm, Summit, Es, Escarpment, Sl, basal slopes. Images from NASA's Shuttle Radar Topography Mission (http://www.nasa.gov/home/hqnews/2003/jun/HQ_03204_S_Amer_Space_Radar.html) (courtesy of NASA/JPL-Caltech).

summits are relicts of a former peneplain, called Auyán, which have been isolated topographically by erosion (Briceño & Schubert, 1990). The assemblage of all the tepui summits

constitutes a discontinuous surface of *c.* 5000 km², ranging from 1500 to 3000 m elevation, which is known as Pantepui (Berry *et al.*, 1995; Huber, 1995a). At present, Pantepui is considered a well-differentiated biogeographical province (Huber, 1994).

The diversity and endemism of Guayana are outstanding. For example, the Venezuelan Guayana, the largest and

better-studied part holding *c.* 90% of the tepuis (Steyermark, 1986), has more than 9400 known vascular plant species (Berry *et al.*, 1995), which represents *c.* 3.5% of the estimated global total (Raven & Johnson, 1991), in only *c.* 450,000 km². Of these species, *c.* 23% are endemic to the Venezuelan Guayana and *c.* 40% are endemic to the Guayana Shield (Berry *et al.*, 1995). But in Pantepui, the numbers are still higher. In these summits, more than 2300 species have been reported – which involves an average species/area ratio 20 times higher than the whole Guayana – of which almost 33% are endemic to Pantepui, and near 65% are endemic to Guayana (after data from Berry *et al.*, 1995). Local endemics, i.e. species restricted to a single locality, mountain or river basin, represent more than 13% of the total Guayanan flora. Most of them correspond to the larger tepuian massifs (Berry *et al.*, 1995), where local endemism can involve up to *c.* 54% of the flora (Mount Roraima; Steyermark, 1986).

Concerning global conservation strategies, the Guayana region, together with the Amazon basin, belongs to the only Tropical Wilderness Area defined for America (Mittermeier *et al.*, 1998). Furthermore, the Guayana Highlands are one of the preferential ecoregions (ER-45) defined within the Global 2000 Project of the World Wildlife Fund for the conservation of biodiversity (Olsson *et al.*, 2000). In addition, the Guayana Highlands contain a key Neotropical Plant Diversity Centre, called Pantepui or SA-2, which has been considered crucial for the evolution of not only the Guayanan but also the Amazonian biota (WWF & IUCN, 1997). At present, Guayana has strict conservation rules, and more than 70% of its area is under official protection (Huber, 1995c). The tepui summits are within the protected areas, which, together with their limited accessibility, make them invaluable areas for understanding the origin and maintenance of singular diversity and endemism patterns, and for the derivation of models of biological diversification, as well as for developing improved criteria for planning strategies to preserve biodiversity.

A DIVERSIFICATION MODEL

The maximum downward vertical shift estimated for the last glaciation in the Guayana region was 1100 m (Rull, 2004a). As a consequence, those taxa with present-day lower altitudinal limits of 1100 m or less above the elevation of the surrounding lowlands, would have reached the lowlands, while the others would not (Fig. 2). This situation is expected to have occurred

