SPECIAL ISSUE

Potential migration routes and barriers for vascular plants of the Neotropical Guyana Highlands during the Quaternary

Valentí Rull* and Sandra Nogué

Departament de Biologia Animal, Vegetal i Ecologia, Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, Spain

ABSTRACT

Aim To reconstruct in detail the potential migration routes and barriers for vascular plants from the summits of the Guyana mountains during the Quaternary, in order to test the possibility of migration among them during the glaciations. These changes in connectivity are predicted based on the altitudinal migration of plant communities associated with glacial cooling. To examine the effects of these cycles, the extent of the potential biotic interchange and its influence on patterns of endemism was modelled.

Location The summits of the tepuis or table mountains of the Neotropical Guyana Highlands, which constitute the peculiar and discontinuous Pantepui phytogeographical province (total surface 5000 km^2, altitudinal range 1500–3014 m a.s.l.), and is characterized by a unique and diverse flora with a high degree of endemism.

Methods GIS-based palaeotopographical reconstruction using a high-precision digital elevation model, combined with phytogeographical analysis by means of a data base built up from the *Flora of the Venezuelan Guyana*, which includes the geographical and altitudinal ranges for each Pantepui species.

Results During the Last Glacial Maximum, which serves as a representative of a standard Quaternary glaciation, most migration pathways among tepuis were open for species with lower altitudinal levels (LAL) $\leq$ 1500 m (1678 species or *c.* 69% of the total Pantepui species), and closed for species with LAL $\geq$ 2300 m altitude (*c.* 3%). The species in between these altitudes have intermediate migratory possibilities, depending on the district and the tepui considered. If these local factors are considered, the number of species with no possibility of glacial interchange increases to 202 or *c.* 8% of the total. The strongest topographical barrier separated eastern locations above 1600–1700 m elevation from all others. The highest possibility of interchange was among the tepuis of the eastern sector, in which internal topographical barriers were only effective for species with LALs at or above 1900 m.

Main conclusions The Quaternary evolution of the vascular flora from the Guyana Highlands took place in a predominantly migration-prone, glacial-era landscape, in which more than 70% of the flora (maximum estimate) was able to move from one tepuian district to another, thanks to the downward bioclimatic shift caused by cooling. Interglacials were too short to drive significant evolutionary diversification. A number of present high-altitude local endemics are species that were unable to migrate, even during glaciations. However, some endemic species do appear to have been able to migrate among regions, suggesting that topographical isolation alone is not enough to explain patterns of endemism. Other factors such as tepui summit area, habitat heterogeneity or pre-Quaternary evolution are considered.

*Correspondence: Valentí Rull, Dep. Biologia Animal, Vegetal i Ecologia, Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, Spain.
E-mail: valenti.rull@uab.cat

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V. Rull and S. Nogué

These studies should be complemented with palaeoecological and phylogeographical surveys.

INTRODUCTION

There is an ongoing debate about the role of Quaternary environmental changes as a mechanism for explaining speciation and modern biodiversity patterns (e.g. Bennett, 2004; Lovette, 2005). One view is that Pleistocene glacial/interglacial cycles have been important in shaping the present-day biota (Hewitt, 2000), while others believe that modern species originated mostly in the Tertiary, before the Quaternary glaciations started (Willis & Niklas, 2004; Bush & de Oliveira, 2006). In the Neotropics, the debate about timing of speciation parallels the discussion on diversification mechanisms. Indeed, pre-Quaternary differentiation has been attributed mainly to tectonic, eustatic and orogenic events that occurred during the late Tertiary (Nores, 2004), while Quaternary speciation has been related primarily to climatic cycles, via the refuge hypothesis, which assumes glacial aridity and fragmentation of forest into bioclimatic refugia, thus favouring vicariance (Prance, 1982). Recently, an increasing amount of palaeoecological evidence hardly compatible with the refuge approach has been gathered (Colinvaux et al., 2000) and more varied and complex mechanisms of speciation have been proposed (Bush, 1994; Colinvaux, 1998; Rull, 2005), but climate change remains the main underlying mechanism driving diversification.

A suite of recent DNA-based phylogeographical surveys illustrate both sides of the controversy. For example, a study on parrots of the genus *Pionopsitta* has shown that its species diversified mainly during the Pliocene, between 3.3 and 6.4 Ma, coinciding with tectonic events influencing river dynamics and marine transgressions (Ribas et al., 2005). In the light of these results, the role of Quaternary climatic changes on Neotropical diversification seemed to lose relevance (Bush, 2005). Noonan & Gaucher (2005) found that the extant species of the harlequin toad genus *Atelopus* from the eastern Neotropical Guyana Shield derived from a common ancestor that migrated from the Andes, crossing the Amazon Basin, between 4.7 (late Miocene) and 1.5 (early Pleistocene) Ma. Such migration would have been possible thanks to the climate cooling that marked the initiation of the late Cenozoic glacial cycles, which favoured the invasion of the Amazon lowlands by mountain taxa (Bush, 1994). Thus, present Guyanan species derived from this ancestor diverged very recently, during the last c. 500,000–100,000 years (middle–late Pleistocene), favoured by the ensuing alternation of Quaternary climatic changes and physical isolation of the highland summits, where they evolved (Noonan & Gaucher, 2005).

Similar results were obtained recently with the poison frog *Dendrobates* (Noonan & Gaucher, 2006). In plants, similar analyses carried out on *Inga* (Fabaceae), a species-rich Neotropical tree genus, have shown that speciation was concentrated in the past 10 Myr, with many species arising as recently as 2 Ma, during the Quaternary (Richardson et al., 2001). Phylogeographical analyses within two families of vascular plants from the Neotropical Guyana Highlands, Rapateaceae and Bromeliaceae, suggest a late Miocene to Pliocene origin for several extant genera and subgeneric clades. The results of the study on individual *Stegolepis* (Rapateaceae) species, which is now in progress (Givnish et al., 2004), are awaited with interest, yet, given the former results, a late Pliocene or Pleistocene age for species divergence seems reasonable.

