Departament de Biologia Animal, de
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Universitat Autònoma de Barcelona

Institut Botànic de Barcelona
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i Paleoecologia

Global warming and biodiversity conservation in the Guayana Highlands: paleoecology, biogeography and GIS modeling

Escalfament global i conservació de la biodiversitat a les Terres Altes de la Guayana: paleoecologia, biogeografia i modelització SIG

Sandra Nogué i Bosch

Tesi doctoral
Barcelona, 2009

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Memòria presentada per:

Sandra Nogué i Bosch

Per optar al títol de Doctora per la Universitat Autònoma de Barcelona

Amb el vist-i-plau dels directors de tesi:

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Pels meus pares,

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Molts de vosaltres ja sabeu que fer una tesi no és cosa fàcil i que definitivament no és un procés que es pugui definir com individual. De les moltes coses relacionades amb la tesi, que han passat durant aquests últims anys, la gent que m'ha envoltat és sense cap dubte la més destacable. Moltes d'aquestes persones no saben com d'important ha estat la seva ajuda, consells, ànims i somriures. És per això, que aquestes línies es convertiran en un **moltíssimes gràcies** per a tots ells i elles. A més, a cada capítol s'ha agraït en particular a tota la gent que m'ha donat un cop demà.

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Tot el coneixement botànic de les espècies dels tepuis li dec a Otto Huber. La setmana viscuda entre les Dolomites discutint sobre el canvi climàtic va ser una gran experiència.

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Entre l'UAB i l'Institut, he tingut la sort de passar 4 mesos en el *Metapopulation Research Group* de la Universitat de Helsinki. Estic molt agraïda a l'Ilkka Hanski per haver-me donat l'oportunitat de conèixer el seu grup i per les bones converses i pluges d'idees durant els mesos que va durar la meva estada. També estic molt agraïda a: Mar, Esther, Evgeniy, Otso, Ace, Ayco, Chaozhi, Albert i Yuho per acollir-me tant i tant bé durant els mesos passats a Helsinki. Tot i la foscor de l'ambient, el vostre caliu (i les saunes) van fer que el fred hivernal no fos tan dur! *Kiitos*.

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Endavant amb les pàgines que segueixen!

Montjuïc, Juliol 2009

ÍNDEX

I. ESTRUCTURA

I. ESTRUCTURA DE LA TESI

Aquesta tesi doctoral està organitzada en una introducció, 5 capítols, una discussió i unes conclusions finals. La introducció, la discussió i les conclusions estan escrites en català mentre que els capítols 1 al 5 en anglès i corresponen a articles que ja han estat publicats, revisats o bé estan en la fase final de la seva elaboració. Els capítols 1, 2 i 3 tenen com a tema en comú l'anàlisi paleoecològic. El tema principal dels capítols 4 i 5 és la modelització de la pèrdua de la biodiversitat de plantes vasculars degut al canvi climàtic futur.

Introducció. Es fa una introducció general en català de la temàtica de la tesi. Es descriu l'àrea d'estudi (clima, geologia i biodiversitat vegetal) i el context paleoecològic i paleoclimàtic.

Capítol 1. Lateglacial and Holocene palaeoecology of the Guayana Highlands (northern South America): pollen record from the highest summit of the Chimantá massif. Aquest capítol és un treball paleoecològic detallat del cim més alt del massís del Chimantá. L'anàlisi dut a terme inclou datacions en C14, identificació de pol·len fòssil, espores de fongs, algues i partícules de carbó, amb l'objectiu d'aportar noves dades que ajudin a aclarir la dinàmica de la vegetació al llarg del Tardiglacial i l'Holocè a les Terres Altes de la Guayana.

Capítol 2. Potential migration routes and barriers for vascular plants of the Neotropical Guayana Highlands during the Quaternary. Aquest treball pretén reconstruir en detall les rutes i barreres potencials de les plantes vasculars de les muntanyes de la Guayana durant el Quaternari. Per dur-ho a terme es va combinar l'anàlisi fitogeogràfic i les paleoreconstruccions de la topografia usant eines SIG.

Capítol 3. The use of taxonomic databases in biogeographic analysis: evaluation of the role of historical and geographical factors on the Guayana Highlands endemicity. Aquest capítol analitza els patrons de distribució en altitud de les espècies endèmiques i no endèmiques. Per dur-ho a terme, es va usar la base de dades de PANTEPUI dissenyada en aquesta tesi, i un anàlisi de correlacions de Pearson.

Capítol 4. Modelling biodiversity loss by global warming on Pantepui, northern South America: projected upward migration and potential habitat loss. En aquest capítol s'estudia l'efecte potencial del canvi climàtic per a finals d'aquest segle a les plantes vasculars de Pantepui. Per a tal propòsit, es va calcular el nombre d'espècies que perdien el seu hàbitat degut al desplaçament vertical de les condicions ambientals. Els mètodes emprats van ser: la relació espècies-àrea i l'anàlisi del Desplaçament del Rang Altitudinal (ARD).

Capítol 5. Quantifying the global warming threats on vascular plants of the remote Guayana Highlands. Aquest capítol és un aprofundiment en la comprensió dels risc del canvi climàtic sobre les plantes vasculars de Pantepui, amb èmfasi sobre els efectes de la reducció i fragmentació de l'hàbitat. Per aquest estudi s'ha emprat l'anàlisi del desplaçament del rang altitudinal i el software relatiu a la fragmentació del paisatge "FRAGSTATS", així com l'aplicació de les categories de conservació del *International Union of Conservation of Nature* (IUCN).

Discussió. En aquest apartat es fa una discussió general integrada dels resultats obtinguts, al llargs del diferents capítols, amb èmfasi en les taxes de migració passades i futures.

Conclusions. S'exposen de manera breu les principals conclusions de la tesi, basades en les conclusions de cada capítol.

1. INTRODUCCIÓ

Stegolepis grandi

Els dibuixos reproduïts a les “sub-portades” interiors són extrets de *La Flora of the Venezuelan Guayana* (Steyemark, J.A., Berry, P. & Holst, K. 1995-2005)

1. CONTEXT PREVI I OBJECTIUS GENERALS

Durant les últimes tres dècades, un seguit d'evidències suggereixen que l'augment en la concentració atmosfèrica de diòxid de carboni i metà, procedents d'activitats humanes, ha començat a modificar el clima global (IPCC, 2007). En els últims 140 anys, s'ha calculat un augment mitjà de la temperatura superficial global de 0.61ºC (Houghton *et al*, 2001). Aquest valor, tot i ser elevat, esdevé excepcional quan es compara amb els 0.25 ºC d'augment de la temperatura per mil·lenni, calculats des de l'Últim Màxim Glacial (fa 21000 anys) al Neotròpic (Rull, 2004).

S'ha qüestionat quina serà la resposta de les espècies vegetals (ex: canvis fenològics, fisiològics, de distribució i/o adaptació) i si aquestes seran capaces de sobreviure a un escalfament tan ràpid (Hughes, 2000, 2003; Walther *et al,* 2002; Parmesan & Yohe, 2003; Thomas *et al,* 2004; Jump & Peñuelas, 2005). Evidències palinològiques suggereixen que les espècies de plantes han respòs als canvis ambientals del passat adaptant-se a les noves condicions, migrant cap a les zones on les condicions eren més favorables, fragmentant les seves poblacios o extingint-se (Overpeck *et al*, 1991, 2005; Hughes, 2000; Jump & Peñuelas, 2005). Però, donada la magnitud i velocitat del canvi previst per finals d'aquest segle i l'augment de les activitats humanes, hi ha una seguit d'incògnites sense anàlegs en el passat. Una d'aquestes incògnites seria les conseqüències provinents de les accions directes o indirectes causades per l'home: podran tolerar les espècies la fragmentació provocada per la mà de l'home? Aquesta fragmentació provocarà una major barrera pel que fa a la dispersió de llavors i de gens entre les poblacions? Així mateix, estan obertes moltes altres incògnites pel que fa la capacitat migratòria de les espècies vegetals davant d'un augment de temperatura, tan ràpid i en un període tan curt. Així doncs, cal destacar que no estem davant d'un fenomen futur, sinó que estem davant d'un fenomen actual. Per exemple, les primeres dades de migracions actuals han estat ja recopilades als Alps Austríacs, on s'ha mesurat un ascens mitjà de 4 m per dècada associat a un augment de la temperatura de 0.7 ºC (Grabherr et al, 1994, Pauli et al, 1996). D'estudis com aquest, se n'han realitzat a diferents parts del planeta i, a priori, tots descriuen una migració més o menys acusada (Gottfried *et al*, 1999; Parolo & Rossi, 2007; Kelly & Goulden, 2008; Lenoir et al, 2008). També hi ha treballs basats en la modelització de la distribució de les espècies, que tenen com a objectiu predir l'impacte del canvi climàtic en el futur (Fig 1). Molts d'ells mostren com a resultats un nivell elevat d'extinció. És el cas del treball de Thomas *et al* (2004), on es pronostica que, per exemple, del 15 al 37% de les espècies de mamífers, aus i plantes, de les regions estudiades (Mèxic, Amazònia, Queensland i Sud Àfrica) s'extingirien l'any 2050 (Thomas *et al*, 2004; Thuiller *et al*, 2005; Shoo *et al*, 2005; Engler *et al*, 2009). Alguns d'aquests estudis van més enllà i pronostiquen que un gran nombre d'espècies estarien en Perill Crític segons els criteris de la "*International Union for Conservation of Nature*" (IUCN). Els mateixos autors, però, descriuen les limitacions dels models emprats, com el fet d'assumir que les espècies estan en equilibri amb l'ambient i no considerar les possibles adaptacions o la tolerància al canvi climàtic.

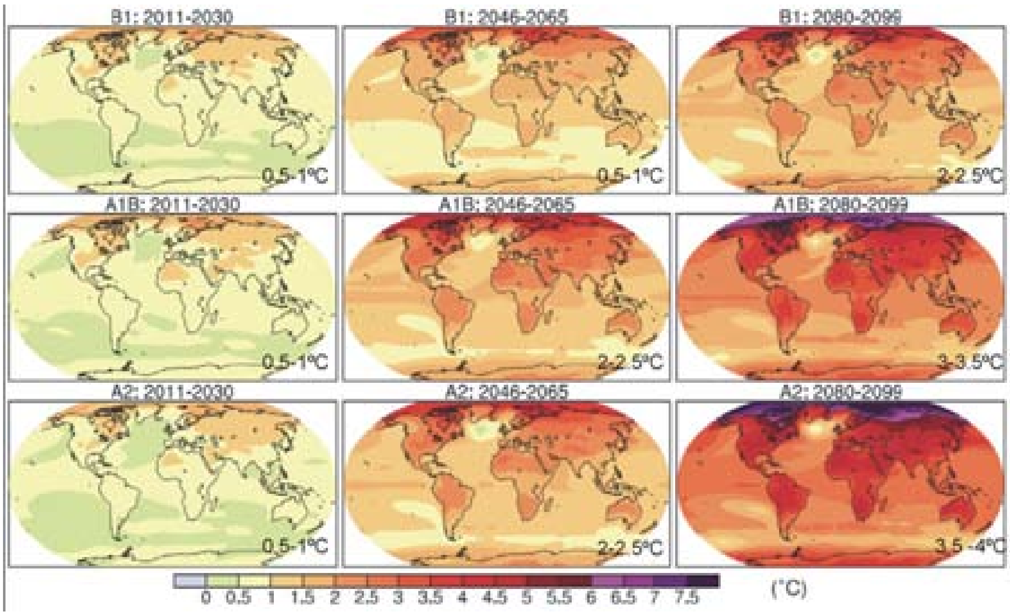


Figura 1. Patrons d'augment de la temperatura durant aquest segle proposats per l'*Intergovernamental Panel on Climate Change* (IPCC, 2007). S'han considerat tres escenaris d'emissió: B1 (baix), A1B (mig) i A2 (alt). A la cantonada dreta a baix, increment de la temperatura previst per a la nostra zona d'estudi (nord de Sud-Amèrica). Modificat de Solomon *et al*. (2007).

Aquesta tesi usa l'estudi combinat del passat i el present per modelitzar el futur aplicat a les plantes vasculars de les Terres Altes de la Guayana (TAG), una remota zona al nord de Sud Amèrica conformada per un conjunt de muntanyes tabulars (conegudes com a *tepuis*), amb un grau d'endemisme excepcional (Berry & Riina, 2005) i on la influència humana és i ha estat nul·la (Fig. 2). Aquest conjunt de característiques han propiciat l'aparició de novel·les fantàstiques com ara el Món perdut de Arthur Conan Doyle

(1912), on es descriuen els tepuis com una terra oblidada per l'evolució i habitada per espècies d'èpoques remotes, apartades de la resta del món. Aquest caràcter de món fantàstic, inaccessible i sagrat també existeix dins les creences populars de les comunitats indígenes (els *Pemons*) que habiten les terres baixes. Ja des dels inicis de les exploracions, les TAG han estat considerades com un arxipèlag d'illes flotants en l'aire (Huber, 1988).

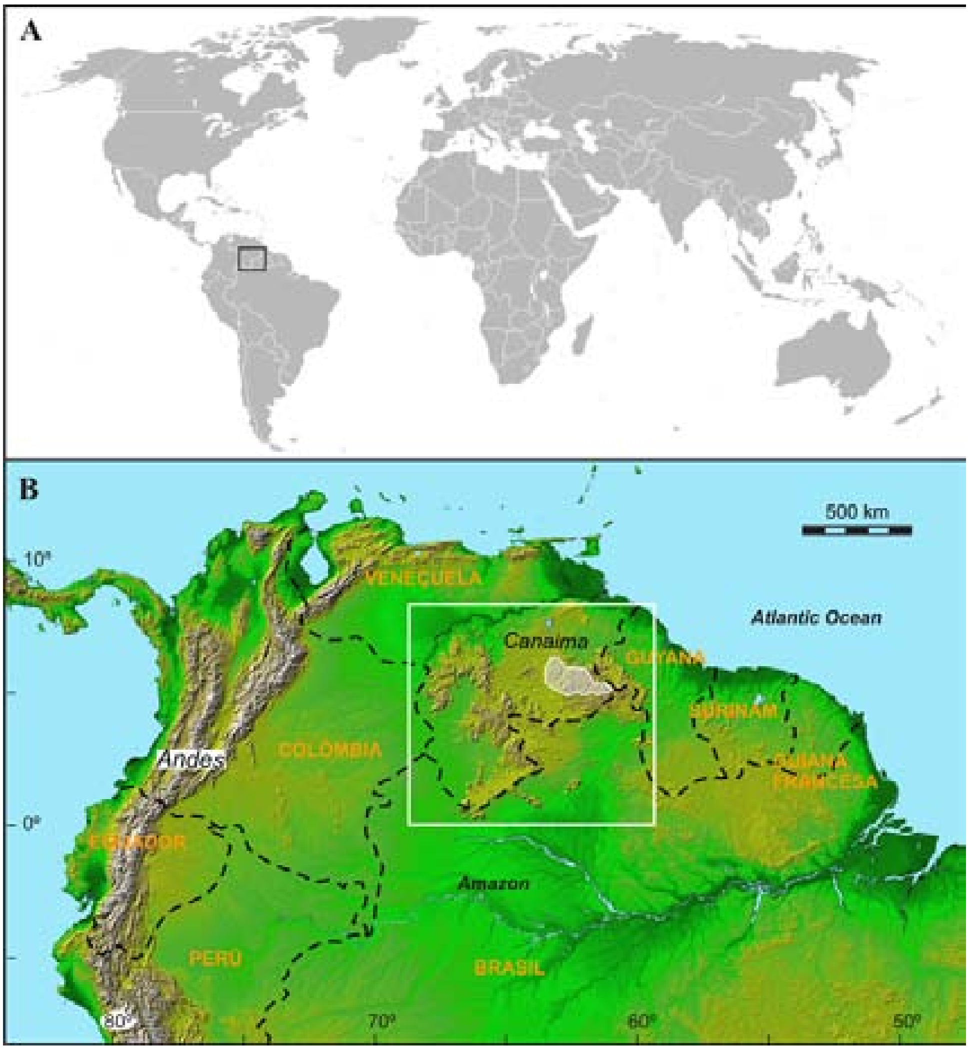


Figura 2. A) Mapa del món mostrant la situació de les Terres Altes de la Guayana (requadre negre). B) Localització al nord de Sud-Amèrica de la regió d'estudi (requadre blanc). Parc Natural de Canaima, sombrejat en blanc.

Recentment, el concepte d'illa ha estat revisat per Whittaker i Fernández-Palacios (2007). Els autors fan una divisió entre les considerades illes veritables (*true islands*) i les illes hàbitat (*habitat islands*). Les TAG s'enquadrarien entre les considerades illes hàbitat, definides com a: *taques d'un habitat diferenciat i isolat respecte d' una matriu hostil* (Whittaker & Fernández-Palacios, 2007). El concepte de taca s'entendria com l'àrea no lineal, diferenciada de l'entorn, mentre que la matriu, consistiria en l'element del paisatge més estès i connectat, o dit d'una altra manera, l'element que envolta la taca (Forman & Godron, 1986). Així doncs, les TAG, juntament amb la *Great Basin* (USA), els llacs continentals (ex, llac Titicaca) o els cims de les muntanyes en general, es poden considerar illes.

La magnitud de la migració ascendent esperada a les TAG, degut a l'escalfament global, està calculada de ser de fins a 700 m (Rull & Vegas-Vilarrúbia, 2006). Una de les possibles conseqüències d'aquest escalfament, seria la disminució de la biodiversitat global del planeta per extinció, a causa de la pèrdua, reducció i fragmentació de l'hàbitat d'un nombre relativament important d'espècies, particularment d'espècies endèmiques. No es pot oblidar que la magnitud d'aquesta extinció dependrà directament de l'altitud i la morfologia de les muntanyes. Per exemple, en les muntanyes més altes amb un pis nival ben desenvolupat, s'espera una menor extinció, ja que la fusió dels gels deixarien noves àrees disponibles per als organismes. D'altra banda, les muntanyes baixes i tabulars tindrien una extinció més elevada a causa de la manca d'espai als cims (Rull & Vegas-Vilarrúbia 2006). Aquest és el cas de les TAG. Un estudi preliminar on s'analitzava l'efecte de l'escalfament sobre 45 espècies de plantes de gèneres endèmics, calculava que entre el 10 i el 35% estaven en risc de perdre el seu hàbitat potencial.

L'objectiu general és avaluar una sèrie de preguntes ecològiques, biogeogràfiques i de la biologia de la conservació a les TAG: quina ha estat la dinàmica de la vegetació en els últims 12000 anys en el cim més elevat? Els últims cicles climàtics del Quaternari (últims 2.6 milions d'anys) han influït potencialment en les migracions de les plantes vasculars? Quines són les espècies amb risc de pèrdua d'hàbitat a causa de l'escalfament global? Aquestes incògnites s'han enfocat des de diferents punts de vista. 1) El paleoecològic, que ens ha aportat eines per tal d'esbrinar l'efecte del factor temps sobre la vegetació dels cims dels tepuis, 2) El d'anàlisis i acumulació de dades de biodiversitat vegetal essencials per poder tenir un sòlid coneixement del grau d'endemisme i poder relacionar-ho amb diferents factors ecològics com són: l'àrea i l'altitud, 3) L'ús de models per predir la possible pèrdua d'hàbitat, entès com a espai climàtic potencial de les espècies endèmiques davant del canvi climàtic previst per aquest segle i finalment, 4) La perspectiva de la biologia de la conservació: quines espècies estan amenaçades i què es pot fer conservar-les? Abans de desengranar tots els objectius, començarem des del principi, explicant: l'àrea d'estudi i el context paleoecològic als tepuis de les Terres Altes de la Guayana.

2. ÀREA D'ESTUDI: LES TERRES ALTES DE LA GUAYANA

2.1 Consideracions prèvies

A la regió de la Guayana, en general, existeix un gradient altitudinal, més o menys continu, on s'han diferenciat tres unitats principals (Huber, 1995a): Terres Baixes (*Lowlands*, 0-500m), Terres Mitjanes (*Uplands* 500-1.500 m) i Terres Altes (*Highlands* 1.500-3.000 m (Fig 3).

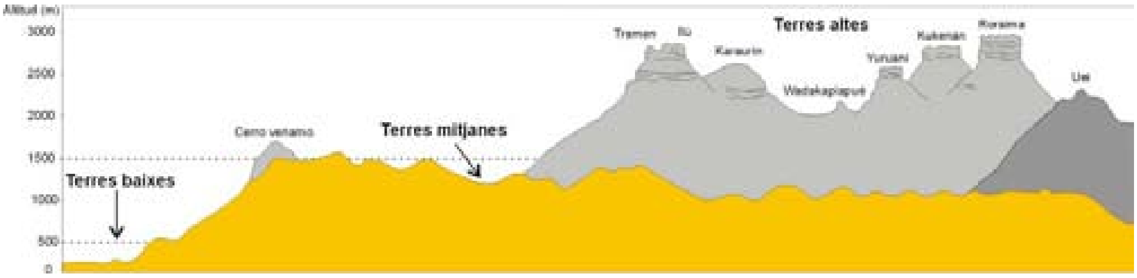
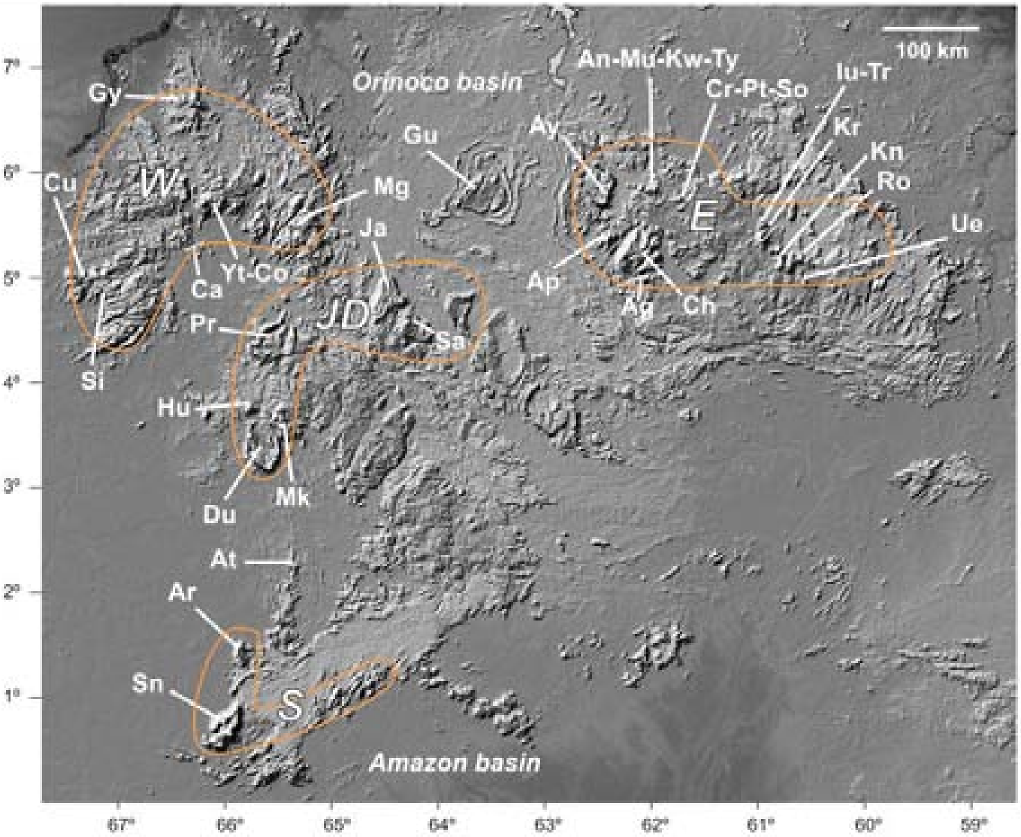


Figura 3. Esquema del gradient altitudinal, on es diferencien les Terres Baixes, Terres Mitjanes i Terres Altes i els tepuis: Tramen, Ilú Karaurín, Wadakapiapué, Yuruaní, Kukenán, Roraima i Uei. Modificat de Huber 1995.

Aquesta tesis està centrada en les Terres Altes, conegudes com a Terres Altes de la Guayana (TAG). En aquest estudi s'usaran dos termes indistintament: TAG i Pantepui. Tot i que cal remarcar que el primer terme és una unitat fisiogràfica i el segon, una unitat biogeogràfica (Huber, 1988) (Fig. 4). La primera vegada que el terme Pantepui va ser usat per definir el conjunt de muntanyes tabulars de Veneçuela va ser el 1955 per Mayr i Phelps. En aquest estudi, prenem la definició de Huber (1988) que defineix Pantepui com una província biogeogràfica, conformada per un conjunt de muntanyes tabulars que s'estenen entre 1500 i 3045 m i que tenen en comú la història geològica,la geomorfologia i atributs biològics que els diferencia de les terres circumdants.



Pantepui s´ha dividit en 4 ditrictes fitogeogràfics: l´est (E), l´oest (W), el Jaua-Duida (JD) i el Sud (S): Angasima (Ag), Aparamán* (An), Aprada* (Ap), **Auyán** (Ay), Carrao (Cr), **Chimantá** (Ch), Ilú-Tramen (Il), Kamarkawaray (Kw), Karaurín (Kr), Kukenán (Kn), Murispán (Mu), **Ptari*** (Pt), **Roraima** (Ro), Sororopán (So), Tereké-Yurén (Ty) i Uei (Ue). **W**: Camani (Ca), Cuao (Cu), Guanay (Gy), Sipapo (Si), Maigualida (Mg),Yaví* (Yv) i Yutajé-CoroCoro (Yt-Co). **JD**: **Duida** (Du), **Huachamacari** (Hu), Jaua (Ja), **Marahuaka*** (Mk), Parú (Pr) i Sarisariñama (Sa). **S:** Aracamuni (Ar), Aratitiyope (At) i Sierra Neblina (Sn) (Modificat de Rull & Nogué, 2007)

Figura 4. Descripció de Pantepui i imatge radar (NASA/JPL-Caltech), que mostra les TAG i els tepuis distribuïts en districtes (modificat de Rull & Nogué, 2007). * tepuis amb els cims relativament isolats (Huber, 1988). En negreta: tepuis ben explorats (Huber, 1995).

2.2 Les Terres Altes de Guayana

Les Terres Altes de la Guayana (TAG), amb una extensió d'aproximadament 6600 km^2, es troben localitzades entre la conca de l'Orinoco al nord i l'Amazònia al sud amb les coordenades 1º-7º N i 59º-67º W (Fig. 4). Pràcticament, la seva totalitat es troba a dins de Veneçuela (90%), tot i que també es troben als països adjacents de Colòmbia, Brasil, Suriname i Guyana (Steyermark *et al*, 1995-2005). El tret fisiogràfic més característic és la presència d'una cinquantena de muntanyes tabulars (tepuis), terme que significa brots de pedra en la llengua indígena Pemón (Huber, 1988). Els tepuis en si es poden trobar de forma individual (la majoria) o agrupats en massissos (ex. Auyán i Chimantá). Tots ells presenten uns grans penya-segats i valls més o menys inclinades que els separen de les Terres Mitjanes i Baixes. Tot i el seu aparent aïllament, pocs d'ells estan considerats totalment aïllats: Aparamán, Aprada, Ptarí, Marahuaka i Yaví (Huber, 1988) (Fig. 4). La superfície dels cims dels tepuis és molt variada, sent la més comú entre 200 i 500 km^2 (Steyermark *et al*, 1995-2005). Podem trobar tepuis configurats per una combinació de tepuis interns i externs, valls, rius i cascades. La diferència principal entre un tepui extern i intern és la seva exposició a factors ambientals, com són els vents alisis, i/o a les possibles pertorbacions provinents de les terres mitjanes i/o baixes, com serien els focs. L'altura màxima dels tepuis és de 3014 m (Sierra Neblina), encara que la majoria dels tepuis es troben entre 2.000 i 2.600 m (Rull, 2009).

2.3 Geologia i geomorfologia

La zona d'estudi ocupa el sector nord oriental de l'Escut de la Guayana. L'Escut està constituït essencialment per roques ígneo-metamòrfiques (principalment granits i gneis), formades al Precàmbric (entre 2700 i 3500 milions d'anys abans del present, MA), i una capa de roques sedimentàries (gresos i quarsites) que es coneixen amb el nom de grup Roraima, ubicades sobre el conjunt de roques ígneo-metamòfiques (Briceño & Schubert, 1990). Aquest Escut és un residu de l'antic Escut de Gondwana, que va iniciar la seva fragmentació ara fa entre 100 i 150 Ma en el Juràssic-Cretàcic. En aquest període hi va haver l'obertura de l'Atlàntic i la formació de les conques fluvials de l'Orinoco i l'Amazones, i es va iniciar un llarg procés de meteorització i erosió que s'estén fins avui dia (Briceño & Schubert, 1990; Edmond *et al,* 1995). L'erosió de la capa de roques sedimentàries no ha estat un procés continu, sinó que, com a resultat dels llargs períodes d'estabilitat de l'escut, s'han format sis nivells de superfícies d'erosió, sent la superior la que correspondria a la majoria dels cims dels tepuis (Briceño & Schubert, 1990). La intensitat d'erosió més elevada ha tingut lloc a l'oest i al sud, on els tepuis són menys freqüents i estan més separats uns dels altres (Huber, 1995a).

2.4 Clima

Les condicions climàtiques a Pantepui són típicament equatorials, caracteritzant-se per una poca variabilitat tèrmica al llarg de l’any i amb fortes oscil·lacions diàries (10 ºC) (Huber, 1995a). Pel que fa a la precipitació, s’estima que els cims dels tepuis reben, com a terme mitjà, de 2500 a 4000 mm de pluja anuals, sense estació seca. A més, hi ha un aportació addicional d’humitat per la freqüència i persistència de la boira (Huber, 1995a). El gradient adiabàtic d’aquestes muntanyes és de -0.6 ºC/ 100 m (Galán, 1992; Huber, 1995a). Un altre paràmetre important a l’ambient tepuià és la freqüència dels vents alisis provinents del nord-est, que poden arribar a ràfegues de 50 km/h (Huber, 1992; Huber, 1995 b) (Fig. 5).

Tenint en compte aquestes característiques, es pot distingir tres tipus principals de zones climàtiques: 1) el clima premontà alt i molt humit, amb una temperatura mitjana anual d’entre 17 i 21 ºC i un precipitació mitjana estimada de 2500 mm, present als cims compresos entre 1500 i 1700 m, 2) el clima montà baix i molt humit, amb una temperatura mitjana anual de 14 a 17 ºC i una pluviositat mitjana anual de 2500 a 3000 mm, present als tepuis amb cotes entre 1700 i 2000 m, 3) el clima montà extremadament humit, amb una temperatura mitjana anual de 10 a 14 ºC i una elevada radiació solar. Aquest clima es troba a les cotes més elevades dels tepuis (superiors a 2200 m) i presenta una pluviositat elevada de 3000 a 4000 mm. Els registres climàtics no han registrat mai temperatures per sota de 0 ºC, ni s’ha observat fins ara la formació de gel a cap del tepuis (Huber, 1995a).

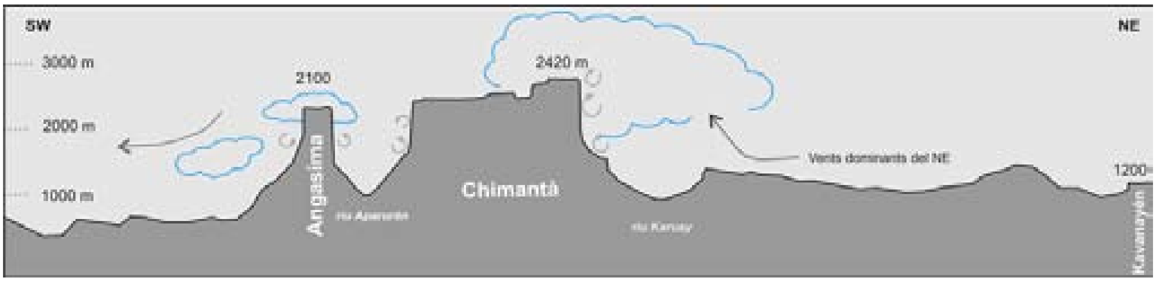


Figura 5. Tall esquemàtic de la circulació atmosfèrica i les altituds. Modificat de Huber (1995). Veure Fig 4 per la seva ubicació.

2.5 . Biodiversitat vegetal

2.5.1 Endemismes

Des del punt de vista florístic, s'han documentat 2447 espècies de plantes vasculars a Pantepui (Berry & Riina, 2005). La majoria de les famílies són d'Angiospermes (130), seguides pels Pteridòfits (24) i Gimnospermes (2) (Berry & Riina, 2005). La família més representada és la de les Orchidaceae, amb 258 espècies, les Melastomataceae (147), les Asteraceaea (140) i les Rubiaceae (133) (Berry & Riina, 2005). Pel que fa als gèneres, tres superen les 40 espècies: *Psychotria* (Rubiaceae), *Schefflera* (Aralaiceae) i *Xyris* (Xyridaceae). Des del punt de vista fitogeogràfic, el 70% dels gèneres són de distribució neotropical, el 22% són Paleotropicals, el 4% són de distribució temperada i el 4% són cosmopolites (Berry & Riina, 2005). La flora vascular de les TAG té un elevat grau d'endemisme, comparable al de moltes illes oceàniques (Rull, en premsa), on hi destaquen 23 gèneres endèmics d'aquestes terres (Berry & Riina, 2005): *Achnopogon, Chimantaea, Glossarion, Huberopappus, Quelchia, Tyleropappus* (Asteraceae), *Brewcaria* (Bromeliaceae), *Tepuia* (Ericaceae), *Celiantha*, *Neblinantha* (Gentianaceae), *Pyrrorhiza* (Haemodoraceae), *Comoliopsis, Mallophyton, Ochthephilus* (Melastomataceae), *Adenanthe, Adenarake* (Ochnaceae), *Aracamunia* (Orchidaceae), *Marahuacea* (Rapateaceae), *Coccochondra*, *Coryphothamnus* (Rubiaceae), *Rutaneblina* (Rutaceae), *Saccifolium* (Saccifoliaceae) i *Achlyphila* (Xyridaceae).

Els tepuis amb més espècies endèmiques de Pantepui són: el massís del Chimantá (258) i Sierra Neblina (140) (Fig 6). Pel que fa als tepuis que contenen més espècies endèmiques locals, descrites com aquelles espècies que només es troben en un sol tepui, són: els Chimantà (102), Sierra Neblina (132), Auyán (32) i Roraima (17) (Berry & Riina, 2005).

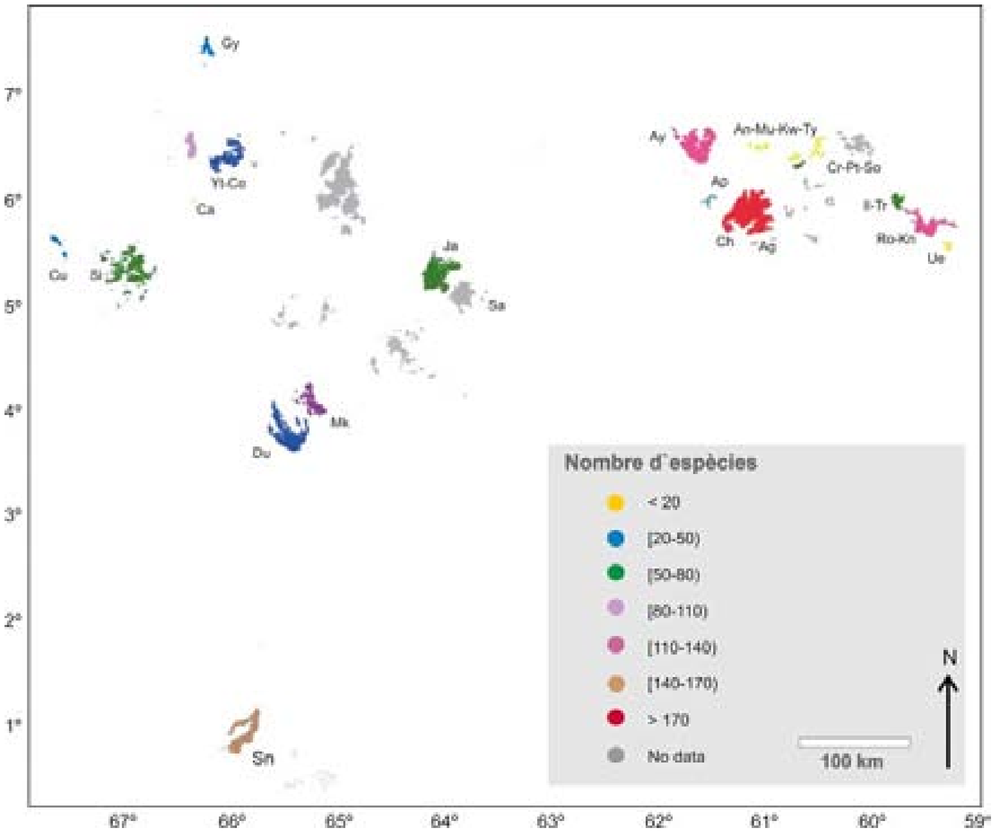


Figura 6. Nivell d'endemisme dels tepuis més estudiats. Dades de Berry & Riina (2005).

2.5.2 La vegetació

Els tipus de vegetació que es troben a les TAG es resumeixen en quatre formacions (Huber, 1995b)(Fig. 7): boscos, arbustars, herbassars i formacions pioneres. Les formacions més esteses en els tepuis són les arbustives i les herbàcies, seguides per les pioneres i, finalment, els boscos.

Formació boscosa

On els penya-segats no interrompen la continuïtat topogràfica entre el pendent i el cim, es pot observar, entre els 1700 i 1900 m, el límit superior dels boscos montans mesotèrmics. A partir d'aquest nivell altitudinal, es troben els boscos tepuians pròpiament dits (Huber, 1995b). Aquests, amb una alçada de 4 a 8 m, es presenten en dues formes principals: el bosc de galeria i el bosc baix sobre diabases. Bàsicament, la diferència entre els dos recau en la menor o major presència del gènere *Bonnetia* (Bonnetiaceae). Els boscos tepuians estan dominats per *Bonnetia roraimae* (Bonnetiaceae), amb presència de *Podocarpus sp.* (Podocarpaceae)*, Magnolia tepuiana* (Magnoliaceae)*, Schefflera* (Araliaceae) i *Weinmannia* (Cunoniaceae), amb un sotabosc frondós de *Orectanthe* (Xyridaceae), *Brocchinia* (Bromeliaceae) i herbes bambusoidees com les espècies del gènere *Myriocladus*. En el bosc baix sobre diabases, els gèneres dominants són *Stenopadus* (Asteraceae) i *Podocarpus* (Podocarpaceae), mentre que *Bonnetia* no és tan abundant. També s'observa una freqüència més elevada de *Spathelia chimantensis.* Al sotabosc (quan hi és present) s'han observat vàries espècies arbustives com: *Psycothria* (Rubiaceae), *Clusia* (Clusiaceae), *Poecilandra sclerophylla* (Ochnaceae), *Miconia acutifolia* (Melastomataceae). L'estrat herbaci està dominat per gramínies (principalment *Panicum eligulatum*) i Cyperaceae (*Everardia* i *Rynchospora*) (Huber, 1992).

Formació arbustiva

La formació arbustiva, d'una alçada entre 0.5 a 3 m, és la dominant i més desenvolupada en els cims. En general, en els tepuis es distingeixen dos tipus d'arbustars: els arbustars tepuians i els arbustars paramoides. Els primers, representats a tots els cims, estan adaptats als ambients rocosos i accidentats. Algunes famílies importants són: Apocynaceae, Aquifoliaceae, Asteraceae, Clusiaceae, Ericaceae, Melastomataceae, Myrsinaceae, Ochnaceae, Rubiaceae i Theaceae. Els arbustars paramoides són exclusius del massís del Chimantá i els tepuis veïns (Aparamán, Auyán i Murisipán). Estan dominats per una de les tres espècies del gènere endèmic de compostes anomenat *Chimantaea: Chimantaea humilis, Chimantaea lanocaulis* i *Cimantaea mirabilis.* El nom d'arbustar paramoide prové de la similitud fisiognòmica amb els dominats per *Espeletia* (Asteraceae), típics dels *pàramos* andins (Huber 1995 a). Els páramos són biomes herbàcis-arbustius del Andes, que s'estenen des de 2900 m fins al límit de les neus perpètues aproximadament a 4700 m (Luteyn, 1999).

Formació herbàcia

Les formacions herbàcies cobreixen grans extensions en els cims tepuians. Se'n coneixen dos tipus: praderies i herbassars tepuians. Les praderies es localitzen en zones de valls inundades. Estan dominades per grans colònies d'espècies graminoides com *Rhynchocladium* (Cyperaceae), juntament amb *Syngonanthus* (Eriocaulaceae) i molses (*Sphagnum*). També es troben colònies d'una bambusàcia (*Aulonemia*), una Iridàcia (*Trimezia chimantensis*) i una herba paràsita, el *Thesium tepuiense* (Santalaceae). Els herbassars tepuians creixen sobre sòls menys inundats, com són les torbes. Estan dominats pels gèneres *Stegolepis* (Rapateaceae) i *Xyris* (Xyridaceae), amb la presència de Ciperàcies (*Everardia* i *Lagenocarpus*) i Sarracinàcies (*Heliamphora*). Un fet significatiu és que les gramínies, grans dominadores de moltes comunitats herbàcies tropicals, són poc importants a les TAG (Huber, 1995a).

Formació pionera

Una considerable porció dels cims estan constituïts per superfícies de roca nua. Les formacions pioneres creixen sobre les superfícies rocoses. La colonització d'aquestes superfícies comença per l'establiment de cianòfits (*Stigonema*), seguit per líquens (*Cladonia* i *Cladina*). Una vegada s'ha format una capa de substrat orgànic, les herbàcies troben les condicions adequades i són les predominants en els estats avançats de la colonització (Huber, 1992).

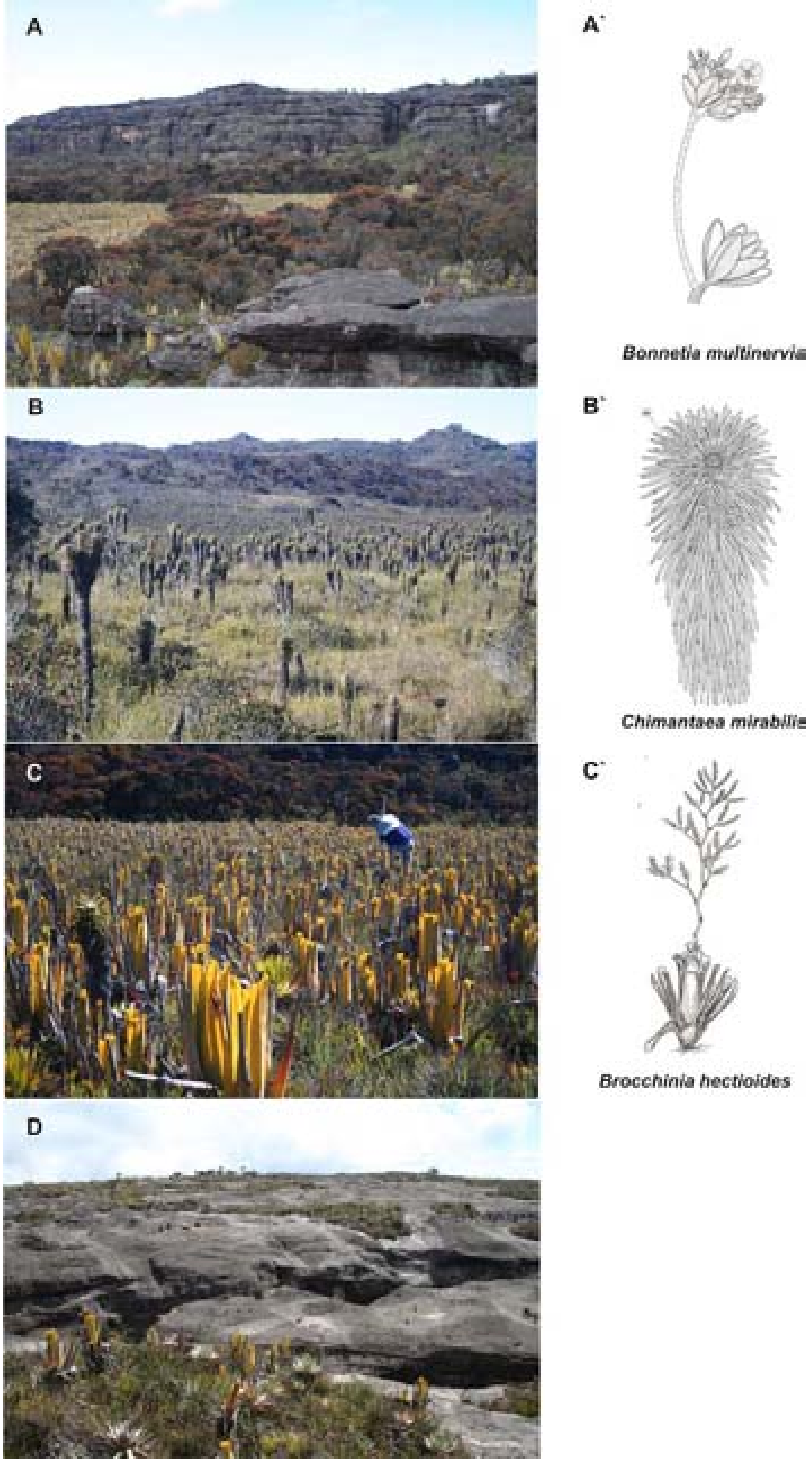


Figura 7. Exemples de les 4 formacions vegetals característiques dels cims dels tepuis: A) bosc, B) arbusts, C) herbassars i D) pioneres. A la dreta, detall de l'espècie dominant de cada formació, de dalt a baix*:* A') *Bonnetia multinervia,* B') *Chimantaea mirabilis* i C') *Brocchinia hectioides.* Fotos de les formacions vegetals de Nogué S. Detalls reproduïts de la Flora de la Guayana Veneçolana de Steyermark *et al* (1995-2005).

2.6 Conservació

Més del 70% del territori de la Guayana es troba sota protecció oficial (Huber, 2001). Aquesta regió ha estat considerada una àrea preferencial dins dels programes dels principals organismes dedicats a la conservació de la biodiversitat global. Per exemple, va ser declarada una "prioritat global" a la reunió de Paramaribo (2002), en la que hi van participar la *International Union for the Conservation of Nature* (IUCN), la *United Nations Developement Program* (UNDP), *Conservation International* (CI) i *Guayana Shield Initiative* (GSI) (detalls a http://www.guianashield.org). Les TAG han estat incloses en el *World Wildlife Fund* (WWF) "*Global 2000 project*" com l'ecoregió ER-45, i han estat definides com una *WWF/IUCN Neotropical Plan Diversity Centers* (Pantepui o SA-2), considerat crucial per l'evolució de la Guayana i la biota de l'Amazònia (IUCN, 2000). Pel que fa a les proteccions internacionals, l'àrea de Canaima, ubicada al sud-est de Veneçuela, va ser nomenada patrimoni de la humanitat per l'Organització de les Nacions Unides per l'Educació, la Ciència i la Cultura (UNESCO) l'any 1994 (Huber, 1995a) (Fig 1).