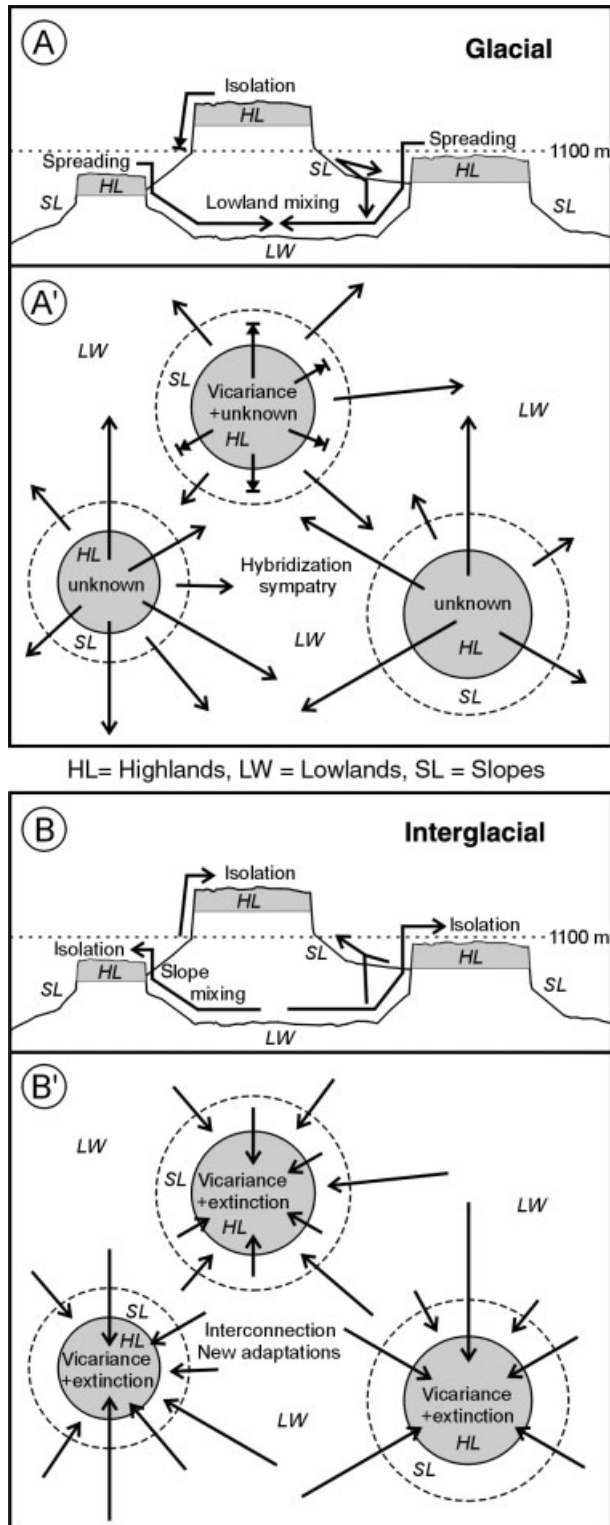


Figure 2 Schematic representation of the diversification model proposed in this paper, representing the main evolutionary events during glacial and interglacials. The events are represented in idealized cross-sections (A and B) and the corresponding aerial views (A' and B'). The straight dotted lines in A and A' with the 1100 m label represents the altitudinal limit above which the tepui summits have been isolated from lowlands, even during glacial phases. Highlands are highlighted in grey and the slopes are indicated by dotted lines in aerial view (A' and B'). Solid arrows indicate the proposed sense of biotic migration in each case.

for every glacial period, although with different intensity. Therefore, a number of taxa have had repeated opportunities for mixing in the lowlands, thus favouring sympatric speciation, hybridization and polyploidy, while others have remained isolated on summits and have experienced long-term vicariance. These vertical migrational phenomena are expected to have occurred only in mountains with a base–summit difference of < 1100 m, and with physical connections between their summits and the lowlands. The altitude criterion is fulfilled only by slightly above 50% of the tepuis plant species (Rull, 2004b,c). Among them, in spite of the isolated appearance of the tepuis at first sight, the vast majority of these table mountains have potential migrational pathways through gentle valleys and ridges (Huber, 1988). As a result, biotic mixing by vertical migration has been possible only in about half of the tepuis. In these highest tepuis, however, taxa from the slopes would have also migrated to lowlands thus contributing to the biotic mixing. In addition, the downward displacement of environmental conditions created an ‘extra space’ at the top of the highermost mountains probably occupied by nowadays unknown taxa and vegetation types (see following section). As glacial conditions have prevailed for 80% of the time during the last 2 Myr (Willis & Whittaker, 2000), these evolutionary processes are assumed to have been dominant during the late Cenozoic.

In the interglacials, the biota migrated upward, attaining a situation similar to the present, which is, in fact, an interglacial (Fig. 2). Lowland taxa migrated to the slopes of the higher tepuis and the summits of the lower ones, thus escaping from extinction and promoting some genetic mixing between lowlands and highlands at these intermediate altitudinal environments (Steyermark & Dunsterville, 1980). Other taxa would have reached the tepui summits with an altitudinal offset of < 1100 m. The general ascent prevented the extinction of many lowland and midland taxa, but produced range shrinking and probably extinction in the highermost biota, because of the loss of the extra habitats created at the mountaintops in glacial times. The surviving high-altitude taxa were pushed up and restricted to the highermost tepui summits, in a patchy environment like that of the present-day (Huber, 1992, 1995b), in which vicariance is favoured by isolation. Evolutionary change, however, is not expected to be as intense as in glacial phases, because of the comparatively short duration of interglacials (Petit *et al.*, 1999).

After repeated glacial/interglacial cycles – *c.* 40 cycles in the last 2.5 Myr (Raymo, 1994) – many taxa have had the potential for migration from one summit to another, thus increasing the gene pool of the summit biota, while others would have developed new adaptations to lowland conditions and remained there, as is supported by the current occurrence of patches of tepuian-like vegetation in the lowlands (Huber, 1995b). Under these conditions, speciation opportunities are expected to have been very high and extinction rates reduced, because many migrational possibilities remained open, and also because the complex structural topography of the Guayana Highlands (Briceño & Schubert, 1990) determined

a high environmental heterogeneity, favourable for niche diversification. Therefore, in spite of some interglacial extinction in the mountaintops, the result should be a net increase in biodiversity and endemism. It should be noted that, under this model, and contrary to the tenets of the refuge theory, fragmentation and vicariance were dominant during interglacials, while spreading and mixing were characteristic of the glacial phases.