The region of the Guyana Highlands is especially well suited for testing phylogeographical hypotheses (Rull, in press). This region is situated between the Orinoco and the Amazon basins in northern South America (Fig. 1), and is characterized by the peculiar flat-topped table mountains, the tepuis, separated from the surrounding lowlands by sheer cliffs (Fig. 2). The assemblage of these summits, with an elevation of between 1500 and 3000 m, is a distinct and discontinuous biogeographical province called Pantepui, of about 5000 km^2 (Berry et al., 1995). The Pantepui vascular flora has striking richness and patterns of endemism. Indeed, of the 2447 known species, 1517 (63%) are endemic to the Guyana Shield, 1034 (42%) are endemic to Pantepui and 617 (25%) are local endemics (i.e. endemic to a single tepui) (Berry & Riina, 2005). The uniqueness and high degree of specialization of the Pantepui flora and vegetation has been recognized for quite some time (Berry & Riina, 2005; Huber, 2005; and references therein), and has generated much discussion about their origin. The defenders of the lost world (LW) hypothesis had proposed a long history of evolution in isolation since the late Jurassic–Cretaceous (Maguire, 1970). However, further studies revealed unknown floristic relationships that were compatible with the vertical displacement (VD) hypothesis, which proposes intermittent biotic mixing between highlands and lowlands due to the Quaternary glacial/interglacial alternation (Steyermark & Dunsterville, 1980; Huber, 1988). Recent palynological data indicate that both LW and VD mechanisms are needed to explain the characteristics of the Pantepui flora (Rull, 2004a,b), and a combined LW/VD approach has been used to explain the present-day biogeography of the Pantepui flora (Rull, 2004c).
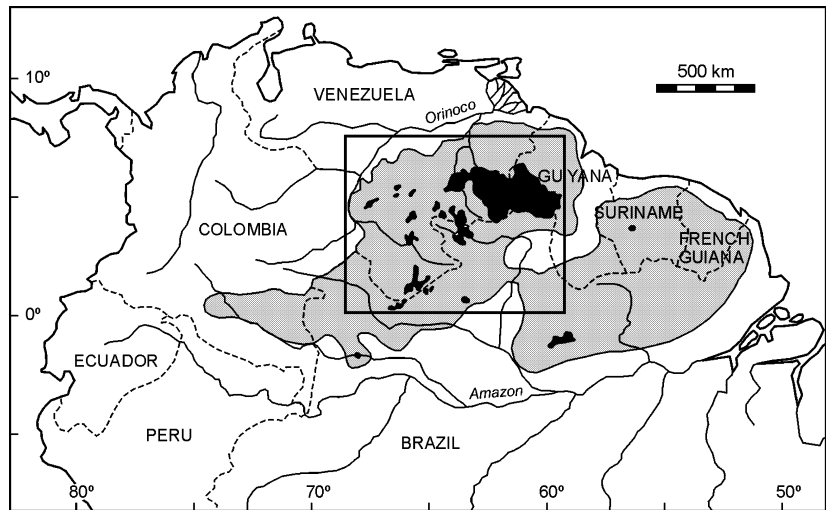
Figure 1 Map of northern South America showing the extension of the Guyana Shield (grey area), the Roraima Group (black patches) and the zone under study (rectangle).

The possible relationship between speciation and Quaternary climatic changes in the Guyana Highlands has been explored recently, and a tentative diversification model has been proposed (Rull, 2005). According to this model, the main diversification events occurred during glacials, when tepuian biotas migrated downslope owing to cooling. This movement allowed dispersal among the tepuis by way of the lowlands and promoted the reunification of diverging gene pools and the possibility of new genetic combinations as individuals from different populations hybridized, thus providing the necessary migration pathways for gene flow among tepuian summits. During the interglacials, upslope retraction would have favoured isolation and extinction by habitat loss in the highlands. In this way, the successive alternation of Quaternary glacial and interglacial events, combined with the complex topography and habitat heterogeneity of the Guyana Highlands, would have resulted in a net increase in biodiversity and endemism (Rull, 2005). In order to test this diversification model for the Guyana Highlands, detailed physiographical studies using geographical information system (GIS) tools have been proposed, in combination with palaeoecological analyses of suitable sediments and phylogeographical surveys of keystone taxa (Rull, 2004c, 2005). At issue is the magnitude and extent of the assumed glacial biotic spreading, key parameters delineating potential migrational pathways and biogeographical barriers for tepui biotas. According to Huber (1988), besides the apparent inaccessibility of the tepuian summits, very few are totally 'suspended in the air' by vertical cliffs, and numerous river valleys and ridges physically connect the tepui summits with the surrounding lowlands thus providing potential migration routes. However, a detailed reconstruction of such potential pathways is still unavailable.

This study aimed to reconstruct in detail the maximum surface area that could have been occupied by the Pantepui flora during a glaciation, and to locate potential migrational pathways and dispersal barriers for its vascular flora. This analysis is carried out using GIS. The Last Glacial Maximum

(LGM), which occurred around 21,000 yr BP, is used as a model, as it was among the coldest Quaternary glaciations (Mix et al., 2001); hence, the downslope biotic migration and the probability of biotic interchange among tepuis is expected to have reached its maximal extent. Glacial phases have been notably longer than interglacial ones, so it is believed that boreal continents have been glaciated for around 80% of the time since the beginning of the Quaternary (Willis & Whittaker, 2000). Interglacials are viewed as comparatively short warmings of duration 10–20 ka, which occurred every 80 or 90 ka within a dominant glacial Quaternary climate (Bush et al., 2001). Therefore, the palaeotopographical reconstruction presented here, with the corresponding differences in magnitude, is assumed to have been the dominant scenario for the Quaternary evolution of the Pantepui biota. The possible influence of these palaeogeographical patterns on present-day endemism patterns is discussed, but this is an issue that needs further study for a definite assessment.

MATERIALS AND METHODS

Study area

The Guyana Highlands are situated between about 1° and 7° N and 59° and 67° W (Figs 1 & 2). The tepuis are modelled on the quartzites and sandstones of the Precambrian Roraima Group, overlying the igneous–metamorphic Guyana Shield, which is part of the South American old core (Briceño & Schubert, 1990; Gibbs & Barron, 1993). In the eastern tepuis, the Roraima Group forms an almost continuous cover and reaches a lower limit between 400 and 1200 m, whereas in the west and south the sandstone cover has been eroded more intensely, and the tepuis are less frequent, more distant from one another and surrounded by lowlands of 100 m elevation or less (Huber, 1988, 1995) (Fig. 1). This landscape dissection could provide more suitable conditions for lowland corridors of connectivity for Pantepui elements in the east and greater isolation in the west. Pantepui has been subdivided into four
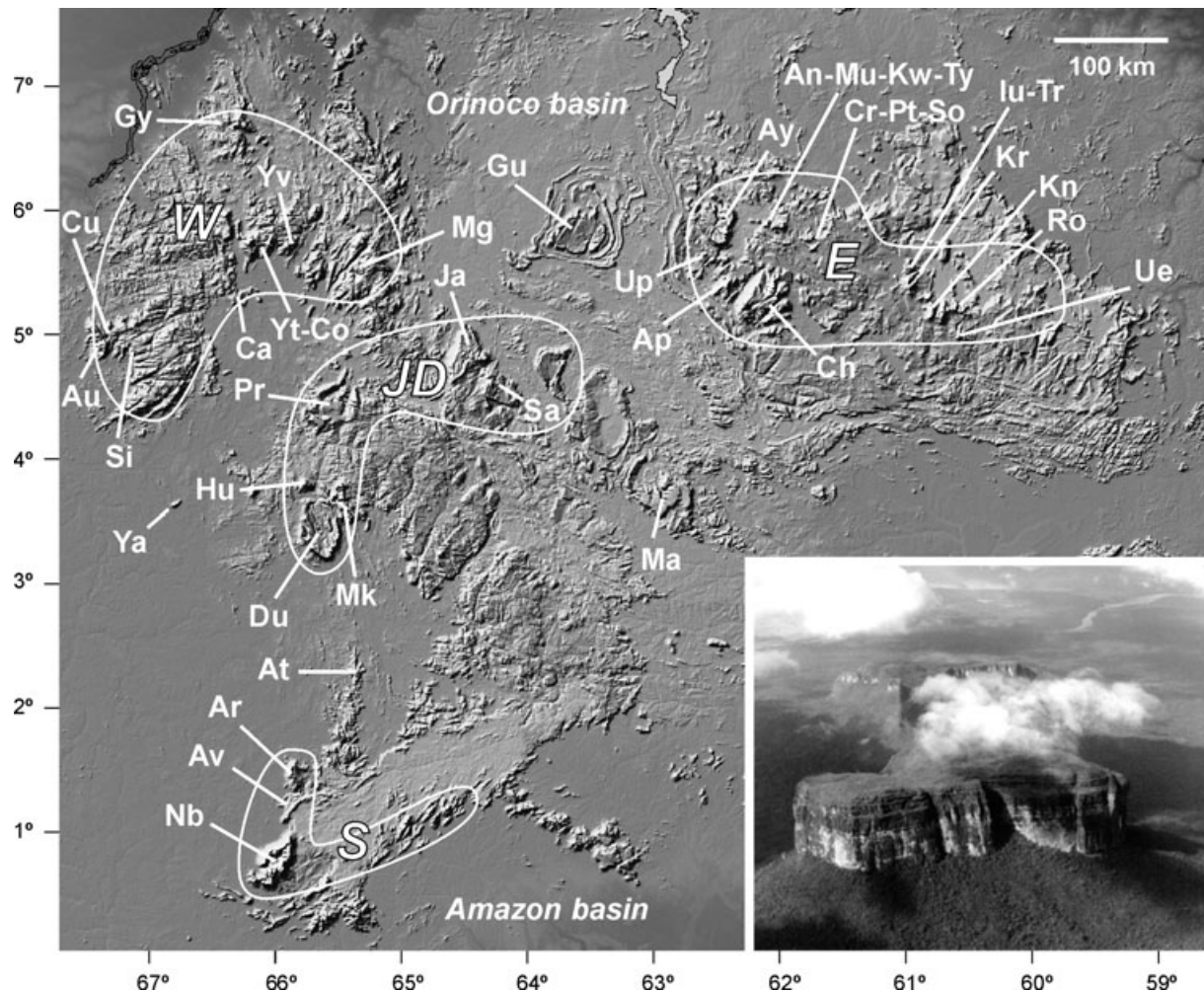
Figure 2 Radar image (courtesy of NASA/JPL-Caltech) showing the Guyana Highlands. The better-known tepuis from a botanical point of view (Berry & Riina, 2005) are indicated, sorted by districts. Eastern district (E): An, Aparamán; Ap, Aprada; Ay, Auyán; Ch, Chimantá; Cr, Carrao; Iu, Ilú; Kn, Kukenán; Kr, Karaurín; Kw, Kamarkawarai; Mu, Murisipán; Pt, Ptari; Ro, Roraima; So, Sororopán; Tr, Tramén; Ty, Tereké-yurén; Ue, Uei; Up, Uaipán. Western district (W): Au, Autana; Ca, Camani; Co, Corocoro; Cu, Cuao; Gy, Guanay; Si, Sipapo; Yv, Yaví; Yt, Yutajé. Jaua-Duida district (J-D): Du, Duida; Ja, Jaua; Hu, Huachamacari; Mk, Marahuaka; Pr, Parú; Sa, Sarisariñama. Southern district (S): Ar, Aracamuni; Av, Avispa; Nb, Neblina. Others: At, Aratitiyope; Gu, Guaiquinima; Ma, Marutaní; Ya, Yapacana. A typical tepuian lanscadpe corresponding to the Cerro Venado and the Gran Sabana lowlands (background) is displayed in the lower right-hand corner.