Veneçuela té una remarcable tradició en la protecció d'àrees, que es va iniciar al 1937 (Huber, 2001) amb la creació de dues figures de conservació: Parcs Naturals (NP) i Monuments Naturals (MN). A la Guayana Veneçolana, hi ha 7 PN i 29 MN que pertanyen a una unitat administrativa anomenada "*Instituto Nacional de Parques*" (INPARQUES). Pel que fa a la nostra zona d'estudi, tots els tepuis estarien protegits des del 1991 (Huber, 2001) (Taula 1). La IUCN ha definit una sèrie de sis categories (Ia, Ib, II, III, IV, V i VI) de gestió de parcs i zones protegides a nivell internacional (IUCN, 1994). Les categories Ia i Ib són categories de protecció estricte. La Ia (reserva natural estricte) té com a objectiu la conservació a nivell regional nacional o global d'ecosistemes i espècies que es veurien dràsticament afectats per la presència d'activitats humanes. La Ib (àrea natural silvestre) és una categoria que protegeix la integritat ecològica a llarg termini de les àrees naturals no pertorbades per activitats humanes i lliures d'infraestructures modernes. En el nostre cas, els tepuis estarien protegits sota les categories II (Parcs Naturals) i la III (Monuments Naturals) (Taula 1). Aquestes dues categories destaquen per la protecció de la integritat dels ecosistemes (II) o àrees amb una singularitat natural a destacar (III). La diferència entre les dos categories és, bàsicament, que la categoria II és més restrictiva i inclou l’exclusió de les activitats d’explotació.

La categoria IV (àrea de gestió d’hàbitat i espècies) té com a finalitat mantenir, conservar i restaurar de manera activa les espècies i els hàbitats. La categoria V (paisatge terrestre o marí protegit), té els objectius similars als de la cateogria IV: protegir i mantenir, però en aquest cas, paisatges terrestres i marins. Finalment, la categora VI (àrea de gestió protegida) es defineix com la protecció dels ecosistemes naturals i l’ús dels recursos de forma sostenible (IUCN, 1994).

Taula 1. Resum de les dades de protecció oficial dels Parcs Naturals (PN) i dels Monuments Naturals (MN) de la zona d’estudi. L’última columna enumera els tepuis inclosos en cada PN o MN. *World Heritage Site* (WHS). Coordenades extretes del decret número 1233 de creació dels Monuments Naturals del 18 de gener de 1991 (*Gaceta Oficial de Venezuela*, nº 4250). Dades d’àrea, altituds i categories IUCN, extretes del “*World database on protected areas*” (http://www.wdpa.org/).

Nom del PN o MN	localització	Km^2	Altitud (m)	Protecció	IUCN	tepuis
Jaua i Sarisariñama	64º00’W- 5º03’N	3.300	500-3400	PN	II	Jaua i Sarisariñama
Canaima	62º59’W- 6º29’N	30.000	450-2810	PN WHS	II	Auyán, Chimantá, Roraima, Ptarí, I Sororopán
Sierra de la Neblina	65° 54' W- 1° 12' N	13.600	500-3041	PN	II	Sierra Neblina
Duida i Marahuaka	65º35’W- 3º29’N	2.100	250-2880	PN	II	Duida i Marahuaka
Cadena de tepuis orientals	61º03’W- 5º05’ N		800-2700	MN	III	Uei, Kukenan, Yuruaní I Ilú
Guaiquinima	63º 42' W- 5º 47' N	1.096	730-1665	MN	III	Guaiquinima
Camani i Morrocoy	66º05’W- 5º 13’ºN	120	850-1.800	MN	III	Camani
Cuao i Sipapo	66º 18’ W- 4º 20’ N	11.205	100-2200	MN	III	Cuao i Sipapo
Parú i Euaja	65º 48’W- 4º 12’ N	400	800 - 1.600	MN	III	Parú
Aratitiyope	65º 35’W- 2º 05’N	3.300	?	MN	III	Aratitiyope
Yutajé i Coro Coro	66º 28’W- 5º 32’N	2.100	1.800	MN	III	Yutajé i Coro Coro

3. EL PASSAT A LES TERRES ALTES DE GUAYANA I TEORIES D'ESPECIACIÓ

3.1 Consideracions prèvies

La paleoecologia, definida com l'ecologia del passat, tracta de l'estudi dels ecosistemes en el passat (Birks & Birks, 1980). Una de les preocupacions d'aquesta disciplina científica és entendre els processos biològics i els impactes dels canvis ambientals sobre els organismes, les comunitats, els ecosistemes i els paisatges, que involucrin períodes de temps més llargs dels que els mètodes ecològics tradicionals usen (Birks & Birks, 1980). En aquest treball ens centrarem en el període Quaternari que abraça el període de temps comprès entre els 2.6 milions d'anys (Ma) i l'actualitat (Gibbard *et al*, 2005). El Quaternari, dividit entre el Pleistocé i l'Holocè, està caracteritzat per l'aparició de l'home i l'alternança de períodes glacials i interglacials. (Roberts, 1998; Willis & Whittaker, 2000). Al llarg d'aquest apartat, s'usaran les següents abreviacions: ka BP per, milers d'anys abans del present i Ma per, milions d'anys abans del present. Si no es diu el contrari, les dates usades es donen sempre en anys calibrats.

3.2 Context paleoecològic i paleoclimàtic

A diferència d'altres zones pròximes com per exemple els Andes, els estudis palinològics a la zona de Pantepui són força recents. En les últimes dècades s'ha anat omplint el buit existent de dades bàsiques necessàries per a una bona interpretació dels anàlisis paleoecològics. Per una banda, la publicació d'una clau palinològica de referència (Rull, 2003) i, per l'altra, la Flora de la Guayana Veneçolana (Steyermark *et al*, 1995-2005), han representat un pas endavant en la identificació i comprensió de la vegetació present a Pantepui. A partir d'aquí, un seguit d'estudis que analitzen el pol·len i les espores fòssils en torberes del massís del Chimantá i el tepui Guaiquinima, han aportat resultats fonamentals de la dinàmica de la vegetació al llarg de l'Holocè. Tanmateix, els sondatges analitzats fins a l'actualtat, no assoleixen una gran antiguitat. En aquest sentit els registres obtinguts al Guaiquinima a una altitud de 1350 m són els que engloben un període de temps més ampli (últims 8.5 ka BP) (Rull, 2005b). En el cas del massís del Chimantá s'han sondejat diferents tepuis: Akopán, Amurí Toronó i Churí, situats entre 1900 i 2250 m d'altitud, que registren la vegetació des de fa 6.5 ka BP (Rull, 2005c). Així doncs, la presència de sediments més antics, com els pertanyents a l'Últim Màxim Glacial (LGM) fa 21000 anys, segueix sent desconeguda a la zona. En canvi, en altres muntanyes Neotropicals sí que s'ha aconseguit obtenir sediments d'aquesta antiguitat. Per exemple estudis als Andes han permès estimar una davallada de la temperatura mitjana de 7 a 8 ºC durant el LGM, que va comportar descens dels pisos de vegetació d'entre 1200 i 1500 m (Rull, 1998; Rull, 1999; Van der Hammen & Hooghiemstra, 2000). A nivell regional, s'ha determinat que, durant el LGM, va tenir lloc, a les muntanyes tropicals, un descens mitjà de les temperatures d'entre 5 i 6 ºC, acompanyat d'una migració altitudinal descendent de la biota d'uns 1100 m (Farrera *et al*, 1999; Bush *et al*, 2001).

En termes generals, s'ha observat manifestacions climàtiques (canvis en la temperatura i d'humitat) locals a Pantepui de fenòmens descrits de caràcter regional (comuns a tot el Neotròpic), que situen les muntanyes de Guayana en un context coherent amb la resta de muntanyes Neotropicals (Rull *et al*, en premsa). És el cas de la fase més humida registrada en el Guaiquinima entre 4.5 i 2 ka BP (Rull, 2005c). L'anàlisi pol·línic va permetre estimar una expansió dels boscos de galeria de *Bonnetia* (Bonnetiaceaea), interpretat com un increment en la relació precipitació/evaporació (P/E), seguida per una substitució d'espècies típiques del bosc montà (Rull, 2005b). Aquest segon canvi en la vegetació suggereix el pas a un període més sec (Rull, 2005b). A nivell regional, la primera fase es correlaciona amb la pujada d'humitat generalitzada per tot el Neotròpic (Marchant & Hooghiemstra, 2004), determinada a partir d'evidències tant terrestres (Gran Sabana), com lacustres (Llac València) i marines (Cariaco).

Els treballs realitzats al Churí, tepui localitzat al massís del Chimantá, a 2250 m, han aportat resultats altament informatius, en part gràcies al fet que es troba situat molt proper a la zona altitudinal de transició entre dues comunitats tepuianes; l'herbassar de *Stegolepis* (Rapateaceae) i la formació arbustiva paramoide de *Chimantaea* (Asteraceae). Els ecotons són reconeguts com a zones adients per detectar canvis en la vegetació, juntament amb les localitats d'alta muntanya (Markgraf, 2001). Aproximadament entre 6.5 fins a 2.5 ka BP, aquest ecotò entre l'herbassar i la formació arbustiva es trobava per sota del Churí, és a dir, per sota dels 2250 m, mentre que la zona d'estudi estava dominada per un arbustar de *Chimantaea*, fet que s'interpreta com un indici de temperatures mitjanes inferiors a les actuals (Rull, 2005c). A partir de 2.5 ka BP, s'observa un augment de la presència de pol·len de *Stegolepis*, gènere típic dels herbassars, que indicaria un ascens de l'ecotò. Així doncs, es va passar d'un arbustar paramoide a un herbassar tepuià. Aquest fet suggereix un augment de la temperatura. S'estima que les oscil·lacions de l'ecotò enregistrades van ser de pocs centenars de metres, equivalents a una variació tèrmica de 1ºC (Rull, 2004; Rull, 2005c). Pel que fa als altres tres sondatges realitzats al Chimantà entre 1900-2100 m d'altitud, només registraren oscil·lacions menors de vegetació. Aquesta constància s'ha interpretat com una evidència de la insensibilitat de les localitats sondejades a les oscil·lacions climàtiques, a causa, a priori, de la seva altitud intermèdia i allunyada dels ecotons sensibles a aquestes oscil·lacions (Rull, 2005c).

3.3 Teories d'especiació

Degut a la naturalesa aïllada dels tepuis, s'han desenvolupat, al llarg dels temps, moltes hipòtesis i teories respecte a l'origen i evolució de la vegetació i la fauna dels seus cims. Ja des del 1967, Mayr i Phelps van recopilar una sèrie de teories ideades, fonamentalment, per explicar l'origen de la fauna (primordialment en referència als ocells) a Pantepui (Mayr & Phelsp, 1967). Totes elles tenen la base comuna de voler explicar l'elevadíssim grau d'endemisme dins la diversitat d'avifauna. Entre elles cal destacar la teoria de l'altiplà (Chapman, 1931), basada en entendre la fauna actual de Pantepui com una porció de la fauna que va quedar després de l'actuació dels processos d'erosió i meteorització de l'altiplà inicial. Una altra teoria a accentuar és la del clima fred (Chapman, 1931), que suggereix que la fauna actual de Pantepui va ser capaç d'arribar-hi quan a les terres baixes hi dominava un clima subtropical durant els períodes freds del Pleistocè. Les tres teories restants (Teoria del canvi d'hàbitat, Teoria de l'especialització i Teoria de la dispersió) es basen en: canvis de preferència d'hàbitat de les espècies d'aus, especialització a zones de penya-segats i dispersió provinent d'altres zones com els Andes. Les hipòtesis actuals usen els mateixos principis establerts per Mayr i Phelps (1967) per debatre l'origen de la vegetació (Rull, 2004; Rull, 2009). Aquestes hipòtesis són: la del Món Perdut (Maguire, 1970), la del Desplaçament Vertical (Steyermark & Dunsterville, 1980) i la més recent que sintetitza les dues anterioirs (Rull, 2005 a). La primera hipòtesis, la del Món Perdut (Maguire, 1970) defensa que la diferenciació genètica que origina les espècies té lloc exclusivament per especiació al·lopàtrica, és a dir, per aparició de barreres reproductives, normalment geogràfiques o topogràfiques. Per tant, sosté la idea de què la flora originada en el Juràssic i/o el Cretàcic (200-150 Ma BP) persisteix a l'actualitat (Maguire, 1970). La hipòtesis dels Desplaçament Vertical (Steyermark & Dunsterville, 1980) proposa que les espècies de Pantepui van poder descendir dels cims i dispersar-se a través de les terres baixes, facilitant, d'aquesta manera, el flux genètic entre els diversos tepuis. Recentment, s'ha descrit la última hipòtesis, que es podria definir com el resultat de la combinació de les dues anteriors (Rull, 2005a) (Fig.8). Durant els períodes glacials, molt més llargs que els interglacials, les espècies es veien obligades a migrar cap avall, propagant-se a través de les Terres Baixes. Durant els interlacials, períodes més càlids, s'obria de nou la possibilitat de tornar a migrar cap amunt, arribant a nous tepuis.

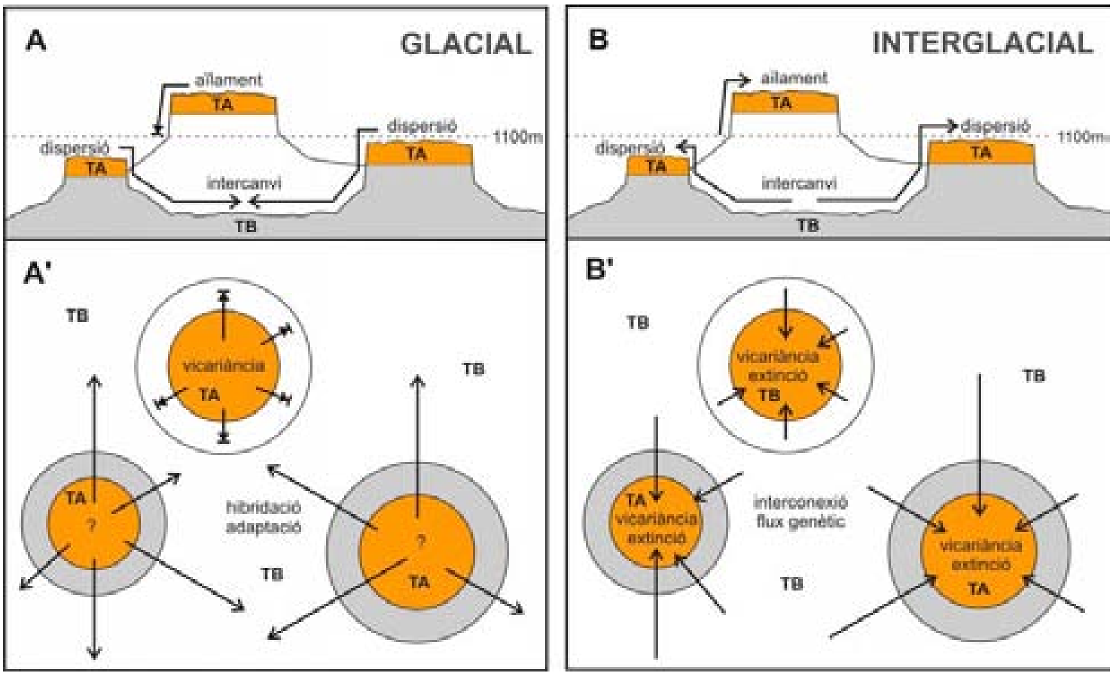


Figura 8. Representació gràfica de la hipòtesi de síntesis. A i A' representen la situació glacial en secció i en planta, respectivament. B i B' representen el mateix per una interglacial. TA= Terres Altes, TB = Terres Baixes. La línia de punts indica el límit (1100 m) per sobre la qual les espècies de TA no arriben a les TB durant una glaciació (Rull, 2005a).

El resultat final seria el flux de gens entre tepuis, afavorint així la radiació adaptativa. Al mateix temps, alguns individus no haurien aconseguit arribar a les Terres Baixes, quedant aïllats inclús durant els períodes glacials, i diferenciant-se per vicariància. L'extinció per l'absència de les condicions ambientals adequades també s'esperaria que fos superior durant els interglacials (Fig. 8). Segons aquest model, l'alternança glacial-interglacial hauria comportat un augment net de la diversitat biològica i del grau d'endemisme i podria explicar el fet que Pantepui sigui un centre tan important d'endemisme (Rull, 2004, 2005 a, 2009).

4. OBJECTIUS

En aquest context general d'interrelació entre la paleoecologia i la biogeografia, els objectius concrets de la tesis són:

1) Datar i analitzar palinològicament els sediments més antics obtinguts a l'actualitat del cim més elevat dels tepuis (Capítol 1).
2) Identificar els canvis climàtics a partir de l'estudi palinològic dels sediments i clarificar l'estabilitat de la vegetació tepuiana durant l'Holocè suggerida en estudis paleoecològics previs (Capítol 1).
3) Reconstruir les rutes i barreres potencials de migració per a les plantes vasculars dels tepuis durant el Quaternari (Capítol 2).
4) Testar la hipòtesi dels desplaçaments verticals/aïllament en els tepuis (Capítol 2).
5) Crear una base de dades de les espècies de plantes vasculars de Pantepui (Capítol 3).
6) Determinar l'efecte de l'àrea i l'altitud sobre la riquesa d'espècies (3).
7) Aplicar el model de Desplaçament del Rang Altitudinal i relació espècies-àrea per analitzar les conseqüències, sobre les plantes vascular de Pantepui, de la migració altitudinal de les condicions climàtiques degut a l'escalfament global (Capítol 4 i 5).
8) Identificar les espècies de plantes vasculars potencialment amenaçades per l'escalfament global i proposar algunes eines de conservació (capítol 4 i 5).
9) Analitzar les possibles conseqüències de la fragmentació i la pèrdua de l'hàbitat a les TAG (capítol 5).
10) Comparar les taxes de migració naturals (des del darrer màxim glacial) amb les pronosticades per aquest segle, sota les hipòtesis d'escalfament existents (discussió).

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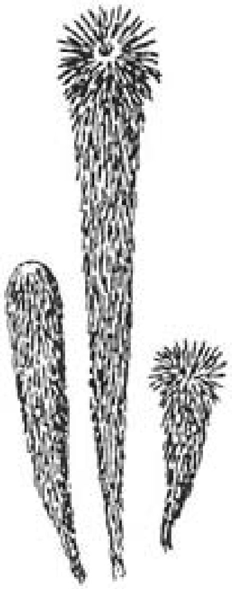
2. CAPÍTOL 1

Lateglacial and Holocene palaeoecology of the Guayana Highlands (northern South America): pollen record from the highest summit of the Chimantá massif.



Chimantaea mirabilis

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ABSTRACT

The previously recorded vegetation constancy atop some summits of the Guayana tabular mountains (or *tepuis*), during most of the Holocene, led to the hypotheses of either environmental stability or site insensitivity. As high-mountain biomes are considered to be specially well suited to record past environmental changes, a palynological study on the uppermost summit of the Chimantá massif was designed to test these possibilities. A peat sequence was obtained spanning the last ~13.0 cal kyr BP. Peat accumulation rates were highly variable and the resolution was low for the Lateglacial and the mid-Holocene, and high for the mid-late Holocene. The 12.7-4.3 cal kyr BP interval was characterized by extreme environments and poor vegetation cover, likely due to oscillating (dry/wet) and windy climates. Around 4.3 cal kyr BP, the modern vegetation established and remained virtually unchanged until today, minor paleoenvironmental changes recorded in other sequences around 2.5 cal kyr BP were not detected here. The main paleoclimatic trends found show a good agreement with other neotropical records, especially from Lake Valencia and the Cariaco Basin. It is concluded that high-altitude tepuian sites are useful to record paleoenvironmental changes of moderate to high intensity but, once a dense vegetation cover is established, gentle shifts remain hidden due to the buffer capacity of plant communities. The best sites for paleoecological research atop the tepuis are those lying on or near altitudinal ecotones, especially between the meadows and the paramoid shrublands (~2200 m elevation). Sites within the meadow domain, as most of the studied so far, are relatively insensitive to Holocene paleoenvironmental changes.

1. INTRODUCTION

The Guayana Highlands (GH), i.e. the summits of the typical Guayana table mountains or *tepuis*, are known by their remoteness and pristinity, as well as for their amazing biodiversity and the high number of endemic species on their summits (e. g. Mayr & Phelps, 1967; McDiarmid & Donnelly, 2005; Berry & Riina, 2005; Berry *et al*, 1995). As a consequence, the GH have been considered an important center of neotropical speciation (Funk & Brooks, 1990). The origin of such biotic features has been largely debated and different hypotheses have been proposed, most of them related to Quaternary climatic changes (Mayr & Phelps, 1967; Huber, 1988; Rull, 2004a, 2005a). In spite of the nowadays apparent placidity of the Guayana Highlands' ecosystems, and the lack of direct human disturbances (Huber, 1995b), their biota seems to be seriously threatened by the ongoing global warming, which might derive in the extinction of a considerable number of species by habitat loss if the IPCC predictions are realized (Rull & Vegas-Vilarrúbia, 2006; Nogué *et al*, 2009). The study of ecological reorganizations linked to past climatic shifts is important to assess the response of the GH biota to environmental changes, thus providing more reliable criteria to predict the eventual future reactions to the projected global warming.

Compared to other neotropical regions, the paleoecological and paleoclimatic study of the GH is relatively recent. The first analyses reported the absence of late Pleistocene sediments, leading to the hypothesis of extended aridity in the entire Guayana region before the Holocene (Schubert & Fritz, 1985; Schubert *et al*, 1986); however, further work changed this view. Indeed, some records from the plains around the tepuis documented temperature and moisture changes during the LGM and across the Pleistocene/Holocene boundary (Bush *et al*, 2004; Rull, 2007). Atop the tepuis, the oldest sediments found so far are around 8 cal kyr BP old and since then a more or less continuous record is available (Rull, 1991). So far, the more remarkable findings are a phase of increased hydrological balance (as measured by the precipitation/ evapotranspiration ratio or P/ETP) between about 4.5 and 2.0 cal kyr BP, recorded in the Guaiquinima massif, and a slight increase in temperature (~1 ºC) detected in a tepui from the Chimantá massif (Churí-tepui), starting around 2.5 cal kyr BP (Rull, 2004b, c, 2005b). The results of further studies from other Chimantá tepuis (Acopán, Amurí and Toronó) were confusing because they did not record any significant vegetational and climatic change during the last 6000 cal kyr, just minor reorganizations likely associated to local ecological shifts (Rull, 2005c). From these studies, it was not clear if the apparent lack of changes was due to either climatic and ecological stability or to site insensitivity. The first possibility did not agree with the results obtained in the Churí-tepui, where an upward shift of the ecotone was recorded (Rull, 2004b, c). Furthermore, site insensitivity seemed to be favored by the fact that the Acopán, Amurí and Toronó cores were obtained around 2000 m, where altitudinal shifts are more difficult to record due to the lack of an altitudinal ecotone in the vicinity (Rull, 2005c). To solve this dilemma, new studies were proposed on high-mountain localities, considered to be among the most sensitive biomes to environmental changes (Diaz & Bradley, 1997). Here, we report the results of pollen analysis from a peat core obtained in the highest peak of the Chimantá massif, the Euroda-tepui (~2700 m elevation), spanning from around 13 cal kyr BP to the present.

2. MATERIAL AND METHODS

2.1 Study area

The Guayana Highlands lie on the Precambrian Guayana Shield, in northern South America (Fig. 1), and are developed on the quartzites/sandstones of the Roraima Group, with localized diabase intrusions (Briceño & Schubert, 1990). The tepuis are remnants of ancient erosion surfaces that have been isolated by denudation due to the Gondwana breakup and the formation of the extensive Orinoco and Amazon river basins (Briceño & Schubert, 1990). The Chimantá massif is among the largest and highest tepuian complexes, with an area of about 900 km^2 (~600 km^2 in the summits), and almost 2700 m altitude in its highest summit, the Eruoda-tepui. The massif is surrounded by the Gran Sabana (GS) midlands, around 800 m elevation. The Chimantá summit is shaped by a combination of several internal and external tepuis separated by deep, densely vegetated internal valleys. The external tepuis are more exposed to the action of strong winds and fire events lighted in the neighbor plains of the Gran Sabana. Climatic data available for this area are very scarce, but enough to define its climate as very wet, with high pluviosity (3350 mm/year), high relative humidity, low evapotranspiration (820 mm/year), and intense trade winds. The annual average temperature is around 14 ºC at 2200 m elevation, with an adiabatic lapse rate of -0.6 ºC /100 m altitude (Galán, 1992).

As in the whole Guayana region, the vegetation shows an altitudinal pattern, from midlands (500-1500 m elevation) to highlands (>1500 m) (Huber, 1992, 1995a). The Gran Sabana is covered by savanna vegetation, dominated by grasses, with gallery forests along the rivers and on humid slopes. The slopes, the transition between the Gran Sabana plains and the vertical cliffs of the Chimatá, extend from 800 m to 2000 m and are covered by evergreen upper mountain forests dominated by *Bonnetia* (Bonnetiaceae), *Podocarpus* sp. (Podocarpaceae), *Magnolia* (Magnoliaceae), *Schefflera* sp. (Araliaceae) and *Weinmannia* (Cunoniaceae), with a dense understory with *Orectanthe* (Xyridaceae), *Brocchinia* (Bromeliaceae) and bambusoid grasses, mainly *Myriocladus*. These forests also appear in some parts of the summits, especially on diabase intrusions, along rivers and creeks, and in humid depressions. The Chimantá summits are located between 2000 and 2700 m, and are characterized by a mosaic of bare rock, pioneer vegetation, tepuian forests, herbaceous formations, and paramoid shrublands (Huber, 1995a). Pioneer communities are composed mainly of algae (*Stigonema*) and lichens (*Cladonia*, *Cladina*, *Siphula*) growing directly on rocks. The forests are mostly situated along rivers, and dominated by *Bonnetia roraimae*, with *Schefflera chimantensis* and *Sch. umbellata* (Araliaceae), *Spathelia chimantensis* (Rutaceae), *Stenopadus chimantensis* (Asteraceae) and *Malanea mycrophylla* (Rubiaceae). Among herbaceous communities, grasslands and meadows are the more important. Grasslands are restricted to flooded plains on the center of the massif, and are characterized by grasses (*Cortaderia*, *Aulonemia*), and sedges (*Cladium*, *Rhycocladium*, *Rhycospora*). The meadows are broad-leaved communities dominated by *Stegolepis ligulata*, which is endemic to the Chimantá, with *Xyris*, *Everardia* and *Lagenocarpus* (Cyperaceae), *Lindmannia* and *Brocchinia* (Bromeliaceae), *Heliamphora* (Sarraceniaceae), and *Syngonanthus* (Eriocaulaceae). Shrubs occur as small clusters or isolated. Shrublands are the more developed and diverse communities of the Chimantá. The more characteristic, the paramoid shrublands, are exclusive of this massif, and are dominated by some species of *Chimantaea* (*Ch. humilis*, *Ch. lanocaulis*, *C. viridis*), a genus endemic of the Chimantá and few other neighbor tepuis. The herbaceous stratum is dominated by the bambusoid *Myriocladus* (Poaceae), and several Xyridaceae, Cyperaceae and Eriocaulaceae, as well as *Lindmannia*, *Everardia* and *Heliamphora*.

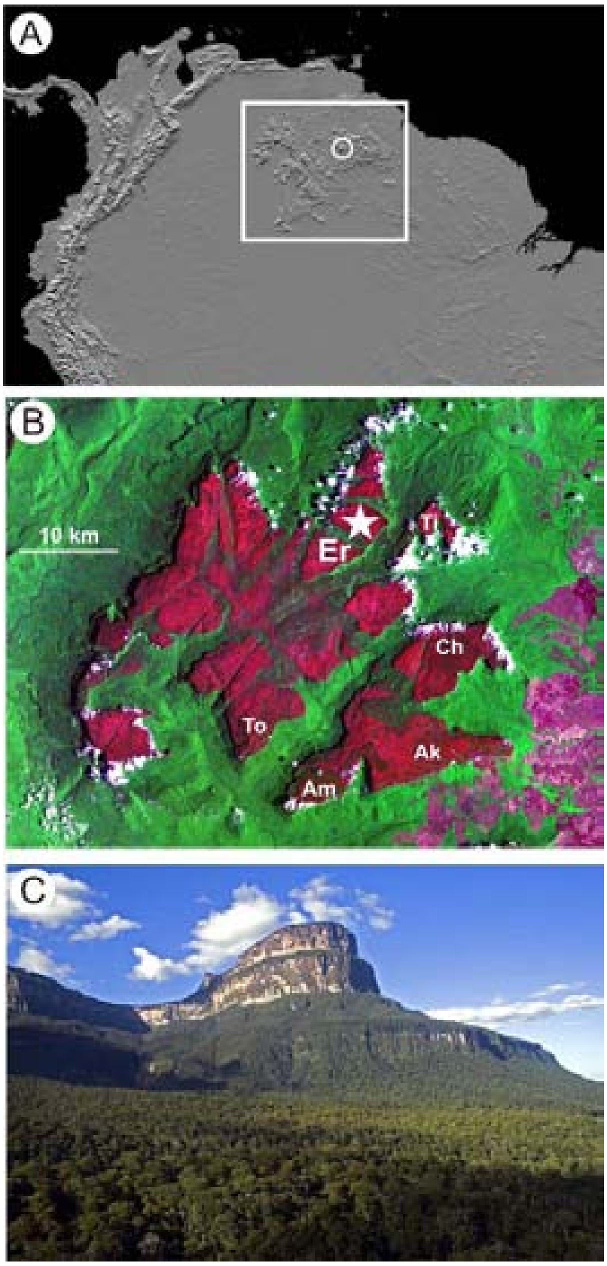

Figure 1. Location map. A) Map of northern South America, showing the location of the Guayana Highlands (square) and the Chimantá massif (open circle). Courtesy of NASA/JPL Caltech. B) Radar image of the Chimantá massif, indicating the sites mentioned in the text. The coring site is indicated by a star. Er = Eruoda, Ti = Tirepón, Ak = Akopán, Am = Amurí, Ch = Churí, To = Toronó. Courtesy of ANAPRO Digital. C) Helicopter view of the southern cliffs of the Tirepón-tepui, in the vicinity of the Eruoda summit, as an example of the typical tepuian topography (Photo V. Rull).

2.2 Sampling site

The Eruoda is an external tepui located to the NE of the Chimantá massif and represents its highest summit, reaching 2698 m elevation (Fig.1). The sampling bog (5º 22’ Lat N, 62º 05’ Lat W; 2627 m elevation) was located in a high and slightly SW-inclined plateau surrounded by a rock wall 10-30 m high. The bog is around 2 m deep and supports a dense meadow dominated by *Brocchinia hechtioides* (Bromeliaceae), *Orectanthe sceptrum* (Xyridaceae), *Nietneria paniculata* (Liliaceae), *Everardia* sp. (Cyperaceae) and *Xyris* sp. (Xyridaceae), with *Paepalanthus* and *Syngonanthus* (Eriocaulaceae), *Lagenocarpus* (Cyperaceae), *Heliamphora minor* (Sarraceniaceae), *Isidrogalvia schomburgkiana* (Liliaceae) and *Lindmania* cf. *subsimplex* (Bromeliacaeae). This community is surrounded by *Bonnetia roraimae* plots, in the contact with the rock wall, and by small and shallow pools on open rocks cavities, partially filled with algal masses, in the opposite side. In the vicinity, typical tepuian gallery forests of *B. roraimae* and paramoid shrublands of *Chimantaea lanocaulis* and *Ch. humilis* are frequent. Other ligneous species observed in the site are: *Maguireothamnus speciosus* and *Aphanocarpus steyermarkii* (Rubiaceae), *Chimantaea espeletoidea, Ch. mirabilis, Ch. eriocephala* and *Stomatochaeta condensata* (Asteraceae), *Schefflera* cf. *cavigera* (Araliaceae), *Clusia* sp. (Clusiaceae) *Mycerinus chimantensis* and *Ledothamnus decumbens* (Ericaeae), and *Cyrilla racemiflora* (Cyrillaceae). A 1.77-m peat core named PATAM 6-A07 was obtained using a Russian borer (4 drives of 50 cm each), coring was stopped when underlying bedrock was encountered. The uppermost 25 cm were of water and no peat was recovered. The rest of the core was sampled in the field and a total of 75 peat samples (1 each 2 cm) were obtained, to produce a high-resolution record. A surface sample was taken in the same coring site for comparison.

2.3 Sample processing, identification, counting and interpretation

From each sample, 3 g were used for chemical processing, after addition of *Lycopodium* spore tablets (batch nº 124961; 12,542 spores/tablet). We proceeded with the standard pollen protocol, with KOH, HCl and HF digestions, and acetolysis (Bennett & Willis, 2001). Slides were mounted with silicone oil without sealing. One to five slides per sample were counted until a minimum of 300 pollen grains and fern spores were attained, but counts were continued until the diversity did not change significantly (Rull, 1987). The pollen sum (ΣP) includes all pollen types except Cyperaceae, pteridophyte spores were also excluded. Fungal spores, algae remains and charcoal particles were counted as groups and referred to the pollen sum for percentage. The identification was based mainly on Salgado-Labouriau & Villar (1992) and Rull (2003), with the help of other neotropical and general keys and atlases, mainly Roubik & Moreno (1991) Tryon & Lugardon (1991), Herrera & Urrego (1996) and Colinvaux *et al*. (1999). Pollen diagrams were plotted and zoned with the software *psimpoll* version 4.10 (Bennett, 2005). The zonation was carried out through the Optimal Splitting by Information Content (OSIC) method, and its significance was tested with broken-stick model (Bennett, 1996). Only pollen types over 3% were considered for zonation. Radiocarbon dating was carried out in the in the University of California and Beta Analytic Inc., and radiocarbon dates were calibrated according to Reimer *et al*. (2004) using with CALIB version 5.0.2. The interpretation of pollen trends was based on the known environmental requirements of the involved taxa (Steyermark *et al*, 1995-2005; Marchant *et al*, 2002; Rull, 2003), as well as on the available modern analog stidues (Rull, 2005c).

3. RESULTS AND INTERPRETATION

3.1 Dating and accumulation rates

Nine radiocarbon dates were obtained in the Eruoda core, ranging from 10,630 to 150 ^{14}C yr BP (~12,700 to 100 cal kyr BP) (Table 1). This gave an average of about 170 years between adjacent pollen samples, thus providing a centennial resolution. However, peat accumulation rates have been highly variable, and this average is meaningless. The age-depth model shows three main phases (Fig. 2): I) extremely low accumulation rates of less than 1 mm per century (0.006 mm/y; $r^2 = 0.988$) in average before 4.2 cal kyr BP, II) a sudden increase of around 310 times this magnitude (1.886 mm/y; $r^2 = 0.994$), from 4.2 to 2.4 cal kyr, and III) a further lowering of 11 times (0.166 mm/y; $r^2 = 0.992$) between 2.4 cal kyr BP and 100 years ago.

Thus, the real time resolution of the pollen record varies from 1680 years per sampling interval (y/si) in phase I, to 11 y/si in phase II, and 115 y/si in phase III. Therefore, the resolution of the pollen record varies from millennial (phase I) to decadal (phase II) to centennial (phase III).

Table 1. Radiocarbon dating of Eruoda tepui core (PATAM6 A07). Macro = Macroscopic plant remains, Pollen = Pollen residues, pe = point estimation (median).

Depth (cm)	Lab code	Material	^{14}C BP	cal BP (2σ)	cal BP (pe)
32-34	BETA 251878	Macro	150 ± 40	54-152	103
66-68	UCI 43698	Macro	2430 ± 20	2356-2496	2426
96-98	UCI 43699	Macro	3625 ± 20	3868-3948	3908
114-116	UCI 43700	Macro	3685 ± 20	3970-4088	4029
132-134	YCI43701	Macro	3735 ± 20	4069-4151	4110
156-158	UCI 43702	Macro	3820 ± 20	4149-4290	4220
170-172	BETA 242283	Macro	3860 ± 40	4218-4413	4316
172-176	UCI 37503	Macro	7690 ± 20	8420-8523	8472
175-177	BETA 243847	Pollen	10,630 ± 60	12,573-12,821	12,697

The average accumulation rates for each of these phases were used to calculate the age of each individual pollen sample and, as a consequence, the age of the boundaries between pollen zones (see below). The major break in accumulation rates between phases I and II suggests the possibility of a hiatus between them. Alternatively, the low rates of phase I may be interpreted in terms of a discontinuous accumulation process, frequently interrupted by non-accumulation and/or peat removal periods. Peat accumulation is largely controlled by climate (Clymo, 1978; Barber, 1981, 1982). In the tropics, humid climates facilitate accumulation by favoring permanent flooding and low pH conditions, which delay the organic matter decomposition (Meadows, 1988). On the contrary, drier climates favor oxidation thus hindering accumulation and/or removing previously accumulated peat (Chateauneuf *et al*, 1986). Therefore, a drier climate might be inferred for phase I, which suddenly changed to a very humid one during phase II, and ended with the establishment of modern conditions, starting around 2.4 cal kyr BP. As modern climates are already very humid (3300 mm of total annual precipitation), the conditions during phase II may be considered per-humid.

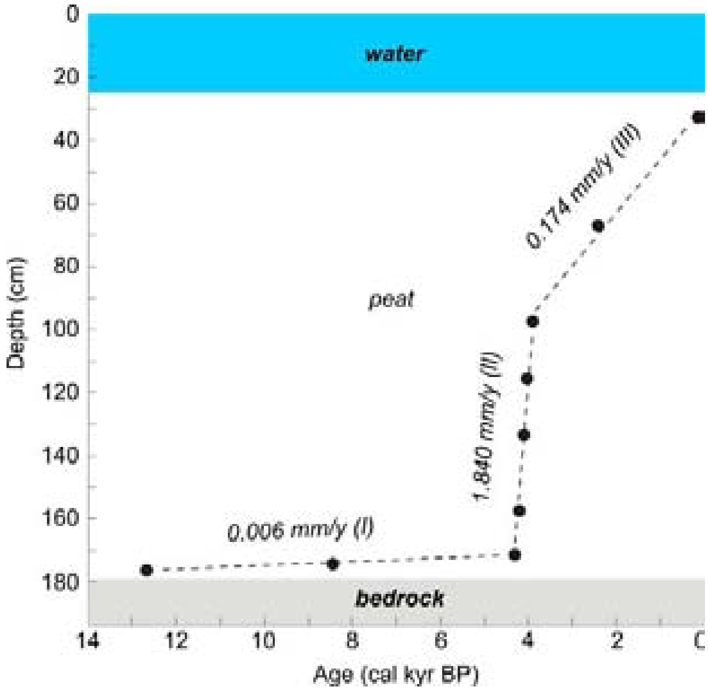

Figure 2. Depth-age curve for core PATAM6 A07 based on ^{14}C dating and calibration. The average accumulation rates in mm/year (obtained by linear regression) are indicated. The white area correspond to peat, the grey area are either water or bedrock, as indicated.

3.2 Modern pollen assemblage in relation to vegetation

The pollen assemblage of the surface sample is dominated by herbs (~67%), while trees and shrubs reach almost one third of the pollen sum (Table 2). Among herbs, the dominants are Cyperaceae, *Xyris* and Poaceae (>15% each), followed by *Brocchinia* and *Heliamphora* (1-5%), the others being below 1%. Pollen from ligneous plants is dominated by Melastomataceae and Urticales (>10%), with Myrsinaceae, *Weinmannia* and Ochnaceae between 1% and 2%, and *Cyrilla*, Guttiferae and Palmae under 1%. The more abundant pteridophytes are the psilate monoletes and triletes (5-15%), followed by *Cyathea* (~4%). When compared with modern vegetation, these results show both similarities and differences, depending on the taxa considered. Cyperaceae and *Xyris* coincide in both the pollen assemblage and the local vegetation as dominants, but Poaceae is clearly overrepresented in the pollen assemblage, as no species of this family have been found to be important in local vegetation. Grasses are not an important component of the tepuian vegetation in general (Huber, 1992, 1995a), thus its relatively high abundance in the Eruoda surface sample should be attributed to the high dispersion power (likely by wind) of this pollen type, and the proximity of the Gran Sabana plains, dominated by grass savannas. It is also interesting that *Brocchinia, Heliamphora* and Eriocaulaceae, which are among the more conspicuous components in the bog, are underrespresented in the pollen assemblage. Concerning ligneous plants, the differences are even greater, as none of the important pollen types correspond to the dominant species in the sampling site and vice-versa. Indeed, no Melastomataceae and Urticales species have been found to be important in the vegetation around the bog, suggesting wind dispersion of these pollen types from forests situated at lower elevations. Conversely, the absence of pollen from *Bonnetia* and *Chimantaea*, which species are very well represented in the surrounding vegetation, is also noteworthy. This is likely due to the low dispersal ability of these pollen types because of their low productivity, large size and morphology, which is more suggestive of animal pollination (Rull, 2003). In the case of *Bonnetia* pollen, a previous study showed that this pollen is a good indicator of the local occurrence of dense *Bonnetia* forests atop the tepuis, as its percentage dramatically drops from >10% inside the forest to <1% shortly beyond its ecotone with the tepuian meadows (Rull, 2005c). The relatively high abundance of the dominant spores also contrasts with the vegetation at the sampling site, where no ferns have been found to be important. Again, wind dispersal from lower altitudinal levels, mainly forests, seems to be important for these types.

3.3 Paleoecological trends

The results of the pollen analysis are displayed in a percentage diagram (Fig. 3), which is dominated by Poaceae and *Xyris*, followed by Melastomataceae, Urticales and *Brocchinia*. The more abundant spores are the psilate monoletes and triletes. Cyperaceae (not included in the ΣP), is also important though more variable, attaining peak values up to 500%. In summary, the average composition of the diagram is relatively constant, and similar to the modern sample discussed above (see also Table 2). Algae remains, fungi spores and charcoal particles are more variable, as shown by the occurrence of frequent local peaks (Fig. 4). A zonation was attempted using only pollen types, and four pollen zones were found to be significant, but the differences with respect to the general pattern are minor:

Table 2. Palynolomorph assemblage of the surface sample taken near the coring site, expresed in percentage of the pollen sum (ΣP).

Pollen types	**% (P)**
Trees & shrubs	
MELASTOMATACEAE	13.3
URTICALES	9.5
MYRSINACEAE	2.2
Weinmannia	1.6
OCHNACEAE	1.3
Cyrilla	0.9
GUTTIFERAE	0.6
PALMAE	0.3
Total	29.7
Herbs	
CYPERACEAE	22.8
Xyris	18.4
POACEAE	16.5
Brocchinia	5.4
Heliamphora	1.6
Drosera	0.9
LILIACEAE	0.6
ERIOCAULACEAE	0.6
Total	66.8
Other pollen types	
EUPHORBIACEAE	3.5
Pretidophytes	
Triletes (psilate)	14.9
Monoletes (psilate)	6.6
Cyathea	3.8
POLYPODIACEAE	0.6
LYCOPODIACEAE	0.3
Monoletes (verrucate)	0.6
Other palynomorphs	
Algae	17.4
Fungi	89.2

EUR-1 (177-172 cm, 3 samples, 12.7-4.3 cal kyr BP). This is the more different pollen zone of the sequence, characterized mainly by the relatively low *Xyris* abundance (<25%), as compared to the rest of the diagram. The low abundance of Urticales, the presence of *Chimantaea* and the absence of *Bonnetia* are also noteworthy. In the pteridophyte spores, the main differences are the maximum of *Cyathea* and the low percentages of psilate monoletes. Fungi are almost absent whereas algae show a striking peak, mainly due to *Pseudoschizaea*, a palynomorph of algal aspect but of still unknown affiliation, which is consistently found in environments submitted to frequent flooding-desiccation cycles (Scott, 1992). The pollen assemblage of this zone has no modern analogs among the surface samples studied so far (Rull, 1991, 2005c), which hinders a sound vegetation reconstruction, but the dominance of wind-transported pollen (trees from lower elevations and Poaceae) and the minimum of *Xyris* and Cyperaceae suggest a poor local vegetation cover. This, together with the low peat accumulation rates and the peak of *Pseudoschizaea*, point towards an unstable climate unfavorable for the development of a dense vegetation cover. It is interpreted that the sampling site was mostly bare rock with small intermittent ponds, and the vegetation was in early colonization stages.

EUR-2 (172-72 cm, 50 samples, 4.3-2.7 cal kyr BP). The pollen assemblage of this zone is very similar to the modern pollen assemblage, including the absence of *Bonnetia* and *Chimantaea* (except for sporadic occurrences of the later). Some minor variations occur within the zone, as for example local peaks of *Cyrilla*, Ericaceae, Urticales, Melastomataceae and Cyperaceae that could be due to local reorganizations within a general vegetation pattern of a peat bog like the present. There are no manifest absences and/or additions to the flora as compared to today, hence, it can be concluded that most of the plants that occur nowadays have already colonized the site. Major spores follow the same pattern, and the less abundant fluctuate a little more. For instance, *Cyathea* drops at the beginning and disappears around the middle of the zone, coinciding with an increase of *Lycopodium cernuum* and *Polypodium* (verrucate), which are more abundant in the upper half, where Polypodiaceae disappears. The whole picture (including peat accumulation rates) indicates a strong increase in the hydrological balance (P/ETP) leading to the establishment of the present vegetation. Algae remains and fungi spores, though highly fluctuating, are more abundant in the lower half, up to around 4.0 cal kyr BP, coinciding with the phase of higher peat accumulation rates, while charcoal particles show a pronounced peak at 3.9 cal kyr BP. All the charcoal particles are smaller than 100 μm which, in the Guayana region, is indicative of regional fires (Rull, 1999). Indeed, there is no any palynological evidence of local vegetation change induced by fire or any other forcing factor. Furthermore, a high proportion of the charcoal particles are morphologically identical to grass phytoliths, suggesting that they were likely originated in the Gran Sabana, where grasses -which are rare in the sampling site and the tepuian vegetation, in general (Huber, 1992, 1995a)- dominate and fires have been frequent during the Holocene (Rull, 1992, 2009b).

EUR-3 (72-44 cm, 14 samples, 2.7-0.9 cal kyr BP). This zone follows the same general patterns that EUR-2 and the modern sample, with some differences in sub-dominant elements, as manifested in the increase of Ochnaceae, and to a lesser extent Euphorbiaceae, and the decrease of Melastomataceae, Urticales and *Cyrilla*. All of them are trees or shrubs not found today around the site, except for *Cyrilla*, which indicates changes in the vegetation elsewhere or in the regional pollen transport. The local vegetation seem to have persisted unchanged. Among pteridophytes, the only change is the occurrence of Polypodiaceae spores in the lower half, and their subsequent disappearance. Fungi spores also show a peak at the beginning and algae remain low during all the zone, suggesting a decrease in the hydrological balance, which is supported by the decrease in peat accumulation rates (Fig. 2). Charcoal particles exhibit their lower values along the core, suggesting a minimum in regional fires.

EUR-4 (44-25 cm, 8 samples, 0.9 cal. Kyr BP to present). In this zone, the pollen assemblage returns to be the same as in EUR-2 and the present, thus indicating the establishment of modern vegetation and climatic conditions. Algae show a consistent increase, not reflected in the peat accumulation rates, suggesting more local flooding. Charcoal particles slightly increase, coinciding with a period of high fire incidence in the Gran Sabana, during the last millennium (Rull, 1999).