GUAYANAN PÁRAMOS?

From an evolutionary perspective, an important consequence of the downward displacement of physical conditions is that environments and organisms inhabiting the highest tepui summits during the LGM and other glacial phases are unknown. According to Schubert & Fritz (1985) and Schubert *et al.* (1986), these summits were too arid to support life during glacial phases, but Rull (2004c) showed that, under the currently accepted LGM climatic conditions for northern South America, a mild and humid climate prevailed in the Guayana Highlands. However, no modern counterparts for the inhabiting biota exist in Guayana. For example, the potential modern analogues for the glacial ecosystems of the tepui summits between 2000 and 3000 m should be hypothetical present-day summits between *c.* 3100 and 4100 m elevation, but the maximum altitude is 3014 m (Huber, 1995a). The only potential modern analogue available at the same latitude is the páramo ecosystem, which occurs in the northern Andes (Fig. 1) between the treeline (*c.* 3000 m) and the snowline (4500–4800 m) (Luteyn, 1999). The páramos are open herbaceous communities with characteristic columnar rosettes (caulirossulae) of several species of the genus *Espeletia* (Asteraceae) that characterize these communities and make them unique. Significant biotic affinities have been noted between the Guayana and Andean highlands. Indeed, characteristic animal species and plant genera from the Andes are also found in the tepui summits (Mayr & Phelps, 1967; Huber, 1988). But the more striking parallelism is the occurrence of the so-called paramoid shrublands in the summits of the Chimantá massif, one of the largest tepuian complexes. This vegetation type, physiognomically analogous and floristically similar to the páramos, forms extensive patches up to 2600 m elevation, and is dominated by caulirossulae-form species of the endemic genus *Chimantaea* (Asteraceae) (Huber, 1992, 1995b).

The Andean páramos originated in the late Pliocene or early Pleistocene, when the northern Andes reached the elevation needed to support such high-altitude communities (Van der Hammen & Cleef, 1986). These ecosystems are absent from other neotropical mountains because of their lower elevations, commonly below 3000 m. However, some summit communities slightly below this altitude have been considered analogous to the so-called *subpáramo*, or the transition zone between the upper montane forests and the páramos (Steyermark & Huber, 1978). The absence of páramos or páramo-like communities on these ranges is due to the lack of terrain above 3000 m, just as in the ‘proto-Andes’ before the late Pliocene (Van der

Hammen & Cleef, 1986). During glacial times, however, the páramos occupied a lower altitudinal position – for example, during the LGM, their lower limit was *c.* 2000 m elevation (Van der Hammen & Cleef, 1986) – and probably colonized the highlands of adjacent Neotropical mountain ranges, although there is no proof for that situation so far. In the Guayana Highlands, *c.* 65% of the tepui summits are above 2000 m elevation (Huber, 1995a), but the glacial occurrence of páramo-like communities on them is problematical because of the lack of terrain elevated enough to accommodate them during the interglacial upward migrations. Indeed, if Guayanian páramos had exist sometime, the repeated alternation of up and down displacements must have determined a progressive impoverishment, with maximum extinction rates during interglacials. However, some remnants could have been preserved, such as the present-day paramoid shrublands restricted to the Chimantá massif (Huber, 1992). Therefore, this tepuian complex, mainly those summits above 2000 m, is a preferred target for future palaeoecological studies.

COMPARISON WITH OTHER NEOTROPICAL MOUNTAINS

The páramos experienced repeated downward expansions and upland contractions during the late Cenozoic, due to the alternation of glacial and interglacial phases, respectively. This greatly determined the biotic differentiation patterns of both plants and animals (Vuilleumier, 1969, 1979; Simpson, 1975; Cuatrecasas, 1979). At present, the páramos occur as isolated patches on the highest Andean elevations (Luteyn, 1999), a typical interglacial situation. The diversification model for the Guayana Highlands is more similar to the páramo model than to that derived from the refuge hypothesis because spreading and coalescence was characteristic of glacials, while shrinking occurred in the interglacials, and the highest extinction rates are expected during interglacials (Vuilleumier, 1969). However, the comparatively lower altitude of the Guayana Highlands makes a big difference. In the Andes, the páramo has been ‘refugiated’ to the highest elevations during the interglacials, but such refugia do not exist in Pantepui, so the long-term extinction rates should have been higher. Another difference, derived also from the altitudinal disparity, is that Pantepui taxa have the opportunity of attaining the lowlands during the glaciations, while páramo elements did not. As a consequence, the dispersal capacity and the genetic mixing are expected to have been higher in Guayana.