phytogeographical districts (Fig. 2): Eastern Pantepui (E), Jaua-Duida (JD), Western Pantepui (W) and Southern Pantepui (S) (Berry et al., 1995). The vast majority of the tepuis are in Venezuela, where they attain their maximum development, although some of them can be found in Guyana, Colombia and Brazil (Steyermark, 1986). The altitudes and summit areas of the tepuis are very variable, ranging from < 1000 to 3000 m elevation, and from < 1 to > 1000 km^2 (Huber, 1987, 1995). The highest tepui is the Pico Neblina (3014 m elevation) in the southern Venezuelan border with Brazil (Fig. 2). The tepuis used for the present study are shown in Fig. 2.

Three main physiographical units have been described in the Guyana region, according to altitude and temperature-based climatic types: lowlands (0–500 m), with macrothermic

climates (> 24°C annual average); uplands (500–1500 m), with submesothermic climates (18–24°C) and highlands (> 1500 m), with mesothermic (12–18°C) and submicrothermic (8–12°C) climates. Temperature is the most influential climatic parameter and decreases at a more or less constant rate of 0.6°C for each 100 m increase in altitude (Huber, 1995). Precipitation and seasonality do not show any altitudinal dependence. Indeed, any of the climatic types previously mentioned can have two subtypes according to the total annual precipitation values and their distribution throughout the year, namely tropophilous (1000–2000 mm year^{-1}, two to five dry months) and ombrophilous (> 2000 mm year^{-1}, less than two dry months). Ombrophilous climates dominate in the highlands (Huber, 1995).

The vegetation shows a clear altitudinal arrangement that is consistent with the pattern of lowlands, uplands and highlands (Huber, 1988), and the main controlling parameter is temperature. In this way, a lower and an upper distribution limit (LDL and UDL, respectively) could have been defined for each of the nearly 9400 species known in the Venezuelan Guyana (Steyermark *et al.*, 1995–2005). These environmentally driven altitudinal patterns are also valid for the Guyana Highlands (Huber, 1988). This is worth mentioning because the view of some earlier workers, influenced by the legend of the Lost World (Doyle, 1912), has contributed to a false impression of these summits as exceptional places subjected to unusual ecological and evolutionary rules (discussion in Rull, 2004c).

METHODS

Palaeogeographical reconstructions were performed with MiraMon software (http://www.creaf.uab.es/miramon/), using the digital elevation model from the Shuttle Radar Topography Mission (SRTM) of 3 arcsec (90 m) precision (USGS/NGA/NASA). In order to compare palaeotopographical reconstructions with present phytogeographical patterns, a data base of all the species occurring above 1500 m altitude (i.e. the Pantepui flora) was built up with the Access software package, on the basis of the *Flora of the Venezuelan Guyana* (Steyermark *et al.*, 1995–2005). This information was completed with physiographical and phytogeographical data obtained from different bibliographic sources (Huber, 1987, 1988, 1995; Berry
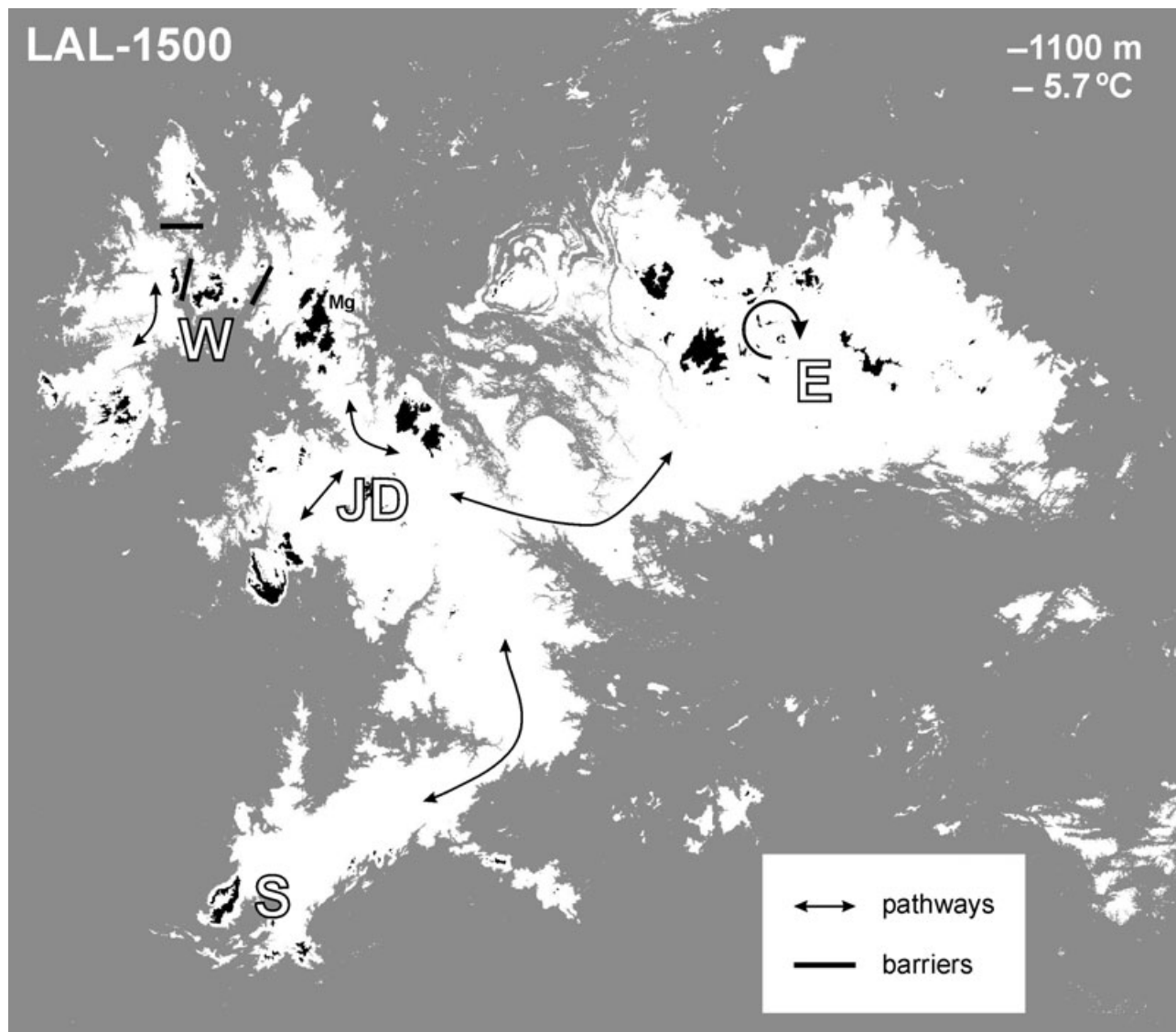