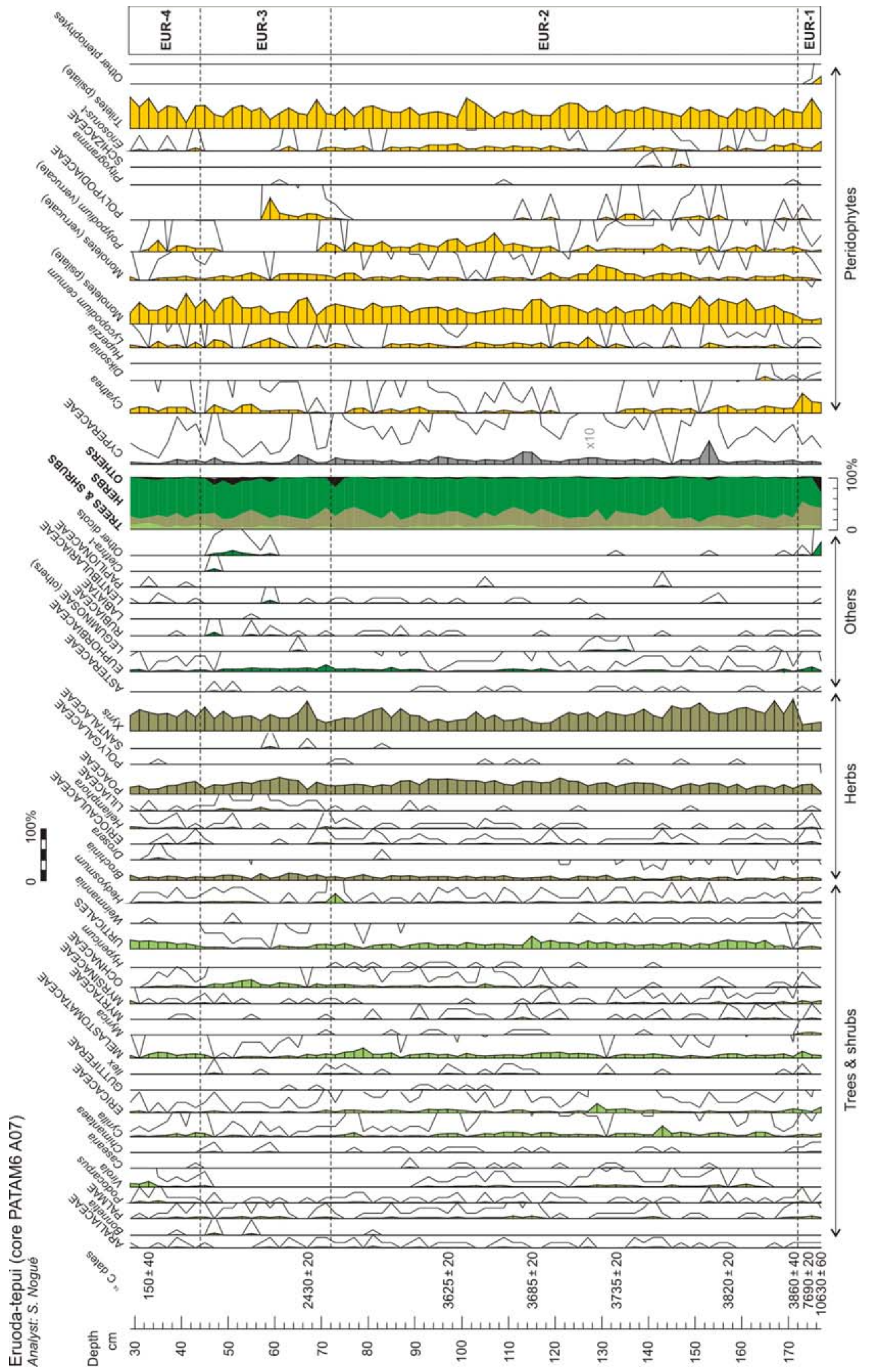

Figure 3. Percentage pollen diagram for core PATAM6 A07. Solid lines represent x10 exaggeration.

4. DISCUSSION AND CONCLUSIONS

4.1 Lateglacial and early Holocene

The Eruoda core PATAM6 A07 extends the paleoecological record of the tepuian summits -which assemblage is called Pantepui (Huber, 1994)- back to 12.7 cal kyr BP, thus allowing reconstruction of the Lateglacial history, which remained unknown so far. However, the low peat accumulation rates recorded since that date to the mid-Holocene (~4 cal kyr BP) prevented a detailed reconstruction of those nearly 9000 years, characterized in the Eruoda summit by bare rock spiked with scattered plant plots and temporary ponds on rock cavities. At first sight, this would suggest arid or semi-arid climates, as proposed by Schubert & Fritz (1985) and Schubert *et al* (1986) but, given the high pluviosity of the site, an improbable decrease of more than 3000 mm/year (>80% of the actual total annual precipitation), would be needed for that (Rull, 2004c). Maximum estimates for the precipitation decrease in northern South America during the LGM, the driest period of the late Pleistocene, are between 30% and 50% (van der Hammen & Hooghiemstra, 2000); therefore, a decrease of >80% during the Lateglacial is unlikely. At present, the precipitation in the Chimantá massif is controlled by the latitudinal movement of the ITCZ, which is over this area from May to September, when precipitation is maximum (400-500 mm/month) and weak SE trade winds dominate. During the rest of the year, when the ITCZ is in its southern position, in the Amazon basin, the precipitation is lower (60-200 mm/month), and strong NE trade winds coming from the north Atlantic predominate (Galán, 1992). The Eruoda-tepui is located at the northeastern edge of the massif (Fig. 1) and is thus very sensitive to these strong NE trades. It is possible that during the Lateglacial and the early-mid Holocene (12.7 to 4.3 cal kyr BP), the intensity of these winds was even stronger and/or they were more extended throughout the year, determining lower precipitations and enhanced evapotranspiration, thus limiting the plant growth and favoring the organic matter decay. Such a situation requires a more southerly position of the ITCZ, which is supported by the Cariaco record, where a cool and dry phase of increased wind-driven marine productivity was recorded during the YD (*ca.* 13.0 to 11.5 cal kyr BP) (Werne *et al*, 2000). Similarly, the Lake Valencia basin was occupied by temporal marshes typical of drier climates, instead of the present lake (Bradbury *et al*, 1981). The early Holocene, however, was characterized in both Cariaco and Valencia by a reverse situation determining a warming trend with increased precipitation (Curtis *et al*, 1999; Haug *et al*, 2001), which contrasts with the interpretation of the Eruoda record. In the Guayana region, the early Holocene warming has been also documented, but it has been associated to a drier phase (Rull, 2007). This apparent disagreement between Valencia, Cariaco and Guayana paleoclimates could be attributed to latitudinal or orographic differences, but the driving mechanisms are still unclear (Rull *et al*, in press).

4.2 Middle to late Holocene

The modern vegetation of the Eruoda summit seems to have been fully established by around 4.3 cal kyr BP, as it occurred in high mountain environments of the northern Andes, above 4000 m elevation (Salgado-Labouriau *et al*, 1988; Rull *et al*, 2005). In the Andes, this required a long, gradual colonization process involving the slow upward migration of species following deglaciation. In the Eruoda, however, all the elements recorded in the pollen sequence were already present since the beginning. The same has been recorded in other tepuian summits (Rull, 1991), and has been explained through the hypothetical existence of microrefugia, where plants survived unfavorable phases - such as the LGM and the YD- and from where they expanded their populations afterwards (Rull, 2009a). Between 4.3 and 4.0 cal kyr BP (the lower half of EUR-2), the high peat accumulation rates, together with the increase of algae, suggest a hydrological balance higher than today, in agreement with previous data from other tepui summits (Rull, 2005c), and also from the Gran Sabana (Rull, 1991, 1992). The present climate is very humid and the rainfall is around four times the evapotranspiration (P/ETP = 4.09) (Galán, 1992); therefore, during that phase, per-humid conditions are suggested. At the same time, climates were also wet in Lake Valencia, where a phase of maximum lake levels has been documented until about 3.0 cal kyr BP (Curtis *et al*, 1999). According to Behling & Hooghiemstra (2001) and Marchant & Hooghiemstra (2004), a generalized shift towards wetter climates occurred in the Neotropics and, in general, in South America around the same dates. The situation changed between 4.0 and 2.7 cal kyr BP, when a return to conditions similar to present are recorded in the Eruoda, coinciding with the beginning of a dry period in the Gran Sabana, the onset of a desiccation trend in Lake Valencia (Rull, 1991, 1992; Curtis *et al*, 1999), and a phase of decreased precipitation in Cariaco, which has been related to shifts in the ITCZ mean position and enhanced ENSO activity (Haug *et al*, 2000). The charcoal peak recorded in Eruoda at

3.9 cal kyr BP roughly coincides with the beginning of this extended dry phase, hence, it is possible that dryness favored an increase in fire incidence in the Gran Sabana, which is the more likely source for the charcoal found atop the Eruoda. Furthermore, some Gran Sabana charcoal records indicate a major fire event around 3.5 cal kyr BP (Fölster, 1992).

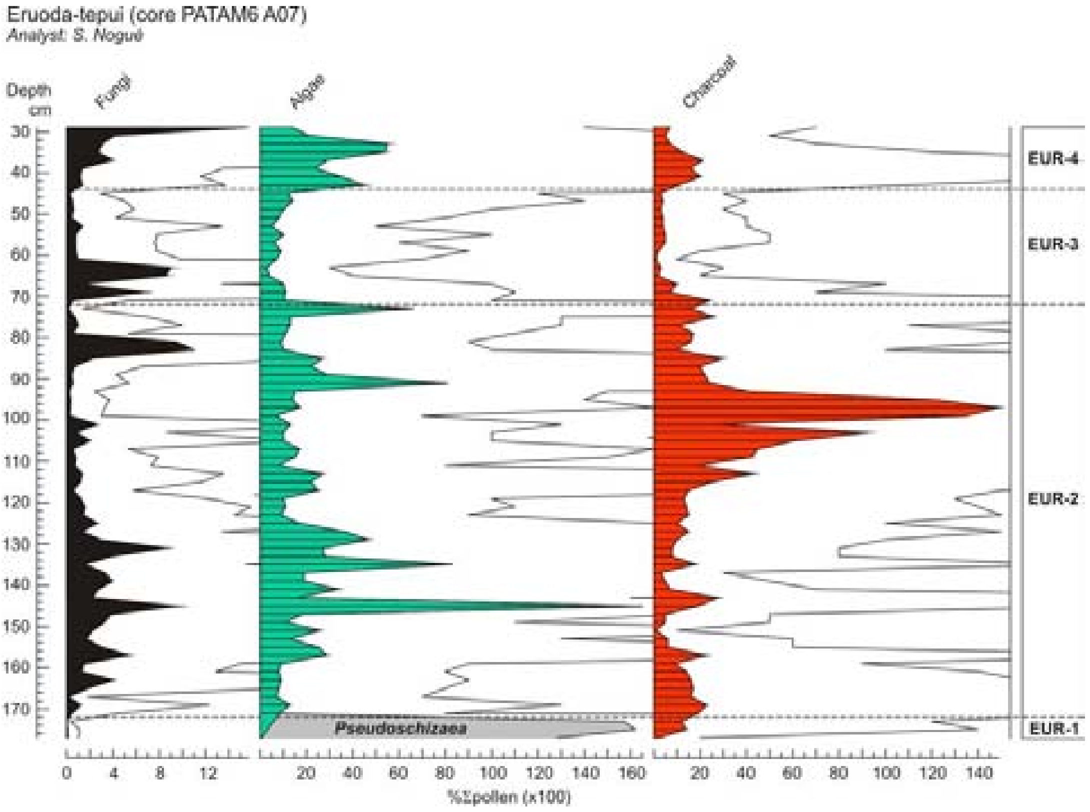

Figure 4. Diagram of fungi spores, algae remains and charcoal particles, expressed as percentages of the pollen sum (ΣP). Solid lines represent x10 exaggeration.

4.3 Vegetation constancy

Despite these inferred moisture variations, the vegetation atop the Eruoda has remained unchanged during the last 4000 years, as it has previously recorded in most tepuian summits of the Chimantá massif (Rull, 2005c). The vegetation shift recorded in the Churí-tepui around 2.5 cal kyr BP, likely due to a gentle temperature increase (Rull, 204a, b), has not been clearly recognized here. In the Eruoda record, this date is slightly above the boundary between pollen zones EUR2 and EUR-3, where small changes in the pollen record, involving mainly allochthonous types (Melastomataceae, Urticales and Ochnaceae), took place. So far, it is not possible to associate these minor shifts with potential environmental variations but, whatever the cause, the local vegetation patterns remained constant. A first conclusion is that variations in the P/ETP balance (as deduced from independent evidence such as peat accumulation rates and algae) from very humid to per-humid and very humid again did not significantly affect the plant community, suggesting a buffering capacity enough to withstand these environmental oscillations without apparent changes. As stated before, it has been asked if the observed vegetation constancy atop the tepuis during the Holocene is due to the absence of environmental disturbances or to site insensitivty (Rull, 2005c). The Churí record previously showed that tepuian communities react to small temperature shifts by altitudinal migration (Rull, 2004a, b). This was favored by the presence, around the coring site (2200 m elevation), of the altitudinal ecotone between the meadows dominated by *Stegolepis* and the *Chimantaea* paramoid shrublands. Such ecotone is clearly distinguishable through pollen analysis, by comparison with modern analogs, as the *Chimantaea* pollen has a very low dispersion power and only occurs within and very close to the paramoids shrublands that dominates (Rull, 1991, 2005c). On the other hand, *Stegolepis* meadows have a definite upper boundary of distribution around 2200 m (Huber, 1992). The Eruoda record has shown that ecosystems from the highermost parts of the Chimantá massif are also sensitive to environmental changes enough to preserve their pollen imprint in the sediments. Therefore, the absence of biotic changes may be attributed, in these cases, to the absence of environmental disturbances of sufficient intensity to affect plant communities. This is the more likely interpretation for the last 4000 years of the Eruoda record. A potential limitation of high-altitude sites is that unfavorable climates determine extreme environmental conditions that may interrupt or eliminate in part the sedimentary record. One advantage is that top-mountain sites are ideal to detect upward altitudinal migrations, with potential for quantitative estimation. For example, in the case of the Eruoda site studied here (around 2700 m), the eventual occurrence of *Stegolepis* meadows (upper limit at 2200 m) would be interpreted in terms of an upward migration of at least 500 m, equivalent to an increase in average temperatures of ~3 ºC. Other sites showing vegetation constancy during the Holocene, as for example Acopán, Amurí and Toronó tepuis, also in the Chimantá massif (Fig. 1), are around 2000 m elevation, within the *Stegolepis* meadows, and far from any altitudinal ecotone. In these cases, site insensitivity cannot be disregarded for gentle environmental changes, but a temperature lowering of >1.2ºC would be enough to determine the downward migration of the *Stegolepis*/*Chimantaea* ecotone around these localities, which are 200 m below. Thus, from the data available so far, it can be concluded that vegetation constancy observed atop the tepuis of the Chimantá massif during the middle to late Holocene is due to the absence of environmental changes of enough intensity to surpass the response threshold of the living communities. A practical conclusion is that the upper altitudinal boundary of *Stegolepis* is one of the best paleoecological prospects atop the tepuis, and sites around this limit are preferred targets for sediment coring. A detailed study of the Pantepui (1500-3000 m elevation) flora and vegetation in relation to altitude would be of great help to plan future sampling programs and interpret their resulting palynological records.

5. ACKNOWLEDGMENTS

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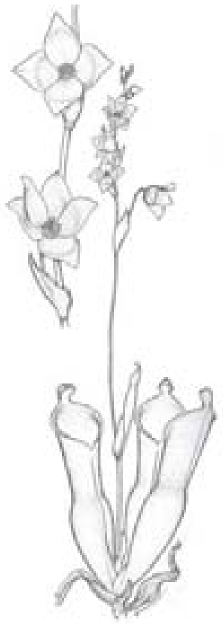
3. CAPÍTOL 2

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



Heliamphora heterodoxa

The main contents of this chapter have been published as:

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ABSTRACT

To reconstruct in detail the potential migration routes and barriers for vascular plants from the summits of the Guayana mountains during the Quaternary, owing to the estimated downward displacement linked to cooling, GIS-based palaeotopographical reconstruction using a high-precision digital elevation model, combined with phytogeographical analysis by means of a database built up from the Flora of the Venezuelan Guayana, were used to measure the extent of the potential biotic interchange and its influence on the endemism patterns. The Quaternary evolution of the vascular flora from the Guayana Highlands took place in a predominantly migration-prone, glacial landscape, in which more than 70% of the flora was able to move from one tepuian district to another, thanks to the downward bioclimatic shift caused by cooling. Interglacials were too short to harbour significant evolutionary rates. A number of present high-altitude local endemisms are species that were unable to migrate, even during glaciations; but others do not, suggesting that topographical isolation alone is not enough to explain endemism patterns. Other factors such as tepui summit area, habitat heterogeneity or pre-Quaternary evolution are considered. These studies should be complemented with palaeoecological and phylogeographical surveys.

1. INTRODUCTION

The Guayana Highlands, between the Orinoco and the Amazon basins in northern South America (Fig. 1), are characterised by the occurrence of peculiar sandstone table mountains or *tepuis* with more or less flat summits of variable extension, separated from the surrounding lowlands by sheer cliffs (Fig. 2). The assemblage of these summits, between 1500 and 3000 m elevation, is a distinct and discontinuous biogeographical province called *Pantepui*, which attain a total of about 5000 km^2 (Berry *et al*, 1995). The Pantepui vascular flora is unique because of its striking richness and high degree of endemism. Indeed, of the 2446 species known so far (ca. 50 species/100 km^2), 1292 (57.8 %) are endemic to the Guayana Shield, 771 (31.5 %) are endemic to Pantepui, and 504 (20.6 %) are local endemics (i.e. endemic to a single tepui) (Chapter 3). The uniqueness and high specialisation degree of the Pantepui flora and vegetation has been recognised since long time ago (Berry & Riina, 2005; Huber, 2005), and has stimulated a debate about their origin. The defenders of the vicariant Lost World (LW) hypothesis proposed a long history of evolution in isolation since the Jurassic-Cretaceous, as the most probable explanation for the high degree of endemism (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 cycles (Steyermark & Dunsterville 1980, Huber 1988). See Rull (2004c) for a more detailed discussion. The last palynological results support 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). Similarly, DNA analysis of Rapateaceae species suggests that both vicariance and long-distance dispersal are needed to account for their biogeographical patterns, even at a continental scale (Givnish *et al*, 2000).

The possible relationship between speciation and Quaternary climatic changes has been explored recently and a tentative diversification model has been proposed (Rull, 2005). According to it, the main diversification events occurred during glacials, when tepuian biotas migrated downslope owing to cooling, thus spreading through the lowlands and promoting sympatric speciation and hybridisation, and providing the necessary migration pathways for gene flow among tepuian summits. During the interglacials, the upslope retraction would have favoured allopatric speciation and extinction by habitat loss. The successive alternation of Quaternary glacial/interglacial cycles, combined with the complex topography and habitat heterogeneity of the Guayana Highlands, would have resulted in a net increase in biodiversity and endemism (Rull, 2005). This model implicitly assumes that a significant part of the genetic structure of the tepuian biota has been shaped during the Quaternary, an idea which is being intensively debated worldwide. One view is that Pleistocene climatic cyclicity has been important in shaping the present-day biota, while others think that modern species originated mostly in the Tertiary or earlier, before the glaciations started (e.g. Bennett, 2004). The debate is especially vivid in the Neotropics, and the Guayana Highlands can significantly contribute to the discussion. In this region, some studies which dated the origin of present-day species using DNA phylogenies support Quaternary evolution for several plant and animal lineages (Givnish *et al*, 2000, Noonan & Gaucher, 2005), while others seem to point towards an earlier origin, more related to river dynamics and marine transgressions than climate (Ribas *et al*, 2005).

In order to test the diversification model for the Guayana Highlands, detailed physiographical studies using geographical information systems (GIS) tools have been proposed, in combination with palaeoecological analyses of suitable sediments and phylogeographical surveys of keystone taxa using DNA sequences (Rull, 2004c, 2005). One of the fundamental questions is the magnitude and the extent of the glacial biotic spreading, to visualise potential migrational pathways and biogeographic barriers among tepuis that can help explain present biogeographical patterns. According to Huber (1988), besides the apparent inaccessibility of the tepuian summits, very few are really isolated, and numerous river valleys and ridges physically connect the tepui summits with the surrounding lowlands thus providing potential migration routes. However, an accurate reconstruction of such pathways among the different tepuis is still unavailable. In this paper, detailed GIS palaeotopographical reconstructions of this type are performed for the Last Glacial Maximum (LGM), occurred around 21,000 years before present (21 ky BP). The LGM is among the more intense Quaternary glaciations (Mix *et al.*, 2001), hence the downward biotic migration and the probability of biotic interchange among tepuis, is expected to have been maximum. The LGM and present scenarios are compared, and the potential consequences for the distribution of vascular plants, the better known organisms from the Guayana Highlands by far, are discussed.

2. MATERIAL AND METHODS

2.1 Study area

The Guayana Highlands are situated between about 1º-7º N and 59º-67º W (Figs. 1 & 2). The tepuis are modelled on the quartzites and sandstones of the Precambrian Roraima Group, overlying the igneous-metamorphic Guayana Shield, which is part of the South American old core (Briceño & Schubert 1990; Gibbs & Barron 1993). The Roraima Group forms a discontinuous sedimentary cover, which contributes to differentiate the eastern and the western parts of Pantepui. At the east, the Roraima Group has a more continuous extension and determines a base level of about 400 to 1200 m for the tepuis, 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).

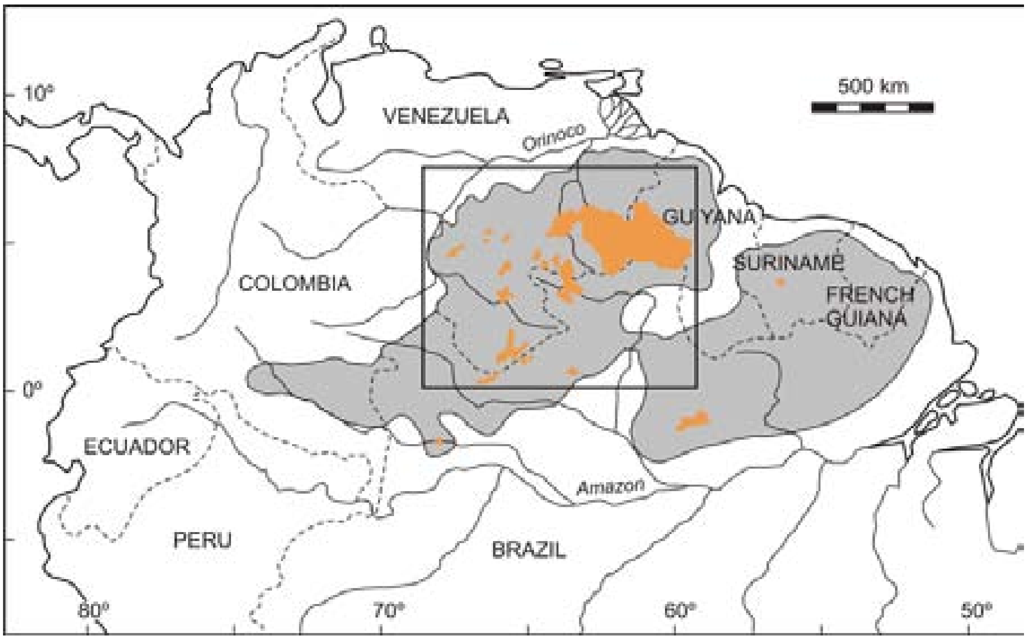

Figure 1. Map of northern South America showing the extension of the Guayana Shield (grey area), the Roraima Group (black patches), and the zone under study (rectangle).

This could theoretically provide more suitable conditions for lowland migration of Pantepui elements in the eastern part. Pantepui has been subdivided into four phytogeographical districts (Fig. 2): Eastern Pantepui district (E), Jaua-Duida District (JD), Western Pantepui District (W) and Southern Pantepui District (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). Both altitude and summit area 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 Figure 2.

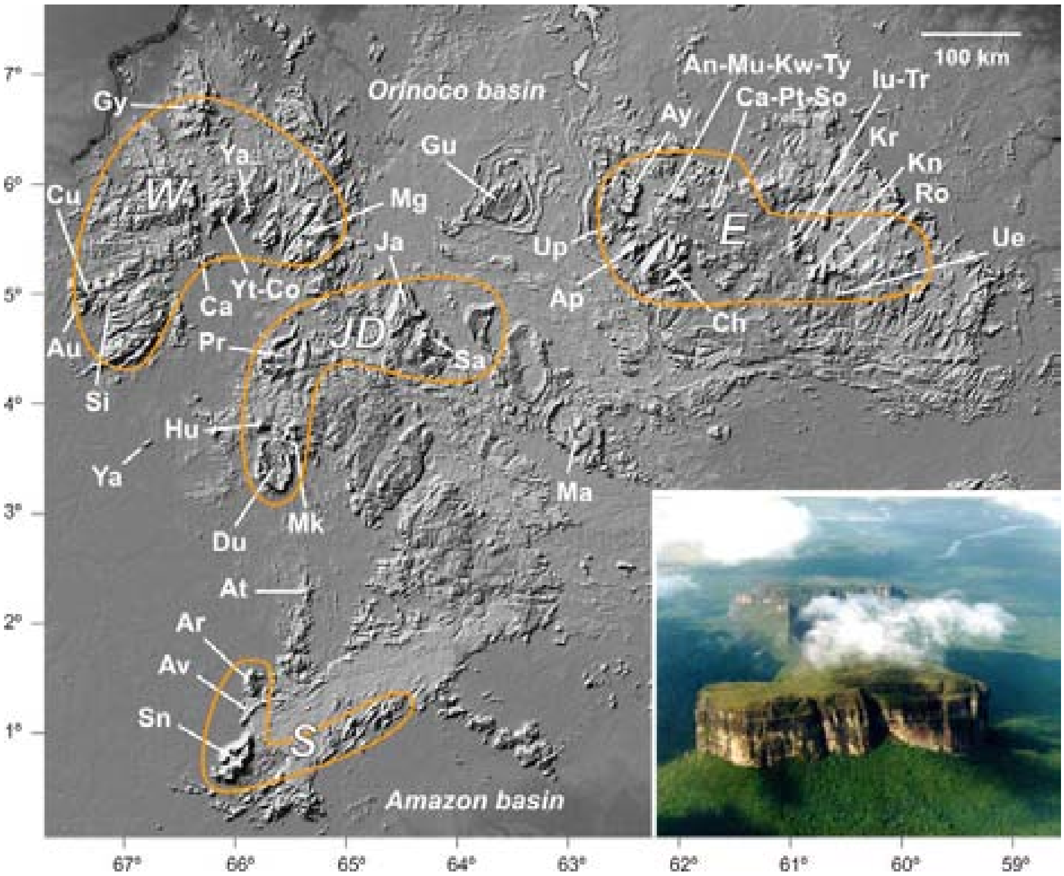

Figure 2. Radar image (courtesy of NASA/JPL-Caltech) showing the Guayana Highlands. The better-known tepuis from a botanical point of view (Berry & Riina, 2005) are indicated, sorted by districts: Eastern district (E): An – Aparamán, Ap – Aprada, Ay – Auyán, Ch – Chimantá, Cr – Carrao, Iu – Ilú, Kn – 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 – Guanaay, Si – Sipapo, Yv – Yaví, Yt – Yutajé; Jaua-Duida district (J-D): Du – Duida, Ja – Jaua, Hu – Huachamacari, Mk – Marahuaka, Pr – Parú, Sa – Sarisariñama; South district (S): Ar – Aracamuni, Av – Avispa, Sn – 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 at the right low corner.

2.2 Data source

Geographical reconstructions were performed with MiraMon software (http://www.creaf.uab.es/miramon/), using the digital elevation model from he Shuttle Radar Topography Mission (SRTM) of 3 arc-second (90 m) precision (USGS/NGA/NASA). In order to compare palaeotopographical reconstructions with present phytogeographical patterns, a database of all the species occurring above 1500 m altitude (i.e. the Pantepui flora) was built up on the basis of the Flora of the Venezuelan Guayana (Steyermark *et al*, 1995-2005). This information was completed with physiographical and phytogeographical data obtained from different bibliographic sources (Huber, 1987, 1988, 1995; Berry *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 considering the currently accepted estimates of 5.7 ºC for temperature dropping and 1100 m for biotic lowering, in this neotropical area (Farrera *et al*, 1999). This procedure assumes no changes in topography since the LGM and, in general, during the Quaternary; a very likely assumption if we consider that the region has not been glaciated, and the erosion rates -mainly due to chemical meteorisation of the Precambrian rocks- have been negligible (Edmond *et al*, 1995).

A terminological remark is necessary, in order to clarify and differentiate concepts such as ‘dispersal’ and ‘migration’ throughout the 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 to the life span of an individual. Pielou (1979) calls ‘diffusion’ to the gradual movement of populations across hospitable terrains for a period of many generations, resulting in the steadily expansion of the range of the involved species. 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 million years BP, or Ma), coinciding with the onset of Northern Hemisphere glaciations (Raymo, 1994).

3. RESULTS

The extent of palaeopantepui (PP) surface during the LGM, which boundaries coincide with the present-day 400-m contour line, is depicted in Fig. 3 and compared with the present-day Pantepui surface. Practically all migration pathways among tepuis and tepuian districts were opened. The only barriers were located within the Western district, and separate all the tepuis expect Maigualida -which is not properly a tepui, but its atop biota falls within the Pantepui province- from the rest. These barriers, however, were narrow and potentially salvable by jump dispersal. The tepuis within the Western district were also separated by thin barriers among them determining three main clusters. This LGM situation, however, is not applicable to all the Pantepui biota, but only to these species having their lower altitudinal limit of distribution (LAL) at or below 1500 m altitude. According to our database, of the 2447 species known in Pantepui, this is the case for 1678 (68.6%) (Table 1). The spreading probabilities for the remaining 769 species (31.4%) have been 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 Western and South districts were narrowed but still active. It is remarkable that the Guaquinima was an isolated tepui for these species. The degree of isolation suddenly increases for species with LAL = 1700 m, which attain 4.6% of the total (Table 1). For them, the four districts were topographically isolated and, furthermore, the tepuis from the south were also detached among them, 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 with LAL = 1800 m (4.8%) the situation is almost the same, but it is noteworthy that the Auyán, from the Esatern 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 Souht districts were hundreds of km wide. Topographical splitting within Jaua-Duida and Eastern districts began for species with LAL = 2000 m and was almost completed for species with LAL = 2300 m (Figs. 6 and 7). The species with LALs above this point (~ 3%) have remained isolated even during the LGM (Fig. 8).

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

It is also possible to estimate the species that were confined to a single tepui during the LGM, with no possibility of migration, by searching in the database the altitude required for a given tepui summit to be isolated and the number of species with LALs at or above this point (Table 2). A total of 202 species (8.3% of the total) are in this situation, most of them (164 or 81%) are endemics to a single tepui or tepuian massif, or to a cluster of neighbour tepuis within the same district (Supplementary material 2). The remaining 19% occur nowadays in more than one district or even in regions adjacent to Guayana.

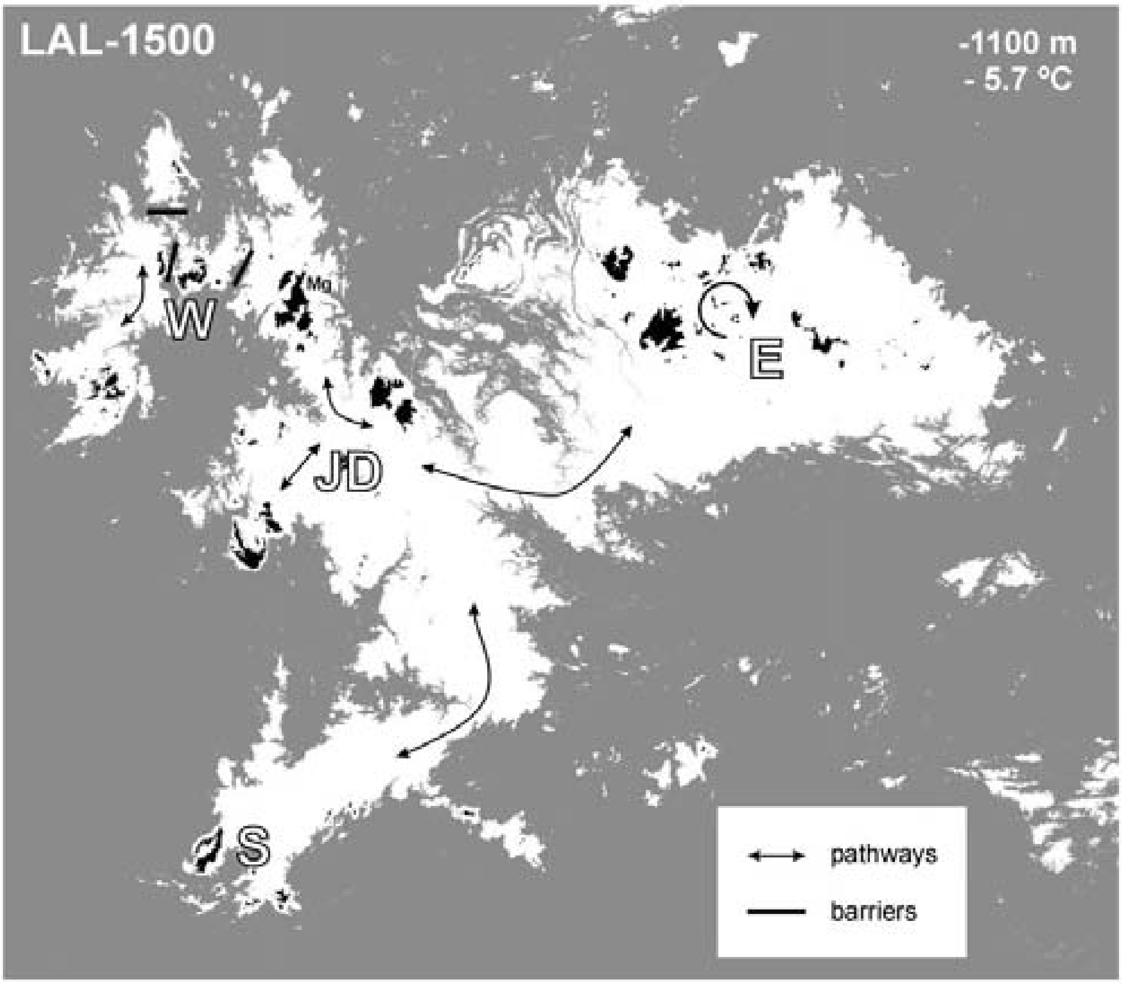

Figure 3. Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 1500 m (white), compared to present-day Pantepui surface (black). Districts are indicated by capital letters (Mg = Maigualida). The estimated downward displacement with respect to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

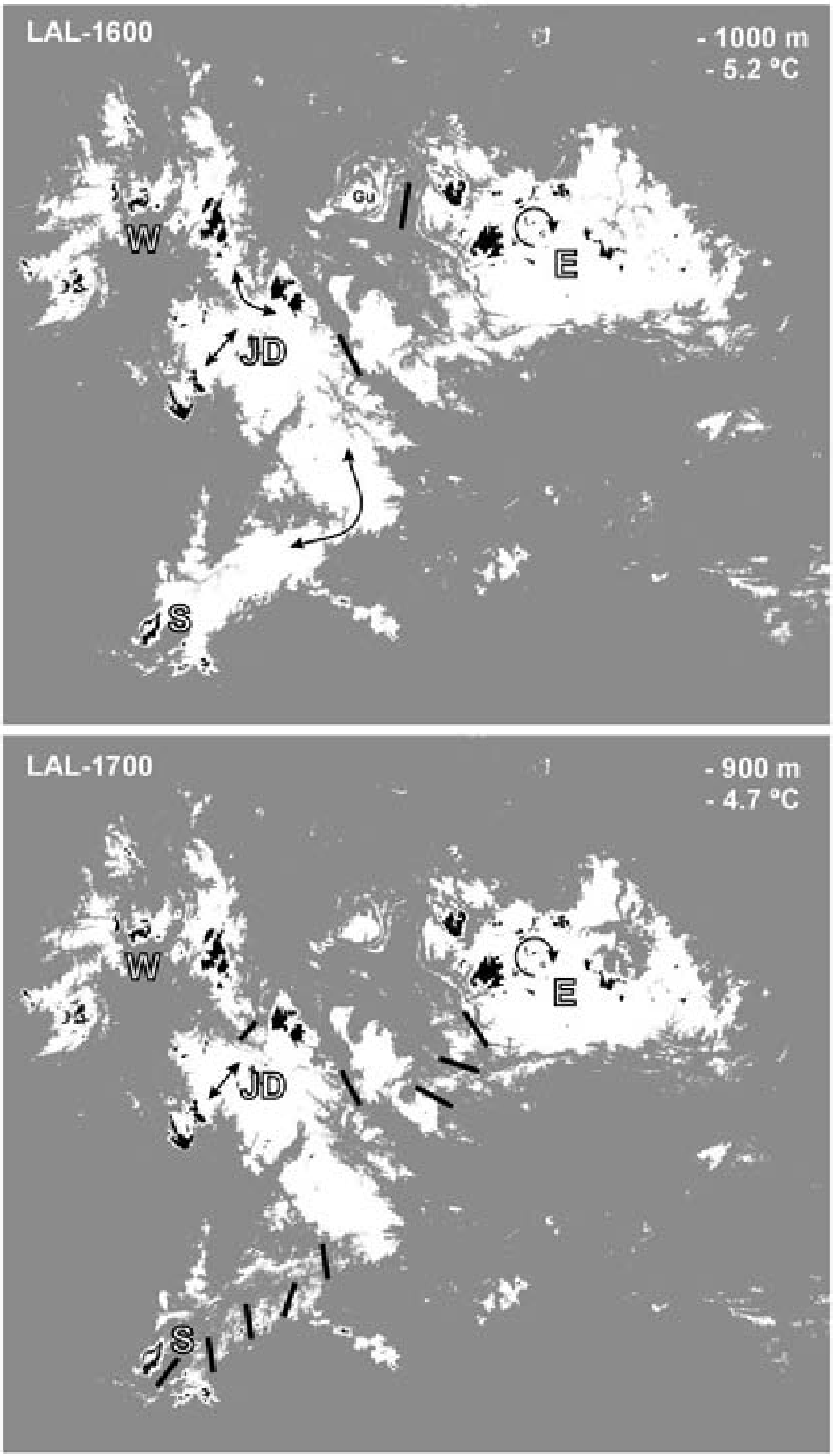

Figure 4. Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 1600 (upper) and 1700 (lower), compared to present-day Pantepui surface (black). Symbols and text as in Fig. 3. Gu = Guaiquinima.

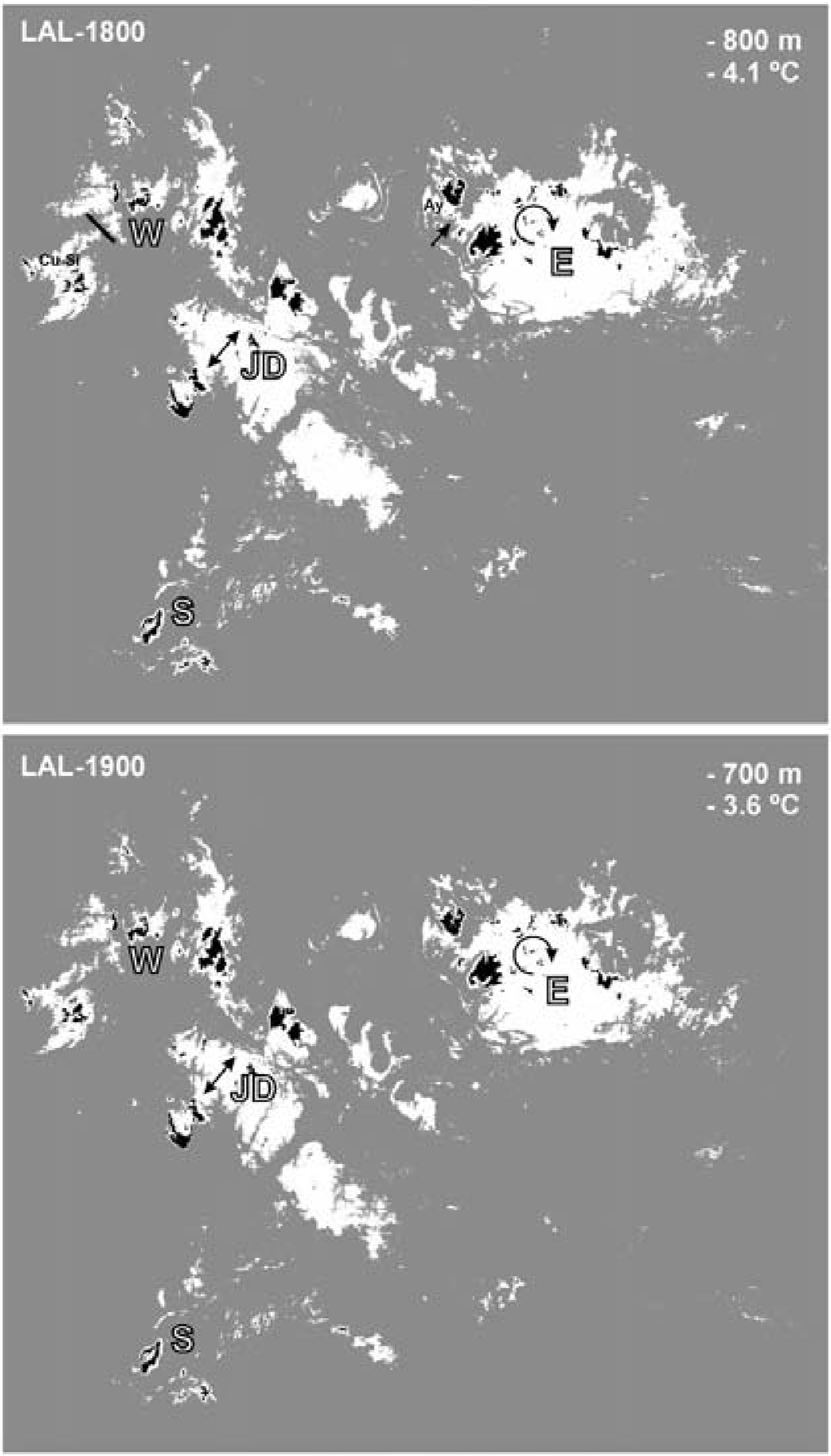

Figure 5. Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 1800 (upper) and 1900 (lower), compared to present-day Pantepui surface (black). Symbols and text as in Fig. 3. Ay = Auyán, Cu-Si = Cuao-Sipapo massif.

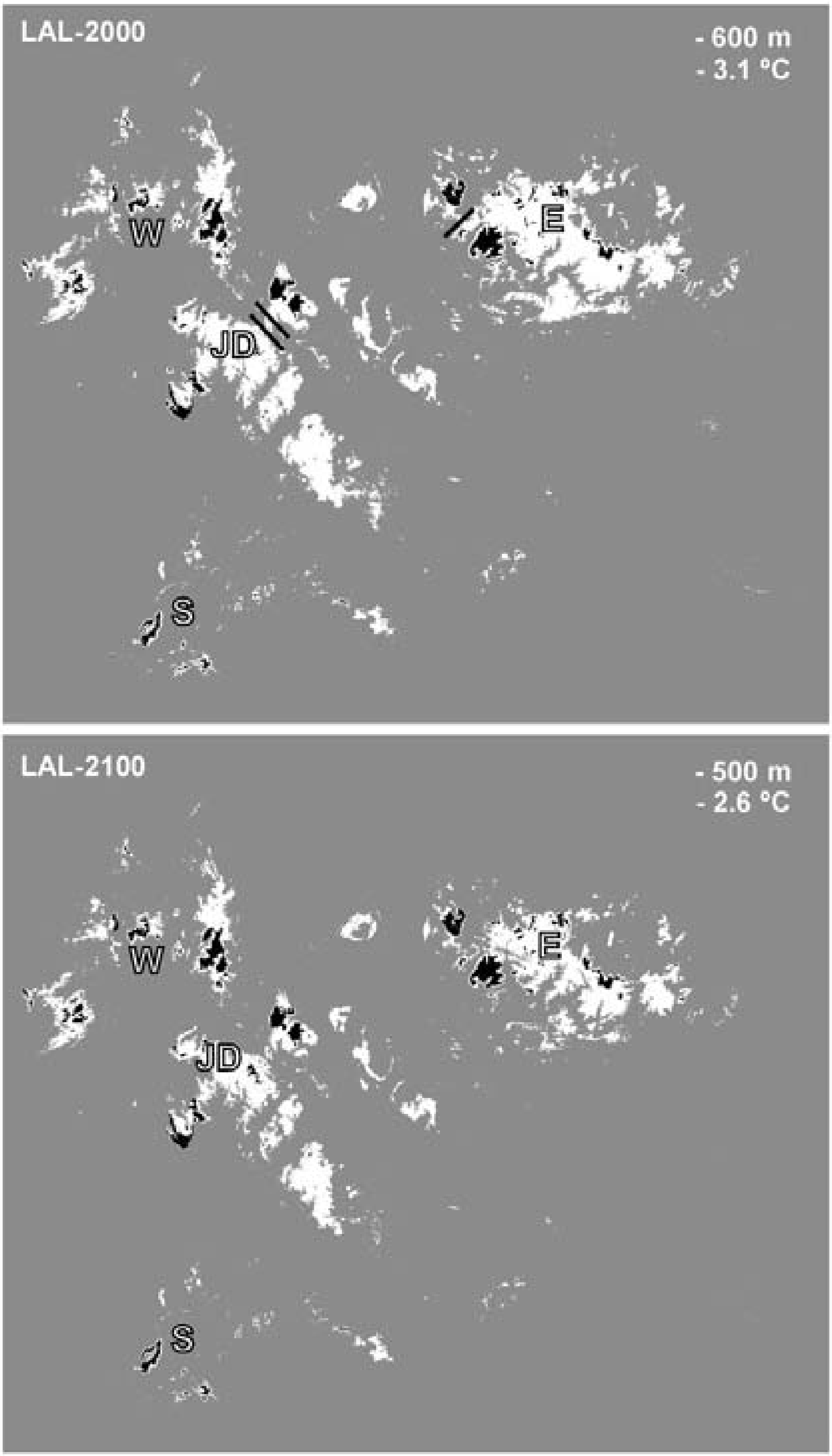

Figure 6. Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 2000 (upper) and 2100 (lower), compared to present-day Pantepui surface (black). Symbols and text as in Fig. 3.