Palaeoecological trends similar to those of the Guayana Highlands have been found in some mid- and low-altitude Neotropical mountains, mainly in Central America and the Andean flanks, in the Amazon basin (Bush & Colinvaux, 1990; Bush *et al.*, 1992, 2004). In them, the glacial downward migration of mountain taxa, due to cooling, is a constant; whereas the assumed upward displacement of lowland forests to hypothetical mountain refugia has not been observed. Bush & Colinvaux (1990) and Bush *et al.* (1992, 2004) concluded that, indeed, endemism centres are a consequence of allopatric

speciation. However, cooling and not aridity was the driving mechanism, while relict montane populations were the evolutionary subjects, instead of lowland forest species. Therefore, the same endemism patterns that had formerly stimulated the development of the refuge hypothesis, led to an almost opposite view of the diversification patterns (Bush & Colinvaux, 1990), and led to the statement that the refuge hypothesis have ‘the facts reversed’ (Colinvaux, 1998). This revised evolutionary model is much more similar to that of Guayana in patterns and processes; however, the peculiar tabular topography of the Guayana Highlands and the more or less isolated nature of the tepuian summits, as compared with other mountains, introduce some significant differences. First, migrational pathways between tepui summits are not continuous, but restricted to valleys and ridges (see above), thus enhancing isolation, habitat heterogeneity, and niche fragmentation. Secondly, the distribution area of many taxa and their populations are, and have been, often disjunct, thus favouring allopatric differentiation, as is reflected in the high degree of endemism. Thirdly, in Guayana, the diversity has been permanently increasing with the glacial/interglacial alternation, because of the occurrence of many speciation opportunities and mechanisms, as well as the reduced extinction rates. Finally, although both diversification models involve the complex interaction of spatial and temporal heterogeneity (through the combination of niche fragmentation by habitat heterogeneity and climatic instability), in Amazonia, environmental shifts are viewed as ‘intermediate disturbances’ (Bush, 1994), while in Guayana they are considered the main forces governing both the timing and the extent of evolutionary processes (*sensu* Bennett, 1997).

FINAL COMMENTS, NEW HYPOTHESES AND FUTURE RESEARCH

The Guayana Highlands are likely to have been influential in current patterns of Neotropical diversity because of their large area and their geographical position, between the Orinoco and the Amazon basins on the one hand, and in contact with the Caribbean and the Amazon (Hylaea) biogeographical regions (Berry *et al.*, 1995), on the other. In this sense, the Guayana Highlands would have been important in promoting the emergence of new taxa, and their subsequent centrifugal spreading to lower terrains during glacial downward migrations, thus acting as ‘biodiversity pumps’ for both inner and coastal lowlands. The tepuian slopes would have been decisive in the evolution of the Guayanian biota because of their intermediate topographical position. Indeed, these almost scientifically unknown forest environments, have harboured both highland and lowland taxa in their vertical migration during glacials or interglacials, respectively, thus becoming key scenarios for genetic interchange and, consequently, decisive evolutionary localities.

The degree of genetic differentiation due to late Cenozoic climatic changes is not known, but it is assumed that it occurred at specific and intra-specific levels (Bush, 1994).

Palynology, perhaps the most utilized palaeoecological tool in the Neotropics, alone is commonly unable to resolve evolutionary phenomena at or below the species level, because of the lack of enough taxonomic discrimination power (Rull, 2003). Molecular phylogenetics, especially DNA analysis, can help through the direct observation of genetic changes, especially at subspecific level. In the region under study, these type of analysis have been successfully performed in the genera *Brocchinia* (Bromeliaceae) and *Stegolepis* (Rapateaceae) (Givnish *et al.*, 1997, 2000). Unfortunately, no combined studies have been developed so far. The coupling of palaeoecological and molecular studies is essential to disentangle evolutionary issues like those devised in this paper (Bennett, 2004).

After this reappraisal of the biological diversification of the Guayana Highlands, a number of new hypotheses to be tested with combined palaeoecological and molecular phylogenetic studies have emerged. Some are of local extent, but of global interest, such as for example the actual magnitude of vertical displacements and their real influence on the evolution of selected key taxa, the existence or not of extensive páramo-like communities during glaciations and their progressive biotic impoverishment, or the role of tepuian slopes in biotic evolution. Others are more general in nature, as for example the potential role of the Guayana Highlands, and possibly other Neotropical mountains, as 'biodiversity pumps' for the surrounding lowlands. The studies needed to test these hypotheses should be multidisciplinary (multiproxy), and should analyse lowland, midland and highland areas simultaneously, to account for vertical shifts and their consequences. Such an effort cannot be undertaken by a single research team, and extensive international cooperation is required. Finally, it should be stated that any ecological or biogeographical interpretation of the Guayanian biota should consider that the present-day situation is part of an interglacial: a short period in which isolation and vicariance are prevailing, contrary to the 'normal' glacial conditions, which have been probably the dominant ecological theatre for the Guayanian evolutionary play.

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BIOSKETCH

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