Figure 3 Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 1500 m (white), compared with present-day Pantepui surface (black). Districts are indicated by capital letters (Mg = Maigualida). The estimated downward displacement with respect to the present and the corresponding temperature drop, considering the present-day adiabatic lapse rate, is indicated in the upper right-hand corner.

et al., 1995; Berry & Riina, 2005). The palaeotopographical surface representing the extent of the Pantepui province during the LGM (Palaeopantepui-LGM or PP-LGM) was simulated assuming a downward biotic migration accompanying the corresponding decrease in temperature, a common feature in Neotropical mountains (Farrera et al., 1999). Estimates for such a decrease vary according to the site and the proxy used for palaeotemperature, and it was probably not homogeneous over the whole Neotropical area (Bush & Silman, 2004). No data exist for the Guyana Highlands, and we used as a first approach the general estimate for the Neotropics, which is of 5.7°C below present averages, with a corresponding biotic lowering of 1100 m altitude (Farrera et al., 1999). A research programme has started recently to clarify this point in the Guyana region (http://einstein.uab.es/vrull/pantepui/main.htm). Preliminary data suggest temperatures of 2–3°C below present ones for the early Holocene, around 10–11 ka BP (Rull, unpublished data). The nearest site with palaeoclimatic information for the LGM is the Hill of Six Lakes, around 0° latitude, not far from Pico Neblina, to the south (Fig. 2). The invasion of lowland forests by montane trees recorded there is consistent with a minimum LGM biotic descent of 800–900 m and a temperature decrease of 4–5°C; while maximum suggested values are 1000–1100 m and 5–6°C (Bush et al., 2004). Therefore, a similar decrease seems very likely in the Guyana Highlands. If future results indicate a different value, the approach will retain relevance and only some numerical adjustments will be required. It should also be taken into account that factors other than temperature, notably precipitation and atmospheric concentrations of CO_2 among others, could have affected the LGM biota. At present there is not enough information to include these elements in our model, but they should be considered in the future for eventual readjustments. The procedure described here to reconstruct the LGM Pantepui surface also assumes no changes in topography since the LGM and, in general, during the Quaternary. This is a very likely assumption if we consider that the region has not been glaciated, and the erosion rates – mainly due to chemical meteorization of the Precambrian rocks – have been negligible during this period (Edmond et al., 1995).

Once the PP-LGM has been obtained, the critical parameter for inferring the potential for migration across this surface is determined by the lower altitudinal limit (LAL) for each species. This is based on the assumption that LALs are mainly controlled by temperature (see above), and that they were lowered by 1100 m during the LGM. For example, a species with a present-day LAL at 1500 m could have reached the lowlands (400 m) in the LGM and migrated to other tepuis; whereas another with a LAL at 2000 m could only have reached 900 m altitude, and thus has a much more limited migration ability. We used a 1100-m descent because, as stated before, we are interested in the maximum connection probability, but such a decrease has been restricted only to the glacial maxima. For example, it is known that the last glaciation did not consist of a monotonous cooling, but a succession of stadials and interstadials of < 10 ka duration within a maintained cooler period embracing c. 100 ka (e.g. Dansgaard et al., 1993). In this analysis, species have been considered to respond individually to temperature changes, rather than collectively, according to the community to which they belong (Bennett, 1997; Bush et al., 2001). Another parameter used in the analysis is the critical altitude for summit isolation (CAI), or the minimum altitude at which the summit of a given tepui loses effective topographical connection with others through the surrounding uplands or lowlands. Note that CAI is independent of the presence or absence of valleys and ridges able to act as migration routes in the sense of Huber (1988), as it refers to the altitude at which these potential connections become inactive.

Notes on terminology

It is important to define some terms such as dispersal and migration as we use them in this text. According to Pielou (1979), 'jump dispersal' is the movement of individual organisms across great distances, followed by the successful establishment of a population. Jump dispersal usually takes place across inhospitable terrains and is accomplished in a short period of time, comparable with the life span of an individual. Pielou (1979) calls 'diffusion' the gradual movement of populations across hospitable terrains for a period of many generations, resulting in the steady expansion of the range of the species involved. Here we informally equate 'jump dispersal' to 'dispersal' and 'diffusion' to 'migration'. The Quaternary is defined following Gibbard et al. (2005), as the period beginning in the Gauss/Matuyama palaeomagnetic boundary (2.6 Myr BP), coinciding with the onset of Northern Hemisphere glaciations (Raymo, 1994).

Table 1 Distribution of Pantepui vascular plant species according to their lower altitudinal limit (LAL). Data from Steyermark et al. (1995–2005).

LAL (m)	Species (n)	%
3000	0	0.0
2900	0	0.0
2800	1	< 0.1
2700	9	0.4
2600	10	0.4
2500	36	1.5
2400	17	0.7
2300	13	0.5
2200	31	1.3
2100	53	2.2
2000	69	2.8
1900	97	4.0
1800	118	4.8
1700	112	4.6
1600	86	3.5
1500	117	4.8
< 1500	1678	68.6