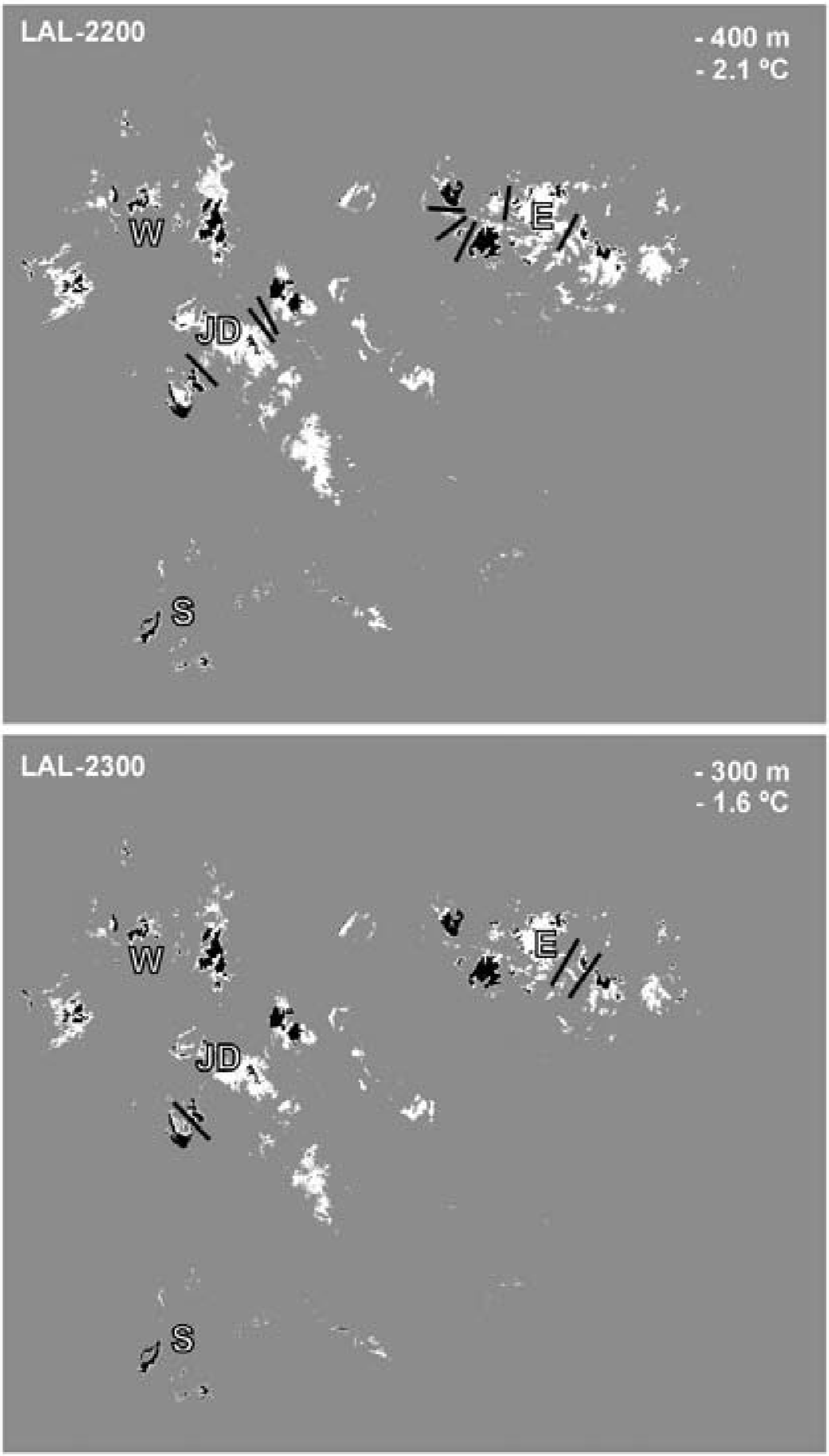

Figure 7. Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 2200 (upper) and 2300 (lower), compared to present-day Pantepui surface (black). Symbols and text as in Fig. 3.

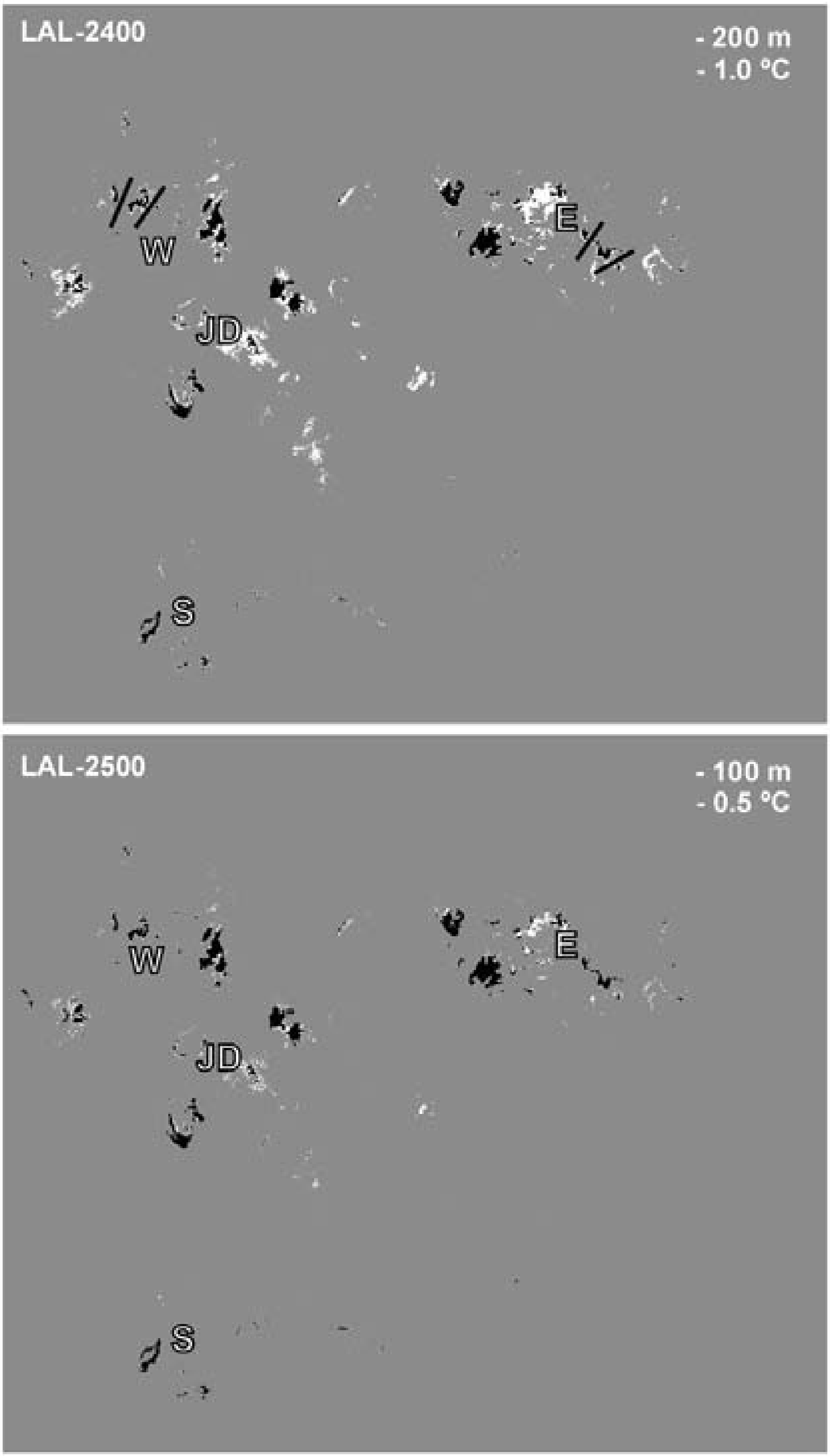

Figure 8. Palaeotopographical reconstruction of the available space for migration, during the LGM, for species with LAL = 2400 (upper) and 2500 (lower), compared to present-day Pantepui surface (black). Symbols and text as in Fig. 3.

4. DISCUSSION AND CONCLUSIONS

During the Quaternary, around 50 climatic cycles of ice expansion and retreat are considered to have occurred in the Northern Hemisphere, with a period of 41 ka since the beginning to about 800 ka BP, and of 100 ka since that time until the present (Raymo & Nisancioglu, 2003). Glacial phases have been notably longer than interglacial ones, so it is believed that boreal continents have been glaciated around 80% of the time since the beginning of the Quaternary (Willis & Whittaker, 2000). In this way, interglacials have been viewed as comparatively short warmings of 10-20 ka duration, which occurred every 80 or 90 ka, within a dominant glacial Quaternary climate. The LGM scenario shown in this paper is considered to be representative of Quaternary glaciation, with the corresponding differences in magnitude. As the LGM has been one of the more intense glaciations of the Quaternary, it can be likely assumed that the migration probability for the Pantepui biota across the lowlands has been maximum. Hence, palaeotopographical reconstructions shown here depict the maximum number and extent of migratory pathways and the minimum number of barriers that have acted during the last 2.6 Ma. In fact, during the last 65 Ma, as the Quaternary has been the colder period since the end of the Cretaceous (Zachos *et al*, 2001).

From a biogegraphical point of view, the situation for the vascular flora of the Guayana Highlands can be represented by a dominant migration-prone environment, spiked by short intervals of isolation atop the tepuis, with important evolutionary consequences (Rull, 2005). According to our results, more than 70% of the flora (see figs. 3 and 4, and Table1) would have been able to migrate and promote gene flux among tepuis during most of the Quaternary. The amount of species with no possibility of migration, even during the LGM, has been estimated in 8%. The remaining percentage have had intermediate probabilities. During interglacials, the situation would have been similar to today, with all species occurring on the tepui summits, almost totally isolated among them. If evolutionary change has taken place during the Quaternary in the Guayana Highlands' vascular flora, it is improbable that this has happened during interglacials, owing to their short duration. Therefore, potential Quaternary evolution has more likely proceeded within a glacial environment with many interchange probabilities among tepuis. In this frame, allopatric speciation able to generate local endemism in the tepuis should have occurred in about 8% of the flora that remained permanently isolated, and also in an additional percentage of highland species with comparatively low spreading probabilities (see Table 1 and Figs. 5 to 7).

Table 2. Comparison between local endemism and the number of species with LALs above the critical isolation altitude for each tepui studied. CAI = Critical altitude for topographical isolation of the tepui during the LGM, SPA = Species with LALs at or above the critical altitude for isolation, END = Endemic species (Berry & Riina, 2005).

Tepui	**district**	**CAI**	**SPA**	**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

The high proportion of local endemisms among the 8% isolated flora supports this view (Supplementary 2). In addition, tepuis like for example Roraima, Marahuaka, Huachamacari, Neblina and Maigualida have approximately the same number of local endemisms and species with LALs above the critical altitude, which also favours the former hypothesis. However, other tepuis as for example Chimantá, Auyán, Duida, Jaua or Parú notoriously deviate from this rule, holding far more endemisms (Table 2). This indicates that evolution in topographical isolation alone is not enough to explain present-day endemism patterns. A common characteristic of tepuis with exceeding endemism is their large summit area, ranging from about 900 to 1200 km^2 (Huber, 1995), which suggests a positive relationship between endemism and area, a dependency recently found in several general ecological and biogeographical studies (Kinzing & Harte, 2000; Ulrich, 2005). Other potential causes for endemism that have to be considered are pre-Quaternary evolution and high microhabitat heterogeneity, resulting in elevated niche diversification (Huber, 1988; Rull, 2005). The study of endemism patterns in the Guayana Highlands and their potential causal mechanisms is a fascinating open field of research that needs further efforts.

The widespread occurrence of species that have remained theoretically isolated throughout the Quaternary (Supplementary material 2) also deserves explanation. It could be speculated that these species were already widespread before the onset of Quaternary glaciations and/or they have a higher potential for successful jump dispersal. Unfortunately, the seed dispersal mechanisms are largely unknown for the Guayanan flora, and a definite answer is not possible. A study on seed dispersal modes carried out in a low sandstone plateau from Colombian Guayana, slightly at the south of the region studied here, showed that wind is the dispersal agent for only 23% of the species, and the dominant agents (~47%) are animals, mainly birds (Arbeláez & Parrado-Rosselli, 2005). This cannot be taken as the rule for highlands, but is indicative of the low importance of anemochory in the region. Concerning birds, there is also a high degree of endemism also among them (Mayr & Phelps, 1967), so the transport probabilities from one tepui to another are not as high as could be *a priori* expected. As a consequence, slow migration through hospitable terrains (i.e. Pielou’s diffusion) seem to have been a determinant spreading mechanism and, therefore, detailed palaeogeographic reconstructions are crucial to unravel palaeobiogeographical processes.

Finally, it should be noted that figs. 3 to 8, besides representing a static geographical picture of the migration possibilities for different species during the LGM, they also reproduce the reduction of the surface available for migration, since the LGM until the present. Assuming that 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 ways 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 likely 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 Guayana Highlands is not yet 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 Guayana Highlands' biota, a multidisciplinary approach is essential. Phylogeographical studies should provide phylogenies and hopefully dating of the main evolutionary events, whereas palaeoecology should inform about the potential causes and forcing factors. The significance of studies like the present is that they provide the necessary detailed palaeogeographical basis for the reconstruction of the evolutionary trends. The combination of these disciplines will hopefully result in a coherent spatial and temporal framework to properly understand environmental and evolutionary processes that have lead to the present-day ecological and biogeographical patterns.

5. ACKNOWLEDGMENTS

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7. SUPPLEMENTARY MATERIAL 2

Supplementary material 2 List of species with lower altitudinal limits (LALs) above the critical isolation altitude for each tepui, according to their endemism patterns. Tepui abbreviations as in Fig. 2.

Endemic to a tepui or tepuian massif

Neblina (n = 56)
Carex neblinensis (Cyperaceae)
Cephalocarpus obovoideus (Cyperaceae)
Drosera meristocaulis (Droseraceae)
Duranta sp.B (Verbenceae)
Elleanthus malpighiiflorus (Orchdaceae)
Epidendrum commelinispathum (Orchidaceae)
Everardia maguireana (Cyperaceae)
Glossarion bilabiatum (Asteraceae)
Graffenrieda fruticosa (Melastomataceae)
Guzmania nubicola (Bromeliaceae)
Heliamphora hispida (Sarraceniaceae)
Hedyosmum neblinae (Chloranthaceae)
Heteropteris neblinensis (Malpighiaceae)
Hypolepis sp. A (Dennstaedtiaceae)
Ilex abscondia (Aquifoliaceae)
Ilex amazonensis (Aquifoliaceae)
Ilex neblinesis (Aquifoliaceae)
Leandra maguirei (Melastomataceae)
Lepidaploa imeriensis (Asteraceae)
Lindmania maguirei (Bromeliaceae)
Lindmania nubigena (Bromeliaceae)
Lindmania sp. A (Bromeliaceae)
Lindmania sp. B (Bromeliaceae)
Macairea neblinae (Melastomataceae)
Macrocarpaea neblinae (Gentianaceae)
Macrocarpaea piresii (Gentianaceae)
Masdevallia manarana (Orchidaceae)
Maxillaria xdunstervillei (Orchidaceae)
Maytenus neblinae (Celastraceae)
Miconia neblinensis (Melastomataceae)
Miconia perobscura (Melastomataceae)
Myriocladus paludicolus (Poaceae)
Navia aloifolia (Bromeliaceae)
Navia crassicaulis (Bromeliaceae)
Navia filifera (Bromeliaceae)
Navia lepidota (Bromeliaceae)
Neblinantha neblinae (Gentianaceae)
Neblinantha parvifolia (Gentianaceae)
Neblinathamnus argyreus (Rubiaceae)

Neurolepis diversiglumis (Poaceae)
Pentacalia neblinensis (Asteraceae)
Persea croatii (Lauraceae)
Philodendron nebulense (Araceae)
Philodendron simulans (Araceae)
Phyllanthus jablonskianus (Euphorbiaceae)
Piptocarpha sp.A (Asteraceae)
Psittacanthus montis-neblinae (Loranthaceae)
Schefflera pallens (Araliaceae)
Schefflera simplex (Araliaceae)
Selaginella beitelli (Selaginellaceae)
Tyleria aristata (Ochnaceae)
Tyleria pendula (Ochnaceae)
Tyleria spectabilis (Ochnaceae)
Tyleria tremuloidea (Ochnaceae)
Vriesea maguirei (Bromeliaceae)
Xyris neblinae (Xyridaceae)
Xyris valdeapiculata (Xyridaceae)
Xyris xiphophylla (Xyridaceae)

Marahuaka (n = 25)
Aulonemia sp. C (Poaceae)
Brachionidium julianii (Orchidaceae)
Brewcaria marahuakae (Bromeliaceae)
Carex marahuakana (Cyperaceae)
Ceradenia arthrothrix (Grammitidaceae)
Ditassa olivaestevae (Asclepiadaceae)
Ditassa juliani (Asclepiadaceae)
Due marahuacensis (Asteraceae)
Eleocharis atrospiculata (Cyperaceae)
Helonoma chiropterae (Orchidaceae)
Isoëtes vermiculata (Isoëtaceae)
Lepanthes marahuacensis (Orchidaceae)
Lindmania arachnoidea (Bromeliaceae)
Lindmania marahuakae (Bromeliaceae)
Macrocarpaea marahuacae (Gentianaceae)
Marahuacaea schomburgkii (Rapateaceae)
Peperomia marahuacensis (Piperaceae)
Pterozonium retroflexum (Pteridaceae)
Rhamnus marahuacensis (Rhamnaceae)
Schefflera marahuacensis (Araliaceae)
Selaginella marahuacae (Selaginellaceae)
Siphocampylus tillettii (Campanulaceae)
Stegolepis terramarensis (Rapateaceae)
Steyerbromelia discolor (Bromeliaceae)
Thelypteris binervata (Thelypteridaceae)

Maigualida (n = 20)
Blepharodon magualidae (Asclepiadaceae)
Byrsonima baccae (Malpighiaceae)

Byrsonima huberi (Malpighiaceae)
Calea sp. B (Asteraceae)
Chromolaena ternicapitulata (Asteraceae)
Cuphea maigualidensis (Lythraceae)
Huberopappus maigualidae (Asteraceae)
Justicia huberi (Acanthaceae)
Leandra gorzulae (Melastomataceae)
Macrocentrum huberi (Melastomataceae)
Marlierea foveolata (Myrtaceae)
Ouratea maigualidae (Ochnaceae)
Palicourea ottohuberi (Rubiaceae)
Pitcairnia cana (Bromeliaceae)
Schefflera argophylla (Araliaceae)
Schefflera brachypodia (Araliaceae)
Schefflera huberi (Araliaceae)
Schefflera longistyla (Araliaceae)
Schefflera umbraculifera (Araliaceae)
Siphocampylus sp. A (Campanulaceae)

Roraima-Kukenán (n = 11)
Bejaria imthurnii (Ericaceae)
Ceradenia fragillima (Grammitidaceae)
Hymenophyllum sp. A (Hymenophyllaceae)
Hypericumraimense (Clusiaceae)
Ilex apicidens (Aquifoliaceae)
Liparis verticillata (Orchidaceae)
Octomeria monticola (Orchidaceae)
Pleurothallis rhombipetala (Orchidaceae)
Schefflera dissidens (Araliaceae)
Stegolepis huberi (Rapateaceae)
Xyris kukenaniana (Xyridaceae)

Chimantá (n = 7)
Ditassa colellae (Asclepiadaceae)
Elaphoglossum steyermarkii (Dryopteridaceae)
Everardia lanata (Cyperaceae)
Lindmania saxicola (Bromeliaceae)
Paepalanthus apacarensis (Eriocaulaceae)
Rondonanthus flabelliformis (Eriocaulaceae)
Vaccinium steyermarkii (Ericaceae)

Guanay (n = 5)
Biophytum sp. B (Oxalidaceae)
Calea esposi (Asteraceae)
Clusia radiata (Clusiaceae)
Microlicia guanayana (Melastomataceae)
Schefflera guanayensis (Araliaceae)

Ilú-Tramén (n = 5)
Heliamphora elongata (Sarraceniaceae)

Heliamphora ionasii (Sarraceniaceae)
Miconia huberi (Melastomataceae)
Pagamea magniflora (Rubiaceae)
Symbolanthus aureus (Gentianaceae)

Huachamacari (n = 3)
IIlex cowanii (Aquifoliaceae)
Myrcia gentryi (Myrtaceae)
Schefflera huachamacarii (Araliaceae)

Camani (n = 2)
Calea camani (Asteraceae)
Symbolanthus camanensis (Eriocaulaceae)

Guaiquinima (n = 2)
Daphnopsis guanaye (Thymeleaceae)
Ilex parvifructa (Aquifoliaceae)

Aprada (n = 2)
Lindmania sp. C (Bromeliaceae)
Rondonanthus caulescens (Eriocaulaceae)

Murisipán (n = 1)
Paepalanthus holstii (Eriocaulaceae)

Endemic to a district

East (n = 14)
Chimantaea lanocaulis (Asteraceae) – Ch, Mu
Cybianthus wurdackii (Myrsinaceae) – Ay, Ch, Kw, Pt
Ditassa roraimensis (Asclepiadaceae) - Iu/Tr, Kw, Ro
Epidendrum alsum (Orchidaceae) – Ro and neighbouring tepuis
Epidendrum montigenum (Orchidaceae) - Iu/Tr, Kn, Ch, Ro
Ilex summa (Aquifoliaceae) – An, Ay, Kw
Ledothamnus sessiliflorus (Ericaceae) - Iu/Tr, Kr, Kn, Ro
Lepanthes unitrinervis (Orchidaceae) - Iu/Tr, Ro
Octomeria dentifera (Orchidaceae) – Ch, Ro
Octomeria connellii (Orchidaceae) - Iu/Tr, Ro
Schefflera umbellata (Araliaceae) - Iu/Tr, Kn, Ro, Yu
Syngonanthus tiricensis (Eriocaulaceae) – Ap, Ch
Weinmannia guyanensis (Cunoniaceae) – Ch, Ro, Yu
Xyris concinna (Xyridaceae) – Iu/Tr, Kn, Ro, Uei

West (n = 6)
Axonopus sp. A (Poaceae) – Co, Gy
Guayania yaviana (Asteraceae) - Co, Gy, Yv
Lindmania cylindrostachya (Bromeliaceae) – Gy, Yt
Ocotea huberi (Lauraceae) – Co, Gy
Symbolanthus yaviensis (Gentianaceae) – Gy, Yv, Yt
Tococa bolivarensis (Melastomataceae) – Gy, Yv, Yt

Jaua-Duida (n = 4)
Adelobotrys duidae (Melastomataceae) - Du, Hu, Mk
Koanophyllon tatei (Asteraceae) - Ja, Du, Hu, Mk, Pr
Mycerinus sclerophyllus (Ericaceae) – Du, Mk
Tyleria grandiflora (Ochnaceae) - Du, Hu, Mk

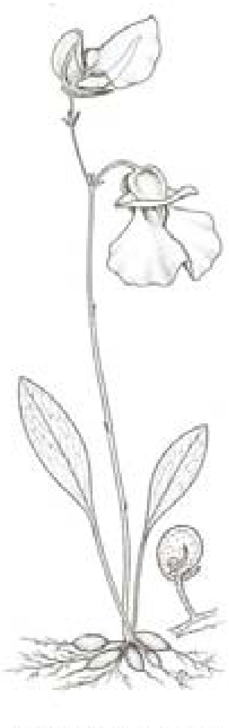
South (n = 1)
Orthaea wurdackii (Ericaceae) – Ar/Av, Nb*

Widespread (n = 38)

Baccharis densa (Asteraceae) – Iu/Tr, Kn, Ro, Mk
Clusia pachyphylla (Clusiaceae) – Gu, Ja, Mg, Co, Du, Yv, Yt
Coccochondra laevis (Rubiaceae) – Mg, Pr
Cybianthus quelchii (Myrsinaceae) - An, Ay, Ch, Gu, Pt, Ro, Ma, Si, Nb
Daphnopsis steyermarkii (Thymeleaceae) – Ja, Ch, Mk, Nb, Mg
Dendrophthora raraimae (Viscaceae) - Ay, Ja, Iu, Ch, Hu, Ro, Mk
Drimys roraimensis (Winteraceae) – Ay, Ch, Ro, Mk, Pr, Si, Nb
Drosera hirticalyx (Droseraceae) – Mk, Nb
Dugandiodendron Pttepuianum (Magnoliaceae) – Pt, Ro, Mg
Eleocharis squamigera (Cyperaceae) – Ay, Ch, Ro, Nb
Eriocaulon jauense (Eriocaulaceae) – Ja, Mg, Co, Yt
Gaultheria setulosa (Ericaceae) - Iu/Tr, Kn, Ro, Mk
Huperzia robusta (Lycopodiaceae) - Ay, Ch, Gy, Yv, Yt
Hymenophyllopsis dejecta (Hymeophyllopsidaceae) – Kn, Ch, Pt, Ro, Mk, Nb
Ilex huachamacariana (Aquifoliaceae) – Ay, Hu
Ilex venezuelensis (Aquifoliaceae) – Ja, Ch, Du, Nb
Lindsaea mesarum (Dennstaedtiaceae) – Ay, Kw, Ch, Du, Mk, Yv, Nb
Mikania michelangeliana (Asteraceae) – Mk, Nb
Myrcia sipapensis (Myrtaceae) – Si, Nb
Myrcia kylistophylla (Myrtaceae) – Ja, Mg
Myriocladus exsertus (Poaceae) - Ar, Du, Hu, Mk, Yt
Myriocladus exsertus (Poaceae) – Ar/Av, Du, Hu, Mk, Yt
Octomeria anomala (Orchidaceae) – Ma, Mk
Palicourea wurdackiana (Rubiaceae) – Mg, Yt
Pernettya marginata (Ericaceae) – Ay, Iu, Kn, Ch, Pt, Ro, Mk, Nb
Podocarpus acuminatus (Podocarpaceae) – Ch, Nb
Podocarpus roraimae (Podocarpaceae) – Ch, Ro, Nb
Podocarpus steyermarkii (Podocarpaceae) – Cr, Pt, Ja, Up, Yv, Nb
Schefflera jauaensis (Araliaceae) – Ja, Mg
Schefflera tremuloidea (Araliaceae) – Mk, Nb
Stegolepis albiflora (Rapateaceae) – Ja, Sa, Mg
Styrax guanayanus (Styracaceae) – Gy, Ja
Thelypteris arborea (Thelypteridaceae) – Iu, Ch, Ro, Mk, Nb
Tibouchina dissitiflora (Melastomataceae) - Av, Co, Gy, Yt, Nb
Vellosiella spathacea (Scrophulariaceae) – Ap, Ay, Iu, Pt, Ro, So, Nb
Xyris bicostata (Xyridaceae) – Hu, Mk, Nb
Xyris delicatula (Xyridaceae) - Ay, Gy, Si
Xyris riparia (Xyridaceae) – Ch, Gu

4. CAPÍTOL 3

The use of taxonomic databases in biogeographic analysis: evaluation of the role of historical and geographical factors on the Guayana Highlands.



Utricularia alpina

The contents of this chapter are in preparation to be sumitted as:
Nogué, S., Rull, V., Vegas-Vilarrúbia, T., Capdevila, A. & Huber, O The use of taxonomic databases in biogeographic analysis: evaluation of the role of historical and geographical factors on the Guayana Highlands.

ABSTRACT

The Pantepui Database is an open continuously growing taxonomic database that allows searching and browsing the vascular plants of the Venezuelan Guayana Highlands (GH) and their geographic distribution. This paper uses the database to analyze the elevation patterns and distribution rang of these plants I order to elucidate potential causes for the high degree of diversity and endemism observed. Species richness and endemic richness (for local endemics, Pantepui endemics and Guayana endemics) vary along elevation gradients. The maximum of species endemic to Pantepui is recorded at 2000 m, above the altutde of maximum richness, and the maxima of Guayana endemics and non-endemics (1500-1800 m). Statistical analysis showed that Pantepui endemics have significant negative correlations with area and positive significant correlations with elevation. On the contrary, Guayana endemics and non-endemic spceies show opposed correlation trends. Local endemics show little relationship with both altitude and area. The maximum number of local endemism showed a pattern of occurrence which might be related with altitudes with small or null connection possibilities even during glacials. It is concluded that patterns of endemism are due to both present-day geographic factors (area and altitude) and historic processes, as linked to the Quaternary glacial cycles.

1. INTRODUCTION

There is a growing recognition that historical factors influence the present patterns of species richness (Bennet, 2004). In the case of mountains, upward and downward vegetation shifts during the Quaternary climatic oscillations have been proposed as one of the mechanisms which shaped current biogeographic patterns due to the expansion of cool-adapted species in colder phases, followed by fragmentation and isolation during warmer phases (Noonan & Gaucher, 2005; Rull, 2008). The study of changes in species richness along elevational gradients is useful to understand the origin and evolution of endemism patterns (Kessler, 2002). Grytnes and McCain (2007) classified the hypotheses commonly used to explain altitudinal richness patterns into four categories: historical, climatic, spatial and biotic. Historical hypotheses are based on processes occurring across evolutionary timescales. Climatic hypotheses, are related mainly to temperature decrease with altitude, and also to mid-altitude rainfall peaks. Temperature is commonly cited as the main cause affecting elevation patterns, as it is known that climatic tolerance of species constrains their altitudinal range (Rahbek, 1997; Körner, 2000; Lomolino, 2001). Spatial hypotheses are based on species-area relationships, which predict more species in elevation belts that cover more area. Finally, biotic hypotheses are related to species habitat specialization (Kruckenberg & Rabinowitz, 1985; Lomolino, 2001; Grytnes & McCain, 2007; McCain, 2007).

Elevation patterns of endemism have been studied in mountain ranges worldwide. This is the case of the Himalayan mountains (Vetaas & Grytnes, 2002; Grytnes & Vetaas, 2002), Braulio Carrillo National Park in Costa Rica (Kluge & Kessler, 2006), Helen mountain in China (Jiang *et al*, 2007), and the Ecuadorian tropical Andes (Kessler, 2002). Results vary among studies and groups of organisms (Kluge & Kessler, 2006), being the main conclusion that the larger amount of endemic species is found higher in elevation than total species richness peaks (Vetaas & Grytnes, 2002; Grytnes & Vetaas, 2002, Kluge & Kessler, 2006).

In the Neotropical Guayana Highlands (GH) of northern South America, a large amount of vascular plant phytogeographic information has been gathered during the last century, especially in the summits of the typical sandstone table mountains or *tepuis*, which summits and upper slopes, above 1500 m elevation, form the Pantepui biogeograhic province (Huber, 1988b). The GH have been also recognized as an important centre of Neotropical plant diversity and endemism (Huber, 1988a; Givnish *et al.*, 2000; Maguire, 1970; Steyermark, 1979; Funk & Brooks, 1990). Previous attempts to quantify species richness and endemism, describe floristic patterns, and compare the GH flora with other regions may be found in Maguire (1970), Steyermark (1979), Huber (1988a), Rull (2004), Berry & Riina (2005), and Steege (2005). Concerning potential historical processes involved in shaping the GH vascular plant diversity, a recent study suggested a speciation model based on altitudinal migrations linked to the glacial-interglacial alternation during the Quaternary (Rull, 2005). It has been estimated that nearly 70 % of the GH vascular plant species would have been able to move among tepuis by downward migration triggered by glacial cooling (Rull & Nogué, 2007). Knowledge about biodiversity and geographical distributions of species is useful not only to study their driving processes, but also to plan their conservation. Recently, databases of regional and local floras -as for example that of the Global Biodiversity Information Facility (GBIF)- have been successfully used to model species distribution for conservation purposes Thuiller *et al*, 2005; Tsoar *et al*, 2007).

In this paper, we introduce the PANTEPUI database containing all the known vascular plants of the GH and their geographical distribution, as a tool for analyzing elevational patterns and evaluate: 1) the potential occurrence of altitudinal gradients in species richness, 2) potential differences between endemic and non-endemic species patterns across elevation gradients, 3) the occurrence of general endemism patterns, and 4) the potential historical factors involved in the origin of the observed patterns.

2. MATERIAL AND METHODS

2.1 Study area

The Pantepui province ranges between 1500 and 3014 m altitude (Huber, 1988b), with a composite area of around 6.000 km ^{2} (Nogué *et al*, 2009) representing a small proportion (<1%) of the total area of the whole Guayana region (Huber, 1995). Considering this small area, the vascular plant richness and endemism per unit area of the tepuis are comparatively higher than those of the Guayana midlands and lowlands, below 1500 m (Steyermark & Berry, 1995-2005; Berry & Riina, 2005). The climate is characterized by a very high precipitation (2500 to 4000 mm/year), high relative humidity, and frequent trade winds. Temperature ranges between 14 and 21 ºC, with an adiabatic lapse rate of - 0.6 ºC /100 m altitude (Galán, 1992; Huber, 1995). Politically, most tepui summits belonging to Pantepui (90%) are in Venezuela, with a few exceptions in Guyana and Brazil. In this paper, the Venezuelan tepuis are analyzed.

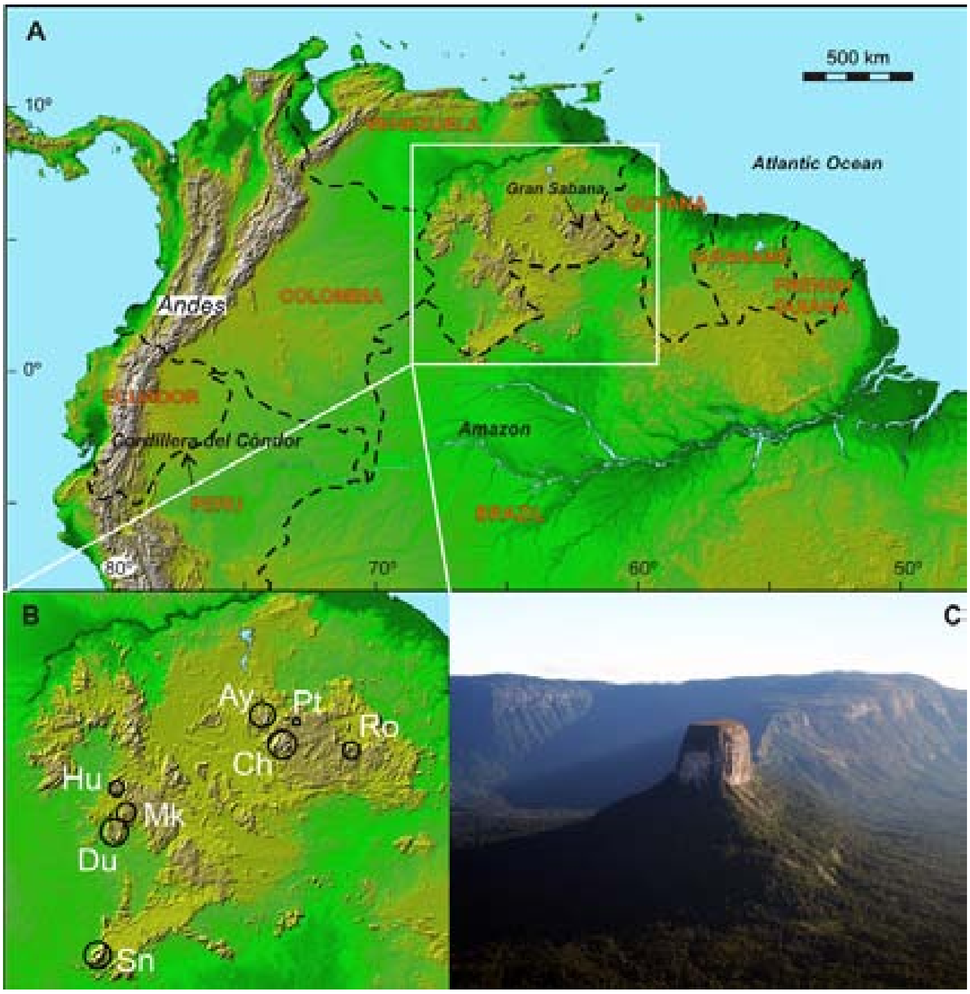


Figure 1. A) Location map of the Guayana Highlands and the main localities described in the chapter. The white square is the study area. B) The tepuis analyzed are encircled and written in white: Auyán (Ay), Chimantá (Ch), Duida (Du), Huachamacari (Hu), Marahuaka (Mk), Ptarí (Pt), Roraima (Ro) and Sierra Neblina (Sn). C) Typical Guayana Highlands landscape (photo: S. Nogué).

The vegetation of the Guayana region is arranged in an altitudinal pattern, according to the three main physiographic units recognized: lowlands (0-500m), midlands (500-1500 m) and highlands (>1500 m) (Huber, 1995a). The Gran Sabana midlands, at the base of most tepuis, are dominated by grasses, with gallery forests along the rivers. The tepuian slopes, the transition between the Gran Sabana plains and the vertical cliffs of the tepuis, extend from 800 m to 2000 m are covered by evergreen mountain forests, which can also occur in some parts of the summits, especially on diabase intrusions, along rivers and creeks, and in humid depressions. Most of the tepui summits are above 1800 m (Huber, 1994), and are characterized by a mosaic of pioneer vegetation, tepuian forests, broad-leaved meadows, and paramoid shrublands (Huber, 1995). There are some singular elements, as for example, the genus *Chimantaea* (Asteraceae), endemic to a single tepuian massif (the Chimantá) and its surroundings, which dominates the so-called paramoid shrublands. Meadows are dominated by *Stegolepis* (Rapateaceae), another endemic genus. The more characteristic forests atop the tepuis are the gallery forests dominated by *Bonnetia* (Bonnetiaceae) which occur along rivers and water courses.

2.2 Raw data

The database, called PANTEPUI, was designed using Microsoft Office Access 2003. It contains all the Pantepui species mentioned and described in the *Flora of Venezuelan Guayana* (Steyermark *et al*, 1995-2005), which have been manually extracted. A total of 2446 species were found to occur in the Pantepui province, as defined above (Huber, 1988b). The information recorded for each species is categorized by species, genus and family names, altitudinal distribution boundaries (maximum and minimum elevation reported), the tepuis in which it occurs, and their geographic distribution. Species' elevation ranges are given in 100-m intervals (Steyermark *et al*, 1995-2005). The geographic entities considered are the tepuis, the tepuian massifs, the Pantepui districts (Eastern, Jaua-Duida, Southern, and Western) (Berry *et al*, 1995), the Venezuelan political subdivisions or states (Bolívar, Amazonas and Nueva Esparta), the Venezuelan natural regions (Venezuelan Andes, Coastal Range, Gran Sabana and Caribbean Island), as well as other regions and countries of occurrence of the species considered (Africa, Antillas, Argentina, Barbados, Belize, Bolivia, Brazil, Chile, Colombia, Costa Rica, Cuba, El Salvador, Ecuador, French Guiana, Guatemala, Guiana, Honduras, Jamaica, Mexico, Nicaragua, Panama, Paraguay, Peru, Puerto Rico, Suriname, Uruguay and Venezuela).

The design of the PANTEPUI database enables users to query and search its contents based on species and site attributes. The raw data are subdivided by 7 tables and, due to the fact that each record must be unique, we adopted numeric Id codes to identifying each record in the table, which are created using an auto-numbering feature (Id primary key). The 7 tables are organized in four master tables, called *ms tables* (*ms species*, *ms tepui*, *ms tepui massif* and *ms sites*) which contain the species, tepuis and site data. There are also three data tables called *in tables* (*in species tepui*, *in species sites* and *in sites*) that indicate which record of the master table relates to what other master table record. Thus both types of tables (*ms* and *in*) are related by one-to-many relationships. These relationships are depicted in figure 2.

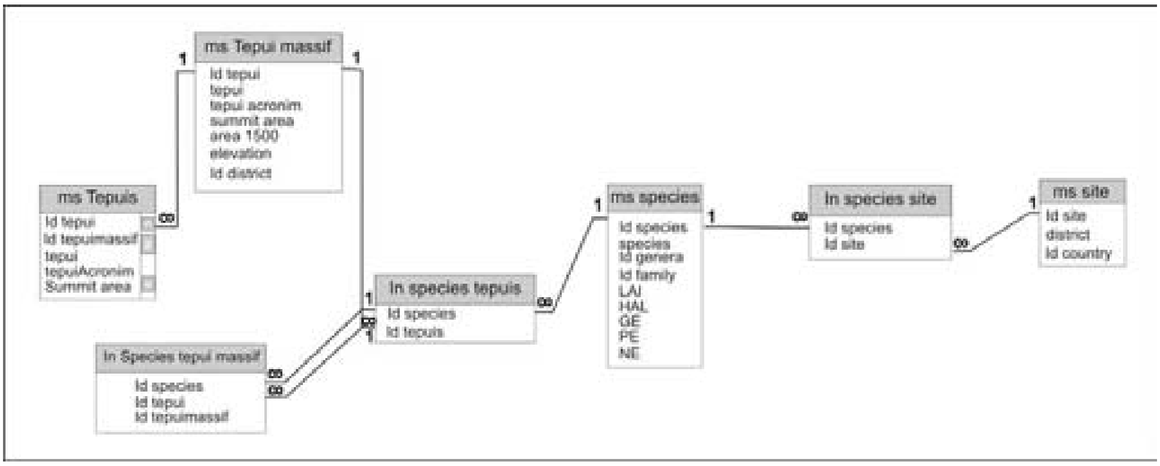


Figure 2. Simplified diagram of the PANTEPUI database showing the relationships between the different tables.

2.3 Analytical methods

Analyses were conducted at regional (the whole Guayana region) and local (each individual tepuis) scales. The local approach considered only the better explored tepuis (Auyán, Chimantá, Duida, Huachamacari, Marahuaka, Neblina, Ptarí, Roraima and Sierra Neblina) (Table 1) (Huber, 1988b). At a regional scale, we considered the following parameters: richness (R), Guayana Endemics (GE), non-endemics (NE) and Pantepui endemics (PE). At a local scale, we considered the local richness (R), the local endemics (LE), the non-endemic elements (NE), the Guayana endemics excluding the Pantepui endemics (GE*), and the Pantepui endemics excluding the local endemics (PE*). Areas represent the surface between a given altitudinal interval and the next, and were calculated using a digital elevation model from the Shuttle Radar Topography mission (SRTM) of 3 arc sec (90 m) precision using ArcGis version 9.3 (see supplementary material 3). Correlation analysis used the Pearson product-moment correlation coefficient using SPSS version 15.0.

3. RESULTS

3.1 General patterns

According to the PANTEPUI database, of the 2446 known Pantepui species of vascular plants, 1292 (52.8%) are endemic of Guayana (GE) and, among them, 771 species (31.5% of the total and 59.7% of GE) are endemic of Pantepui (PE). Therefore, 1154 species (47.2%) are non-endemic (NE). Local endemics (LE) - species occurring in one single tepui- include 504 species (20.6% of the total and 65.4% of the PE).

GE are widespread around Bolívar and Amazon states. Among NE species, 29.5 % are also present in the Venezuelan Andes, 13.1 % occur in the Coastal Range and 25.4 % are widespread across the neotropics, as for example 62.7% in Brazil, 53.4 % in Colombia, 52.6 % in Guyana, 35.7% in Ecuador, 25.4 % in Suriname, and 19.0% in French Guayana. Within Pantepui, many species are very restricted in their geographical range. For example, only 0.5% and 0.4% of GE and PE, respectively, are widespread, contrasting with NE (20.3%). Local endemics are also frequent, including 65.4% (504). Moreover, 19.3% (149) occurs in two tepuis, 6.1% (47) in 3 tepuis and 3.4% (26) in 4 tepuis (Fig 3).

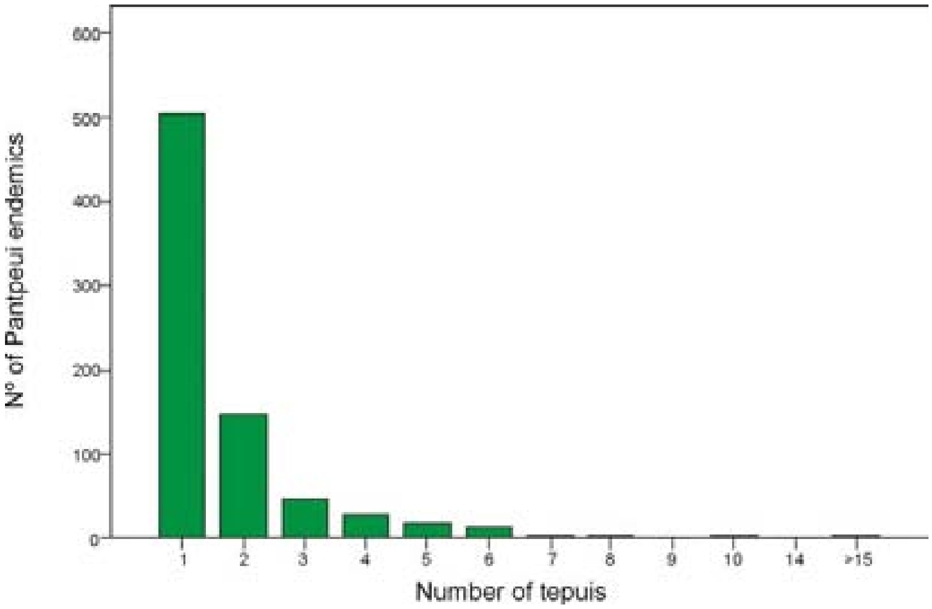


Figure 3. Species geographic distribution. This figure show how many species occurs in one, two, etc, tepuis.

The tepuis selected for this study showed a high level of endemism (Table 1), with an average percentage around 30% for the PE, except for the Huachamacari (11.8%). The highest percentage of LE is around 11% and the minimum 2.3 %.

Table 1.Results of the PANTEPUI database for the better known tepuis. R: species richness, PE: Pantepui endemics, LE: local endemics.

Tepui	R	PE	%	LE	%
Auyán (Ay)	467	158	33.8	32	6.9
Chimantá (Ch)	676	233	34.5	76	11.2
Duida (Du)	242	49	20.25	18	7.4
Huachamacari (Hu)	127	15	11.8	3	2.4
Marahuaka (Mk)	355	104	29.3	28	7.9
Ptarí (Pt)	286	68	23.8	7	2.5
Roraima (Ro)	383	144	37.6	9	2.4
Sierra Neblina (Sn)	433	156	36.0	10	2.3

3.2 Altitudinal gradient

The range size for each species is defined as the difference between its upper and lower altitudinal boundaries. Pantepui endemics (PE) have an average range size of 360 m, while Guayana endemics (GE) and non-endemics (NE) have range sizes of 635 m and 1209 m, respectively. At a regional scale, richness (R) shows an increasing trend from 0 to 1500 m a small plateau between 1500 to 2000 m and a steep decrease towards 3000 m (Fig 4 A). The non-endemic species (NE) display a similar trend with a sharp peak at 1500 m while the Guayana endemics (GE) peaks around 1800-2000 m elevation (Fig 4 A). The Pantepui endemics (PE) also show a monotonic pattern increase between 1500 and 2000 m and a decrease afterwards, but with a minor peak around 2500 m (Fig 4B).

