OPINION PAPER

Unexpected biodiversity loss under global warming in the neotropical Guayana Highlands: a preliminary appraisal

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Abstract

The fully vegetated summits of the table mountains that form the Guayana Highlands (GH), in northern South America, hold amazing biodiversity and endemism levels, and unique vegetation types. In spite of their present-day healthy appearance, their biota is seriously threatened of habitat loss by upward displacement, because of the projected warming for the end of this century. Available data are still insufficient for a definite assessment, but preliminary estimations based on representative endemic vascular plant species show that roughly one-tenth to one-third of them would loss their habitat with the 2–4 °C temperature increase predicted for the region by AD 2100. Given the underlying endemism, the eventual loss of biodiversity will be of global nature. Other mountain ranges around the world with similar characteristics of the GH, namely topographical isolation, high endemism and absence of nival stage because of the lower altitude, would be under similar unexpected risk, and should be urgently considered for conservation purposes.

Keywords: biodiversity, conservation, endemism, extinction, global warming, Guayana, habitat loss, high mountains, migration, tropics

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Introduction

Among the predicted consequences of global change, there is a generalized biodiversity loss, which could be especially significant in high-latitude and high-mountain biomes (McCarthy et al., 2001; Chapin et al., 2004). On high-mountain biomes, the main reason is the displacement of environmental conditions to higher altitudes because of global warming, and the consequent community fragmentation and/or habitat loss for taxa living on climatically extreme environments above the treeline (Dirnböck et al., 2003; Körner, 2004; and literature therein). Upland biotic migrations and corresponding community reorganizations following the recent warming trend started at the beginning of the industrial era (ca. AD 1750) have been already documented, in temperate mountains (Grabherr et al., 1994; Pauli et al., 1996; Keller et al., 2000; Dullinger et al., 2003; Parmesan & Yohe, 2003; Root et al., 2003). Tropical mountains,

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however, have been largely ignored in this respect. In general, it is believed that the tropics are prone of suffering intensified aridity episodes or catastrophic events (cyclones, floodings, etc.), rather than habitat loss, as a consequence of climatic change (McCarthy et al., 2001). In particular, tropical mountain biotas are believed to be more threatened by changes in land-use intensity (Molau, 2004). However, upward migration has been recognized as a crucial biogeographical factor in tropical mountains, in relation to past and future climate changes (Bush, 2002). Here, the case of the neotropical Guayana Highlands (GH) is analysed to illustrate the potentially severe consequences of the predicted 21st century warming on highland biotas from tropical mountains, even on those of low/medium altitude, with no permanent snow and fully vegetated summits, presently under favourable mild and wet climates. This is still a preliminary overlook, because of the lack of data detailed enough for a more definite assessment. The main aim is to make evident the potential and unexpected danger for these and other similar tropical mountain areas, in order to promote

more detailed studies hopefully leading to suitable conservation strategies.

The GH

The GH, situated between the Amazon and the Orinoco basins (Fig. 1), are the assemblage of the more or less flat tops of remote and spectacular table mountains, the tepuis, which form the discontinuous Pantepui biogeographical province, of about 5000 km^2 and 1500–3000 m elevation (Huber, 1994). In the present context, the terms GH and Pantepui are roughly equivalent and will be used with the same physiographical meaning. The tepuis have been developed by long-term erosion of the Precambrian sandstone/quartzites of the Roraima Formation, which are part of the Guayana Shield (Briceño & Schubert, 1990). More than 100 of these mountains are known, most in Venezuela, albeit few lie on Brazil, Colombia and Guyana (Steyermark, 1986). The more common altitude of the tepui summits is between 2000 and 2600 m, with a maximum of 3014 m at Sierra de la Neblina, in the border between Venezuela and Brazil (Berry et al., 1995). The GH climate is mild and perhumid. Mean annual temperature is between 12 °C and 18 °C with negligible seasonal oscillations, and total annual rainfall averages 2500–3500 mm, without dry season (Berry et al., 1995).