RESULTS

Assuming a constant 5–6°C cooling and consequent lowering of floral limits, the lower bound (1500 m) of the potential area occupied by the Palaeopantepui (PP) during the LGM coincided with the present-day 400-m contour line (Fig. 3). The resulting potential connectivity along low elevational migrational paths between tepuis could have greatly increased gene flow. The only barriers were located within the Western district, separating all the tepuis except Maigualida (which is not properly a tepui, but its summit biota falls within the Pantepui province) from the rest. These barriers, however, were narrow (1 or few tenths of a kilometre) and potentially crossed by jump dispersal. The tepuis within the Western district were also separated by thin barriers that delineated three main subclusters. This LGM situation, however, is not applicable to all the Pantepui biota but only to these species having their LAL of distribution at or below 1500 m altitude.
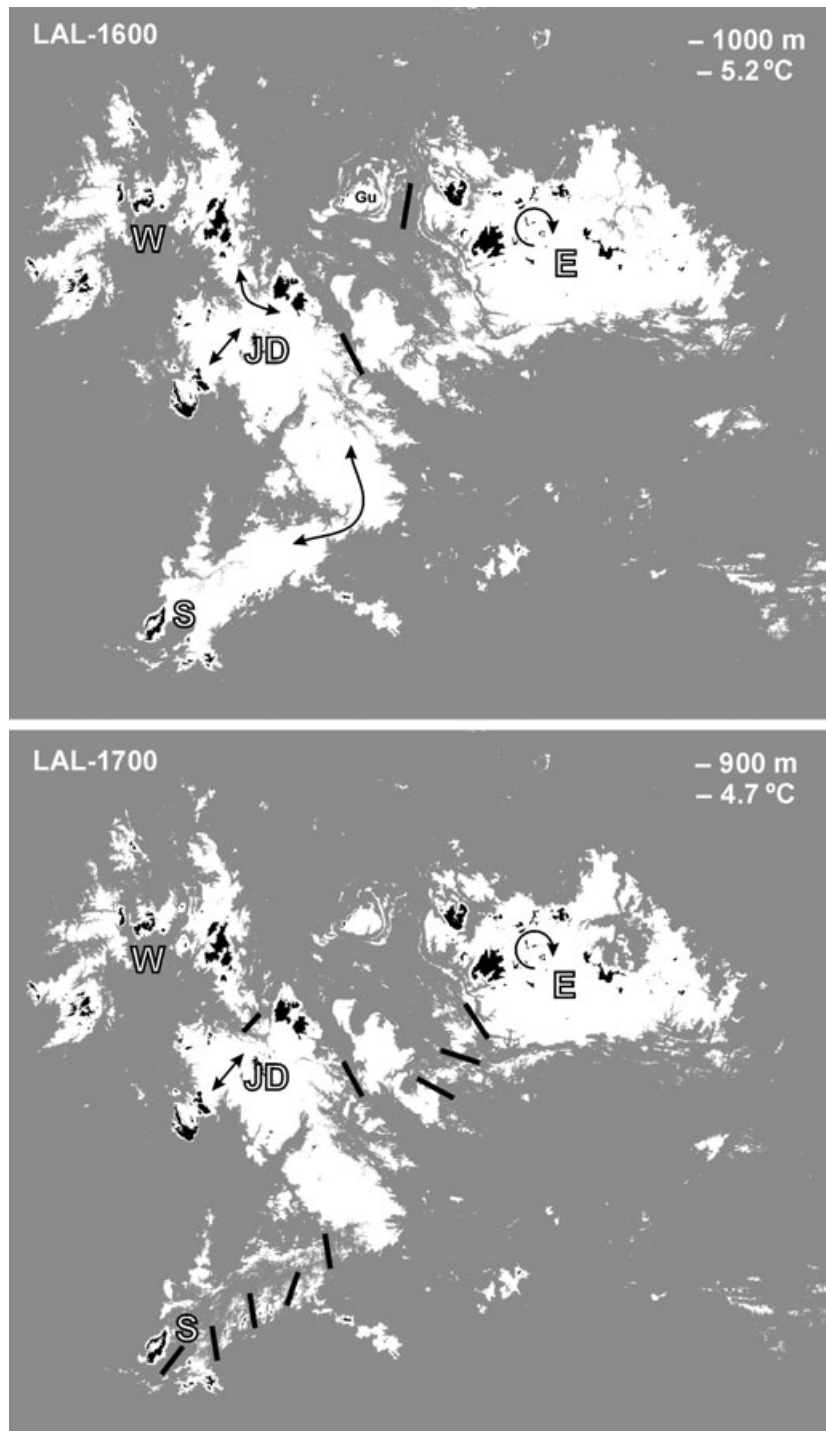

Figure 4 Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 1600 (upper) and 1700 (lower), compared with the present-day Pantepui surface (black). Symbols and text as in Fig. 3. Gu = Guaiquinima.

V. Rull and S. Nogué

According to our data base, of the 2447 species known in Pantepui, this is the case for 1678 (68.6%) (Table 1). The potential for dispersal of the remaining 769 species (31.4%) was lower. For the 86 species (3.5%) with LAL = 1600 m, few additional narrow barriers were located around the centre, preventing direct contact, and therefore migration, among the Eastern district and the rest of the tepuis (Fig. 4). The passages connecting Jaua-Duida with the Western and Southern districts were narrowed but still active. It is

remarkable that Guaquinima was an isolated tepui for these species.

The degree of isolation suddenly increases for the 4.6% of species with LAL = 1700 m, (Table 1). For them, the four districts were topographically isolated and, furthermore, the tepuis from the south were also isolated from one another, as is the case for many tepuis from the Western district (Fig. 4). Migration within the tepuis of the Eastern district was still possible, as it was for those of Jaua-Duida district. For species
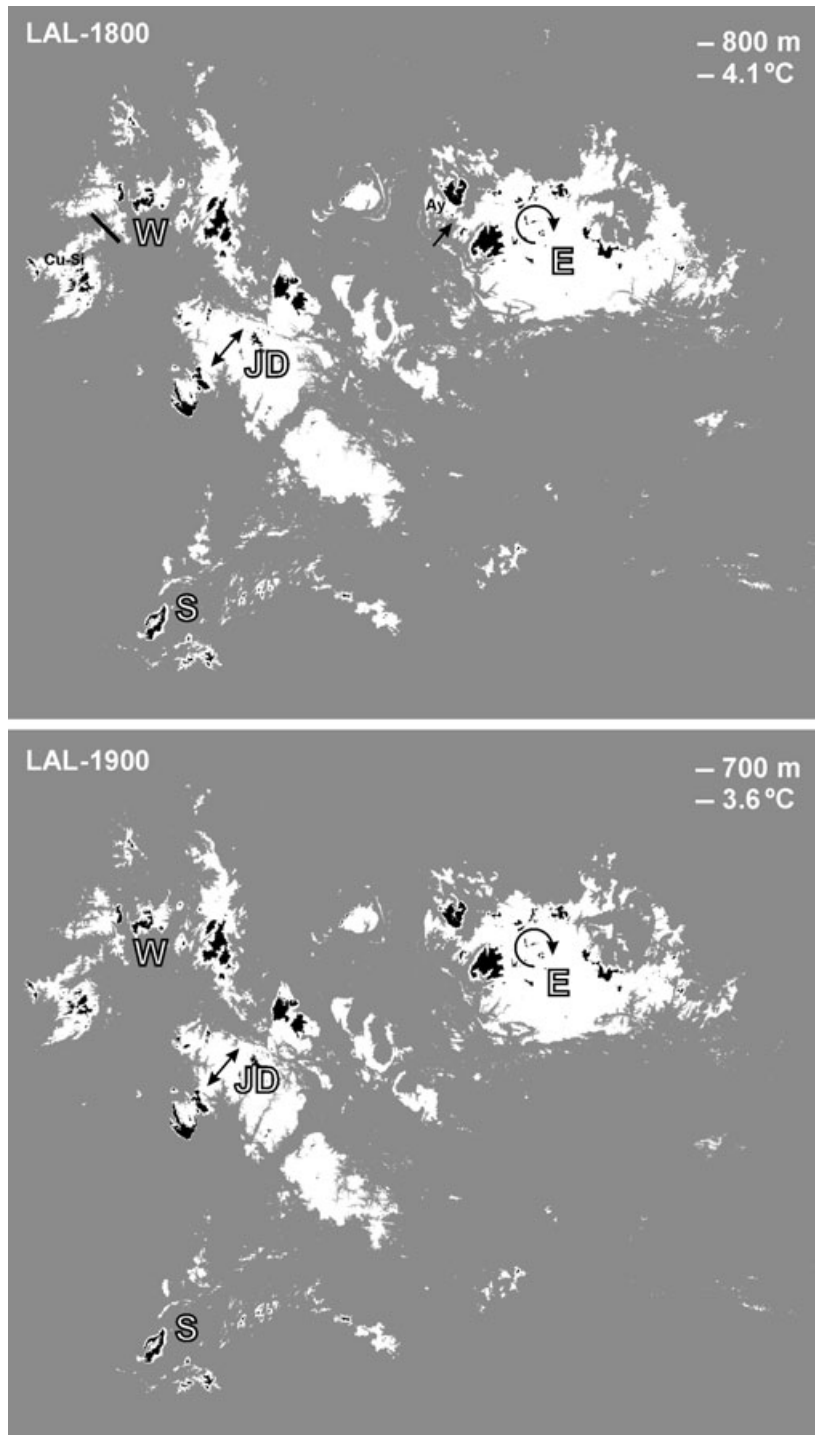