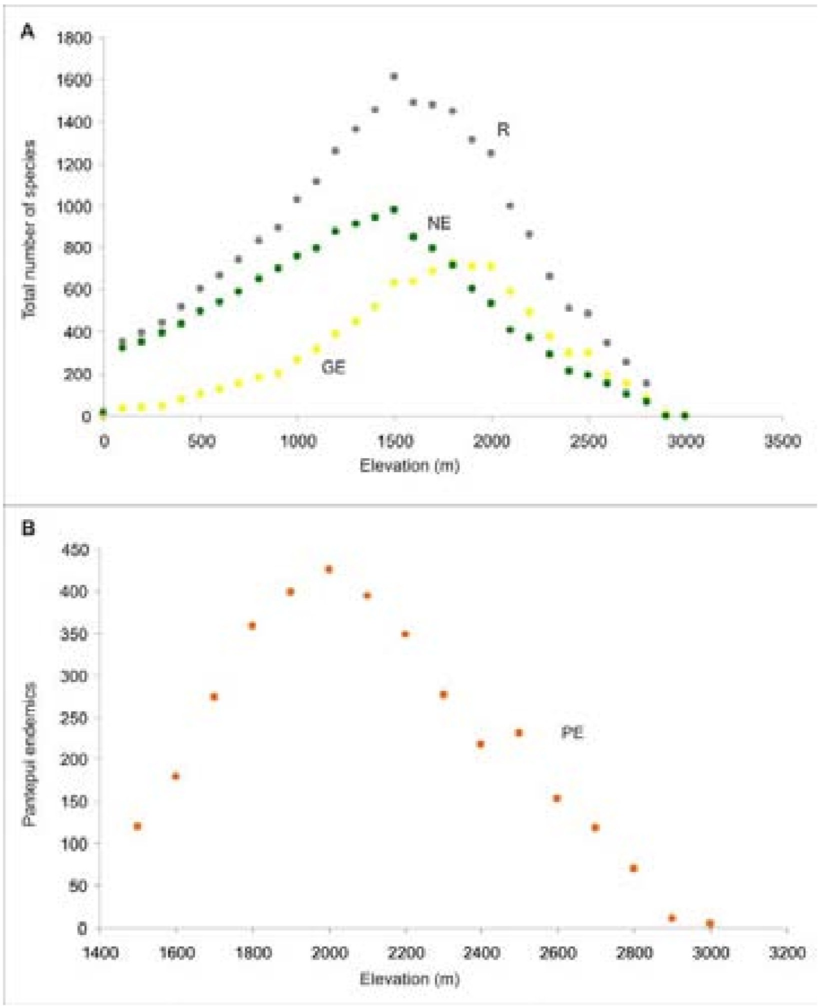


Figure 4. Variation in diversity along the elevational gradient in the Guayana Highlands. A) Non-endemics (NE), Guayana endemics (GE) and species richness (R); B) Pantepui endemics (PE).

Figure 5 and 5 cont (A to H) shows the elevation patterns for each tepui analyzed, for local endemics (LE) and Pantepui endemics excluding LE (PE*). Almost all tepuis display an unimodal pattern for both parameters, with three exceptions: 1) Huachamacari, in which PE* increases monotonically, 2) Roraima, where LE decrease with altitude, and 3) Ptari, with an increasing pattern in LE. Interestingly, LE peaks at the same or at lower altitudes than PE*.

Figure 5 and 5 cont (A’ to H’) shows the elevation pattern for each tepui considering the Guayana endemics excluding the Pantepui endemics (GE*), the non-endemics (NE) and the richness (R). For GE* and NE, almost all the tepuis display a general decrease, except for the Roraima, in which NE peaks around 1800 m, and Sierra Neblina, with a plateau between 1500 and 1800. Richness patterns are more heterogeneous. In the Duida, Huachamacari, Marahuaka and Ptarí, there is a decrease towards the higher elevations, whereas in the others a unimodal pattern can be observed, peaking at different altitudes: Auyán (1800 m), Chimantá (1600 m), Roraima (2000 m) and Sierra Neblina (1800 m).

3.3 Correlations

The results of correlation analysis are shown in Table 2. Local endemics (LE) only show significant correlations (always positive) in three cases, two with area (Chimantá and Neblina) and one with elevation (Marahuaka). In the case of PE*, almost all correlations with area are significant and negative (except for the Duida), while correlations with elevation are usually positive (except for the Sarisariñama) and significant in half the cases. For GE*, NE and R, correlations with elevation are always highly significant and negative, whereas correlations with area are always positive and generally significant, with a few exceptions.

Table 2. Correlations with area and elevation, for the selected tepuis. See table 1 for acronyms (* p< 0.05, ** p< 0.001).

tepui	**LE**		**PE***		**GE***		**NE**		**R**	
	area	**elev**	**area**	**elev**	**area**	**elev**	**area**	**elev**	**area**	**elev**
Ay	-0.35	-0.10	-0.79*	0.50	0.85**	-0.99**	0.78**	-0.98**	0.6	-0.89**
Ch	0.72**	0.14	0.64*	0.16	0.40	-0.99**	0.45	-0.99**	0.67*	-0.88**
Du	0.41	-0.40	-0.58	0.59	0.98**	-0.99**	0.91**	-0.92**	0.96**	-0.97**
Hu	-0.50	0.24	-0.93*	0.98**	0.74	-0.91*	0.91*	-0.99**	0.81	-0.94*
Mk	0.033	0.57*	-0.56*	0.39	0.72**	-0.99**	0.70**	-0.99**	0.69**	-0.96**
Pt	0.57	-0.32	-0.87**	0.77**	0.92**	-0.99**	0.78**	-0.92**	0.71*	-0.92**
Ro	-0.42	0.48	-0.81**	0.83**	0.87**	-0.99**	0.69**	-0.89**	0.50	-0.71**
Sn	0.58*	-0.41	0.79**	-0.75**	0.86**	-0.98**	0.90**	-0.98**	0.91**	-0.97**

4. DISCUSSION

Our general results have been compared with those of previous studies (Table 3). On our database the degree of Pantepui endemicity is closer to that of Berry *et al*. (1995) than in Berry and Riina (2005). Our number of Guayana endemics is the lowest (1292). Overall, richness values are the most consistent among the three studies. These differences are likely due to differences in data availability. In the case of Berry *et al*. (1995), the data were compiled 10 years before the completion of the whole Flora (Steyermark *et al*, 1995-2005), and based on preliminary checklists and manuscripts. In the case of Berry & Riina (2005), the authors specify that their compilation was made on the basis of current and pending volumes of the Flora.

Tabla 3. Comparison of vascular plant richness and endemism in Pantepui

	Berry *et al*, 1995	**Berry & Riina, 2005**	**This paper**
Richness	2322	2447	2446
Guayana endemics	1517	1517	1292
Pantepui endemics	766	1034	771

In our case, the PANTEPUI database benefits from the final publication of all the volumes. It is expected that the number of species of Pantepui will increase with new studies and the number of endemics will decrease as more phytogeographic information is available from the Neotropics. For example, recent studies in the Cordillera del Cóndor, adjacent to the Ecuadorian and Peruvian Andes, have reported several genera and species that were previously considered Guayana and Pantepui endemics (Neill, 2005; Ulloa & Neill, 2006) (Fig 1).

The results of the biogeographic analysis can be summarized in two main points.
First, PE peaks at higher elevation (2000 m) than the GE (1800 m), NE (1500 m) and R (1500 m) (Fig 4). The same results have been obtained along the longest altitudinal gradient known, in the Himalayas (Vetaas & Grytnes, 2002; Grytnes & McCain, 2007), and also on Neotropical mountains from Central and South America, including the Andes (Kessler, 2002; Kluge & Kessler, 2006). Second, R, NE, GE*, and PE* significantly correlate with both area and elevations but LE do not. An additional striking feature is that, whereas the more endemic species (LE and PE) are generally unimodal or increasing, the NE and GE* show decreasing trends. Among the more accepted hypotheses about factors determining endemicity are habitat specialization (Kruckenberg & Rabinowitz, 1985), topographic isolation and habitat fragmentation at higher elevations (Vetaas & Grytnes, 2002). Our results show that endemic species have the narrower geographic and elevational range size among the species considered in this study, suggesting some degree of habitat specialization. Unfortunately, the lack of studies on biotic and abiotic niche features for the Pantepui species, prevents any definitive assessment. Regarding the isolation hypotheses, correlation analysis may provide some clues. The fact that PE* is positively associated to elevation and negatively correlated with area (Table 2) is consistent with a high degree of isolation and habitat fragmentation. The same pattern has been found in several studies on other mountain ranges and is commonly cited as an explanation for endemism trends in altitude (Kruckenberg & Rabinowitz, 1985; Kessler, 2002; Vetaas & Grytnes, 2002). Furthermore, the peaks of PE* are commonly located between 1800 and 2400 m altitude (Figs 5 and 5 cont), where most of the highly fragmented and isolated tepuian summits occur (Huber, 1995) (Supplementary material 3).
Correlation patterns for R, NE and GE* are opposed to those of Pantepui endemics, that is, positive with area and negative with altitude (Table 2).

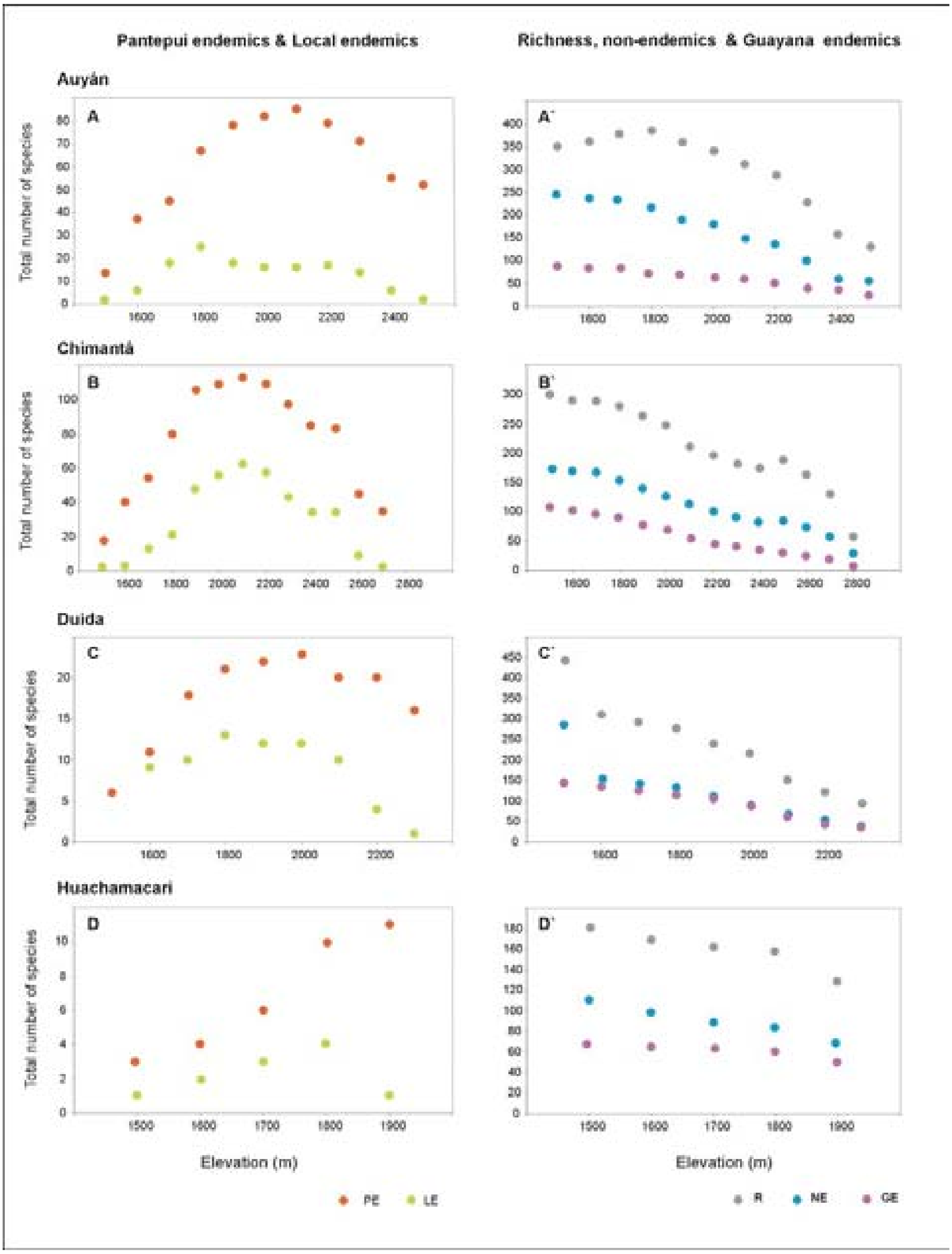


Figure 5. Variation along the Pantepui elevation gradient of Pantepui endemics (PE) and local endemics (LE), Guayana endemics (GE), non-endemics (NE) and Richness (R)for the individual tepuis considered.

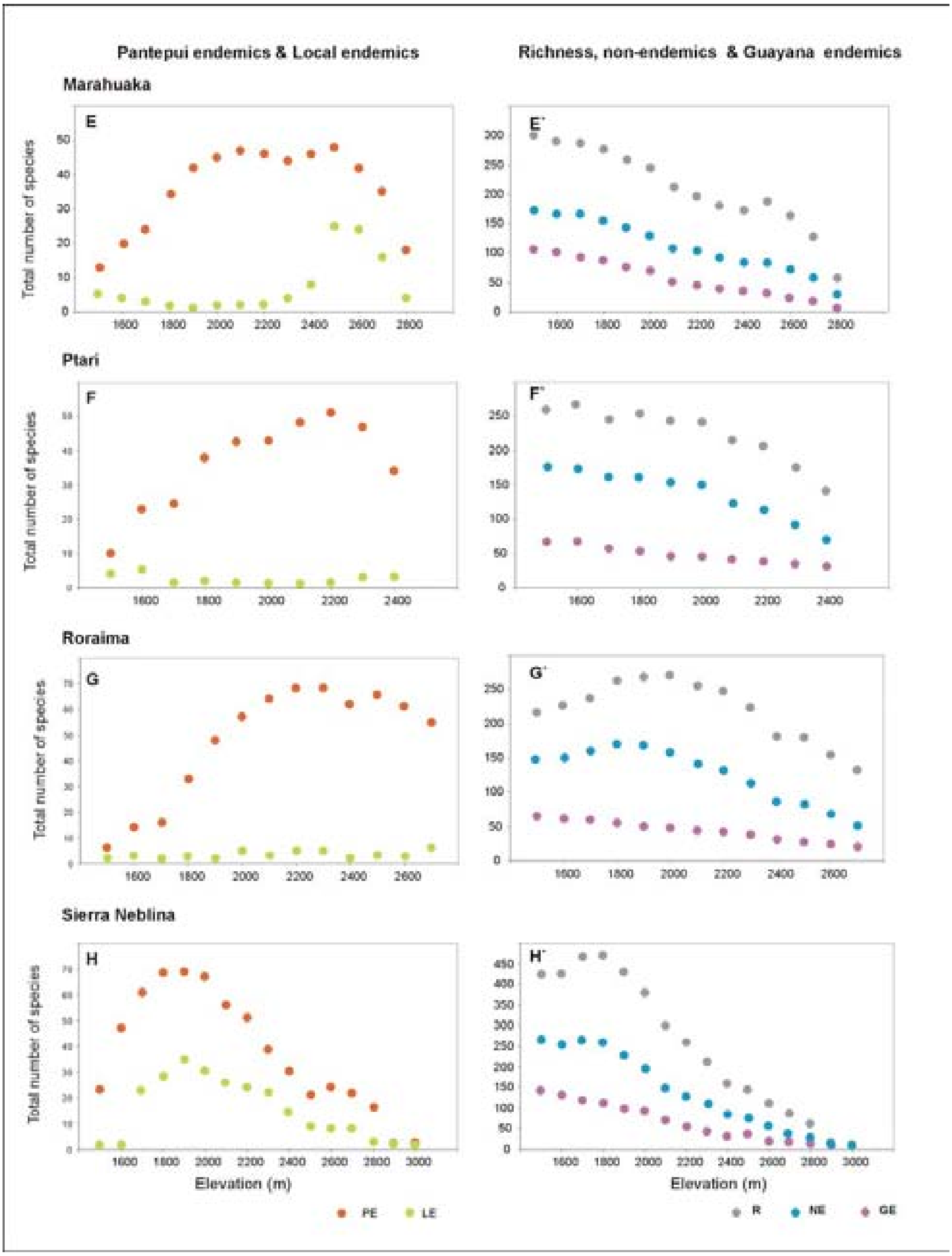


Figure 5 (cont). Variation along the Pantepui elevation gradient of Pantepui endemics (PE), local endemics (LE), Guayana endemics (GE), non-endemics (NE) and Richness (R) for the individual tepuis considered

This follows the predictions of island biogeography, that smaller islands (which area decrease with altitude) are inhabited by less species (McArthur & Wilson, 1967). Contrastingly, LE show little relationship to both altitude and area. The only significant values obtained were in the Chimantá and Neblina with area and in Marahuaka with elevation (Table 2). Potential explaining factors for this lack of pattern may be microhabitat specialization and historical processes. The first are difficult to evaluate at the present state of knowledge, due to the mentioned lack of appropriate ecological studies, but the second may be analyzed in the light of the available paleoecological records. Quaternary climatic oscillations would have created the conditions for fragmentation and isolation atop the tepuis (interglacials), followed by mixing and interchange (glaciations), thus contributing to high speciation rates and increase of local endemism levels in the summits (Rull, 2005). In a previous study, where the potential migration routes for vascular plants were reconstructed, the critical altitude for topographical isolation (CAI) was defined as the minimum altitude at which the summit of a given tepui losses the possibility of biotic interchange with others, through the surrounding lowlands, during a glaciation (Rull & Nogué, 2007) (Table 4). Interestingly, LE peaks often occur close or above the CAI, except for Duida and Ptarí (Table 4), indicating that the maximum levels of local endemism occur at altitudes with small or null connection possibilities even during glacials, when the probability of migration and interchange among tepuis was maximum (Rull & Nogué, 2007).

Table 4. Comparison of the elevation maximum of local endemics (LE) with Critical Altitude for topographical Isolation (CAI) during the Last Glacial Maximum (Rull & Nogué, 2006). See table 1 for acronyms.

Tepui	Elev	CAI	LE
Ay	2450	2000	1800
Ch	2650	2200	2100
Du	2358	2300	1800
Hu	1900	1600	1800
Mk	2800	2300	2500
Pt	2400	2600	1600
Ro	2723	2400	2700
Sn	3014	1700	1900

In Chimantá and Auyán, LE peaks are slightly lower (100-200 m) than CAI, suggesting that other mechanisms, such as habitat heterogeneity and long-distance dispersal, may have also operated. These results support that a significant part of the genetic structure of the LE has been shaped during the Quaternary, a hypotheses that is being intensively debated and is gaining support worldwide (Noonan & Gaucher, 2005; Rull, 2005; Rull & Nogué, 2006; Rull, 2008, and literature therein).

5. ACKNOWLEDGMENTS

I would like to thank I. Hanski, O. Ovaskainen, E. Sebastián and E. Meike for guidance and support during my stay in the Metapopulation Research Group (University of Helsinki). This research has been supported by the Biodiversity Conservation Program of the BBVA Foundation (project BIOCON 2004-90/05) and a PhD travel grant from the *Generalitat de Catalunya* (BE-2007).

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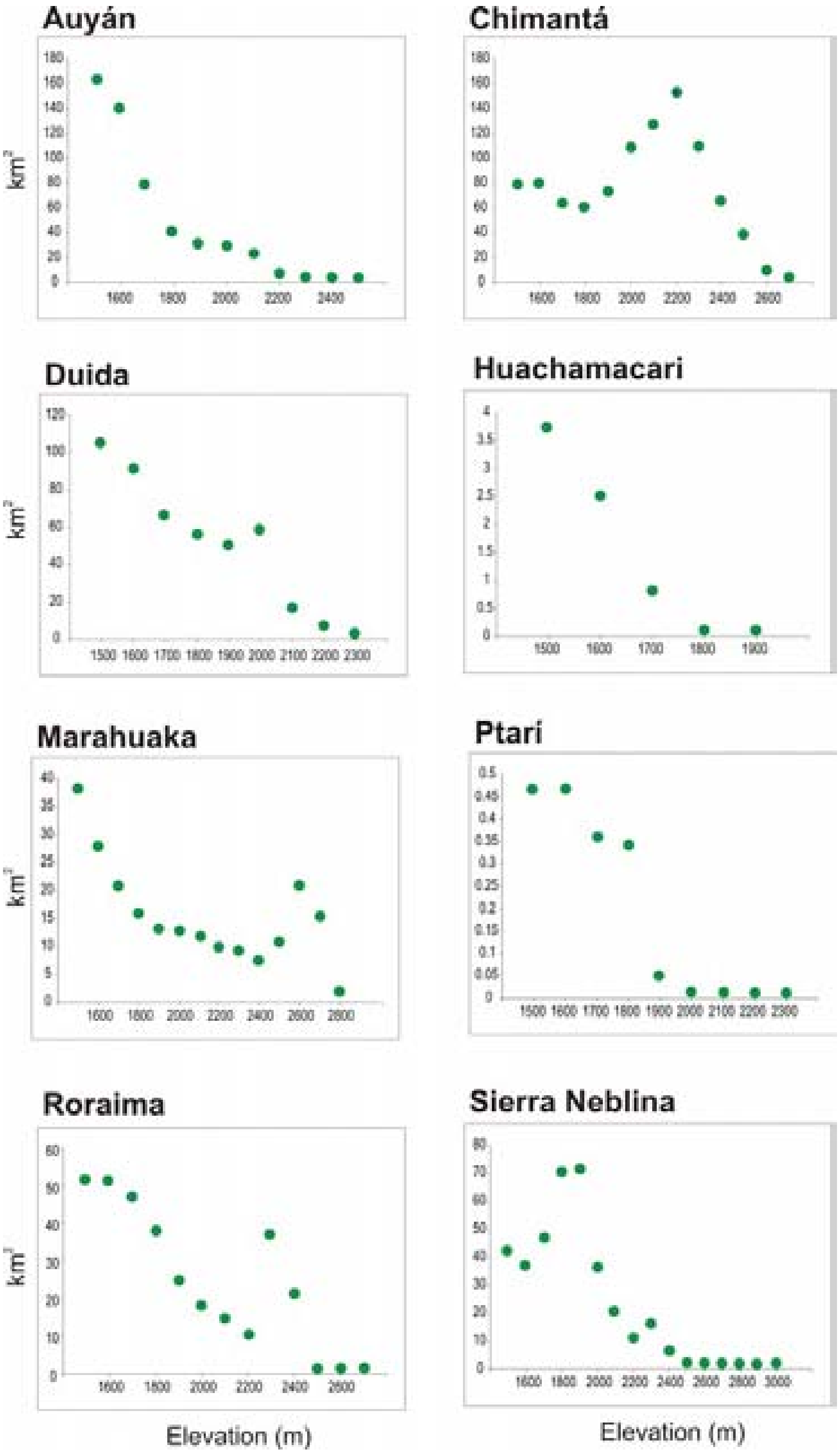
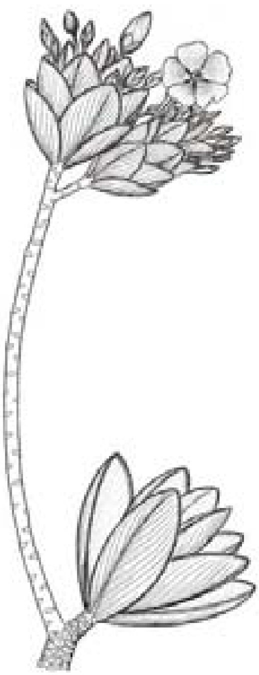
7. SUPPLEMENTARY MATERIAL 3

Supplementary material 3. Areas between the altitudinal intervals considered in the analysis, calculated using a digital elevation model from the Shuttle Radar Topography mission (SRTM) of 3 arc sec (90 m) precision using ArcGis version 9.3.



5. CAPÍTOL 4

Modeling biodiversity loss by global warming on Pantepui, northern South America: projected upward migration and potential habitat loss



Bonnetia multinervia

The main contents of this chapter have been published as:
Nogué, S., Rull, V. & Vegas-Vilarrúbia, T. (2009) Modelling biodiversity loss by global warming on Pantepui, northern South America: projected upward migration and potential habitat loss. Climatic Change, 94, 77-85.

ABSTRACT

This work aims to estimate the potential effects of the global warming projected for the 21st century on the biodiversity of a remote and pristine region of the Neotropics called Pantepui. Habitat loss and fragmentation by upward migration of bioclimatic conditions is analyzed using Species-Area Relationships (SAR) and Altitudinal Range Displacement (ARD) analysis. The ARD is a tool that uses the present-day lapse rate to estimate the upward migration of the species based on the global warming predicted by the IPCC. The results show that around 80% of the vascular flora, ca. 1700 species of which up to 400 would be Pantepui endemics, are threatened of extinction. These estimates should be considered preliminary, but the danger is real. Therefore, suitable conservation or mitigation strategies are needed.

1. INTRODUCTION

The global warming predicted for the end of the present century due to the enhancement of the greenhouse effect is unprecedented in the recent earth history (Houghton *et al*, 2001). The warming is already affecting an increasing number of organisms, which respond in a variety of ways, including changes in their geographical and altitudinal distribution (Hughes, 2000; Parmesan, 2006; Rull & Vegas-Vilarrúbia, 2006; Raxworthy *et al*, 2008; Sekercioglu *et al*, 2008). In mountain environments, the usual consequence is an upward biotic migration following the altitudinal displacement of suitable environmental conditions (e. g. Grabherr *et al*, 1994; Gottfried *et al*, 1999; Dirnböck *et al*, 2003; Peñuelas & Boada, 2003; Araújo *et al*, 2005; Bowman, 2005; Graumlich *et al*, 2005; Sphen & Körner 2005; Williams *et al*, 2005; Wilson *et al*, 2005). If current temperature projections are realistic, upward bioclimatic displacements of the order of 500 to 700 m are expected to occur for AD 2100 (Hughes, 2000; Rull & Vegas-Vilarrúbia, 2006). As a consequence, species inhabiting high elevations are threatened of extinction by habitat loss.

Tropical mountains seem not to be an exception. For example, Foster (2001) suggested the future warming-driven extinction of mountaintop species in tropical cloud forests from Central America. In the Guayana Highlands of northern South America, Rull and Vegas-Vilarrúbia (2006) estimated that up to one third of the vascular plant species analyzed would lose their habitat by AD 2100, owing to the ongoing global warming. However, this was the result of a preliminary survey based on a limited species selection, and a thorough study including the bulk of known endemic species was recommended. This paper aims to fill the gap by evaluating the potential risk of extinction of all the known vascular plants of this region, with emphasis on endemic species, using all the taxonomical and phytogeographical information available so far. This is a thorough, species-level analysis, oriented not only to estimate a percentage of potential habitat loss, but also to identify individually all the threatened species and classify them according to their vulnerability. The resulting information will be of utility for planning biodiversity conservation in the Guayana region.

2. MATERIAL AND METHODS

2.1 Study area

Pantepui is a discontinuous biogeographical province of the Guayana Highlands (Fig. 1), constituted by the assemblage of the flat summits of numerous table mountains or *tepuis* (Fig. 2). The whole Pantepui surface is of some 6000 km^2 and ranges from 1500 to 3000 m altitude (Huber, 1994). This province lies on the Precambrian Guayana Shield, which had been separated from the African Shield by continental drift, leading to the formation of the Atlantic Ocean, around 80-100 million years ago (Edmond *et al*, 1995). The tepuis are remnants of ancient erosion surfaces that have been isolated by denudation due to the Gondwana breakup and the formation of the extensive Orinoco and Amazon river basins (Briceño & Schubert, 1990).

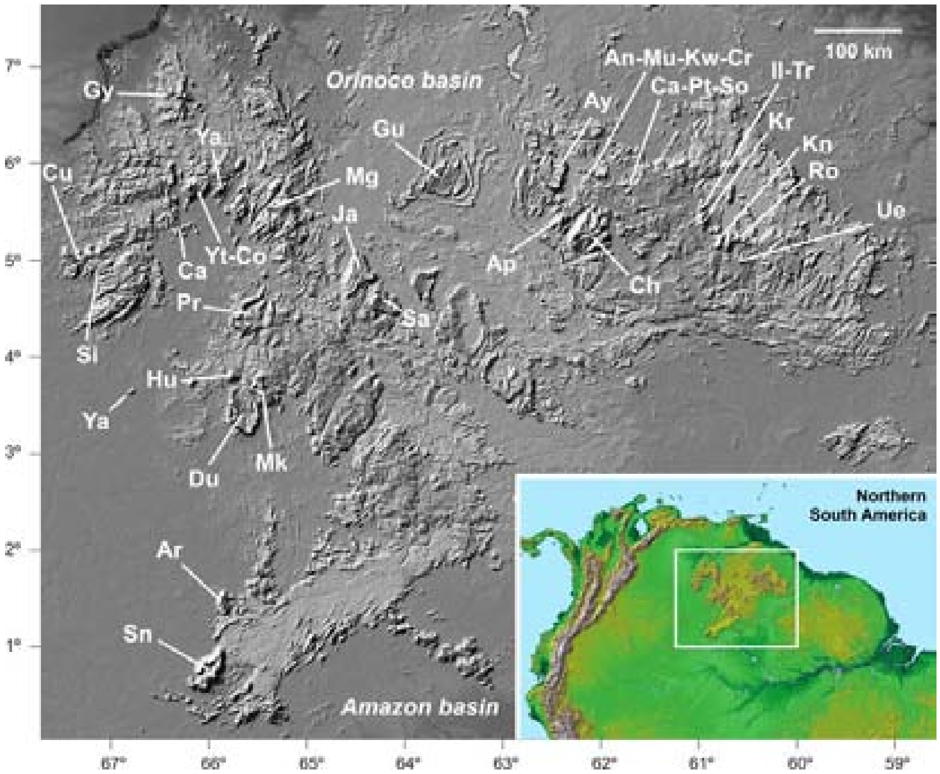


Figure 1. Radar image of the Guayana Highlands (courtesy of NASA /JPL-Caltech), indicating the tepuis studied: An = Aparamán, Ag = Angasima, Ap = Aprada, Ar = Aracamuni, Ay = Auyán, Ca = Camani, Ch = Chimantá, Co = Coro-coro, Cr = Carrao, Cu = Cuao, Du = Duida, Gu = Guaiquinima, Gy = Guanay, Hu = Huachamacari, Iu-Tr = Ilú-Tramén, Ja = Jaua, Kn = Kukenán, Kr = Karaurín, Kw = Kamarkawarai, Mk = Marahuaka, Mu = Murisipán, Nb = Neblina, Pr = Parú, Pt = Ptari, Ro = Roraima, Sa = Sarisariñama, Si = Sipapo, So = Sororopán, Ue = Uei, Yt = Yutajé, Yu = Yuruaní, Yv = Yaví.

Pantepui is mostly inaccessible, and still pristine (Rull, 2007). The uniqueness of the Panteui biota, as well as its striking degree of biodiversity and endemism, are well known and have been recognized for long time (Huber, 2005). This is especially manifest in vascular plants, the better known organisms of the region (Steyermark *et al*, 1995-2005), with ca. 630 genera and more than 2300 species, of which 57.8 % are endemic to the Guayana Shield, 31.5 % are endemic to the Guayana Highlands, and around 20 % are endemic to a single tepui (chapter 3). Unfortunately, besides the general physiographical, climatic and biological features mentioned, Pantepui remains still largely unknown. More or less detailed studies on climatic variability, soils, hydrology, ecophysiology, or population and community ecology, are still lacking.

2.2 Data analysis

The estimation of potential biodiversity loss was based on two approaches: the Species-Area Relationship (SAR) and the Altitudinal Range Displacement (ARD) analysis. SAR and the Endemic species-Area Relationship (EAR) have been widely used in the estimation of biodiversity reduction by habitat loss by applying the basic Arrhenius equation: $S = S_0A^z$, where S is the total number of species, A the area, and S_0 and z the interception and the slope respectively. (McDonald & Brown, 1992; Halloy & Mark, 2003; Thomas *et al*, 2004; Ulrich, 2005; Wisley *et al*, 2005). EAR has been considered to attain better performances than SAR by several authors (Harte & Kinzig, 1997; Kinzig & Harte, 2000). Four regression equations (SAR1, EA’R1, SAR2 and EA’R2) were tested, considering 771 endemic species (chapter 3) and a total of 2446 species (Berry & Riina, 2005). For this purpose we calculated the total Pantepui area above 1500 m and that of 26 tepuis individually, excluding those with with very small summits. Areas were mesured with a geographic information system (GIS) software (Miramon, 2007) using the digital elevation model from the Shuttle Radar Topography Mission (SRTM) of 3 arcsec (90 m) precision (USGS/NGA/NASA). EA’R1 considers the whole Pantepui surface (A’), and was obtained relating the Pantepui endemics with the area of a set of altitudinal slices resulting from progressive 100-m upward displacement increments (GIS analyses). In this way we obtained the number of species having their lower altitudinal limit in each slice and the corresponding area reduction. SAR2 and EAR2 were built after a selection of tepuis similar to Riina (2003), but using the area and the species number above 1500 m for each tepui (Fig. 1). SAR1 equation was taken directly from Riina (2003), because it relates the summit area and the total number of species (33 tepuis): $S = 39{,}08A^{0.354}$ ($r^2 = 0.706$; $p < 0.0001$), since we counted only endemic species.

The ARD analysis is a simulation aimed to obtain the Projected Altitudinal Range (PAR) and the Projected Available Area (PAA) for each Pantepui endemic species by AD 2100 (Rull & Vegas-Vilarrúbia, 2006, Roxworthy *et al*, 2008). Due to the limited environmental and ecological information available, the potential biotic altitudinal displacement for AD 2100 was estimated using the present altitudinal range of species, the IPCC temperature predictions, and the present moist temperature lapse rate for the region. These data were used to simulate the future altitudinal range for each endemic species. Raw data were from a phytogeographical database including all the Pantepui endemic species, their altitudinal ranges, and their geographical distribution, especially developed for this study after Steyermark *et al*, (1995-2005). Global warming predictions for the so called 'Amazonia' region are of 2–4 ºC, depending on the forecasting model and the scenario considered (IPCC, 2007), and the present lapse rate for the Pantepui region is of 0.6ºC/100 m altitude (Huber, 1995). In this way we obtained an expected upward displacement ranging from 330 m (2ºC) to 670 m (4ºC). The PAA for each species was obtained by high-resolution GIS analysis using the same digital elevation model mentioed before. A given species is threatened of habitat loss if the predicted warming is enough for its LAI to reach the present altitudinal maximum of the species and, as a consequence, both PAR and PAA are zero.

3. RESULTS

Equations obtained are depicted in Fig. 2. The better performance corresponds to EA'R1 ($r^2 = 0.968$; $p < 0.002$). Correlation coefficients are lower, but still significant, for EAR2 ($r^2 = 0.392$; $p < 0.001$) and SAR2 ($r^2 = 0.339$; $p < 0.002$). Using these equations and SAR1, it is possible to estimate the global extinction rates expected for the Pantepui area (Table 1). For total species (SAR1 and SAR2), the extinction risk is high and fairly constant among the different equations. For endemic species, there is a notable difference between EA'R1 (the equation with higher correlation) and EAR2, which predictions are around two to three times higher.

ARD analysis shows that up to 45% of Pantepui endemic species seem to be in danger of extinction by habitat loss by AD 2100 under the 4 ºC scenario (Supplementary material 4.1). Approximately 23% (176 species) would lose their habitat for a 4 ºC increase but not for a 2 ºC warming. The complete species list of endangered species is provided as supporting material (supplementary material 4.2). The families with more endangered species are those with more species endemic to Pantepui, with the exception of Xyridaceae and Poaceae, with relatively few endemic species under risk. Taken individually, the tepuis with intermediate numbers of endemic species (especially Jaua, Sipapo and Parú) are more endangered than those with more endemics (Chimantá, Neblina, Auyán) (Supplemenatry material 4.3).

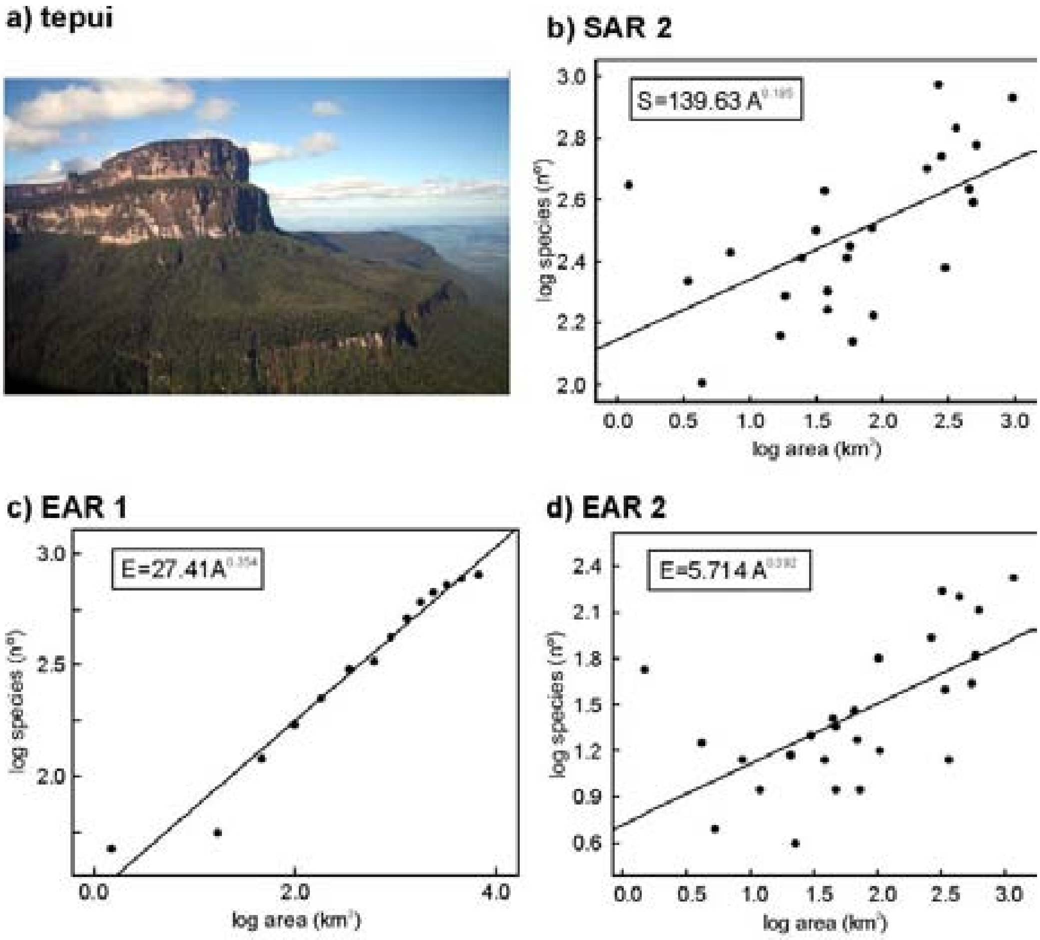


Figure 2. Example of a tepui, showing the characteristic flat summit (a), and regression plots of the three species-area models obtained in this study (b, c, d).

PAA analysis provided maps of potential habitat distribution for all the species not under risk of total habitat loss (412 to 588, or 55% to 78%, respectively), for each tepui (Fig. 3). Virtually all the species analyzed in this way show a fragmented PAA by AD

2100. Globally, the total Pantepui surface reduction is of 68% (2 ºC) to 90% (4 ºC), which explains the high extinction rates derived from SAR and EAR equations.

Table 1. Estimates of the number of species living and extinct by habitat loss by AD 2100 in Pantepui, using the species-area models considered in this study and the two extreme IPCC scenarios. Extinction rates have been calculated as percentages of present-day total (2446) and endemic (771) species of Pantepui.

model (scenario)	living	extinct	% extinct
SAR1 (2ºC)	589	1733	70.1
SAR1 (4ºC)	393	1929	78.9
SAR2 (2ºC)	622	1700	69.5
SAR2 (4ºC)	498	1824	74.6
EAR1 (2ºC)	545	209	27.1
EAR1 (4ºC)	348	406	52.7
EAR2 (2ºC)	115	639	82.9
EAR2 (4ºC)	74	680	88.2

4. DISCUSSION AND CONCLUSION

Due to the scarcity of ecological information available so far for the study area, our results should be considered a first approach to the potential effects of the global warming in Pantepui. SAR estimates are congruent , but EAR ones are not (Table 1). Given the higher correlation coefficient of EA'R1, this equation is tentatively preferred to EAR2. Estimates of potential extinction for endemic species based on EAR are consistently higher than those obtained using ARD (Tables 1, 2 and 3). This would be due to the fact that ARD only measures habitat loss, while EAR implicitly includes other ecological forcings into play. It should be noted that both PAR and PAA are merely spatial components of the corresponding species' niches, so they should be considered as maximum (habitat) conditions for life. The inclusion of other components, such as substrate availability and biotic interactions, would constrain the potential niche and reduce the survival expectation. Other possible warming-related causes of extinction are secondary extinction, due to the extinction of dominant and keystone species (Ebenman & Jonsson, 2005), and competitive exclusion because of the upward migration of successful invaders from lowlands and midlands (Clubbe, 1996). Hence, the potential extinction estimated according to PAR and PAA modeling should be viewed as a minimum expectation.

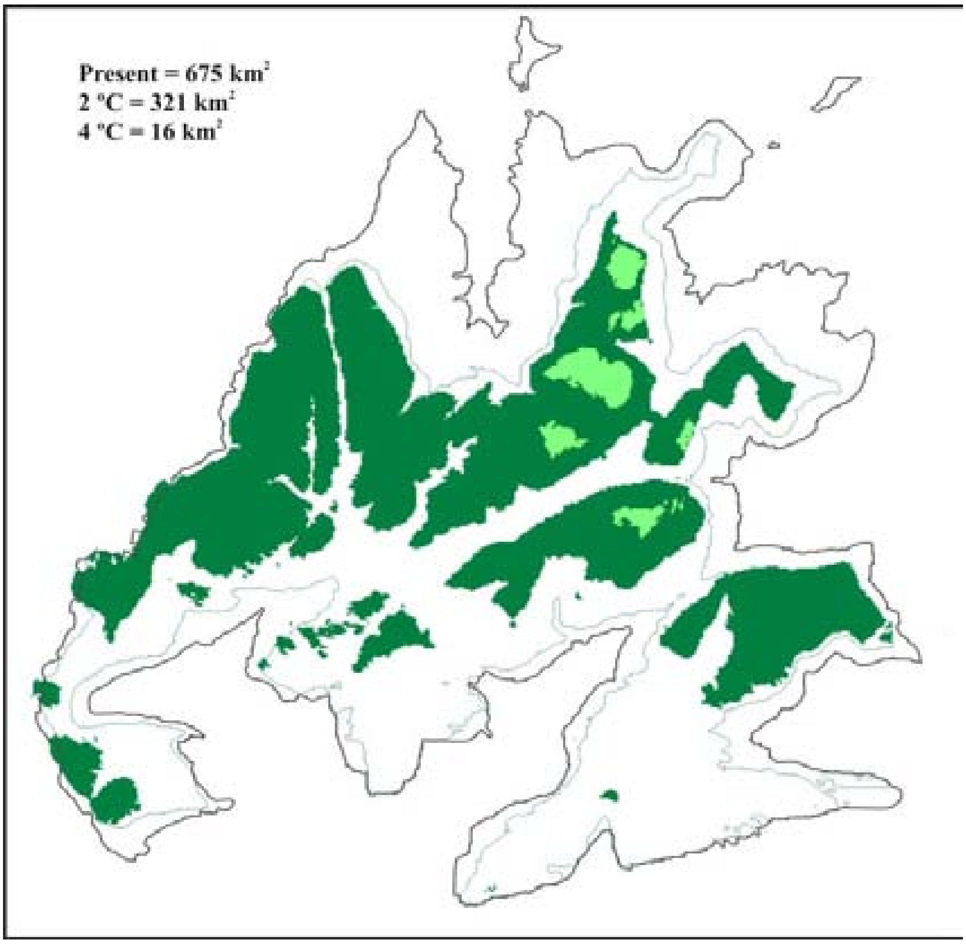


Figure 3. Projected Available Area (PAA) for AD 2100 using GIS modelling. The external solid contour is the Pantepui lower boundary (1500 m elev.), the dashed contour is the present-day Lower Distributin Limit (LDL) of the involved species, the dark-gray area is the PAA considering a 2 ºC warming, and the light-gray area is the PAA for a 4 ºC increase. The surface values for each situation are indicated. This example illustrates the case of 6 species of *Chimantaea* (Asteraceae), a genus endemic to the Chimantá massif and some adjacent tepuis.

In summary, according to the SAR/EAR models, the expected extinction by global warming for Pantepui vascular plant species by AD 2100 is of the order of 80% (> 1700 species), and the extinction of Pantepui endemics would be between around 30-50% (ca. 200 to 400 species). The risk of total habitat loss would affect between 20% and 45% of endemics (ca. 170 to 340 species), which have been identified individually. The relatively flat topography of the tepui summits (Fig. 2) is a crucial differential feature that enhances habitat loss because it prevents the threatened species to migrate upwards (Rull & Vegas- Vilarrúbia, 2006). Moreover, the PAA maps obtained should be analyzed to evaluate potential additional extinction risk by critical habitat reduction and fragmentation. Pantepui is considered to be an important speciation center for the Guayana and the Amazon regions (Rull, 2005). Therefore, a reduction of 70-90% in its surface, as predicted by our analyses, would seriously compromise the capacity of generating new biodiversity in the future (Rosenzweig, 2001).

The conclusions of this study are preliminary and should be revised in the future, when more environmental and biological data are available for Pantepui. However, the danger is real and preliminary estimations such as those presented here are necessary to start planning biodiversity conservation policies. The next step is to classify the endangered species according to the international conservation criteria (IUCN, 2001; Miller *et al*, 2007), a task which is now in progress (Nogué *et al*, 2008). Futher developments include the *in situ* periodical monitoring of upward displacement using standradized methodologies, under the framework of the GLORIA network (http://www.gloria.ac.at/)

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7. SUPPLEMENTARY MATHERIAL 4

Supplementary material 4.1 Results of ARD analysis for all the Pantepui endemic species, considering the two IPCC extreme scenarios for AD 2100. The values are the number of species of each family that would be extinct by habitat loss. The complete species list is provided as supplementary material. Abbreviations: Asp = Aspleniaceae, Cae = Caesalpinaceae, Cap = Capriofilaceae, Cya = Cyatheaceae, Dio = Dioscoreaceae, Dry = Dryopteridaceae, Ela = Elaeocarpaceae, Fab = Fabaceae, Fla = Flacourtiaceae, Hug = Hugoniaceae, Hym = Hymenophyllopsidaceae, Hyme = Hymenophyllaceae Iri = Iridaceae, Iso = Isoëtaceae, Len = Lentibulariaceae, Lyc = Lycopodiaceae, Lyt = Lythraceae, Mag = Magnoliaceae, Mim = Mimosaceae, Nyc = Nyctaginaceae, Oxa = Oxalidaceae, Pol = Polygalaceae, Pte = Pteridaceae, Rha = Rhamnaceae, Ros = Rosaceae, Sap = Sapindaceae, Sol = Solanaceae, Sty = Styracaceae, The = Thelypteridaceae, Thy = Thymeleaceae, Verb = Verbenaceae, Voc = Vochysaceae.