Figure 5 Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 1800 (upper) and 1900 (lower), compared with the present-day Pantepui surface (black). Symbols and text as in Fig. 3. Ay, Auyán; Cu-Si, Cuao-Sipapo massif.

with LAL = 1800 m (4.8%) the situation is almost the same, but it is noteworthy that the Auyán, from the Eastern district, was only connected by a narrow corridor, and the Cuao-Sipapo massif, of the Western district, was detached by a barrier (Fig. 5). The same scenario is valid for species with LAL = 1900 m (4.0%), although in this case the barriers among Eastern, Jaua-Duida and Southern districts were hundreds of kilometres wide. Topographical splitting within the Jaua-Duida and Eastern districts began for species with

LAL = 2000 m and was almost completed for species with LAL = 2300 m (Figs 6 & 7). The species with LALs above this point (c. 3%) have remained isolated even during the LGM (Fig. 8). It is also possible to estimate the species that were confined to a single tepui even during the LGM, with no possibility of migration, by examining the number of species in the data base with LALs at or above the CAI for each tepui (Table 2). A total of 202 species (8.3% of the total) are in this situation, most of them (164 or 81%) being endemic to a single
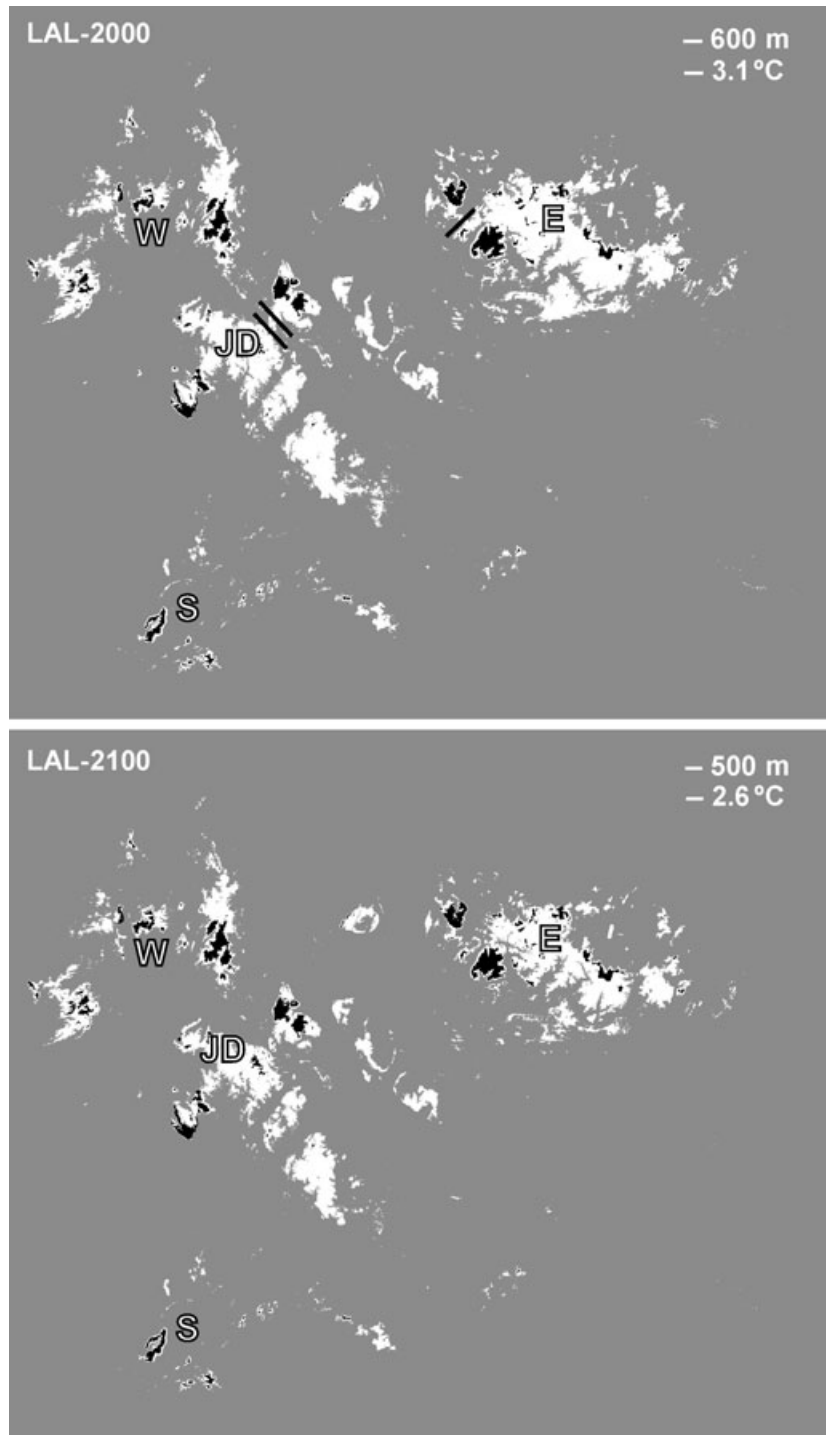

Figure 6 Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 2000 (upper) and 2100 (lower), compared with the present-day Pantepui surface (black). Symbols and text as in Fig. 3.
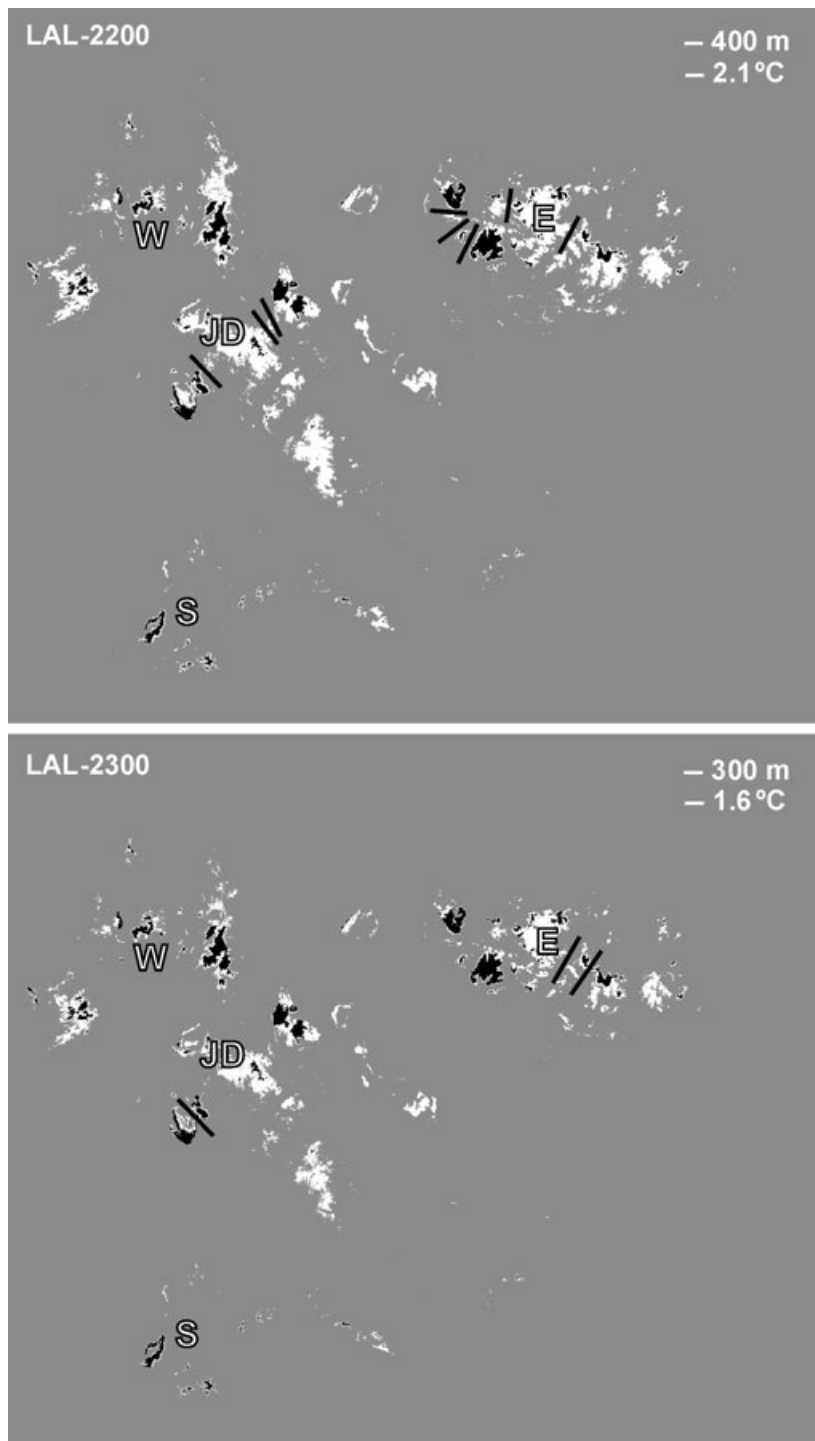
Figure 7 Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 2200 (upper) and 2300 (lower), compared with the present-day Pantepui surface (black). Symbols and text as in Fig. 3.

tepui, a tepuian massif or a cluster of neighbouring tepuis within the same district (see Appendix S1 in Supplementary Material). The remaining 19% currently occur in more than one district or even in adjacent regions.

DISCUSSION AND CONCLUSIONS

According to our results, more than 70% of the present flora would have been able to migrate among tepuis during Quaternary glacial maxima. The number of species with no possibility of migration, even during as intense a glacial event as the LGM, is estimated at c. 8%. The remaining 22% have had intermediate probabilities of migration. This scenario of climatic oscillation seems to have been the norm during the Quaternary, with interglacials and peak glacial conditions being too short to account for significant evolutionary diversification across a broad array of species (Bush, 2005). Despite the instability of glacial climates (Dansgaard *et al.*,
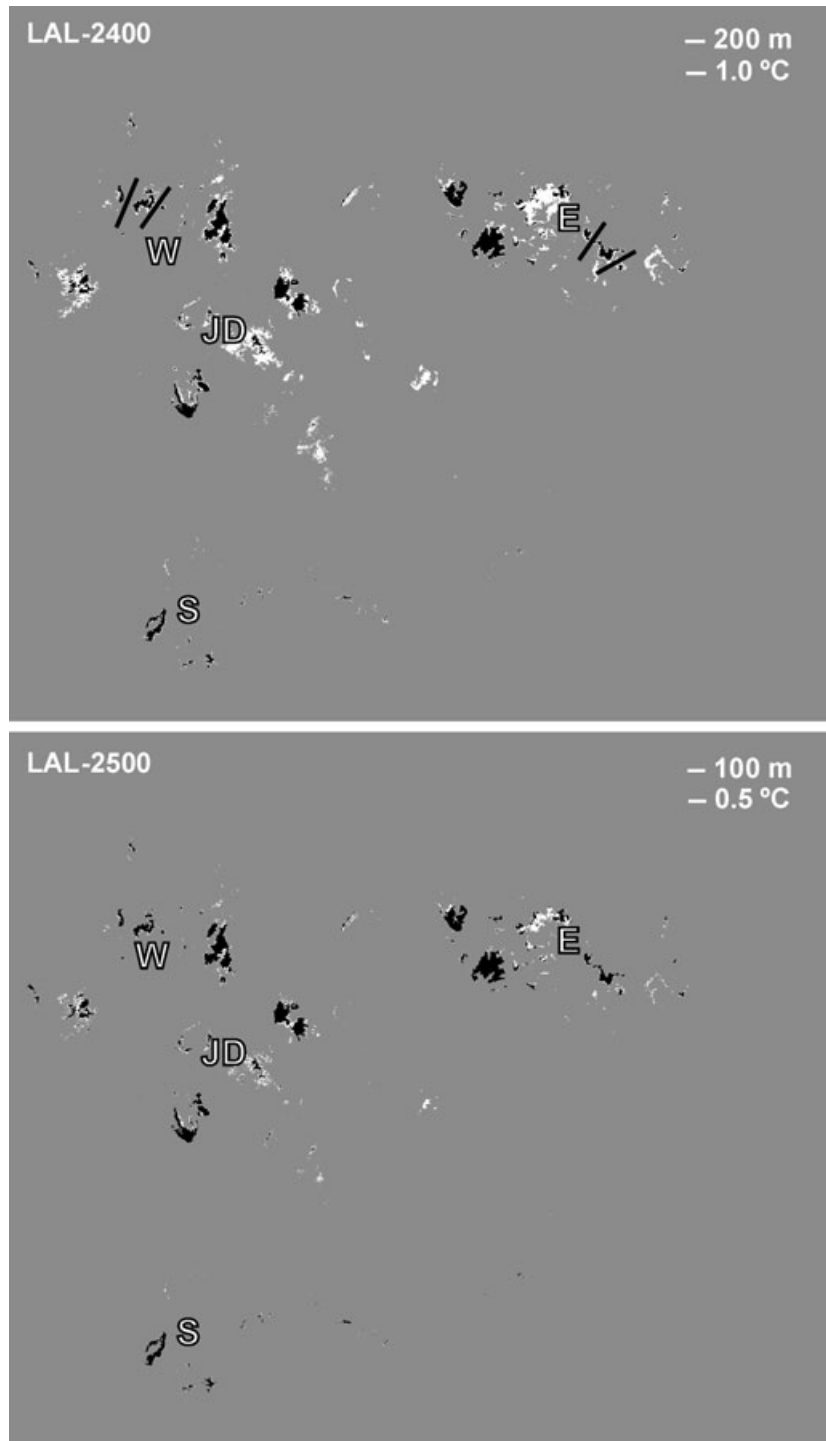
Figure 8 Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 2400 (upper) and 2500 (lower), compared with the present-day Pantepui surface (black). Symbols and text as in Fig. 3.