Family	2ºC	4ºC
Asteraceae	15	31
Bromeliaceae	14	29
Orchidaceae	12	20
Rubiaceae	10	21
Eriocaulaceae, Melastomataceae	9	19
Araliaceae, Ericaceae	7	15
Asclepiadaceae, Gentianaceae	7	13
Aquifoliaceae	5	8
Bonnetiaceae	4	8
Cyperaceae	4	6
Ochnaceae, Piperaceae	4	5
Clusiaceae	3	5
Lauraceae, Myrtaceae, Xyridaceae	3	6
Rapateaceae	3	7
Apocynaceae, Campanulaceae	2	2
Cunoniaceae, Grammitidaceae, Sarraceniaceae	2	3
Euphorbiaceae	2	6
Myrsinaceae	2	5
Poaceaea	2	9
Cya, Dio, Hug, Hyme, Iso, Len, Mim, Nyc, Pte, Thy	1	1
Fab, Rha, Sty, The, Voc	1	2
Malpighiaceae, Selaginellaceae	1	3
Rutaceae	1	4
Acantaceae, Proteaceae,Viscaceae	0	2
Asp, Cae, Cap, Dry, Ela, Fla, Hym, Iri, Lyc, Lyt, Mag Oxa, Pol, Ros, Sap, Sol, Ver	0	1
Total	166 (22.0%)	343 (45.5%)

Supplementary material 4.2 List of the Pantepui endemic species threatened of total habitat loss under a 4 ºC warming, according to ARD analysis. Crosses indicate the species that lose their habitat even with a warming of 2 ºC. The tepuis in which each species occurs at present is also indicated (abbreviations as in Figure 1).

Families	Endemic species	2ºC	Tepuis
Acanthaceae	*Justicia huberi*		Ma
	Justicia paruana		Cu, Si, Pr
Apocynaceae	*Aspidosperma glaucum*	+	Si
	Mandevilla aracamunensis	+	Ar, Av
Aquifoliaceae	*Ilex apicidens*	+	Kn, Ro
	Ilex parvifructa	+	Gu
	Ilex ptariana		Ro, Pt
	Ilex summa	+	Kw, An, Ay
Araliaceae	*Schefflera argophylla*		Ma
	Schefflera auyantepuiensis		Ay
	Schefflera brachypodia	+	Ma
	Schefflera contracta		Ja
	Schefflera dissidens	+	Ro
	Schefflera gracillima		Ja
	Schefflera guanayensis		Gy
	Schefflera hitchcockii		Co, Yt, Yv
	Schefflera marahuacensis	+	Mk
	Schefflera paruana		Pr
	Schefflera sipapoensis		Cu, Si
	Schefflera steyermarkii		Ja
	Schefflera umbellata	+	Il-Tr, Kn, Ro
Asclepiadaceae	*Blepharodon magualidae*		Ma
	Cynanchum chimantensis		Ch
	Cynanchum paraquense		Cu, Si
	Ditassa acerifolia	+	Yv
	Ditassa colellae		Ch
	Ditassa duidae		Du, Mk
	Ditassa juliani		Du, Mk
	Ditassa obovata		Co, Pt
	Ditassa olivaestevae	+	Du, Mk
	Ditassa ottohuberi	+	Co, Yt
	Ditassa roraimensis	+	Ro, Il-Tr, Kw
	Ditassa sipapoana	+	Si
	Matelea fucata		Pr
Aspleniaceae	*Asplenium cowanii*		Pr
Asteraceae	*Achnopogon steyermarkii*		Ay
	Baccharis densa	+	Du, Il-Tr, Kn, Ro, Mk
	Calea camani	+	Ca
	Calea esposi		Gy
	Calea phelpsiae	+	Yv
	Calea politii	+	Si
	Calea sp. A		Sa
	Calea sp. C	+	Co
	Calea sp. E	+	Co
	Chimantaea lanocaulis		Mu, Ch

	Chimantaea rupicola		Ch
	Chionolaena latifolia		Mk
	Chromolaena ternicapitulata	+	Ma
	Duidaea marahuacensis		Du, Mk
	Glossarion bilabiatum		Nb
	Gongylolepis paruana	+	Pr
	Huberopappus maigualidae	+	Ma
	Lepidaploa auyantepuiensis		Ay
	Piptocarpha jauaensis		Ja
	Piptocoma areolata		Cu, Si
	Quelchia conferta		Ro, Kn, Yu, Il-Tr
	Quelchia eriocaulis		Ch
	Quelchia x grandifolia		Ch
	Stenopadus jauensis		Ja
	Stomatochaeta acuminata	+	Ag
	Tyleropappus dichotomus		Du, Mk
	Verbesina angusta		Ch
Bonnetiaceae	*Bonnetia bolivarensis*	+	Pt
	Bonnetia chimantensis		Ay, Ap, Ch
	Bonnetia euryanthera	+	Ja
	Bonnetia fasciculata		Ch
	Bonnetia liesneri	+	Ar, Av
	Bonnetia ptariensis	+	Pt
	Bonnetia roseiflora		Ja
Bromeliaceae	*Brewcaria marahuacae*	+	Mk
	Brocchinia hitchcockii	+	Pr
	Connellia caricifolia		Ro, Kn, Yu, Il-Tr
	Connellia varadarajanii		Ay
	Lindmania arachnoidea		Mk
	Lindmania argentea		Ch
	Lindmania cylindrostachya		Yt, Gy
	Lindmania maguirei		Ar, Av, Nb
	Lindmania marahuacae	+	Du, Mk
	Lindmania phelpsiae	+	Pr
	Lindmania riparia		Ay
	Lindmania saxicola	+	Ch
	Lindmania simithiana		Ay
	Lindmania sp. C	+	Ap
	Lindmania steyermarkii		Ch
	Lindmania tillandsioides		Ch
	Navia colorata		Pr
	Navia incrassata		Ja
	Navia involucrata	+	Pr
	Navia lactea		Cu, Si
	Navia lanigera	+	Ca
	Navia lasiantha		Ja
	Navia mima		Cu, Si
	Navia patria	+	Ar, Av
	Navia terramarae	+	Ar, Av
	Pitcairnia kunhardtiana		Cu, Si
	Pitcairnia phelpsiae	+	Yv
	Steyerbromelia discolor	+	Du, Mk
Campanulaceae	*Siphocampylus* sp. A	+	Ma
	Siphocampylus tillettii	+	Du, Mk
Capriofilaceae	*Viburnum* sp.A		Ch

Clusiaceae	*Clusia duartei*		Cu, Si
	Clusia phelpsiae		Yv
	Clusia radiata	+	Gy
	Hypericum roraimense	+	Ro
Cunoniaceae	*Weinmannia corocoroensis*	+	Co
	Weinmannia guyanensis		Ch, Ro
	Weinmannia ilutepuiensis		Il-Tr
	Weinmannia laxiramea		Ro, Kn, Ch
Cyatheaceae	*Cyathea liesneri*	+	Ar, Av
Cyperaceae	*Carex marahuacana*	+	Du, Mk
	Cephalocarpus dracaenula		Ay
	Eleocharis atrospiculata		Du, Mk
	Everardia lanata	+	Ch
	Everardia maguireana	+	Ar,Av, Nb
	Everardia vareschii		Ay, Ch, Yt
	Rhynchospora pallida	+	Ca
Dioscoreaceae	*Dioscorea sororopana*	+	So, Pt
Dryopteridaceae	*Elaphoglossum steyermarkii*		Ch
Elaeocarpaceae	*Sloanea carrenoi*		Ja
Ericaceae	*Bejaria imthurnii*	+	Kn, Ro
	Bejaria neblinensis		Ar, Av, Nb
	Gaultheria setulosa	+	Du, Il, Kn, Mk, Ro
	Ledothamnus jauaensis		Ja
	Ledothamnus sessiliflorus	+	Kr, Il-Tr, Kn, Ue
	Mycerinus sclerophyllus		Du, Mk
	Notopora auyantepuiensis		Ay
	Notopora chimantensis		Ch
	Tepuia intermedia		Ay
	Tepuia vareschii		Ay
	Thibaudia breweri		Ja
	Thibaudia carrenoi		Ja
	Thibaudia smithiana		Si
	Vaccinium chimantense		Kw, Ty, Mu, An, Ch
	Vaccinium steyermarkii	+	Ch
Eriocaulaceae	*Eriocaulon jauense*		Ma, Yt, Co, Ja
	Leiothrix celiae	+	Yt
	Paepalanthus apacarensis	+	Ch
	Paepalanthus auyantepuiensis	+	Ay
	Paepalanthus cardonae		Ch
	Paepalanthus cristatus		Ay
	Paepalanthus cumbricola		Ch
	Paepalanthus chimantensis		Ch
	Paepalanthus fraternus		Ro, Kn, Il-Tr
	Paepalanthus holstii	+	Mu
	Paepalanthus phelpsiae		Ja
	Paepalanthus roraimense		Ro
	Rondonanthus caulescens	+	Ap
	Rondonanthus flabelliformis	+	Ch
	Rondonanthus roraimae		Ro, It, Kn, Yu
	Syngonanthus macrocephalus	+	Si
	Syngonanthus minutus	+	Ay
	Syngonanthus tiricensis		Ap, Ch
Euphorbiaceae	*Phyllanthus carrenoi*		Ja, Sa
	Phyllanthus chimantae		Ch
	Phyllanthus jauaensis		Ja

	Phyllanthus minutifolius	+	Si
	Phyllanthus paraqueensis		Cu, Si
	Phyllanthus ventuarii	+	Pr
	Plukenetia multiglandulosa		Pr
Fabaceae	*Aldina elliptica*		Yt
	Dioclea rigida	+	Pr
Flacourtiaceae	*Euceraea sleumeriana*		Sa
Gentianaceae	*Irlbachia phelpsiana*		Pr
	Macrocarpaea marahuacae	+	Mk
	Macrocarpaea piresii		Nb
	Macrocarpaea rugosa		Ch
	Saccifolium bandeirae	+	Nb
	Schultesia subcrenata	+	Ro
	Sipapoantha ostrina		Si
	Symbolanthus aureus	+	Il-Tr
	Symbolanthus sessilis		Ja
Grammitidaceae	*Ceradenia arthrothrix*	+	Mk
	Ceradenia fragillima	+	Ro
	Grammitis sp. A		Kw
Hugoniaceae	*Roucheria* sp. A		Si
Hymenophyllopsidaceae	*Hymenophyllopsis universitatis*		Ay, An, Kw, Ty, Mu
Hymenophyllaceae	*Hymenophyllum* sp. A	+	Kn
Iridaceae	*Trimezia chimantensis*		Ch
Isoëtaceae	*Isoëtes vermiculata*	+	Mk
Lauraceae	*Ocotea atrata*	+	Si
	Ocotea cowaniana	+	Pr
	Ocotea glabra		Kr, Cr
	Ocotea roseopedunculata		Ch
	Ocotea sp. A	+	Ty, Mu
	Ocotea venosa		Du, Mk
Lentibulariaceae	*Utricularia mirabilis*		Cu, Si
Lycopodiaceae	*Huperzia huberi*		Ay, Ch, Yv, Si
Lythraceae	*Cuphea maigualidensis*		Ma
Magnoliaceae	*Dugandiodendron ptaritepuianum*		Ro, Pt, Ma
Malpighiaceae	*Byrsonima huberi*		Ma
	Diacidia stipularis		Pr
	Pterandra flavescens		Cu, Si
Melastomataceae	*Chaetolepis anisandra*		Ro, Ay, Yt, Co
	Ernestia maguirei		So, Pt, Ay
	Graffenrieda cinnoides		Si
	Graffenrieda jauana		Ja
	Henriettella heteroneura		Si
	Leandra gorzulae	+	Ma
	Macrocentrum angustifolium		Si
	Macrocentrum huberi	+	Ma
	Macrocentrum maguirei		Yu, Co
	Mallophyton chimantense		Ch
	Miconia cacumina		Ro
	Miconia huberi	+	Il-Tr
	Miconia neblinensis		Ar, Av, Nb
	Microlicia guanayana		Gy
	Tibouchina sipapoana	+	Si
	Tibouchina steyermarkii		Ja
Mimosaceae	*Inga bijuga*	+	Pt, So

Myrsinaceae	*Cybianthus crotonoides*		Cr, Pt, Ty, Mu, An, Ay, Kw
	Cybianthus julianii	+	Du, Mk
	Cybianthus sipapoensis		Cu, Si
	Cybianthus wurdackii		Pt, Ay, Ch
Myrtaceae	*Marlierea foveolata*		Ma
	Myrcia compta		Cu , Si
	Myrcia induta	+	Pr
	Myrcia kylistophylla		Ja, Ma
Nyctaginaceae	*Neea guiquinimae*	+	Gu
Ochnaceae	*Adenarake macrocarpa*		Cu, Si
	Ouratea obovata		Cu, Si
	Ouratea paruensis		Pr
	Tyleria breweriana	+	Ja
	Tyleria phelpsiana		Ja
Orchidaceae	*Aracamunia liesneri*	+	Ar
	Brachionidium julianii	+	Mk
	Cleistes huberi		Ro, Kn, Yu, Il-Tr, An
	Dryadella lueriana	+	Gu
	Epidendrum alsum	+	Ro
	Epidendrum montigenum	+	Ro, Kn, Il-Tr, Ch
	Epidendrum stalkyi		Ja
	Helonoma chiropterae	+	Du, Mk
	Lepanthes marahuacensis	+	Du, Mk
	Lepanthes unitrinervis	+	Ro, Il-Tr
	Liparis verticillata	+	Kn
	Maxillaria colemanii	+	Ve
	Octomeria anomala	+	Du, Mk
	Octomeria connellii	+	Il-Tr, Ro
	Octomeria dentifera		Ro, Ch
	Octomeria monticola	+	Kn, Ro
	Octomeria sp. A		Cu, Si
	Octomeria splendida		Ja, Sa
	Pleurothallis callifera		Pt, Ch
	Pleurothallis rhombipetala	+	Ro
	Prescottia auyantepuiensis		Ay
	Trichosalpinx oxychilos		Ja
	Trichosalpinx steyermarkii		Ay
Oxalidaceae	*Biophytum* sp. B		Gy
Piperaceae	*Peperomia delascioi*		Du, Il, Mk, Ro
	Peperomia marahuacensis	+	Mk
	Peperomia yutajensis		Co, Yt
	Piper mosaicum	+	Ar
	Piper subalpinum	+	So, Cr, Pt
Poaceae	*Aulonemia chimantaensis*		Ch
	Aulonemia deflexa		Ro, Pt, It
	Aulonemia jauaensis		Ja
	Aulonemia sp. C	+	Du, Mk
	Axonopus gracilis		Cu, Si, Yt
	Axonopus magallanesiae		Ja
	Dichanthelium telmatun		Ay, Il, Ue
	Myriocladus involutus		Ch
	Neurolepis diversiglumis		Ar, Av, Nb
	Panicum jauanum		Ja
Polygalaceae	*Polygala sipapoana*		Si, Cu

Proteaceae	*Panopsis ornatinervia*		Ch
	Roupala paruensis	+	Pr
	Roupala sororopana		Ro, So, Ay, Ch
Pteridaceae	*Pterozonium retroflexum*	+	Mk
Quinaceae	*Froesia gereauana*		Si
Rapateaceae	*Epidryos* sp. A		Cu, Si
	Marahuacaea schomburgkii		Mk
	Stegolepis huberi	+	Ro, Kn
	Stegolepis jauaensis		Ja, Sa
	Stegolepis microcephala		Ja
	Stegolepis terramarensis	+	Du, Mk
Rhamnaceae	*Rhamnus longipes*	+	Pr
	Rhamnus marahuacensis		Du, Mk
Rosaceae	*Prunus espinozana*		Ja
Rubiaceae	*Chiococca auyantepuiensis*		Ay
	Chiococca lucens	+	So
	Coccochondra laevis		Ma, Pr
	Malanea jauaensis		Ja, Sa
	Merumea coccocypseloides		Cu, Si
	Neblinathamnus brasiliensis	+	Ar, Av
	Pagamea diceras	+	Pr
	Pagamea magniflora	+	Il-Tr
	Palicourea ottohuberi	+	Ma
	Palicourea pensilis		Ch
	Palicourea wurdackiana		Ma, Yu
	Psychotria carrenoi		Ja
	Psychotria celiae		Nb
	Psychotria cerronis		Ja, Sa
	Psychotria oblita		Ar, Av, Il-Tr, Ro, Yu
	Psychotria phelpsiana	+	Sa
	Remijia aracamuniensis	+	Ar, Av
	Remijia sipapoensis		Cu, Si
Rutaceae	*Raveniopsis capitata*		Ja, Pr
	Raveniopsis fraterna		Ch
	Raveniopsis paruana	+	Pr
	Raveniopsis tomentosa		Ay
Sarraceniaceae	*Heliamphora elongata*	+	Il-Tr
	Heliamphora folliculata		An, Mu, Ty, Kw
	Heliamphora ionasii	+	Il-Tr
Selaginellaceae	*Selaginella marahuacae*	+	Mk
	Selaginella rhodostachya		Ro, Kn
	Selaginella tyleri		Du
Solanaceae	*Solanum tepuiense*		Pr, So
Styracaceae	*Styrax guanayanus*		Ja, Gy
	Styrax sipapoanus		Cu, Si
Thelypteridaceae	*Thelypteris binervata*	+	Du, Mk
	Thelypteris pilosissima		Ro
Thymeleaceae	*Daphnopsis guaiquinimae*	+	Gu
Verbenaceae	*Duranta* sp.A		Ch
Viscaceae	*Dendrophthora densifrons*		Ro, Ch
	Dendrophthora microsoma		Ja
Vochysaceae	*Vochysia ortegae*		Cu, Si
Xyridaceae	*Abolboda dunstervillei*	+	Ar, Av
	Xyris aracamunae	+	Ar
	Xyris concinna	+	Ro, It, Kn, Ue

Xyris consolida		Pt, Ue
Xyris kukenaniana	+	Kn
Xyris schneeana		Ch
Xyris toronoana		Ch

Supplementary material 4.3 Results of ARD analysis applied to each tepui individually. The number of present-day endemic species, and those under risk of extinction by habitat loss at the two extreme scenarios of the IPCC for AD 2100 are given.

Tepui	present	extinct (2ºC)	%	extinct (4ºC)	%
Chimantá	212	8	3.8	46	21.7
Neblina	158	3	1.9	9	5.7
Auyán	132	4	3.0	31	23.5
Roraima	113	17	15.0	36	31.9
Marahuaka	87	24	27.6	35	40.2
Jaua	67	4	5.9	40	59.7
Ilú-Tramén	64	14	21.9	22	34.4
Sipapo	56	30	53.6	37	66.1
Kukenán	54	12	22.2	20	37.0
Ptarí	54	3	5.6	13	24.1
Duida	44	6	13.6	15	34.1
Parú	29	13	44.8	23	79.3
Yutajé	25	2	8.0	15	60.0
Aprada	22	2	9.1	5	22.7
Sororopán	20	4	20.0	10	50.0
Aparamán	18	1	5.6	7	38.9
Aracamuni	17	9	52.9	9	52.9
Kamarkawarai	17	3	17.6	7	41.2
Yuruaní	17	2	11.8	7	41.2
Murisipán	16	2	12.5	6	37.5
Guanay	16	1	6.3	8	50.0
Coro-coro	15	7	46.7	9	60.0
Huachamacari	14	5	35.7	8	57.1
Yaví	14	4	28.6	8	57.1
Sarisariñama	14	2	14.3	11	78.6
Guaiquinima	13	4	30.8	4	30.8
Carrao	9	4	44.4	6	66.7
Angasima	9	1	11.1	1	11.1
Karaurín	9	1	11.1	2	22.2
Cuao	7	1	14.3	5	71.4
Camani	5	4	80.0	4	80.0
Uei	5	2	40.0	3	60.0

6. CAPÍTOL 5

Quantifying the global warming threats to vascular plants of the remote Guayana Highlands

Heliamphora nutans

The contents of this chapter are in preparation to be sumitted as:

Nogué, S., Vegas-Vilarrúbia, T., Rull, V., Safont, E. & Huber, O Quantifying the global warming threats to vascular plants of the remote Guayana Highlands

ABSTRACT

To analyse the effects of global warming on the endemic vascular plants of the Guayana Highlands (GH), located in northern South America, we used several methods. First, we applied the Altitudinal Range Displacement (ARD) analysis. The ARD is a tool that uses the present-day lapse rate to estimate the upward migration of the species based on the global warming predicted by the IPCC, and allows to estimate the potential habitat loss of each specie. Second, we developed future landscape reconstructions of the expected upward displacement using GIS modeling, which was then analysed using FRAGSTATS at a landscape level. Five fragmentation indexes were determined: total area, number of patches, larger patch index (LPI), landscape division index (LSI) and landscape shape index (LDI). Considering the warmest scenario predicted, 40 % of the endemic species would be at risk of habitat loss. Among these species there are endemic genera from this region. All the species threatened by total habitat loss would be classified as critical endangered by the IUCN. Fragmentation analysis showed that the current GH landscape is fragmented (the values of LSI and LDI are the highest) and that future changes in landscape configuration would not increase habitat fragmentation. The decreasing trend of these two indexes suggests a reduction in the complexity of the landscape. The highest LPI index is obtained in the warmest scenario, which determines that the 46 % of the remaining habitat would be comprised in one patch coinciding with the Chimantá massif.Combined *in situ* and *ex situ* conservation actions are proposed.

1. INTRODUCTION

During the past two centuries, the so-called Anthropocene, an acceleration of the warming of the planet, has taken place, caused in part by human activities (Crutzen & Stoermer, 2000). In the last 140 years global average temperatures have already risen 0.6 ºC, and they continue to increase (Houghton *et al*, 2001). There is now substantial evidence linking the present climate change to biological responses to warming, such as variations in species distributions, abundances and extinctions (Hughes, 2000; Parmesan & Yohe, 2003; Root *et al*, 2003; Solomon *et al*, 2007). In mountain biomes, the projected consequence of global warming is an upward biotic migration of 500 to 700 m as a result of the altitudinal displacement of suitable environmental conditions (Hughes, 2000). As a consequence, species inhabiting the highest elevations are threatened with habitat loss and fragmentation (Grabherr *et al*, 1994; Gottfried *et al*, 1999; Araújo & Rahbek, 2006; Lenoir, 2008; Sekercioglu *et al*, 2008). Several studies have modelled future species distributions according to the predictions of the Intergovernmental Panel on Climate Change (IPCC), projecting a high risk of extinction due to habitat loss by the end of the century. A study based on bioclimatic envelopes applied to different biomes from tundra to tropical forest estimates that by 2050 between 15 and 37% of species may go extinct for the above reason (Thomas *et al*, 2004). Also, Williams *et al* (2003) suggest that with a 3.5 ºC temperature increase, Australian endemic rainforest vertebrates will undergo dramatic declines in distribution.

Currently, there are some attempts to use the International Union of Conservation of Nature (IUCN) Red List criteria to categorize extinction risk due to global warming (Thomas *et al*, 2004; Shoo *et al*, 2005; Thuiller *et al*, 2005). For example, it is expected that 22% of European plants will become critically endangered and 2% extinct by 2080 (Thuiller *et al*, 2005). The IUCN Red List of threatened species is an essential source of information to guide conservation efforts, and represents a significant advance in the risk classification of threatened species (Keith *et al*, 2000; Lamoreux *et al*, 2003; Rodrigues *et al*, 2006). Studies which apply the IUCN Red List criteria to their projections are important for providing a perspective on the species level impacts of expected changes.

The Guayana Highlands (GH) in northern South America, also known as Pantepui, are known for their peculiar table mountains locally called *tepuis* (Huber, 1987). It is a unique place due to the striking degree of biodiversity and endemism in both plants (Berry & Riina, 2005) and different animal groups (Mayr & Phelps, 1967; Huber, 1992 b). The largely undisturbed biota, as evidenced by the very low number of introduced species in the flora (Huber, 1995b), is also exceptional. Except for some tourism mainly on the Roraima and Auyán tepui mountains, human activities are practically nonexistent (Huber, 1995b). Paleoecological data also show evidence of no human perturbations during the last 12000 years, including fire events (Huber, 2001; Rull, 2005; Chapter 1) which are typical of other mountain tops (Halloy & Mark, 2003).

The potential consequences of global warming for the GH vascular flora have been recently studied using the species-area relationship (SAR) and the simple Altitudinal Range Displacement (ARD) analysis (Rull & Vegas-Vilarrúbia, 2006; Nogué *et al*, 2009). Estimates presented in the first study using the ARD methodology indicate that up to 45% of the species within a selected group of genera will lose their habitat by 2100, owing to ongoing global warming (Rull & Vegas-Vilarrúbia, 2006). A more comprehensive study using SAR predicted an extinction of more than 1700 species in the GH (Nogué *et al*, 2009). In addition to habitat loss, habitat reduction and fragmentation is expected to occur to a greater extent on tabular tepuis than on other conical mountains (Rull & Vegas-Vilarrúbia, 2006). In this study, we assess the potential extinction vulnerability of the endemic vascular plants of the entire GH area due to the expected upward displacement of suitable habitat conditions as a result of global warming. We used the ARD, as this methodology has been successively applied in the GH and is especially well suited for evaluating the effect of the upward migration on mountain ecosystems (Rull & Vegas-Vilarrúbia, 2006; Raxworthy *et al*, 2008; Sekercioglu *et al*, 2008; Nogué *et al*, 2009). The objectives of this paper are: a) to evaluate the risk of extinction by habitat loss over different periods of time (between the present day and 2030, 2065 and 2099) predicted in the last IPCC assessment (Solomon *et al*, 2007), b) to analyse habitat fragmentation at a landscape level and c) to classify threatened species according to the current IUCN criteria.

2. MATERIAL AND METHODS

2.1 Study area

The GH and the tropical Andes are the highest mountain regions located around the Amazonian basin in northern South America (Fig 1). The majority of the GH summits form the Pantepui biogeographical province, which is about 6000 km^2 in area with a 1500-3014 m elevation range (Huber, 1988). Pantepui's main physiographic characteristic is the assemblage of isolated table mountains or tepuis. The tepuis are remnants of ancient erosion surfaces of the Precambrian sandstone Roraima Formation (Briceño & Schubert, 1990). Four main phytogeographical districts have been defined within Pantepui (Fig 1): Eastern (E), Jaua Duida (JD), Western (W) and Southern (S) (Berry *et al*, 1995).

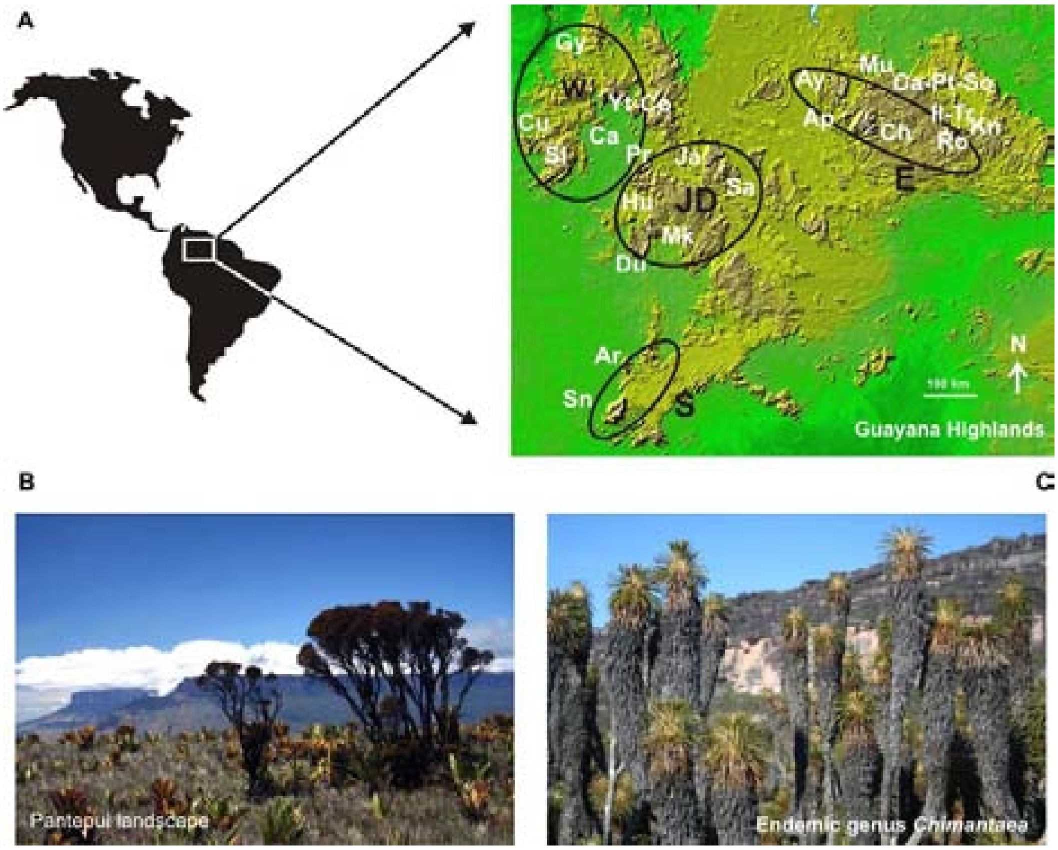

Figure 1. Location map. A) On the left: Geographic location of the Guayana Highlands (GH) (square); on the right: radar image of the GH showing the tepuis involved in the analysis and the districts. B) Typical Pantepui landscape. C) Typical paramoid shrubland with a community dominated by *Chimantaea* (endemic genus) on the Chimantá massif (Photos: S. Nogué).

The tepui summits are characterised by extreme bioclimatic and environmental conditions, including a high total annual average precipitation (2500 to 4000 mm), strong trade winds (50 km/h), high solar radiation and highly acidic soils (Huber, 1995a). Historical expeditions have demonstrated the region's exceptional degree of biodiversity and endemism (Steyermark *et al*, 1995-2005). There are 630 vascular plant genera (23 GH endemics) and 2446 species, of which 31.5 % are endemic to the GH; amazingly, only 0.4 % of the GH endemics species are present on all tepuis (chapter 3). There are 23 endemic genera: *Achnopogon* (Asteraceae), *Achlyphila* (Xyridaceae), *Adenanthe* (Ochnaceae), *Adenarake* (Ochnaceae), *Aracamunia* (Orchidaceae), *Brewcaria* (Bromeliaceae), *Celiantha* (Gentianaceae), *Chimantaea* (Asteraceae), *Coccochondra* (Rubiaceae), *Comoliopsis* (Melastomataceae), *Coryphothamnus* (Rubiaceae), *Glossarion* (Asteraceae), *Huberopappus* (Asteraceae), *Mallophyton* (Melastomataceae), *Marahuacea* (Rapateaceae), *Neblinantha* (Gentianaceae), *Ochthephilus* (Melastomataceae), *Pyrrorhiza* (Haemodoraceae), *Quelchia* (Asteraceae), *Rutaneblina* (Rutaceae), *Saccifolium* (Saccifoliaceae), *Tepuia* (Ericaceae) and *Tyleropappus* (Asteraceae). Plant communities are mostly montane shrublands dominated by Melastomataceae, Ericaceae, Asteraceae and Rubiacaea. Among the herbaceous communities, the more extensive ones are grasslands and meadows dominated by *Stegolepis* (Rapateaceae) and *Rhynchocladium* (Cyperaceae), respectively. Gallery forests, mostly situated along rivers and creeks, are dominated by *Bonnetia* (Bonnetiaceae), *Podocarpus* (Podocarpaceae) and *Schefflera* (Araliaceae). Colonising communities grow on open rocks and are composed mainly of algae and lichens (Huber, 1992 a)

2.2 Data source

The phytogeographic data necessary for this analysis were obtained from the PANTEPUI database (Chapter 3), which is based on the Flora of the Venezuelan Guayana (Steyermark *et al,* 1995-2005). The analyses presented here use a subset of these data containing the 771 GH endemic species. We selected for further analysis the lower altitudinal limit (LAI), the highest altitude limit (HAL) and the highest potential habitat (HPH), represented by the highest tepui summit within the present geographical range of each species. Current climatic data were obtained from Galán (1992), including the Guayana adiabatic lapse rate of -0.6 ºC/100 m elevation. Future temperature projections were derived from the IPCC warming scenarios known as B1, A1B and A2 (Solomon *et al*, 2007). Among them, we considered the two extreme cases B1 and A2 in order to include the whole range of expected variability. The temperature increases predicted for northern South America for three time periods (between the present day and 2030, 2065 and 2099) are: B1) 1, 2 and 2.5 ºC and A2) 1, 2.5 and 4 ºC, respectively.

2.3 Endemic species and the Altitudinal Range Displacement (ARD) analysis

To implement the ARD analysis, it is necessary to define the LAI and the HPH of each endemic species. The objective of the ARD analysis is to estimate the habitat migration needed, in terms of altitudinal displacement, for a complete loss of habitat (UDHL). UDHL is defined as the difference between the HPH and the LAI (UDHL = HPH – LAI). The temperature increase corresponding to UDHL is deduced from the current adiabatic rate (-0.6 ºC/ 100 m). The use of this kind of analysis has increased in recent years in regions of the world where climatic and ecological data are scarce or nonexistent for the study area (Raxworthy *et al*, 2008; Sekercioglu *et al*, 2008; Rull & Vegas-Vilarrúbia, 2006; Nogué *et al*, 2009). The most recent previous study conducted for the GH calculated only the number of species that would suffer total habitat loss by the end of this century, assuming a temperature increase of 2 or 4 ºC (Nogué *et al*, 2009). In this paper, we go further, offering a dynamic analysis where we assess the risk of habitat loss for all the endemic species over the three previously defined time periods. Also, independently of predicted warming, we calculate when all the Pantepui endemic species would suffer total habitat loss and give the temperature required for this to occur.

2.4 Habitat fragmentation

Successive reconstructions of the expected upward displacement of the GH potential habitat are made for comparison purposes. These maps were created using ArcGis version 9.3 and include the following tepuis: Aprada, (Ap), Aracamuni (Ar), Auyán (Ay), Camani (Ca), Chimantá (CH), Cuao (Cu), Duida (Du), Guaiquinima (Gu), Guanay (Gy), Huachamacari (Hu), Ilú-Tramen (I-Tr), Jaua (Ja), Kukenán (Kn), Marahuaka (Mk), Murisipán (Mu), Parú (Pr), Ptarí (Pt), Roraima (Ro), Sarisariñama (Sa), Sipapo (Si), Sierra Neblina (Sn), Sororopán (So), Uei (Ue), Yaví (Yv) and Yutajé-CoroCoro (Yt-Co) (Huber, 1988). Te maps were then reclassified and resampled to permit area comparisons and imported as an ASCII file into FRAGSTATS version 3.3 (McGarigal *et al*, 2002). FRAGSTATS computes several statistic parameters (metrics) for the landscape as a whole. It is a suitable program for quantifying landscape composition and configuration (McGarrigal *et al*, 2002). We captured general uncorrelated landscape metrics to compare the expected successive habitat modifications due to temperature increase. The metrics were selected for calculating: 1) habitat loss (TA and NP), 2) the largest patch index (LPI) and 3) the landscape complexity (LSI and LDI). Total area (TA) and number of patches (NP) are measures describing landscape heterogeneity. Larger patch index (0 <= LPI <=100) is the percentage of the landscape that the largest patch comprises. Landscape division index (LDI) is 0 when the landscape consists of a single patch, achieving its maximum value when the landscape is maximally subdivided. Finally, the landscape shape index (LSI >=1) is a standardized measure, which increases with increasing landscape shape irregularity or increasing amount of edge (McGarrigal *et al*, 2002).

2.5 Classifying the threatened endemic species under the IUCN categories

The IUCN Red List Criteria (version 3.1, IUCN 2001) were applied to classify the endemic species threatened by habitat loss and fragmentation by 2100. Species were classified in three categories considering a 100 year time scale: Critically Endangered (CR), Endangered (EN) and Vulnerable (VU) (IUCN, 2001). The IUCN system measures the symptoms of extinction risk by considering five independent criteria relating to aspects of population loss and decline of habitat. We applied the B2 IUCN criteria, which consider as threatened those species with a very restricted geographical range or area of occupancy (AOO) showing the following symptoms: 1) severely fragmented or known to exist at one to ten locations and 2) a continuing area of occupancy decline (IUCN, 2001). Following these criteria, CR species have a projected area of less than 10 km^2, EN of less than 500 km^2 and VU of less than 2000 km^2 (IUCN, 2001).

3. RESULTS

Figure 2 depicts the increase in the number of species threatened with habitat loss by 2100. By 2030, equivalent to a 1ºC increase in global temperature under both scenarios (B1 and A2), 43 species (5.6 %) would be threatened with habitat loss (Table 2). Among them, the presence of a GH endemic genus with only one species, *Aracamunia liesneri*, is outstanding.

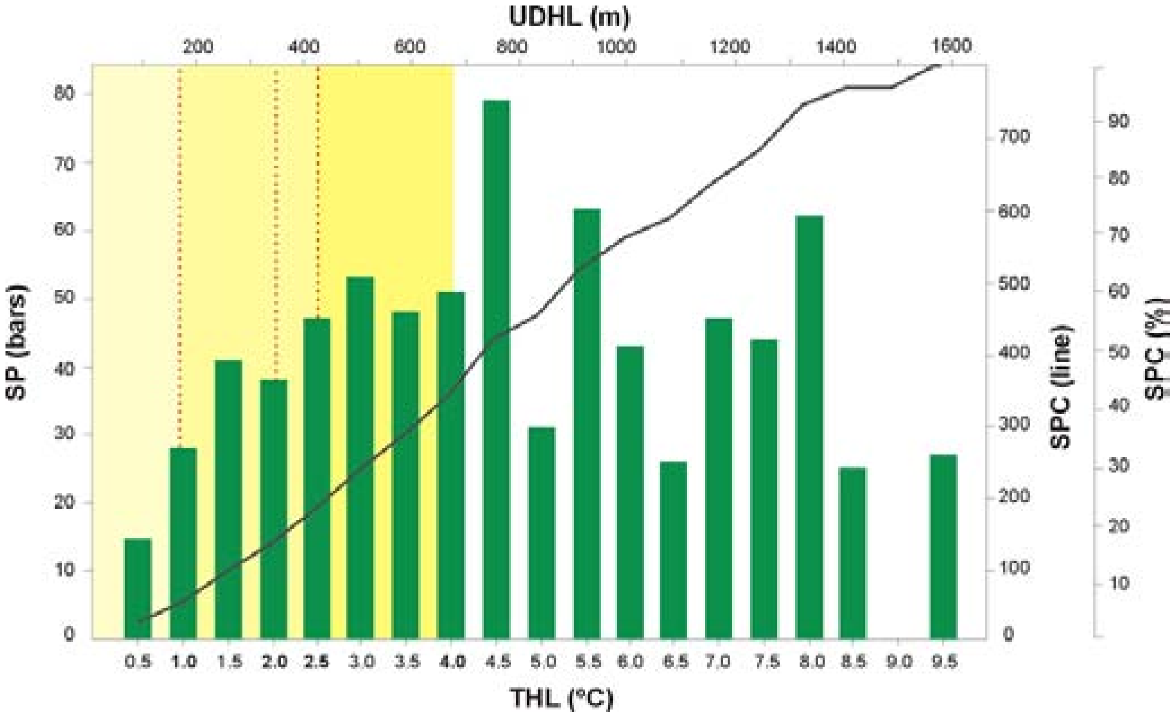

Figure 2. Graphical Altitudinal Range Displacement (ARD) analysis for calculating the risk of habitat loss for the GH's endemic species at 0.5ºC intervals. Bars represent the number of species that would lose the habitat for each interval (scale SPC), whereas continues line represents the accumulative values both in numbers and percentages (SPC scale). THL = temperature increase needed for the total habitat loss, UDHL = altitudinal displacement needed for the total habitat loss. The predicted warming for the three different periods of time (between the present and 2030, 2065 and 2099) are represented in broken lines for B1 and in shade of yellow for A2 scenario. Temperatures in bold are the maximum warming expected for each time interval.

The loss of endemics forecasted for 2065 depends on the scenario used. For B1 (2 ºC), 122 species (15.8%) become threatened while for A2 (2.5 ºC), 169 species become threatened (23%) (Table 2). Among them, some are particularly worth mentioning because of belonging to endemic genera: *Brewcaria marahuacae*, *Chimantaea lanocaulis*, *Coccochondra laevis*, *Glossarion bilabiatum*, *Huberopappus maigualidae*, *Marahuacea schomburkii*, *Saccifolium bandeirae* and *Tepuia vareschii*.

Table 2. Example of two IPCC scenarios (B1 and A2) and three time intervals (2030, 2065 and 2099) (Solomon *et al*, 2007). First two columns, represent the temperature increase expected by the IPCC by each time interval (Solomon *et al*, 2007). Last two columns are the number of threatened species by total habitat lose for each time interval.

Time-period	**B1 (ºC)**	**A2 (ºC)**	**Threatened species B1**	**Threatened species A2**
present	Current	Current	-	-
2030	1	1	43	43
2065	2	2.5	122	169
2099	2.5	4	169	321

Further temperature increases of 2.5 ºC (B1) and 4 ºC (A2) expected by 2099 would increase the number of threatened species, causing 169 (23%) and 321 (41.7%) species, respectively, to completely lose all potential habitats (Table, 2 and Fig 2). Among these species, ten belong to endemic genera: *Achnopogon steyermarkii*, *Adenarake macrocarpa*, *Celiantha imthurniana*, *Quelchia conferta*, *Q. eriocaulis*, *Q. grandifolia*, *Mallophyton chimantense*, *Saccifolium bandeirae*, *Tepuia intermedia* and *Tyleropappus dichotomus*.

None of the 771 species included in this model would have any potential habitat remaining after a 9.5 ºC temperature increase, representing a UDHL higher than 1500 m (Fig 2). Under the examined warming scenarios, between 450 and 602 species not threatened with total habitat loss by 2100, might be heavily affected by severe reduction and/or fragmentation of their habitats.

We present a map showing present-day GH conditions and three representing the successive shrinkage of habitats corresponding to the 1, 2, 2.5 and 4 ºC temperature increases predicted to occur over different time periods (Table 2 and Fig. 3) (Solomon *et al*, 2007). The predicted changes in the total available area are complex and dramatic (Figs 3 A-3 E). Changes are significant (40% of habitat lost) even with a 1ºC increase in global temperature, which is the expected warming by 2030 under both B1 and A2 scenarios (Table 3).

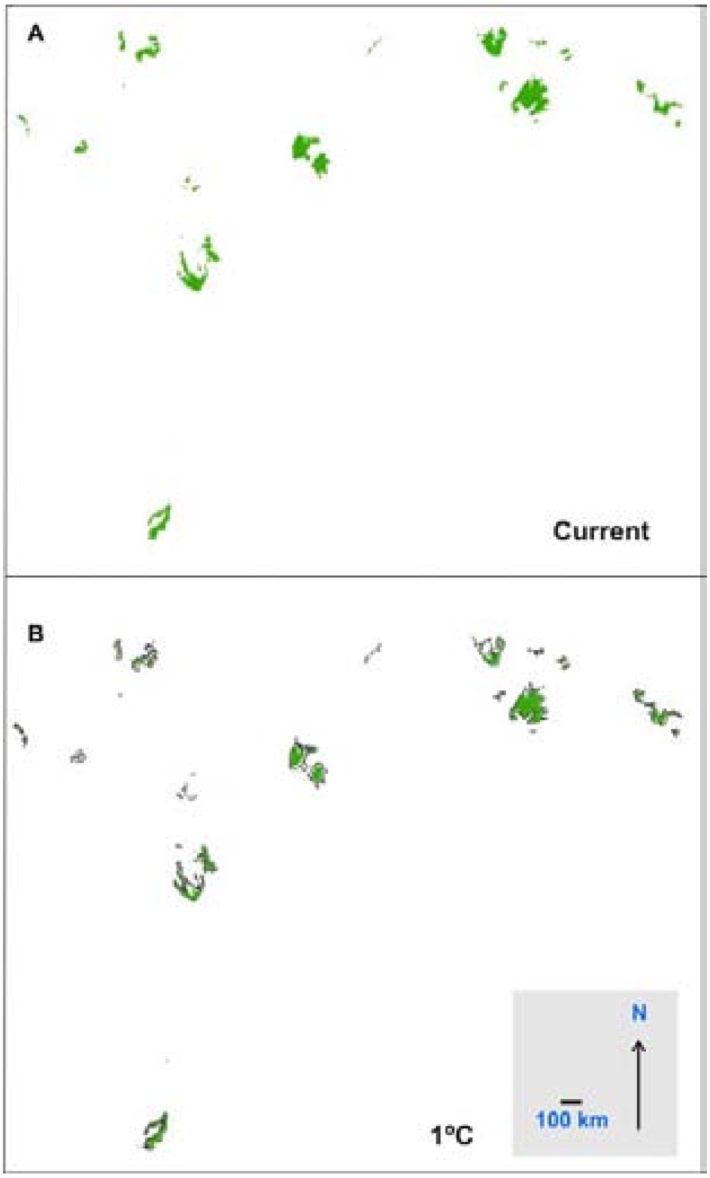

Figure 3. Reconstructions of the current (A) and the habitat reduction of the GH potential habitat due to a 1 ºC (B) temperature increase expected for each scenario studied (B1 and A2). In green the estimated remaining GH habitat with respect to the present day GH surface (black lines).

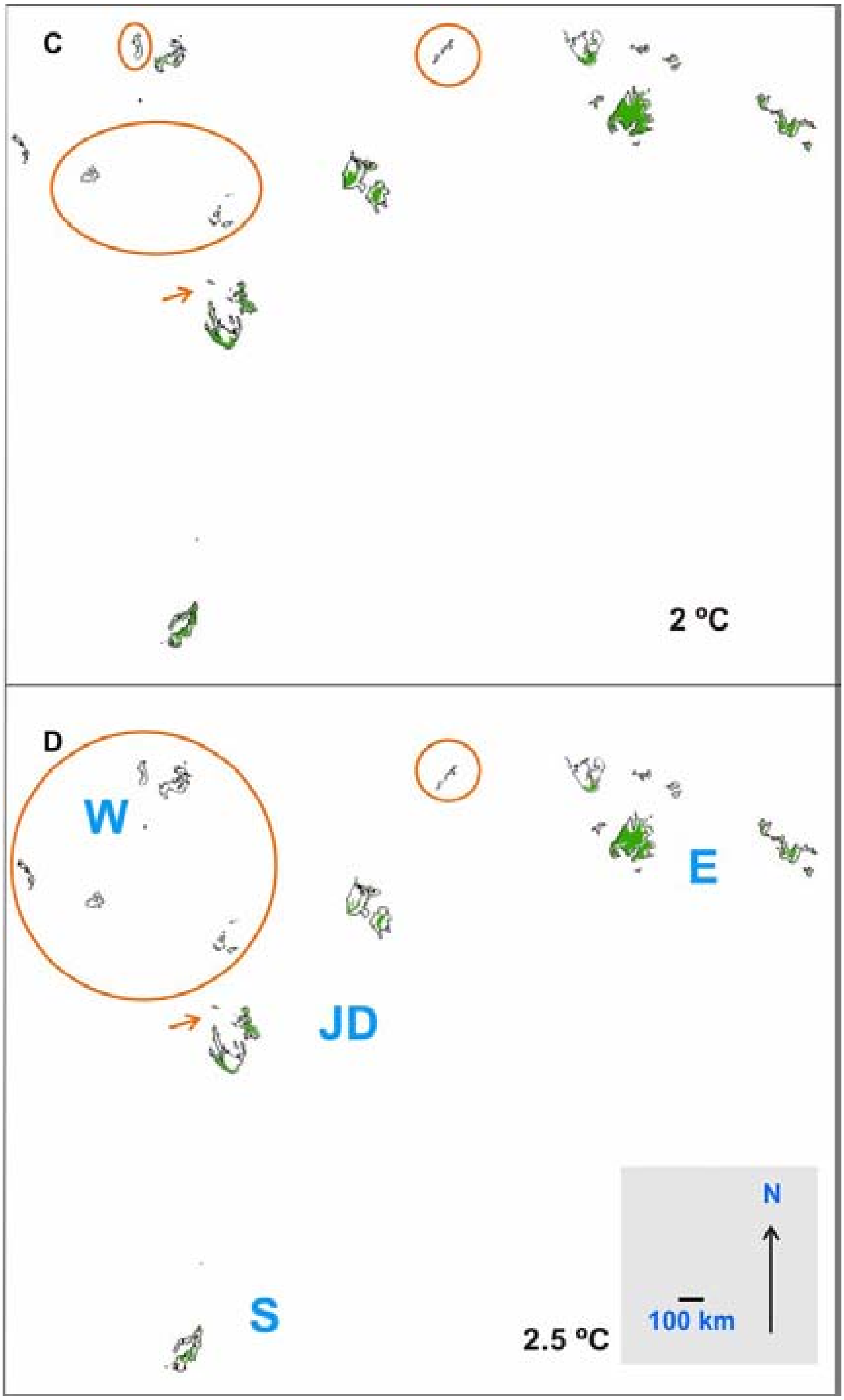

Figure 3 cont. Reconstructions of the habitat reduction of the GH potential habitat due to a 2 ºC (C) and 2.5 ºC (D) temperature increase expected for each scenario studied (B1 and A2). In green the estimated remaining GH habitat with respect to the present day GH surface (black lines). In orange, tepuis suffering fom total habitat loss. See figure 1 for acronyms in blue.