1993; see above), downward biotic spreading has been largely favoured during most of the Quaternary. As a consequence, the vascular flora of the Guyana Highlands has evolved in an environment with many possibilities for interchange among the tepuis, and allopatric speciation atop the tepuis should have taken place mainly in the summits that have remained isolated, even during glaciations. The high proportion of local endemics among the *c.* 8% isolated flora supports this view (Appendix S1). That tepuis such as Roraima, Marahuaka,

Huachamacari, Neblina and Maigualida have approximately the same number of local endemics and species with LALs above the CAI also favours this assumption (Table 2). However, other tepuis such as Chimantá, Auyán, Duida, Jaua or Parú apparently deviate from this pattern, holding far more endemics than other peaks with equivalent histories of isolation. Therefore, evolution in topographical isolation alone is not enough to explain present-day patterns of endemism on the tepui summits, and other relationships should be

Table 2 Comparison between local endemism and the number of species with LALs above the critical isolation altitude for each tepui studied

Tepui	District	CAI	SP > CAI	END
Chimantá	E	2200	13	102
Auyán	E	2000	0	32
Roraima	E	2400	19	17
Ptari	E	2600	0	10
Ilú/Tramén	E	2400	14	7
Sororopán	E	2600	0	8
Kukenán	E	2400	13	4
Kamarkawarai	E	2200	3	1
Uaipán	E	2200	0	1
Aparamán	E	2200	1	0
Murisipán	E	2200	2	2
Aprada	E	2100	3	2
Tereké-Yurén	E	2200	0	0
Uei	E	2400	1	1
Karaurín	E	2300	1	0
Marahuaka	JD	2300	31	36
Duida	JD	2300	1	47
Jaua	JD	2600	0	38
Huachamacari	JD	1600	10	7
Parú	JD	2300	0	28
Sarisariñama	JD	2600	0	5
Neblina	S	1700	112	132
Aracamuni/Avispa	S	1700	2	15
Sipapo	W	2100	0	40
Yutajé	W	2400	0	17
Corocoro	W	2400	0	5
Maigualida	W	1700	29	28
Carrao	W	2600	0	0
Guanay	W	1500	15	6
Yaví	W	2400	0	4
Autana	W	1500	0	0
Cuao	W	2200	0	1
Yapacana	W	1500	0	7
Camani	W	2100	2	3
Guaiquinima		1600	6	12
Marutaní		1800	2	0
Aratitiyope		1600	0	0

CAI, critical altitude for topographical isolation of each tepui during the LGM (deduced from Figs 3–8). SP > CAI, species with LALs at or above the critical altitude for isolation (from the data base). END, endemic species (Berry & Riina, 2005).

examined. For example, it is remarkable that the tepuis with the highest levels of endemism are those with larger summit areas (900–1200 km^2, according to Huber, 1995). This apparent relationship between endemism and area is not unusual (Kinzing & Harte, 2000; Ulrich, 2005). Mechanisms that form the causal link between area and endemism may centre on larger areas having greater microhabitat heterogeneity than smaller ones, especially in reference to edaphic conditions (Berry et al., 1995). Selection for optimal genotypes could result in enhanced niche diversification and endemism (Rull, 2005). Alternatively, the origins of diversity in this part of the

flora may be substantially pre-Quaternary and the oscillations of the last 2 Myr have led to reassembly of communities but only a limited amount of speciation.

Another feature of this data set is the widespread occurrence of some species with narrow elevational tolerances that have probably remained isolated throughout the Quaternary (Appendix S1). These species may have been widespread before the onset of Quaternary glaciations or they may have a higher potential for successful jump dispersal than more locally distributed species. Unfortunately, seed dispersal mechanisms are largely unknown for the Guyanan flora, and a definite answer is not possible. A study on seed dispersal modes carried out on a low sandstone plateau from Colombian Guyana, slightly to the south of the region studied here, showed that wind is the dispersal agent for 23% of the species, and the dominant agents (c. 47%) are animals, mainly birds (Arbeláez & Parrado-Rosselli, 2005). This cannot be taken as the rule for highlands, but is indicative of the comparatively low importance of anemochory in the region. Concerning birds, there is also a high degree of endemism among them (Mayr & Phelps, 1967), so the transport probabilities from one tepui to another are not as high as could be expected a priori. As a consequence, slow migration through hospitable terrains (i.e. Pielou's diffusion) seems to have been the dominant mechanism of biotic exchange. Therefore, detailed palaeogeographical reconstructions like those shown here are important for unravelling palaeobiogeographical processes. However, jump dispersal should not be disregarded if the percentage of anemochory measured in the Colombian plateau (23%) is considered representative of the Guyana region (which is not guaranteed), as it is relatively high for the Neotropics (M.B. Bush, pers. comm.). In addition, the possible influence of rare and atypical events of long-distance dispersal should be also taken into account (Wilkinson, 1997), though their potential consequences are difficult to measure and are highly unpredictable (Clark et al., 2003).

Finally, it should be noted that Figs 3–8, besides representing a static geographical picture of the migration possibilities for different species during the LGM, also show the post-LGM contraction of available migration corridors. Assuming that the adiabatic lapse rate has not changed significantly during this time, an estimated temperature difference with respect to the present can be computed for each of these surfaces. In this way it is possible to infer the potential migration routes and barriers for a given species at a given time slice, knowing its present LAL and past temperature trends. As the LGM has been one of the more intense glaciations and present-day temperatures are the highest recorded so far, the palaeotopographical reconstructions shown here probably cover the entire range of possibilities for the Quaternary and could be used to reproduce the whole story. So far, however, palaeoclimatic information from the Guyana Highlands is not yet extensive enough for a suitable reconstruction of this type, but this seems to be a promising tool for the future. In order to understand the origin of the biota of the Guyana Highlands,

a multidisciplinary approach is essential. Phylogeographical studies should provide phylogenies and hopefully dating of the main evolutionary events, whereas palaeoecology should be able to inform us about the potential causes and forcing factors. In addition, phylogeographical surveys can contribute to the improvement of palynologically based mapping of past plant populations and estimations about their spreading rates, which can be especially inaccurate in the case of diffuse populations (McLachlan & Clark, 2004; McLachlan *et al.*, 2005). The significance of studies such as ours is that they provide the necessary detailed palaeogeographical basis for the reconstruction of evolutionary trends. The combination of all these disciplines will hopefully result in a coherent spatial and temporal framework for understanding environmental and evolutionary processes that have led to the present-day ecological and biogeographical patterns. So far, this combination – of which the present paper is a part – suggests that Quaternary environmental changes have been important in promoting biotic differentiation and shaping present-day biodiversity and endemism patterns (see also Rull, in press).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 List of species with lower altitudinal limits (LALs) above the critical isolation altitude for each tepui, according to their endemism patterns.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2006.01602.x (This link will take you to the article abstract).

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BIOSKETCHES

Valentí Rull uses palynology for palaeoecological and palaeoclimatic interpretation, to address ecological, biogeographical and evolutionary problems in both tropical and temperate regions. His current research interests are the historical biogeography of the Neotropics as related to the origin of biodiversity and endemism, the study of climatic change from a palaeoclimatic perspective and the palaeoecology of high-mountain environments, especially the Andes and the Pyrenees.

Sandra Nogué is doing her PhD thesis on the conservation of biodiversity, in face of the threat of global warming, on the Guyana Highlands. She combines palaeoecological and present-day phytogeographical data with GIS modelling.

Editor: Mark Bush

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