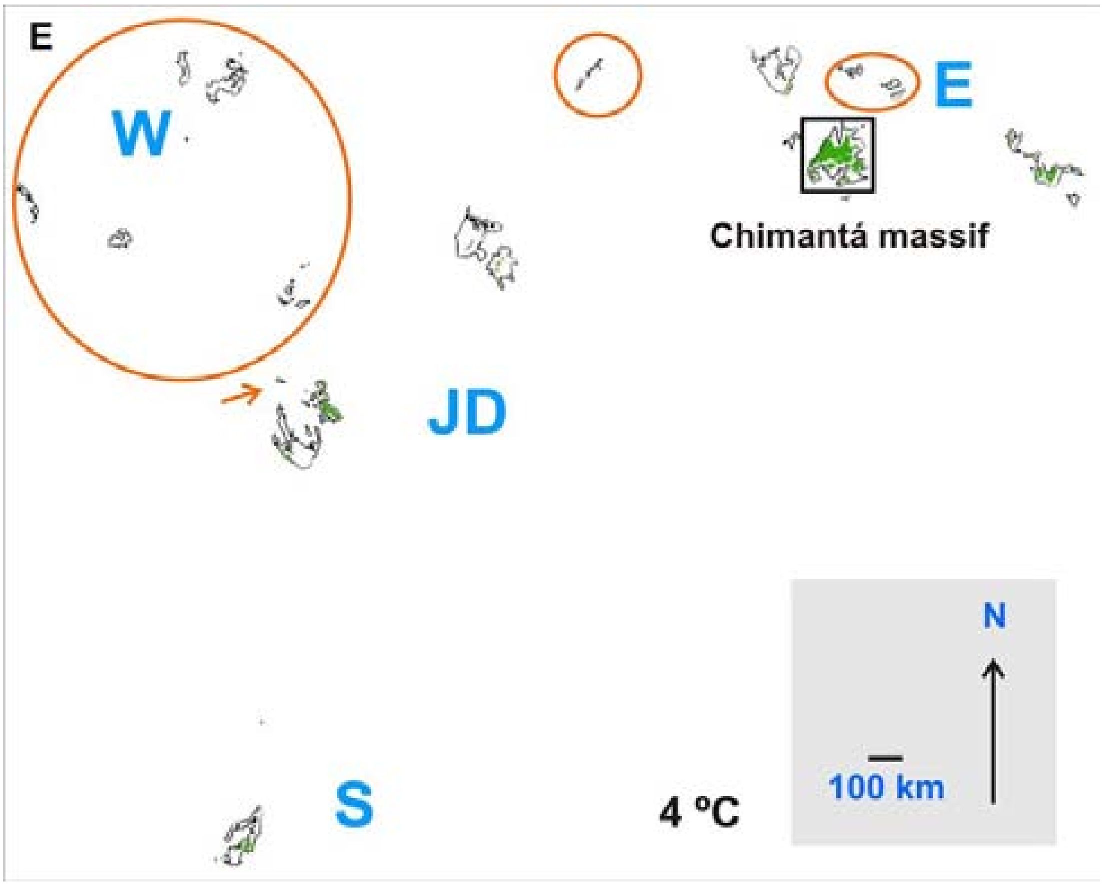

Figure 3 cont. Reconstructions of the habitat reduction of the GH potential habitat due to a 4 ºC (E) temperature increase expected for each scenario studied (B1 and A2). In green the estimated remaining GH habitat with respect to the present day GH surface (black lines). In orange, tepuis suffering from total habitat loss. See figure 1 for acronyms in blue.

The current largest single patch (LPI) comprises 21% of the available habitat. This patch belongs to the Chimantá massif located in the eastern district. The highest largest patch index (LPI) is obtained in the warmest scenario (A2) and also occurs on the Chimantá massif (46.19%). The landscape division index (LDI) and landscape shape index (LSI) show a decreasing trend, suggesting a reduction of landscape complexity with warming (Table 3).

Table 3. Summary FRAGSTATS metrics. Changes in the predicted area (TA) and percentual loss between brackets, number of patches (NP), landscape division index (LDI), landscape proximity index (LPI) and landscape shape index (LSI).

Climate scenario	TA (km^2)	NP	LPI	LDI	LSI
Current	4826.50	102	21	0.91	12.08
1 ºC	2888.18 (40%)	100	29.77	0.87	11.56
2 ºC	2071.97 (57%)	81	37.24	0.83	10.31
2.5 ºC	1306.83 (73%)	70	39.89	0.81	9.09
4 ºC	743.58 (84.6%)	64	46.19	0.76	8.46

3.1 IUCN classification

According to the B2 IUCN criterion, for the B1 and A2 warming scenarios by 2100, 410 species (41.6%) and 294 species (23%), respectively, would be included in the Critically Endangered category, as less than 10 km^2 of habitat would remain available to assure their survival. A total of 452 species (B1) and 360 species (A2) would be Endangered, with less than 500 km^2 of habitat remaining. Finally, for B1, 25 species would be listed as Vulnerable with a remaining habitat less than 1000 km^2.

For both scenarios the less threatened species are those occurring on more than two tepuis.. The families with the highest numbers of Critically Endangered species are: Asclepiadaceae, Eriocaulaceae, Iridaceae, Hymenophyllaceae and Vochysiaceae (Supplementary material 5).

4. DISCUSSION

The results obtained by the ARD analysis suggest that a high number of Pantepui endemic species (22% for B1 and 41.6 % for A2) would become severely threatened, completely losing their potential habitat due to successive temperature increases by the end of this century. However, in the worst-case scenario, if temperatures increase faster than expected, these results would underestimate the potential extinction for each scenario (Fig 2). Our results are coherent with other studies of current and future climate-realted changes in avian distributions, Malagasy amphibian and alpine plant species due to climate change (Hughes, 2000; Raxworthy *et al*, 2008; Sekercioglu *et al*, 2008). All these studies suggest that an upward shift in species is likely to be in progress today (Solomon *et al*, 2007). Although the complete loss of potential habitat may not cause species to go extinct, it will certainly make the species extremely vulnerable due to the severe habitat reduction expected by the end of this century (Williams *et al*, 2003; Thomas *et al*, 2004). There will surely be significant variations between species. Some species will suffer less than predicted or survive owing to greater tolerance to temperature increases, while other species will decline faster than expected (Hughes, 2000, 2003; Walther *et al*, 2002). Interactions with other biotic (competition, predation) and abiotic (moisture, edaphic conditions) factors may influence a positive or negative outcome (Clubbe, 1996).

FRAGSTATS metrics showed for the end of this century a general decrease in total area (84.6%) in number of patches (37.2 %) and in the landscape shape index (LSI) and landscape division index (LDI). These results emphasize that the present-day GH landscape is already fragmented as it has the largest number of patches (102), LDI (0.91) and LSI (12.08), suggesting a naturally heterogeneous landscape otherwise common in alpine environments due to a pronounced topography (Körner, 2002). Values occurring under warming scenarios may be interpreted as the response to a severe habitat reduction (Table 2) and patch losses (from 102 to 64) which lead to a less patchy landscape configuration (lower LDI) with less amount of landscape edge (less LSI). Populations inhabiting these small and isolated patches could be threatened by inbreeding depression, a serious problem for their survival, which, in the case of severe inbreeding, could lead to population extinctions (Shaffer, 1981). The extinction of species belonging to endemic genera represents a significant loss of genetic diversity and an associated reduction in evolutionary potential within Guayana (Rull & Vegas-Vilarrúbia, 2006).

The only FRAGSTATS metric with an increasing trend is the largest patch inex (LPI). This index show that after 4 ºC of warming, corresponding to the end of this century (A2), the Chimantá massif would comprise 46.19 % (343.58 km^2) of the remaining GH potential (Fig 3 E). This is a meaningful result with respect to conservation management, as the Chimantá massif stands out as the best massif for the implementation of *in situ* strategies. The current size, number of endemic species (212), including an endemic genera (Berry & Riina, 2005), and the existing official protection (Canaima National Park and World Heritage Site) support the suitability of the

Chimantá massif for the development of *in situ* strategies to address global warming. Of these strategies, the most necessary are: developing guidelines for the management of the area, maintaining viable populations and preventing the introduction of invasive species (IUCN, 2008b). There are some limitations to this approach. First, the habitat area expected to remain at the end of this century is very small, if species survival is to be ensured. Second, 55 (25%) of the endemic species occurring in the Chimantá massif would be threatened by total habitat loss after a 4 ºC increase. Finally, species occurring in other tepuis would continue being threatened by habitat loss. Thus, it is necessary to combine *in situ* strategies with other actions in order to conserve the highest number of endemic species. In a recent study, germplasm banks (seeds and spores), botanical gardens and assisted migration were proposed as potential *ex situ* conservation strategies for the GH vascular plants species (Rull *et al*, 2009).

Recent studies have used the IUCN Red List Criteria to attempt to quantify potential extinctions derived from climate change and have widely discussed the possible misapplication and uncertainties, for example, those related to species' responses to future climate change (Thomas *et al*, 2004; Akçakaya *et al*, 2006; Mace, 2008). The most common misapplication is including arbitrary changes to temporal scales (Akçakaya *et al*, 2006). The IUCN Red List criteria assesses population declines up to a maximum of 100 years into the future (IUCN, 2001), which is in agreement with the 100 year period we use in our analysis. Also, at the IUCN World Conservation Congress (2008) the fact that over one million species may be at extinction risk due to climate change was highlighted, and therefore the development of climate change guidelines for Red List assessments was recommended (chapter 4.016 in IUCN, 2008a; Marris, 2008). Our estimations of extinction risk due to climate change show that between 294 (B1) and 410 (A2) species would reach the Critically Endangered category of the IUCN system (IPCC, 2001). In addition, 360 (A2) to 452 (B1) would be consideredEndangered and, under the B1 scenario, 25 species would be considered Vulnerable.

With the objective of comparing the results obtained in this work with the real, present-day state of conservation of Pantepui endemic species, we conducted an extensive search of the Red List of Threatened Species, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) database and the Red Book of the Venezuelan Flora (RBVF) (Llamozas *et al*, 2003). We found that 17 GH endemic species (2.2%) are officially protected under the IUCN Red List of threatened species. CITES and the Red Book of the Venezuelan Flora include only one species each, *Inga bijuga* (Fabaceae) and *Bonnetia ptariensis* (Bonnetiaceae), respectively. Of these officially protected species, 11 turned out to be Critically Endangered for A2 and 6 for B1, based on the ARD analysis and the IUCN criteria used in this study (Table 4). In the IUCN analysis we obtained that 294 to 410 species would be included in the Critically Endangered category. The 17 current protected species represent the 4.1 and 5.7 % of them. It is surprising this small number of GH endemic species currently under official protection. Due to the high level of endemism, it would be expected more concern about the protection of this unique region of the World.

We are aware that the main limitation of this study is considering temperature as the only factor affecting endemic species as a result of global warming. However, it is worth remembering that temperature is the determining factor of the altitudinal distribution of the mountainous communities in the Guayana (-0.6ºC/100 m altitude) (Galán, 1992), whereas other climatic variables, such as precipitation, do not show any altitude dependence in this region (Huber, 1995a). Environmental heterogeneity, more detailed biogeographical patterns and ecophysiological characteristics of each species should be considered, but the necessary data are not yet available. We hope that in the future these data will be available and that it becomes possible to use more complex methods without losing reliability. The second limitation of this study is related to the overestimation or underestimation of the IPCC warming estimates. The ARD analysis, which is intended to be a useful forecasting tool for conservation purposes, allows temperature values to be easily changed. The third limitation is the lack of knowledge concerning species' responses to increasing temperature. This can be approached in different manners: 1) undertaking floristic comparisons between current and historical inventories and 2) future monitoring of the current altitudinal migration.

Table 4. Species listed on: Red List of Threatened Species (IUCN) (http://www.iucnredlist.org/), Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)(http://www.cites.org/esp/resources/species.html) and the Red Book of the Venezuelan Flora (RBVF) (Llamozas *et al*, 2003). The two last columns (B1-A2) refer to the ARD classification following the IUCN criteria. CR: Critical Endangered, EN: Endangered, VU: Vulnerable, LC: least concern, LR/nt: near threatened; LR/lc: least concern, DD: Data Deficient.

Endemic sp	**IUCN**	**RBVF**	**CITES**	**B1**	**A2**
Ilex cowanii	VU	-	-	CR	CR
Ilex gleasoniana	LR/nt	-	-	EN	EN
Ilex huachamacariana	LR/nt	-	-	CR	CR
Ilex parvifructa	VU	-	-	CR	CR
Ilex venezuelensis	LR/nt	-	-	EN	CR
Bonnetia bolivarensis	VU	-	-	CR	CR
Bonnetia celiae	VU	-	-	VU	CR
Bonnetia chimantensis	VU	-	-	VU	CR
Bonnetia fasciculata	LR/nt	-	-	EN	CR
Bonnetia maguireorum	VU	-	-	EN	EN
Bonnetia mutinervia	VU	-	-	EN	EN
Bonnetia ptariensis	CR	CRD1	-	CR	CR
Bonntia rubicunda	VU	-	-	EN	EN
Inga bijuga	VU	-	END	CR	CR
Podocarpus roraimae	LC	-	-	EN	EN
Podocarpus steyermarkii	LR/lc	-	-	EN	CR

Although at this stage the ARD is a simplified model of the expected dynamic response of the GH vegetation to climate change, in combination with the analysis of habitat fragmentation it has become a useful tool for providing important information to guide conservationists in developing strategies to cope with climate-related changes by identifying the species and the landscape locations that are likely to be most affected.

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SUPPLEMENTARY MATERIAL 5

Supplementary material 5. IUCN classification for all the Pantepui endemic species analyzednin this study..

Species	Family	2.5 ºC	4ºC
Abolboda ciliata	Xyridaceae	EN	EN
Abolboda dunstervillei	Xyridaceae	EN	EN
Abolboda neblinae*	Xyridaceae	EN	EN
Abolboda uniflora	Xyridaceae	CR	CR
Achlyphila disticha	Xyridaceae	EN	EN
Achnopogon steyermarkii	Asteraceae	CR	CR
Achnopogon virgatus	Asteraceae	EN	EN
Adelobrotis duidae	Melastomataceae	EN	CR
Adenanthe bicarpellata*	Ochnaceae	EN	EN
Adenarake macrocarpa	Ochnaceae	CR	CR
Adenarake muriculata*	Ochnaceae	EN	EN
Ageratina roraimensis	Asteraceae	CR	CR
Ageratum ballotifolium	Asteraceae	EN	EN
Aldina elliptica	Fabaceae	EN	CR
Amanoa steyermarkii	Euphorbiaceae	EN	EN
Aracamunia liesneri	Orchidaceae	CR	CR
Arthrostylidium schomburgkii	Poaceae	EN	EN
Aspidosperma steyermarkii	Apocynaceae	EN	CR
Aspidosperma glaucum	Apocynaceae	EN	CR
Asplenium cowanii	Aspleniaceae	CR	CR
Aulonemia chimantaensis	Poaceae	EN	EN
Aulonemia deflexa*	Poaceae	CR	CR
Aulonemia jauaensis	Poaceae	CR	CR
Aulonemia sp. C	Poaceae	CR	CR
Axonopus gracilis	Poaceae	CR	CR
Axonopus magallanesiae	Poaceae	CR	CR
Axonopus sp. A	Poaceae	EN	EN
Ayensua uaipanensis	Bromeliaceae	EN	EN
Baccharis densa	Asteraceae	CR	CR
Baccharis wurdackiana	Asteraceae	EN	EN
Bejaria imthurnii	Ericaceae	CR	CR
Bejaria neblinensis	Ericaceae	CR	CR
Biophytum sp. B	Oxalidaceae	CR	CR
Blechnum atropurpureum	Blechnaceae	EN	EN
Blepharodon grandiflorus subsp crassifolius*	Asclepiadaceae	EN	EN
Blepharodon magualidae	Asclepiadaceae	EN	CR
Bonnetia ahogadoi	Bonnetiaceae	EN	EN
Bonnetia bolivarensis	Bonnetiaceae	CR	CR
Bonnetia celiae	Bonnetiaceae	EN	CR
Bonnetia chimantensis	Bonnetiaceae	CR	CR
Bonnetia euryanthera	Bonnetiaceae	CR	CR
Bonnetia fasciculata	Bonnetiaceae	CR	CR
Bonnetia liesneri	Bonnetiaceae	CR	CR
Bonnetia maguireorum	Bonnetiaceae	EN	EN
Bonnetia multinervia	Bonnetiaceae	EN	EN
Bonnetia ptariensis	Bonnetiaceae	CR	CR
Bonnetia roraimae	Bonnetiaceae	VU	EN

Bonnetia roseiflora	Bonnetiaceae	CR	CR
Bonnetia rubicunda*	Bonnetiaceae	EN	EN
Bonnetia steyermarkii	Bonnetiaceae	EN	CR
Bonnetia wurdackii	Bonnetiaceae	EN	EN
Borreria cataractarum*	Rubiaceae	EN	EN
Brachionidium julianii	Orchidaceae	CR	CR
Brachionidium longicaudatum	Orchidaceae	CR	CR
Brachionidium neblinense	Orchidaceae	EN	EN
Brewcaria duidensis	Bromeliaceae	EN	EN
Brewcaria marahuacae	Bromeliaceae	CR	CR
Brocchinia hitchcockii	Bromeliaceae	CR	CR
Brunellia comocladifolia	Brunelliaceae	EN	EN
Brunellia neblinensis	Brunelliaceae	EN	EN
Bulbophyllum geraense*	Orchidaceae	EN	EN
Byrsonima chalcophylla*	Malpighiaceae	EN	EN
Byrsonima huberi	Malpighiaceae	EN	CR
Calea camani	Asteraceae	CR	CR
Calea esposi	Asteraceae	CR	CR
Calea lucida	Asteraceae	EN	EN
Calea neblinensis	Asteraceae	EN	EN
Calea phelpsiae	Asteraceae	CR	CR
Calea politii	Asteraceae	CR	CR
Calea sp. A	Asteraceae	CR	CR
Calea sp. B	Asteraceae	EN	EN
Calea sp.C	Asteraceae	EN	CR
Calea sp.E	Asteraceae	EN	CR
Calycolpus alternifolius	Myrtaceae	EN	E
Carex marahuacana	Cyperaceae	CR	CR
Carex neblinensis*	Cyperaceae	EN	EN
Carex roraimensis*	Cyperaceae	EN	EN
Catostema durifolius	Bombacaceae	EN	CR
Cavendishia neblinae	Ericaceae	EN	EN
Celiantha bella	Gentianaceae	EN	EN
Celiantha chimantensis	Gentianaceae	EN	EN
Celiantha imthurniana	Gentianaceae	EN	CR
Cephalocarpus dracaenula*	Cyperaceae	EN	EN
Cephalocarpus obovoideus*	Cyperaceae	EN	EN
Ceradenia arthrothrix	Grammitidaceae	CR	CR
Ceradenia fragillima	Grammitidaceae	CR	CR
Ceradonia microcystis	Grammitidaceae	EN	CR
Cestrum racemosum	Solanaceae	EN	EN
Chaetolepis anisandra	Melastomataceae	EN	CR
Chaetolepis phelpsiae subs chimantensis	Melastomataceae	EN	EN
Chimantaea humilis	Asteraceae	EN	EN
Chimantaea acopanensis	Asteraceae	EN	EN
Chimantaea cinerea	Asteraceae	VU	EN
Chimantaea eriocephala	Asteraceae	EN	EN
Chimantaea espeletoidea	Asteraceae	CR	CR
Chimantaea huberi	Asteraceae	EN	EN
Chimantaea lanocaulis	Asteraceae	VU	CR
Chimantaea mirabilis	Asteraceae	EN	EN
Chimantaea rupicola	Asteraceae	CR	CR
Chiococca auyantepuiensis	Rubiaceae	CR	CR
Chiococca lucens	Rubiaceae	CR	CR

Chionolaena latifolia*	Asteraceae	CR	CR
Chorisepalum rotundifolium*	Gentianaceae	EN	EN
Chromolaena ternicapitulata	Asteraceae	EN	CR
Chusquea linearis	Poaceae	VU	E
Cladocolea roraimensis	Loranthaceae	EN	EN
Cleistes huberi	Orchidaceae	CR	CR
Cleistes stricta	Orchidaceae	EN	EN
Clidemia andersonii	Melastomataceae	EN	EN
Clidemia duidae	Melastomataceae	CR	CR
Clusia duartei	Clusiaceae	CR	CR
Clusia fabiolae	Clusiaceae	EN	CR
Clusia pachyphylla	Clusiaceae	EN	CR
Clusia parvifolia	Clusiaceae	EN	EN
Clusia phelpsiae	Clusiaceae	CR	CR
Clusia phelpsiana	Clusiaceae	EN	EN
Clusia ptaritepuiensis	Clusiaceae	EN	EN
Clusia radiata	Clusiaceae	CR	CR
Coccochondra laevis	Rubiaceae	EN	CR
Comolia coriacea	Melastomataceae	EN	CR
Comolia montana	Melastomataceae	CR	CR
Comoliopsis neblinae*	Melastomataceae	EN	EN
Connellia augustae	Bromeliaceae	EN	CR
Connellia caricifolia	Bromeliaceae	CR	CR
Connellia quelchii	Bromeliaceae	EN	CR
Connellia varadarajanii	Bromeliaceae	CR	CR
Cordia roraimae	Boraginaceae	EN	EN
Cortaderia roraimensis	Poaceae	VU	E
Coryphothamnus auyantepuiensis	Rubiaceae	EN	EN
Croton roraimensis	Euphorbiaceae	EN	CR
Cuphea maigualidensis	Lythraceae	EN	CR
Cyathea intramarginalis	Cyatheaceae	EN	EN
Cyathea liesneri	Cyatheaceae	CR	CR
Cybianthus agostinianus	Myrsinaceae	CR	CR
Cybianthus agostinianus	Myrsinaceae	EN	CR
Cybianthus crotonoides	Myrsinaceae	EN	CR
Cybianthus huberi	Myrsinaceae	EN	EN
Cybianthus julianii	Myrsinaceae	EN	EN
Cybianthus piresii*	Myrsinaceae	EN	EN
Cybianthus plowmanii*	Myrsinaceae	EN	EN
Cybianthus ptariensis	Myrsinaceae	EN	CR
Cybianthus quelchii	Myrsinaceae	EN	CR
Cybianthus sipapoensis	Myrsinaceae	CR	CR
Cybianthus spathulifolius	Myrsinaceae	CR	CR
Cybianthus steyermarkianus	Myrsinaceae	EN	EN
Cybianthus wurdackii	Myrsinaceae	CR	CR
Cynanchum chimantensis	Asclepiadaceae	CR	CR
Cynanchum paraquense	Asclepiadaceae	CR	CR
Daphnopsis guaiquinimae	Thymeleaceae	CR	CR
Daphnopsis steyermarkii	Thymeleaceae	EN	CR
Dendrophthora densifrons*	Viscaceae	CR	CR
Dendrophthora microsoma	Viscaceae	CR	CR
Dendrophthora nitidula	Viscaceae	EN	EN
Dendrophthora roraimae	Viscaceae	EN	CR
Diacidia rufa*	Malpighiaceae	EN	EN

Diacidia stipularis	Malpighiaceae	CR	CR
Dichanthelium telmatun	Poaceae	CR	CR
Dicymbe yutajensis	Caesalpinaceae	EN	CR
Dioclea rigida	Fabaceae	CR	CR
Dioscorea sororopana	Dioscoreaceae	CR	CR
Diplazium roraimense*	Dryopteridaceae	EN	EN
Disterigma cuspidatum	Ericaceae	EN	EN
Ditassa acerifolia	Asclepiadaceae	CR	CR
Ditassa colellae	Asclepiadaceae	CR	CR
Ditassa duidae	Asclepiadaceae	CR	CR
Ditassa juliani	Asclepiadaceae	CR	CR
Ditassa obovata	Asclepiadaceae	CR	CR
Ditassa olivaestevae	Asclepiadaceae	CR	CR
Ditassa ottohuberi	Asclepiadaceae	EN	CR
Ditassa roraimensis	Asclepiadaceae	EN	CR
Ditassa sipapoana	Asclepiadaceae	CR	CR
Drimys roraimensis	Vochysiaceae	EN	CR
Drosera hirticalyx	Droseraceae	EN	EN
Drosera meristocaulis	Droseraceae	EN	EN
Dryadella lueriana	Orchidaceae	CR	CR
Dugandiodendron chimantense	Magnoliaceae	EN	EN
Dugandiodendron ptaritepuianum	Magnoliaceae	EN	CR
Duidaea marahuacensis	Asteraceae	CR	CR
Duranta sp. B	Verbenaceae	EN	EN
Duranta sp.A	Verbenaceae	CR	CR
Elaphoglossum antioquianum	Dryopteridaceae	VU	EN
Elaphoglossum hayesii	Dryopteridaceae	EN	EN
Elaphoglossum steyermarkii	Dryopteridaceae	CR	CR
Eleocharis atrospiculata	Cyperaceae	CR	CR
Eleocharis squamigera	Cyperaceae	EN	EN
Elleanthus gracilis	Orchidaceae	EN	EN
Elleanthus malpighiiflorus*	Orchidaceae	EN	EN
Elvasia brevipedicellata	Ochnaceae	EN	EN
Epidendrum violascens	Orchidaceae	EN	CR
Epidendrum alsum*	Orchidaceae	CR	CR
Epidendrum commelinispathum*	Orchidaceae	EN	EN
Epidendrum montigenum*	Orchidaceae	CR	CR
Epidendrum sp. A	Orchidaceae	EN	CR
Epidendrum stalkyi	Orchidaceae	CR	CR
Epidryos sp. A	Rapateaceae	CR	CR
Episcia sp. B	Gesneriaceae	EN	EN
Eriocaulon jauense	Eriocaulaceae	EN	CR
Eriosourus paucifolius	Pteridaceae	VU	E
Ernestia maguirei	Melastomataceae	CR	CR
Euceraea sleumeriana	Flacourtiaceae	CR	CR
Eugenia tepuiensis	Myrtaceae	EN	EN
Euplassa chimantensis	Proteaceae	EN	EN
Everardia disticha	Cyperaceae	VU	EN
Everardia lanata	Cyperaceae	CR	CR
Everardia longifolia	Cyperaceae	EN	CR
Everardia maguireana*	Cyperaceae	CR	CR
Everardia montana subsp duidae	Cyperaceae	EN	EN
Everardia montana subsp guaiquinimae	Cyperaceae	EN	EN
Everardia montana subsp ptariensis	Cyperaceae	EN	EN
Everardia montana subsp velutina	Cyperaceae	EN	EN

Everardia vareschii	Cyperaceae	CR	CR
Faramea yutajensis	Rubiaceae	EN	CR
Froesia gereauana	Quinaceae	EN	EN
Gaultheria setulosa	Ericaceae	EN	CR
Glossarion bilabiatum*	Asteraceae	CR	CR
Glossarion rhodanthum	Asteraceae	EN	EN
Gongylolepis bracteata	Asteraceae	EN	EN
Gongylolepis fruticosa	Asteraceae	EN	EN
Gongylolepis glaberrima	Asteraceae	CR	CR
Gongylolepis jauanensis	Asteraceae	EN	EN
Gongylolepis paruana	Asteraceae	CR	CR
Graffenrieda cinnoides	Melastomataceae	CR	CR
Graffenrieda fruticosa	Melastomataceae	EN	EN
Graffenrieda jauana	Melastomataceae	EN	CR
Graffenrieda reticulata	Melastomataceae	EN	EN
Graffenrieda sessilifolia subsp cardonae	Melastomataceae	EN	EN
Graffenrieda sessilifolia subsp sessilifolia	Melastomataceae	EN	EN
Graffenrieda steyermarkii	Melastomataceae	EN	EN
Grammitis sp.A	Grammitidaceae	EN	CR
Guayania roupalifolia	Asteraceae	VU	EN
Guayania yaviana	Asteraceae	EN	EN
Guzmania nubicola*	Bromeliaceae	EN	EN
Guzmania terrestris	Bromeliaceae	EN	EN
Hedyosmum neblinae*	Chloranthaceae	EN	EN
Heliamphora chimantensis	Sarraceniaceae	EN	EN
Heliamphora elongata	Sarraceniaceae	CR	CR
Heliamphora folliculata	Sarraceniaceae	EN	CR
Heliamphora hispida	Sarraceniaceae	EN	CR
Heliamphora ionasii	Sarraceniaceae	CR	CR
Heliamphora minor	Sarraceniaceae	EN	CR
Helonoma chiropterae	Orchidaceae	CR	CR
Henriettella heteroneura	Melastomataceae	CR	CR
Heteropterys neblinensis	Malpighiaceae	EN	EN
Hirtella cowanii	Chrysobalanaceae	EN	EN
Hirtella orbicularis	Chrysobalanaceae	EN	EN
Houlletia roraimensis*	Orchidaceae	EN	EN
Huberopappus maigualidae	Asteraceae	EN	CR
Huperzia beitelii	Lycopodiaceae	EN	CR
Huperzia huberi	Lycopodiaceae	CR	CR
Huperzia intermedia	Lycopodiaceae	EN	EN
Huperzia robusta	Lycopodiaceae	CR	CR
Hymenophyllopsis ctenitoides	Hymenophyllopsidaceae	EN	EN
Hymenophyllopsis dejecta	Hymenophyllopsidaceae	EN	EN
Hymenophyllopsis incognita	Hymenophyllopsidaceae	EN	EN
Hymenophyllopsis steyermarkii	Hymenophyllopsidaceae	EN	EN
Hymenophyllopsis universitatis	Hymenophyllopsidaceae	EN	CR
Hymenophyllum sp.A	Hymenophyllaceae	CR	CR
Hypericum marahuacanum	Clusiaceae	EN	CR
Hypericum roraimense	Clusiaceae	CR	CR
Hypolepis sp. A	Dennstaedtiaceae	EN	EN
ilex abscondida	Apocynaceae	EN	CR
ilex abscondida	Aquifoliaceae	EN	EN
Ilex acutidenticulata	Aquifoliaceae	VU	EN

Ilex apicidens	Aquifoliaceae	CR	CR
Ilex cowanii	Aquifoliaceae	CR	CR
Ilex cowanii	Aquifoliaceae	EN	EN
Ilex culmenicola	Aquifoliaceae	CR	CR
Ilex gleasoniana	Aquifoliaceae	EN	EN
Ilex huachamacariana	Aquifoliaceae	CR	CR
Ilex macarenensis*	Aquifoliaceae	EN	EN
Ilex maguirei	Aquifoliaceae	EN	EN
Ilex marginata	Aquifoliaceae	EN	EN
Ilex neblinensis*	Aquifoliaceae	EN	EN
Ilex parvifructa	Aquifoliaceae	CR	CR
Ilex ptariana*	Aquifoliaceae	CR	CR
Ilex solida	Aquifoliaceae	CR	CR
Ilex summa	Aquifoliaceae	EN	CR
Ilex tepuiana*	Aquifoliaceae	EN	EN
Ilex tiricae	Aquifoliaceae	EN	EN
Ilex venezuelensis	Aquifoliaceae	EN	CR
Ilex yutajensis	Aquifoliaceae	EN	EN
Inga bijuga	Mimosaceae	CR	CR
Irlbachia phelpsiana	Gentianaceae	CR	CR
Isoëtes vermiculata	Isoëtaceae	CR	CR
Ixora intropilosa*	Rubiaceae	EN	EN
Justicia huberi	Acanthaceae	EN	CR
Justicia paruana	Acanthaceae	CR	CR
Koanophyllon tatei	Asteraceae	EN	EN
Langsdorffia hypogaea	Balanophoraceae	EN	EN
Leandra gorzulae	Melastomataceae	EN	CR
Leandra longisepala	Melastomataceae	EN	EN
Leandra maguirei*	Melastomataceae	EN	EN
Leandra procumbens	Melastomataceae	CR	CR
Ledothamnus atroadenus	Ericaceae	EN	EN
Ledothamnus decumbens	Ericaceae	EN	EN
Ledothamnus jauaensis	Ericaceae	CR	CR
Ledothamnus luteus	Ericaceae	EN	EN
Ledothamnus sessiliflorus	Ericaceae	CR	CR
Leiothrix celiae	Eriocaulaceae	EN	CR
Lepanthes marahuacensis	Orchidaceae	CR	CR
Lepanthes unitrinervis	Orchidaceae	CR	CR
Lepidaploa auyantepuiensis	Asteraceae	CR	CR
Lepidaploa imeriensis	Asteraceae	EN	EN
Lindmania brachyphylla	Bromeliaceae	EN	CR
Lindmania cylindrostachya	Bromeliaceae	EN	CR
Lindmania arachnoidea	Bromeliaceae	CR	CR
Lindmania argentea	Bromeliaceae	CR	CR
Lindmania aurea	Bromeliaceae	EN	EN
Lindmania longipes	Bromeliaceae	EN	EN
Lindmania maguirei*	Bromeliaceae	CR	CR
Lindmania marahuacae	Bromeliaceae	CR	CR
Lindmania minor	Bromeliaceae	EN	EN
Lindmania navioides	Bromeliaceae	EN	EN
Lindmania nubigena	Bromeliaceae	EN	EN
Lindmania oliva-estevae	Bromeliaceae	EN	EN
Lindmania phelpsiae	Bromeliaceae	CR	CR
Lindmania riparia	Bromeliaceae	CR	CR

Lindmania saxicola	Bromeliaceae	CR	CR
Lindmania simithiana	Bromeliaceae	CR	CR
Lindmania sp. A*	Bromeliaceae	EN	EN
Lindmania sp. B*	Bromeliaceae	EN	EN
Lindmania sp. C	Bromeliaceae	CR	CR
Lindmania stenophylla	Bromeliaceae	EN	EN
Lindmania steyermarkii	Bromeliaceae	CR	CR
Lindmania subsimplex	Bromeliaceae	EN	EN
Lindmania tillandsioides	Bromeliaceae	CR	CR
Lindsaea mesarum	Dennstaedtiaceae	VU	EN
Lindsaea parkeri*	Dennstaedtiaceae	EN	EN
Liparis verticillata	Orchidaceae	CR	CR
Lueddemannia pescatorei	Orchidaceae	EN	EN
Macairea cardonae	Melastomataceae	EN	CR
Macairea linearis	Melastomataceae	EN	EN
Macairea neblinae	Melastomataceae	EN	EN
Macrocarpaea marahuacae	Gentianaceae	CR	CR
Macrocarpaea neblinae	Gentianaceae	EN	EN
Macrocarpaea piresii	Gentianaceae	CR	CR
Macrocarpaea rugosa	Gentianaceae	CR	CR
Macrocentrum angustifolium	Melastomataceae	CR	CR
Macrocentrum huberi	Melastomataceae	EN	CR
Macrocentrum maguirei	Melastomataceae	CR	CR
Maguireothamnus speciosus	Rubiaceae	EN	CR
Maguireothamnus speciosus subsp jauaensis	Rubiaceae	EN	EN
Malanea auyantepuiensis	Rubiaceae	EN	EN
Malanea jauaensis	Rubiaceae	CR	CR
Mallophyton chimantense	Melastomataceae	CR	CR
Mallophyton chimantense	Melastomataceae	EN	EN
Mandevilla aracamunensis	Apocynaceae	CR	CR
Manettia calycosa	Rubiaceae	EN	EN
Marahuacaea schomburgkii	Rapateaceae	CR	CR
Marlierea foveolata	Myrtaceae	EN	CR
Marlierea rugosior	Myrtaceae	EN	EN
Masdevallia manarana	Orchidaceae	EN	EN
Matayba spruceana	Sapindaceae	CR	CR
Matelea fucata	Asclepiadaceae	CR	CR
Maxillaria colemanii	Orchidaceae	EN	EN
Maxillaria schlechteri*	Orchidaceae	EN	EN
Maxillaria x dunstervillei*	Orchidaceae	EN	EN
Maytenus neblinae	Celastraceae	EN	EN
Megalastrum crenulans	Dryopteridaceae	EN	EN
Meriania broccha	Melastomataceae	EN	EN
Merostachys maguireorum	Poaceae	EN	EN
Merumea coccocypseloides	Rubiaceae	CR	CR
Miconia cacumina*	Melastomataceae	CR	CR
Miconia dioica	Melastomataceae	EN	EN
Miconia huberi	Melastomataceae	CR	CR
Miconia iluensis	Melastomataceae	EN	CR
Miconia neblinensis*	Melastomataceae	CR	CR
Miconia perobscura	Melastomataceae	EN	EN
Miconia rupestris*	Melastomataceae	CR	CR
Microlicia guanayana	Melastomataceae	CR	CR
Mikania duidensis	Asteraceae	VU	EN

Mikania marahuacensis	Asteraceae	CR	CR
Mikania michelangeliana*	Asteraceae	EN	EN
Mikania neblinensis	Asteraceae	EN	EN
Moronobea intermedia*	Clusiaceae	EN	EN
Mycerinus chimantensis	Ericaceae	EN	EN
Mycerinus sclerophyllus	Ericaceae	CR	CR
Myrcia exploratoris	Myrtaceae	EN	CR
Myrcia bonnetiasylvestris	Myrtaceae	EN	CR
Myrcia bonnetiasylvestris	Myrtaceae	EN	EN
Myrcia compta	Myrtaceae	CR	CR
Myrcia gentryi	Myrtaceae	CR	CR
Myrcia gentryi	Myrtaceae	EN	EN
Myrcia induta	Myrtaceae	CR	CR
Myrcia kylistophylla	Myrtaceae	EN	CR
Myrcia ptariensis	Myrtaceae	EN	EN
Myrcia salticola	Myrtaceae	CR	CR
Myrcia sipapensis	Myrtaceae	EN	EN
Myrcia sp. C	Myrtaceae	EN	EN
Myrcia tepuiensis	Myrtaceae	EN	CR
Myrica rotundata	Myricaceae	EN	EN
Myriocladus cardonae	Poaceae	EN	EN
Myriocladus churunensis	Poaceae	EN	EN
Myriocladus distantiflorus	Poaceae	EN	CR
Myriocladus exsertus	Poaceae	EN	CR
Myriocladus involutus	Poaceae	CR	CR
Myriocladus paludicolus*	Poaceae	EN	EN
Myriocladus sp A	Poaceae	EN	EN
Myriocladus steyermarkii	Poaceae	EN	EN
Myrsine coriacea subsp reticulata	Myrsinaceae	EN	EN
Myrsine macrocarpa	Myrsinaceae	EN	EN
Myrsine minima	Myrsinaceae	EN	E
Myrsine perpauciflora	Myrsinaceae	EN	EN
Navia aloifolia	Bromeliaceae	EN	EN
Navia colorata	Bromeliaceae	CR	CR
Navia crassicaulis	Bromeliaceae	EN	EN
Navia filifera	Bromeliaceae	EN	EN
Navia glauca	Bromeliaceae	CR	CR
Navia incrassata	Bromeliaceae	CR	CR
Navia involucrata	Bromeliaceae	CR	CR
Navia lactea	Bromeliaceae	CR	CR
Navia lanigera	Bromeliaceae	CR	CR
Navia lasiantha	Bromeliaceae	CR	CR
Navia lepidota	Bromeliaceae	EN	EN
Navia mima	Bromeliaceae	CR	CR
Navia patria	Bromeliaceae	CR	CR
Navia scopulorum	Bromeliaceae	EN	EN
Navia terramarae	Bromeliaceae	CR	CR
Navia xyridiflora	Bromeliaceae	EN	EN
Neblinantha neblinae	Gentianaceae	EN	EN
Neblinantha parvifolia	Gentianaceae	EN	EN
Neblinathamnus argyreus	Rubiaceae	EN	EN
Neblinathamnus brasiliensis	Rubiaceae	EN	EN
Neea guiquinimae	Nyctaginaceae	CR	CR
Neotatea duidae	Clusiaceae	EN	EN

Neurolepis diversiglumis	Poaceae	CR	CR
Notopora auyantepuiensis	Ericaceae	CR	CR
Notopora cardonae	Ericaceae	EN	CR
Notopora chimantensis	Ericaceae	CR	CR
Notopora smithiana	Ericaceae	EN	EN
Ocotea atrata*	Lauraceae	CR	CR
Ocotea cowaniana	Lauraceae	CR	CR
Ocotea glabra	Lauraceae	EN	CR
Ocotea huberi	Lauraceae	EN	EN
Ocotea julianii	Lauraceae	EN	EN
Ocotea perrobusta	Lauraceae	EN	EN
Ocotea roseopedunculata	Lauraceae	CR	CR
Ocotea sp. A	Lauraceae	EN	CR
Ocotea tillettsiana*	Lauraceae	EN	EN
Ocotea venosa	Lauraceae	CR	CR
Ocotea wurdackiana*	Lauraceae	EN	EN
Octomeria splendida	Orchidaceae	CR	CR
Octomeria anomala	Orchidaceae	EN	EN
Octomeria connellii	Orchidaceae	CR	CR
Octomeria dentifera*	Orchidaceae	CR	CR
Octomeria monticola*	Orchidaceae	CR	CR
Octomeria sp. A	Orchidaceae	CR	CR
Oncidium warmingii	Orchidaceae	VU	E
Orectanthe ptaritepuiana*	Xyridaceae	EN	EN
Orthaea wurdackii	Ericaceae	EN	EN
Ouratea maigualidae	Ochnaceae	EN	EN
Ouratea obovata	Ochnaceae	CR	CR
Ouratea paruensis	Ochnaceae	CR	CR
Ouratea ptaritepuiensis	Ochnaceae	EN	EN
Pachira robynsii	Bombacaceae	EN	EN
Paepalanthus apacarensis	Eriocaulaceae	CR	CR
Paepalanthus auyantepuiensis	Eriocaulaceae	CR	CR
Paepalanthus cardonae	Eriocaulaceae	CR	CR
Paepalanthus chimantensis	Eriocaulaceae	CR	CR
Paepalanthus cristatus	Eriocaulaceae	CR	CR
Paepalanthus cumbricola	Eriocaulaceae	CR	CR
Paepalanthus fraternus*	Eriocaulaceae	CR	CR
Paepalanthus fulgidus	Eriocaulaceae	EN	EN
Paepalanthus holstii	Eriocaulaceae	EN	CR
Paepalanthus kunhardtii	Eriocaulaceae	EN	EN
Paepalanthus parvicephalus	Eriocaulaceae	EN	EN
Paepalanthus phelpsiae	Eriocaulaceae	CR	CR
Paepalanthus roraimense*	Eriocaulaceae	CR	CR
Paepalanthus squamuliferus	Eriocaulaceae	EN	CR
Paepalanthus stegolepoides	Eriocaulaceae	EN	EN
Paepalanthus sulcatus	Eriocaulaceae	EN	EN
Paepalanthus sulcatus*	Eriocaulaceae	EN	EN
Paepalanthus turbinatus	Eriocaulaceae	EN	EN
Pagamea diceras	Rubiaceae	CR	CR
Pagamea jauaensis	Rubiaceae	EN	EN
Pagamea magniflora	Rubiaceae	CR	CR
Pagamea magniflora	Rubiaceae	EN	EN
Palicourea obtusata	Rubiaceae	EN	CR
Palicourea ottohuberi	Rubiaceae	CR	CR

Palicourea pensilis	Rubiaceae	CR	CR
Palicourea wurdackiana*	Rubiaceae	CR	CR
Panicum fontanale	Poaceae	EN	EN
Panicum fonticolum	Poaceae	EN	EN
Panicum jauanum	Poaceae	CR	CR
Panopsis ornatinervia	Proteaceae	CR	CR
Panopsis tepuiana	Proteaceae	EN	EN
Passiflora adenopoda	Passifloraceae	EN	EN
Pentacalia neblinensis	Asteraceae	EN	EN
Peperomia celiae	Piperaceae	EN	CR
Peperomia cladara	Piperaceae	VU	EN
Peperomia delascioi*	Piperaceae	EN	EN
Peperomia haematoleptis	Piperaceae	EN	EN
Peperomia marahuacensis	Piperaceae	CR	CR
Peperomia yutajensis	Piperaceae	EN	EN
Perissocarpa steyermarkii	Ochnaceae	EN	EN
Pernettya marginata	Ericaceae	EN	EN
Persea croatii	Lauraceae	EN	EN
Philacra duidae	Ochnaceae	EN	EN
Philacra steyermarkii	Ochnaceae	EN	EN
Philodendron marahuacae	Araceae	EN	EN
Philodendron nebulense	Araceae	EN	EN
Philodendron simulans	Araceae	EN	EN
Phyllanthus carrenoi	Euphorbiaceae	EN	CR
Phyllanthus chimantae	Euphorbiaceae	CR	CR
Phyllanthus jauaensis	Euphorbiaceae	CR	CR
Phyllanthus minutifolius	Euphorbiaceae	CR	CR
Phyllanthus paraqueensis	Euphorbiaceae	EN	EN
Phyllanthus pycnophyllus*	Euphorbiaceae	EN	EN
Phyllanthus ventuarii	Euphorbiaceae	CR	CR
Piper jauaense	Piperaceae	EN	EN
Piper mosaicum	Piperaceae	CR	CR
Piper steyermarkii	Piperaceae	CR	CR
Piper subalpinum	Piperaceae	CR	CR
Piper subduidaense	Piperaceae	EN	EN
Piper toronotepuiense	Piperaceae	EN	EN
Piptocarpha auyantepuiensis	Asteraceae	EN	EN
Piptocarpha jauaensis	Asteraceae	CR	CR
Piptocoma areolata	Asteraceae	CR	CR
Pitcairnia cana	Bromeliaceae	EN	EN
Pitcairnia kunhardtiana	Bromeliaceae	CR	CR
Pitcairnia phelpsiae	Bromeliaceae	CR	CR
Pleurothallis callifera	Orchidaceae	CR	CR
Pleurothallis rhombipetala	Orchidaceae	CR	CR
Pleurothallis stenocardium*	Orchidaceae	EN	EN
Plukenetia multiglandulosa	Euphorbiaceae	CR	CR
Podocarpus acuminatus*	Podocarpaceae	EN	EN
Podocarpus buchholzii*	Podocarpaceae	EN	EN
Podocarpus roraimae	Podocarpaceae	EN	E
Podocarpus steyermarkii	Podocarpaceae	EN	CR
Polygala sipapoana	Polygalaceae	CR	CR
Polystichum platyphyllum	Dryopteridaceae	EN	EN
Prescottia auyantepuiensis	Orchidaceae	CR	CR
Prosthechea jauana	Orchidaceae	EN	EN

Protium ptarianum	Burseraceae	EN	EN
Prunus espinozana	Rosaceae	CR	CR
Psittacanthus montis-neblinae*	Loranthaceae	EN	EN
Psychotria carrenoi	Rubiaceae	EN	CR
Psychotria celiae	Rubiaceae	CR	CR
Psychotria cerronis	Rubiaceae	CR	CR
Psychotria duidana	Rubiaceae	CR	CR
Psychotria jauaensis	Rubiaceae	CR	CR
Psychotria leiantha*	Rubiaceae	EN	EN
Psychotria oblita	Rubiaceae	CR	CR
Psychotria phelpsiana	Rubiaceae	CR	CR
Pterandra flavescens	Malpighiaceae	CR	CR
Pterandra flavescens	Malpighiaceae	EN	EN
Pterozonium cyclophyllum	Pteridaceae	VU	E
Pterozonium cyclosorum	Pteridaceae	VU	E
Pterozonium lineare	Pteridaceae	EN	EN
Pterozonium retroflexum	Pteridaceae	CR	CR
Pterozonium spectabile	Pteridaceae	EN	CR
Pterozonium steyermarkii	Pteridaceae	EN	EN
Purdiaea nutans	Cyrillaceae	EN	EN
Pyrrorhiza neblinae	Haemodoraceae	EN	EN
Quelchia bracteata	Asteraceae	EN	EN
Quelchia cardonae	Asteraceae	EN	EN
Quelchia conferta	Asteraceae	CR	CR
Quelchia eriocaulis	Asteraceae	CR	CR
Quelchia xgrandifolia	Asteraceae	CR	CR
Racinaea tetrantha	Bromeliaceae	EN	EN
Raveniopsis breweri	Rutaceae	EN	EN
Raveniopsis capitata	Rutaceae	CR	CR
Raveniopsis cowaniana	Rutaceae	EN	EN
Raveniopsis fraterna	Rutaceae	CR	CR
Raveniopsis nubicola	Rutaceae	EN	EN
Raveniopsis paruana	Rutaceae	CR	CR
Raveniopsis sericea*	Rutaceae	EN	EN
Raveniopsis steyermarkii	Rutaceae	EN	EN
Raveniopsis tomentosa	Rutaceae	CR	CR
Remijia aracamuniensis	Rubiaceae	CR	CR
Remijia pilosinervula*	Rubiaceae	EN	EN
Remijia sipapoensis	Rubiaceae	CR	CR
Rhamnus chimantensis	Rhamnaceae	EN	CR
Rhamnus longipes	Rhamnaceae	CR	CR
Rhamnus marahuacensis	Rhamnaceae	CR	CR
Rhamnus neblinensis	Rhamnaceae	EN	EN
Rhamnus sipapoensis	Rhamnaceae	EN	EN
Rhynchospora sp. C	Cyperaceae	EN	EN
Rhynchospora pallida*	Cyperaceae	CR	CR
Rogersonanthus coccineus	Gentianaceae	EN	EN
Rogersonanthus quelchii	Gentianaceae	EN	CR
Rondonanthus caulescens	Eriocaulaceae	CR	CR
Rondonanthus duidae	Eriocaulaceae	EN	EN
Rondonanthus flabelliformis	Eriocaulaceae	CR	CR
Rondonanthus roraimae*	Eriocaulaceae	CR	CR
Roucheria sp. A	Hugoniaceae	CR	CR
Roupala paruensis	Proteaceae	EN	EN

Roupala sororopan*	Proteaceae	CR	CR
Rumohra adiantiformis	Dryopteridaceae	EN	EN
Saccifolium bandeirae*	Gentianaceae	CR	CR
Sauvagesia imthurniana	Ochnaceae	EN	E
Scaphyglottis michelangeliorum	Orchidaceae	EN	EN
Schefflera acaropunctata	Araliaceae	EN	CR
Schefflera paruana	Araliaceae	CR	CR
Schefflera argophylla	Araliaceae	EN	CR
Schefflera asymmetrica	Araliaceae	EN	EN
Schefflera auyantepuiensis	Araliaceae	CR	CR
Schefflera brachypodia	Araliaceae	EN	CR
Schefflera chimantensis	Araliaceae	VU	CR
Schefflera clavigera	Araliaceae	EN	CR
Schefflera concolor	Araliaceae	EN	EN
Schefflera contracta	Araliaceae	CR	CR
Schefflera cracens	Araliaceae	EN	EN
Schefflera dissidens*	Araliaceae	CR	CR
Schefflera gracillima	Araliaceae	EN	CR
Schefflera guanayensis	Araliaceae	CR	CR
Schefflera hitchcockii	Araliaceae	EN	CR
Schefflera huachamacarii	Araliaceae	CR	CR
Schefflera huberi	Araliaceae	EN	EN
Schefflera jauaensis	Araliaceae	EN	CR
Schefflera longistyla	Araliaceae	EN	EN
Schefflera marahuacensis	Araliaceae	CR	CR
Schefflera monosperma*	Araliaceae	EN	EN
Schefflera pallens*	Araliaceae	EN	EN
Schefflera paruana	Araliaceae	EN	EN
Schefflera psilophylla*	Araliaceae	EN	EN
Schefflera simplex*	Araliaceae	EN	EN
Schefflera sipapoensis	Araliaceae	CR	CR
Schefflera sp. B	Araliaceae	EN	EN
Schefflera steyermarkii	Araliaceae	CR	CR
Schefflera tremuloidea	Araliaceae	EN	EN
Schefflera ulocephala	Araliaceae	EN	EN
Schefflera umbellata*	Araliaceae	CR	CR
Schefflera umbraculifera	Araliaceae	EN	EN
Schoepfia tepuiensis	Olacaceae	EN	EN
Schradera yutajensis	Rubiaceae	EN	CR
Schultesia subcrenata*	Gentianaceae	CR	CR
Selaginella beitelii	Selaginellaceae	EN	EN
Selaginella breweriana	Selaginellaceae	EN	EN
Selaginella marahuacae	Selaginellaceae	CR	CR
Selaginella neblinae	Selaginellaceae	EN	EN
Selaginella rhodostachya*	Selaginellaceae	CR	CR
Selaginella smithiorum	Selaginellaceae	EN	EN
Selaginella tyleri	Selaginellaceae	CR	CR
Selaginella vernicosa	Selaginellaceae	VU	CR
Sipapoantha ostrina	Gentianaceae	CR	CR
Siphocampylus sp. A	Campanulaceae	EN	CR
Siphocampylus tillettii	Campanulaceae	CR	CR
Siphocampylus tillettii	Campanulaceae	EN	CR
Sloanea carrenoi	Elaeocarpaceae	CR	CR
Solanum capirense	Solanaceae	EN	EN

Solanum tepuiense	Solanaceae	CR	CR
Stegolepis albiflora	Rapteaceae	EN	CR
Stegolepis cardonae	Rapateaceae	EN	EN
Stegolepis choripetala	Rapateaceae	EN	EN
Stegolepis gleasoniana	Rapateaceae	EN	EN
Stegolepis guianensis	Rapateaceae	EN	CR
Stegolepis huberi*	Rapateaceae	CR	CR
Stegolepis humilis	Rapateaceae	EN	CR
Stegolepis jauaensis	Rapateaceae	CR	CR
Stegolepis ligulata	Rapateaceae	EN	EN
Stegolepis maguireana	Rapateaceae	EN	EN
Stegolepis microcephala	Rapateaceae	CR	CR
Stegolepis neblinensis	Rapateaceae	EN	EN
Stegolepis pauciflora	Rapateaceae	CR	CR
Stegolepis terramarensis	Rapateaceae	CR	CR
Stegolepis vivipara	Rapateaceae	EN	EN
Stegolepis wurdackii subsp chimantensis	Rapateaceae	EN	EN
Stelis latisepala	Orchidaceae	EN	EN
Stelis schomburgkii	Orchidaceae	EN	E
Stenopadus chimantensis	Asteraceae	EN	EN
Stenopadus connellii	Asteraceae	VU	EN
Stenopadus huachamacari	Asteraceae	CR	CR
Stenopadus jauensis	Asteraceae	CR	CR
Stenopadus obconicus	Asteraceae	EN	EN
Sterigmapetalum guianense susp guianense*	Rhizophoraceae	EN	EN
Steyerbromelia discolor	Bromeliaceae	CR	CR
Steyerbromelia neblinae	Bromeliaceae	EN	EN
Stomatochaeta acuminata	Asteraceae	CR	CR
Stomatochaeta cymbifolia	Asteraceae	EN	EN
Stomatochaeta steyermarkii	Asteraceae	VU	CR
Styrax guanayanus	Styracaceae	EN	CR
Styrax sipapoanus	Styracaceae	CR	CR
Swartzia roraimae	Fabaceae	EN	EN
Symbolanthus aureus	Gentianaceae	CR	CR
Symbolanthus camanensis	Gentianaceae	CR	CR
Symbolanthus rosmarinifolius	Gentianaceae	EN	CR
Symbolanthus sessilis	Gentianaceae	CR	CR
Symbolanthus yaviensis	Gentianaceae	EN	CR
Symplocos chimantensis	Symplocaceae	EN	EN
Symplocos neblinae	Symplocaceae	EN	EN
Syngonanthus macrocephalus	Eriocaulaceae	CR	CR
Syngonanthus minutus	Eriocaulaceae	CR	CR
Syngonanthus tiricensis	Eriocaulaceae	CR	CR
Tapeinostemon jauaensis	Gentianaceae	CR	CR
Tapeinostemon longiflorum	Gentianaceae	EN	EN
Tapeinostemon rugosum	Gentianaceae	EN	EN
Tectaria lizarzaburui	Dryopteridaceae	EN	EN
Tepuia intermedia	Ericaceae	CR	CR
Tepuia multiglandulosa	Ericaceae	EN	EN
Tepuia speciosa	Ericaceae	EN	EN
Tepuia tatei	Ericaceae	EN	CR
Tepuia vareschii	Ericaceae	CR	CR
Tepuia venusta	Ericaceae	EN	EN
Tepuianthus auyantepuiensis	Tepuianthaceae	EN	EN

Ternstroemia retusifolia	Ternstroemiaceae	EN	EN
Ternstroemia verticillata*	Ternstroemiaceae	EN	EN
Thelypteris arborea	Thelypteridaceae	EN	CR
Thelypteris binervata	Thelypteridaceae	CR	CR
Thelypteris demerarana	Thelypteridaceae	EN	E
Thelypteris pilosissima	Thelypteridaceae	CR	CR
Thibaudia breweri	Ericaceae	CR	CR
Thibaudia carrenoi	Ericaceae	CR	CR
Thibaudia smithiana	Ericaceae	CR	CR
Tibouchina dissitiflora	Melastomataceae	EN	CR
Tibouchina sipapoana	Melastomataceae	CR	CR
Tibouchina steyermarkii	Melastomataceae	CR	CR
Tillandsia turneri	Bromeliaceae	EN	CR
Tococa bolivarensis	Melastomataceae	EN	CR
Tovomita atropurpurea	Clusiaceae	EN	EN
Trichomanes guidoi*	Hymenophyllaceae	EN	EN
Trichomanes roraimense	Hymenophyllaceae	VU	EN
Trichosalpinx oxychilos	Orchidaceae	EN	EN
Trichosalpinx steyermarkii	Orchidaceae	CR	CR
Trimezia chimantensis	Iridaceae	CR	CR
Tyleria aristata	Ochnaceae	EN	EN
Tyleria breweriana	Ochnaceae	CR	CR
Tyleria grandiflora	Ochnaceae	EN	CR
Tyleria linearis	Ochnaceae	EN	EN
Tyleria pendula	Ochnaceae	EN	EN
Tyleria phelpsiana	Ochnaceae	CR	CR
Tyleria spectabilis	Ochnaceae	EN	EN
Tyleria tremuloidea	Ochnaceae	EN	EN
Tyleropappus dichotomus	Asteraceae	CR	CR
Uncinia hamata	Cyperaceae	EN	EN
Utricularia mirabilis	Lentibulariaceae	CR	CR
Utricularia steyermarkii	Lentibulariaceae	EN	EN
Vaccinium chimantense	Ericaceae	VU	CR
Vaccinium roraimense	Ericaceae	EN	CR
Vaccinium steyermarkii	Ericaceae	CR	CR
Vargasiella venezuelana	Orchidaceae	EN	EN
Vellosiella spathacea	Scrophulariaceae	EN	CR
Verbesina angusta	Asteraceae	CR	CR
Viburnum sp.A	Capriofilaceae	CR	CR
Viburnum tinoides	Capriofilaceae	EN	CR
Vochysia ortegae	Vochysaceae	CR	CR
Vochysia rubiginosa	Vochysaceae	CR	CR
Vriesea maguirei*	Bromeliaceae	EN	EN
Weinmannia corocoroensis	Cunoniaceae	EN	CR
Weinmannia guyanensis	Cunoniaceae	EN	CR
Weinmannia ilutepuiensis	Cunoniaceae	CR	CR
Weinmannia laxiramea	Cunoniaceae	EN	CR
Weinmannia laxiramea*	Cunoniaceae	CR	CR
Xyris aracamunae	Xyridaceae	CR	CR
Xyris atriceps subsp atriceps	Xyridaceae	EN	EN
Xyris atriceps subsp chimantensis	Xyridaceae	EN	EN
Xyris atriceps subsp marahuacae	Xyridaceae	VU	EN
Xyris bicostata	Xyridaceae	VU	EN
Xyris byssacea	Xyridaceae	EN	EN

Xyris chimantae	Xyridaceae	EN	EN
Xyris concinna	Xyridaceae	CR	CR
Xyris consolida	Xyridaceae	EN	EN
Xyris culmenicola	Xyridaceae	EN	EN
Xyris decussata	Xyridaceae	EN	E
Xyris delicatula	Xyridaceae	EN	EN
Xyris fuliginea	Xyridaceae	EN	EN
Xyris kukenaniana	Xyridaceae	CR	CR
Xyris lugubris	Xyridaceae	EN	EN
Xyris melanovaginata	Xyridaceae	EN	EN
Xyris neblinae	Xyridaceae	EN	EN
Xyris pratensis	Xyridaceae	EN	EN
Xyris riparia	Xyridaceae	EN	EN
Xyris schneeana	Xyridaceae	CR	CR
Xyris sulcatifolia	Xyridaceae	EN	CR
Xyris toronoana	Xyridaceae	CR	CR
Xyris valdeapiculata	Xyridaceae	EN	EN
Xyris xiphophylla	Xyridaceae	EN	EN

7. DISCUSSIÓ

Tepuia cardonae

1. SÍNTESI

L’espai temporal on s’emmarca aquesta tesi és molt ampli: del Tardiglacial (~ 13000 BP) fins a finals d’aquest segle (2100). Per poder obtenir els resultats ha calgut l’ús d’una sèrie d’eines relacionades amb l’anàlisi de pol·len, així com també eines SIG i base de dades. El nexe d’unió entre els capítols i els corresponents resultats queden palesos en la figura 1.

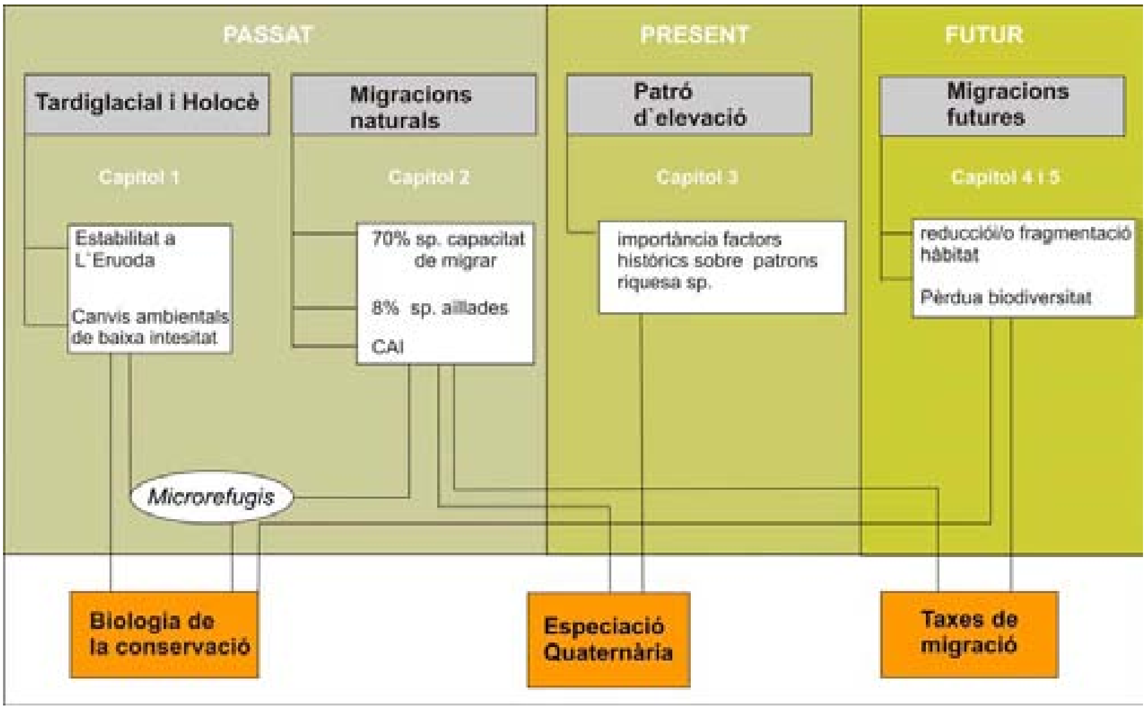

Figura 1. Diagrama dels nexes d’unió, els resultats principals i les aplicacions de la tesi. El gradient de color verd indica l’espai temporal que comprèn la tesi (passat, present i futur). CAI: límit topogràfic crític d’aïllament durant el LGM (capítol 2).

En el capítol 1 es descriu l’anàlisi dels sediments més antics estudiats fins a l’actualitat als *tepuis*. La localitat, situada al tepui Eruoda, és la més elevada dins el massís del Chimantá. L’avantatge principal que presenten les zones altes és la gran sensibilitat envers als canvis climàtics, que les fan ideals per registrar migracions altitudinals. Sorprenentment, la vegetació de l’Eruoda es mostra constant al llarg de l’Holocè. Aquests resultats estan en la línia dels obtinguts a zones altitudinals més baixes, lluny de l’ecotò entre les formacions herbàcies i arbustives. En aquestes zones, l’estabilitat és explicada per l’absència de canvis ambientals o per la insensibilitat de les plantes tepuianes. A partir dels resultats obtinguts a l'Eruoda es conclou que, l'estabilitat obtinguda en els tepuis durant l'Holocè mig i tardà, és deguda a l'absència de canvis ambientals de suficient intensitat com per sobrepassar el llindar de resposta de les comunitats vegetals tepuianes. Aquesta estabilitat, que pot ser clau per analitzar i comprendre la hipotètica existència de microrefugis en els tepuis, explicaria la persistència de la vegetació en fases climàtiques, en principi desfavorables, com l'Últim Màxim Glacial (LGM) fa 21000 anys (Rull, 2009).

Les TAG es caracteritzen per un elevat nombre d'espècies endèmiques de Pantepui i endèmiques locals, que han propiciat un conjunt d'hipòtesis que tenen com a objectiu esbrinar el seu origen. La hipòtesi central d'aquesta tesi es fonamenta en què durant els màxims glacials, les espècies de plantes vasculars dels cims van poder migrar cap avall i propagar-se a través de les terres baixes, mentre que durant els interglacials, van tenir la possibilitat de pujar a nous tepuis (Rull, 2005). El resultat d'aquestes migracions i expansions consistiria en l'existència d'un flux de gens entre tepuis, que afavoriria així la radiació adaptativa. Per altra banda, individus dels cims més alts no haurien pogut arribar a les Terres Baixes i haurien pogut evolucionat per vicariància (Rull, 2005). Així, en el capítol 2 s'ha realitzat una reconstrucció dels possibles espais disponibles per a la migració de les espècies dels tepuis durant l'Últim Màxim Glacial (LGM) i un factor històric anomenat límit topogràfic crític d'aïllament durant el LGM (*critical altitude for topographical isolation*, Rull & Nogué, 2007). La capacitat de migració d'una determinada espècie està relacionada amb el seu límit altitudinal inferior o LAI. Els resultats mostren que, pel 70% de les espècies, totes les possibilitats de migració estaven obertes. Per contra, es van tancar les rutes de migració per al 8% de les espècies, que no haurien pogut sortir de l'actual zona de Pantepui. El 22% restant haurien tingut possibilitats intermèdies de migració. Si es considera que durant els darrers 2.6 milions d'anys, s'han produït al voltant de 40 cicles glacial/interglacials, la possibilitat d'intercanvi biòtic i de flux de gens és evident.

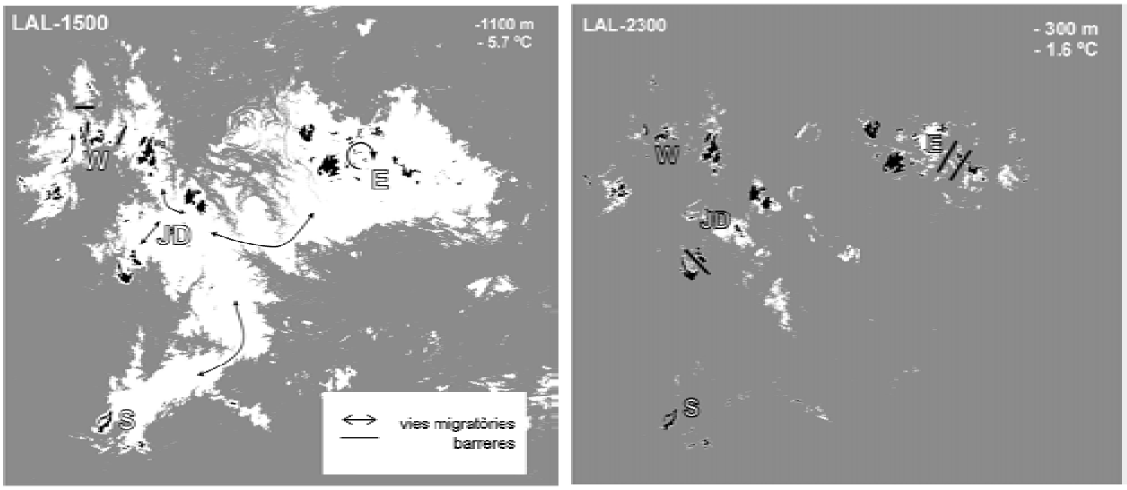

Figura 2. Reconstrucció paleotopogràfica de l’espai disponible durant el LGM per a les espècies amb límit altitudinal inferior (LAI) de 1500 m i 2300 m (blanc) comparat amb la superfície actual de Pantepui (negre). El desplaçament altitudinal i la seva corresponent temperatura, està indicada a la cantonada superior dreta (Rull & Nogué, 2007). W) Districte Oest, E) Districte Est, JD) Districte Jaua-Duida i S) districte Sud.

En el capítol 3 s’ha documentat que les espècies endèmiques locals i les espècies endèmiques de Pantepui (excloent les locals) presenten diferents patrons. Mentre que les espècies endèmiques de Pantepui segueixen un patró que suggereix que l’aïllament i la fragmentació de l’hàbitat han tingut un pes important en la seva distribució, les espècies endèmiques locals presenten una certa independència pel que fa als factors geogràfics, observant-se en canvi, una relació amb el factor històric definit més amunt: el límit topogràfic crític d’aïllament (CAI) durant el LGM del Quaternari. Aquest fet indicaria que els nivells màxims d’endemisme local ocorren a altituds amb petites o nul·les possibilitats de connexió, fins i tot durant l’era glacial, quan la probabilitat de migració i d'intercanvi entre els tepuis era màxima. Això, reforçaria la hipòtesi d’especiació Quaternària de les espècies dels tepuis. Aquesta hipòtesi a nivell global, està sent intensament debatuda. Recentment, s’han aportat noves dades provinents de la filogènia molecular que suggereixen que una gran majoria de les espècies de plantes vasculars neotropicals analitzades tindrien el seu origen en el Quaternari (Noonan & Gaucher, 2005; Rull, 2008).

Al llarg de la tesi s’ha analitzat el desplaçament vertical de les plantes vasculars tant en el passat (capítol 2) com en el que potencialment tindrà lloc en el futur. Pel que fa a les migracions en el futur,s’espera que el canvi climàtic tindrà conseqüències severes sobre les plantes vasculars en els tepuis. Per tal de quantificar els seus efectes, en els capítols 4 i 5 s’han utilitzat tres anàlisis complementaris: la relació espècies-àrea (SAR), l’anàlisi de Desplaçament del Rang Altitudinal (ARD) i el de fragmentació. Tan el SAR com l’ARD preveuen que les espècies de plantes vasculars patiran una davallada a finals de segle. En el capítol 5 s’ha discutit àmpliament que les espècies de les TAG hauran d’assumir una pèrdua superior al 80 % del seu hàbitat potencial. Entre les moltes conseqüències de la fragmentació de l’hàbitat la pèrdua total és la més dràstica. Tot i així, la disminució de les taques d’hàbitat i el conjunt de fragments petits que restarien a finals de segle també podrien comportar importants conseqüències sobre les espècies. En aquest sentit, les poblacions fragmentades i isolades esdevenen més vulnerables per sota d’una certa mida de població (Shaffer, 1981). La probabilitat d’extinció augmentaria si aquestes petites poblacions estiguessin isolades entre elles, ja que la capacitat de colonització per individus d’altres fragments disminueix, així com també, la recolonització dels fragments buits després de l’extinció (Hanski, 1999). En general, es considera que la dispersió és el primer esglaó per l’èxit de la colonització. Però les plantes també necessiten èxit en la germinació, el creixement i la reproducció. S’espera que el canvi climàtic afecti tots aquests processos (Pitelka, 1997). Desafortunadament, els mètodes de dispersió als tepuis no estan estudiats. Un estudi realitzat a les terres baixes de la Guayana Colombiana al sud de les TAG mostra que el 23 % de les espècies són dispersades pel vent i el 47% per zoocòria, sobretot per aus (Arbeláez & Parrado-Rosselli, 2005). La fragmentació i la reducció de l’hàbitat pot ser més greu per les espècies de plantes vasculars dels tepuis que es dispersin per zoocòria ja que la reducció de l’hàbitat també afectaria a les poblacions d’aus, disminuint-ne el nombre d’individus. Com a conseqüència, la dispersió a llarga distància de les llavors es podria veure reduïda (Figuerola, 2007).

2. TAXES DE MIGRACIÓ

2.1 Taxes naturals

La capacitat de les espècies de plantes vasculars de migrar altitudinalment degut als canvis en la temperatura és un tema latent que s’ha anat discutint parcialment al llarg dels capítols. Estudis pol·línics i moleculars han mostrat ser eines importants per determinar aquestes migracions en el passat (Jump & Peñuelas, 2005; Pearson, 2006).

La gran majoria dels estudis realitzats als tepuis són reconstruccions de la vegetació a partir d'anàlisis palinològics. Per tal de poder obtenir dades referents a les possibles taxes de migració en el passat, són necessaris sondatges a diferents altituds. Afortunadament les localitats estudiades fins al moment, estan distribuïdes tant a les TAG com a les Terres Mitges i Baixes. Un clar exemple en migracions altitudinals el podem trobar en l'estudi del sondatge de Mapaurí prop del poble de Santa Cruz, situat a 940 m d'altitud (Rull, 2007). Els resultats d'aquest treball mostren un clar canvi en la composició de la vegetació, produït fa 10200 anys, interpretat com la substitució de la comunitat de bosc ennuvolat mesotèrmic amb *Catostemma* (Bombacaceae) com a gènere dominant, per una altra de sabana formada principalment per gramínies i *Brocchinia* (Bromeliaceae). Actualment, Santa Cruz de Mapaurí té un típic paisatge en mosaic entre sabana i bosc submesotèrmic. El bosc mesotèrmic de *Catostemma* es troba a una franja altitudinal superior, entre 1400 i 2000 m d'altitud a les vessants dels tepuis (Hernández, 1999; Rull, 2007). Així doncs, si comparem l'altitud actual de *Catostema* amb l'obtinguda a Mapaurí, s'obté una variació dels pisos de vegetació de 460 m (1400-940 m) que equivaldria a un augment de la temperatura mitjana de 2.8 ºC, si es té en compte el gradient adiabàtic de la zona de 0.6 per 100 m (Galán, 1992; Rull, 2007). A nivell regional, aquest augment de la temperatura mitjana va formar part de l'escalfament general que hi va haver després de l'Últim Màxim Glacial (21000 anys BP), anomenat *Early Holocene Warming* (a partir dels 11.5 ka BP), que va tenir el seu màxim de temperatura als 6000 anys BP. Aquest màxim es coneix com a *Holocene Thermal Maximum* (10 a 6 ka BP). Si considerem que a partir d'aquest punt les temperatures actuals es van establir, les taxes d'augment de la temperatura des del canvi detectat fins al *Early Holocene Warming*, resultarien ser de ~ 0.70 ºC per mil·lenni el que representaria una taxa de migració altitudinal de 0.11 m per anys o ~110 m per mil·lenni. Aquestes es podrien considerar les taxes naturals per les espècies de la nostra regió d'estudi.

2.2 Taxes presents i futures

A les TAG, el desplaçament altitudinal necessari per a respondre a la mateixa velocitat que el canvi climàtic previst per l'*Intergovernamental Panel on Climate Change* (IPCC), de 2.5 a 4 ºC per a finals del segle, seria de 416 a 670 m, que equivaldria a una taxa de migració de 4.2 a 6.7 m per any. Aquesta taxa si les comparem amb les obtingudes en l’apartat 2.1, representaria entre 38 i 61 vegades les considerades naturals. A altres zones muntanyoses aquest desplaçament altitudinal està projectat de ser de 500 a 700 m (Hughes, 2000), valors similars als obtinguts a les TAG. Com s’ha discutit anteriorment, aquest augment de les temperatures té com a conseqüència la pèrdua i/o fragmentació de l’hàbitat. Aquest càlcul de les taxes de migració sembla molt elevat però hi ha evidències obtingudes durant les últimes dècades on s’evidencia que són possibles.

Per posar en context el desplaçament altitudinal esperat pel futur és essencial revisar si a l’actualitat s’han descrit migracions que puguin ser associades a un augment de la temperatura. En els tepuis, actualment no hi ha dades d’aquestes migracions. És doncs, una incògnita com les espècies tepuianes responen a l’actual augment de les temperatures mitjanes.

Sí que trobem evidències de migracions ascendents d’espècies vegetals de muntanya en altres regions, algunes de les quals es troben resumides a la taula 1.

Taula 1. Exemples de migracions detectades en els últims 100 anys per una selecció de plantes vasculars. * : mitjana dels valors publicats.

continent	regió	nº sp	vegetació	anys	m/any	referències
Americà	Nord Amèrica	52	sotabosc	28*	1.29 *	Matlack , 1994
Europeu	Àustria		alpines	90	0.8	Grabherr *et al*, 1994
Europeu	Sud de Suècia	49	sp de bosc	52.5*	0.53*	Brunet & Oheimb, 1998
Europeu	Bèlgica central	4	herbàcies	84*	0.6*	Bossuyt *et al*, 1999
Americà	Sud Califòrnia	141	arbusts, arbres, agaves	30	3.0*	Kelley & Goulden, 2008
Europeu	França	171	sp de bosc	20	3	Lenoir *et al*, 2008
Europeu	Alps centrals	52	alpines	46	3.42	Parolo & Rossi, 2007
Europeu	Alps del Sud	18 aprox	arbusts i herbàcies	5	Augment en el nombre d’espècies als cims	Erschbamer & Kiebacher, 2009

Entre elles destaquen les migracions d’1 a 5 m en altitud en 30 anys, de les espècies d’arbres i arbusts a les muntanyes de Santa Rosa (USA), a conseqüència d’un augment de les temperatures de 0.4 ºC (Kelley & Goulden, 2008). Estudis als Alps centrals de Parolo i Rossi (2007) han mostrat per 52 plantes una migració de 3.42 m en 46 anys. Als Alps del Sud s'ha detectat, en un període de 5 anys, un augment en el nombre d'espècies als cims més alts (Erschbamer & Kiebacher, 2009).

Aquests resultats evidencien la importància de mesurar aquestes migracions ascendents associades a l'escalfament global registrat en l'últim segle a les TAG. Molts dels resultats de migracions recents exposats en el paràgraf anterior, són fruit d'una xarxa mundial d'observació anomenada *Global Observation Research Initiative in Alpine Environments* (GLORIA, www.gloria.ac.at). Aquesta xarxa monitoritza mitjançant diferents tècniques l'ascens degut a l'escalfament global, de les plantes vasculars d'alta muntanya. És per tant l'opció més adequada a desenvolupar a les TAG.

3. BIOLOGIA DE LA CONSERVACIÓ A LES TERRES ALTES DE LA GUAYANA

Les Terres Altes de la Guayana (TAG), representen un regió pràcticament intacte des del punt de vista de la intervenció humana. La característica de lloc sagrat i inaccessible l'ha preservat de moltes amenaces antròpiques, a diferència d'altres zones naturals com l'Amazònia. A les TAG no hi ha recursos naturals per explotar i el sòl no és adequat per establir-hi cultius i tampoc hi ha evidències que s'hagin realitzat tales ni cremes en els cims. Tanmateix, hi ha dues amenaces que han emergit recentment: l'augment del turisme (Huber, 2001) i l'escalfament global. Afortunadament, el turisme no és massiu. Es compon per petits grups organitzats o participants en esports d'aventura. En aquest sentit, un bon control d'accés i dels permisos constituirien les eines més eficaces per tal de mantenir el seu creixement i el seu impacte. D'altra banda, les conseqüències potencials de l'escalfament global semblen difícils de controlar. En primer lloc la pèrdua d'hàbitat en l'escenari d'escalfament global més dràstic per a finals d'aquest segle és superior al 80% (Capítol 5). Aquesta dada ens porta a no ser gaire optimistes respecte a les accions de conservació a aplicar. D'entrada, degut a aquesta reducció d'hàbitat que porta associada una gran davallada en el nombre d'espècies, es suggereix que les estratègies *ex situ* serien indispensables per tal de conservar el nombre més elevat de biodiversitat (Rull *et al*, 2009). Com van recomanen aquest autors, seria essencial conservar unitats de germoplasma (llavors, espores o altres propàguls) adequades per reproduir l'espècie quan sigui necessari. També es va proposar la creació de jardins botànics en entorns adequats, tractant de reproduir l'hàbitat de les TAG. Això s'aconseguiria mitjançant la creació d'ambients artificials o per la translocació d'espècies en risc a altres llocs, on les condicions es produeixen naturalment. Aquesta translocació es coneix com a migració assistida o colonització assistida (McLachlan *et al*, 2007; Hoegh-Guldberg *et al*, 2008). En aquesta tesi s'ha aportat una dada important que obre les portes a apostar per una combinació d'estratègies *ex situ* i *in situ.* A partir de l'anàlisi de fragmentació s'ha obtingut que, prop del 50% de l'hàbitat resultant per a finals de segle es concentraria en una sola zona: el massís del Chimantá. Aquest massís, com s'ha especificat en el capítol 5, resultaria ser ideal per aplicar estratègies de prevenció d'espècies invasores i adoptar activitats de gestió per tal de preservar la biota.

Al comparar els resultats de la modelització al futur amb els obtinguts a partir de l'anàlisi de pol·len, s'evidencia el gran contrast entre les dades. Mentre que durant l'Holocè els cims dels tepuis s'han mantingut estables, resulta sorprenent la dràstica reducció en el nombre d'espècies previst només en un segle. Aquestes dades paleoecològiques suggereixen dues idees: 1) que possiblement les espècies tepuianes tinguin una major plasticitat fenotípica davant els canvis climàtics, aportant a les espècies una possibilitat més elevada de sobreviure a l'escalfament esperat per a finals de segle i 2) s'ha de valorar també la possible capacitat de les espècies de mantenir poblacions en baixa densitat (microrefugis) quan el clima sigui desfavorable (Rull, 2009). El concepte de microrefugi va sorgir per a explicar la persistència d'espècies i comunitats d'alta muntanya durant l'Últim Màxim Glacial (LGM) en els cims dels tepuis (Rull *et al*, 1988; Rull, 2009). En aquest sentit, els microrefugis, poden tenir un gran potencial per tal d'afrontar la pèrdua de biodiversitat a les TAG. Pearson (2006) els suggereix com a una esperança per a mitigar les conseqüències de les projeccions pel futur.

4. ESTUDIS FUTURS

La combinació de les tres temàtiques principals de la tesi (paleoecologia, canvi climàtic i biogeografia) és essencial per l'estudi del canvi de la vegetació i les respostes de les plantes als canvis ambientals.

Pel que fa a la paleoecologia, una de les principals línies que se'n poden derivar està relacionada amb l'obtenció de noves dades respecte a les taxes Holocèniques de migració de les espècies tepuianes. En aquesta discussió s'han valorat preliminarment, però caldria estudiar acuradament la potencialitat de noves zones d'estudi i de taxons clau. Per poder clarificar la taxa de migració ascendent del gènere *Stegolepis* durant els últims 6000 anys seria interessant estudiar, en el massís del Chimantá una localitat situada al tepui Apakará a 2200 m d'altitud. Aquesta localitat ja ha estat sondejada i processada al laboratori. D'altra banda, el treball de camp dut a terme fins a l'actualitat s'ha centrat majoritàriament en els tepuis localitzats al voltant de la Gran Sabana. Seria interessant, per tant, analitzar algunes localitats situades als tepuis d'altres zones com l'Amazònica per poder establir comparacions entre regions.

En aquesta discussió s'ha exposat la importància de mesurar les migracions actuals. Cal destacar que seria interessant centrar esforços en calcular les migracions històriques, és a dir, les associades a l'escalfament global des de l'inici de l'era industrial. Així, es podria analitzar els efectes de les accions antròpiques indirectes, ja que la influència directa humana a la zona ha estat mínima. Seguint aquesta línia s'ha iniciat un projecte finançat per la Fundació BBVA anomenat PANTEPUI II on l'objectiu principal serà registrar aquestes migracions històriques a les TAG. La metodologia que es preveu emprar està basada en la comparació dels primers inventaris realitzats als tepuis que es van iniciar cap a finals del 1880. D'aquesta manera, es podran calcular o descartar les migracions dels últims 100 anys. D'altra banda, també s'ha destacat la necessitat d'incloure les TAG a la xarxa mundial de monitorització anomenat GLORIA que té com a finalitat registrar els possibles ascensos de la vegetació de muntanya a conseqüència de l'escalfament global durant el segle XXI. Per aconseguir-ho caldrà escollir i instal·lar una Parcel·la d'Observació Permanent i seguir els protocols (Pauli *et al*, 2004).

La necessitat d'usar tècniques basades en la modelització de nínxols ecològics s'ha posat de manifest en els capítols de la tesi basats en els efectes del canvi climàtic futur i passat a les TAG (capítol 2, 4 i 5). Per poder dur a terme aquest anàlisi, caldria obtenir una llista de les espècies a estudiar degudament georeferenciades, com també dades ambientals (clima i topografia, entre altres). La modelització de nínxols ecològics ha aportat dades molt informatives respecte les conseqüències del canvi climàtic futur

(Thomas, 2004; Thuiller, 2005) i la distribució de les espècies durant l'Últim Màxim Glacial (Bonaccorso *et al*, 2006). Aquests models, però, tenen una sèrie de limitacions com la no incorporació de dades referents a la dispersió de les espècies i les interaccions ecològiques. En el nostre cas seria molt interessant la incorporació de dades en el model, referents a les possibles migracions naturals, Holocèniques i futures. D'aquesta manera es podrien obtenir dades molt més precises per modelitzar la distribució de les espècies a les Terres Altes de la Guayana.

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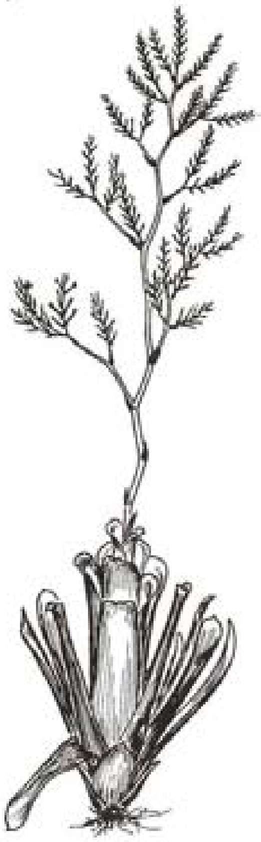
8. CONCLUSIONS



Brocchinia hechtioides

1. CONCLUSIONS

A continuació s’enumeren les principals conclusions de cada capítol d’aquesta tesi doctoral:

- S’ha obtingut una reconstrucció de la vegetació en el cim més elevat del massís del Chimantá, que reflexa una constància en la composició de la vegetació al llarg de l’Holocè.

- La variació en el balanç precipitació/evapotranspiració (P/ETP) no ha afectat significativament la comunitat de plantes, fet que suggereix que la comunitat té una capacitat suficient per suportar aquetes oscil·lacions sense canvis aparents.

- Aquesta constància en la comunitat s’interpreta com a absència de canvis ambientals de suficient intensitat per afectar-les.

- El pic de microcarbons situat a 3.9 cal ka BP, coincideix aproximadament amb l’inici d’una fase regional més seca, que possiblement va afavorir un augment en la incidència d’incendis a la Gran Sabana.

- El cims dels tepuis no han estat afectats per foc ni per altres activitats humanes durant el període estudiat (Holocè).

- Les localitats en zones altes dels tepuis són adequades per registrar canvis paleoambientals moderats, sent les millors zones les que es troben en ecotons, especialment entre la formació herbàcia i l’arbustiva (2200 m).

- S’ha obtingut per a cada tepui el límit topogràfic crític d’aïllament durant el LGM (*critical altitude for topographical isolation*). Aquest límit determina les espècies que romandrien aïllades durant les glaciacions, que és quan la possibilitat de connexió és màxima.

- Més del 70% de les especies van tenir la possibilitat, degut al desplaçament altitudinal de les condicions climàtiques durant les glaciacions, de migrar a les terres baixes i entre tepuis, amb la conseqüent possibilitat d'intercanvi biòtic i de flux genètic.

- El 8% de les espècies, haurien tingut la possibilitat de quedar aïllades durant les glaciacions. En aquest marc, l’especiació al·lopàtrica hauria estat el mecanisme generador d’endemisme en els tepuis. L’alta proporció d’espècies endèmiques locals dins aquest 8% suporta aquesta hipòtesi. El 22% restant va tenir possibilitats intermèdies.

- No es pot assegurar que l’evolució en aïllament topogràfic per si sola sigui suficient per explicar els actuals patrons d’endemisme. L’àrea disponible i la seva heterogeneïtat són factors potencials a considerar.

- La base de dades de PANTEPUI és la primera base de dades que conté totes les espècies de Pantepui (2446) amb la informació biogeogràfica corresponent. Representa una eina primordial que permetrà analitzar hipòtesis biogeogràfiques i patrons de distribució de les espècies dels tepuis.

- Les espècies de les Terres Altes de la Guayana es caracteritzen per tenir un patró unimodal de distribució en altitud. El màxim nombre d’espècies endèmiques de Pantepui es troba a 2000 m, el màxim d’espècies endèmiques de Guayana es troba a 1800 m i el màxim nombre d’espècies no-endèmiques es troba a 1500m.

- L’anàlisi individual per tepui mostra un patró creixent o unimodal en el nombre d’espècies endèmiques, i decreixent en la majoria de les endèmiques de Guayana i no-endèmiques.

- El nombre d’espècies endèmiques de Pantepui (excloent les endèmiques locals) estan positivament relacionades amb l’altitud i negativament amb l’àrea. Pel que fa al nombre d’espècies endèmiques de Guayana i no- endèmiques, la relació és oposada.

- Les possibles causes d’aquest patró en les espècies endèmiques de Pantepui podrien estar relacionades amb: l’especialització de l’hàbitat, l’aïllament topogràfic i l’augment de la fragmentació de l’hàbitat amb altitud.

- El nombre d’espècies endèmiques locals no estan significativament relacionat ni amb l’altitud ni amb l’àrea. Els processos geogràfics juntament amb els històrics, lligats als canvis climàtics del Quaternari explicarien el seu patró de distribució actual. A més, se suggereix que una part important de l’estructura genètica d’aquestes espècies es podria haver format durant el Quaternari.

- D’acord amb la relació especies/area (SAR), l’extinció esperada degut a l’escalfament global per a finals d’aquest segle a les Terres Altes de la Guayana seria aproximadament del 80% (>1700 espècies).

- D’acord amb la relació especies endèmiques/area (EAR), l’extinció esperada per les espècies endèmiques seria del 30 al 50% (200 a 400 espècies endèmiques).

- L’anàlisi de desplaçament del rang altitudinal (ARD) suggereix una extinció per pèrdua d’hàbitat potencial del 20 al 45 % de les espècies endèmiques de Pantepui per a finals d’aquest segle.

- L’extinció possible per pèrdua d’hàbitat no s’ha de considerar la única, ja que cal tenir present també la importància de les possibles extincions secundàries i l’exclusió competitiva degut a la migració altitudinal d’espècies de les terres baixes com també d’espècies invasores.

- Les famílies amb més risc de pèrdua d’hàbitat degut a l’escalfament global són les que tenen més espècies endèmiques de Pantepui, amb l’excepció de les Xyridaceae i les Poaceae.

- Els tepuis amb un nombre mitjà d’espècies endèmiques (especialment el Jaua, Sipapo i Parú) es troba més en risc que els que presenten més espècies endèmiques (Chimantá, Sierra Neblina i Auyán).

- L’anàlisi de desplaçament del rang altitudinal (ARD) en combinació amb l'estudi de la fragmentació de l'hàbitat permet identificar les espècies i les àrees amenaçades per l’escalfament global, afavorint el desenvolupament d’estratègies de conservació.

- D’acord amb el criteri B2 (disminució contínua projectada de l’àrea de l’hàbitat) de l’*International Union of Conservation of Nature* (IUCN), entre 294 i 410 espècies endèmiques estarien sota la categoria de Perill Crític. A més, entre 360 i 452 es considerarien Amenaçades i 25 serien Vulnerables.

- La pèrdua d’hàbitat projectat per un augment de 4 ºC serà superior al 80%. El nombre de taques d’hàbitat disminuirà de 64 a 102. *El landscape shape index* (LSI) i el *landscape division index* (LDI) tenen una tendència decreixent, suggerint una disminució de la complexitat del paisatge.

- Es proposen estratègies de conservació *in situ* (ex: prevenir la introducció d’espècies invasores) en el massís del Chimantá que representarà el 46.19 % (*largest patch index,* LPI) de l’hàbitat de les Terres Altes de la Guayana projectat per a finals d’aquest segle en combinació amb estratègies *ex situ* (ex: bancs de llavors i migració assistida).

Would you tell me, please, which way I ought to go from here?
`That depends a good deal on where you want to get to,' said the Cat.
`I don't much care where-' said Alice.
`Then it doesn't matter which way you go,' said the Cat.

Alice's Adventures in Wonderland
Lewis Carrol