On the tepui summits, biodiversity and endemism are among the world's largest as shown, for example, by vascular plant records, by far the better known Pantepui organisms. Although the flora is still not entirely known, 2322 species of vascular plants have been found in these densely vegetated summits, of which 766 (33.0%) are endemic to the GH, and 1517 (65.3%) are endemic to the Guayana Shield (Berry et al., 1995). Local endemism, i.e. the restriction to one single tepui summit, is outstanding, reaching over 60% in some tepuis (Steyermark, 1986). At supraspecific level, the endemism is also remarkable, including 23 genera and the family Tepuianthaceae (Berry et al., 1995). The origin of such degree of biodiversity and endemism is still controversial. Earlier workers proposed that the GH flora evolved in topographical isolation because of the formation of the tepuis in the late Cretaceous, and vicariance has been the main diversification mechanism (Maguire, 1970). Others, however, believe that biotic connection among tepuis has been possible during the Quaternary glacial cycles by vertical migration, and invoke ecological factors, for example, the spatial distribution of particular edaphic conditions, to explain endemism patterns (Steyermark & Dunsterville, 1980; Huber, 1988; Berry et al., 1995). It has also been proposed that Pantepui would have been a biotic refuge during the glaciations, thus, contributing to the genera-
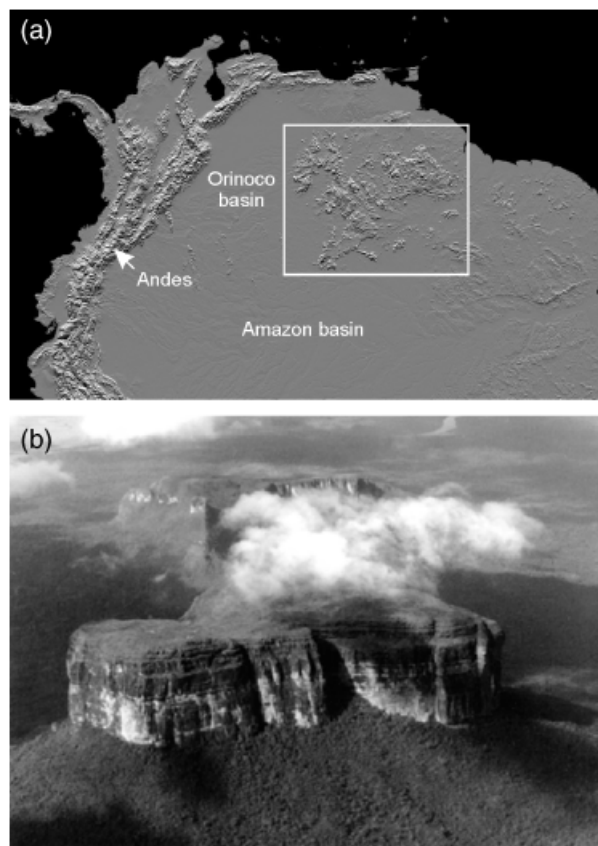

Fig. 1 Location map and typical Guayana Highlands (GH) landscape. (a) Radar image of northern South America showing the location of the GH (rectangle), in relation to the Orinoco and Amazon basins, and the northern Andean range (source image courtesy of NASA/JPL-Caltech). (b) Aerial view of the tepui Cerro Venado (photo by V. Rull).

tion of new endemic species, also by geographical isolation and allopatric speciation (Steyermark, 1979, 1986). But the refuge hypothesis has been severely criticized in the GH, on the basis of palaeoecological evidence (Rull, 2004c). Recently, Rull (2005b) proposed a diversification model linked to glacial–interglacial alternation, without reference to the refuge hypothesis, which involves gene flow among the tepuis – because of the vertical biotic migration – and the interaction of several speciation mechanisms in addition to vicariance.

The GH vegetation is dense and luxuriant, and includes four main categories: forests, shrublands, meadows and pioneer formations. Some peculiar formations belonging to these types are unique and characteristic of the tepui summits. Among forests, the more emblematic and well known are the high-tepui *Bonnetia* forests (Fig. 2), dominated by trees of this Theaceae genus. They grow mostly on peats and mineral soils derived

from diabase intrusions, typically between 1700 and 2600 m, along water courses (gallery forests) and in wet depressions. Physiognomically, the *Bonnetia* forests are low (6–12 m) and with a dense and homogeneous canopy formed by a few species, mainly *B. roraimae*, *B. tepuiensis* and *B. wurdackii* (Berry *et al.*, 1995). Shrublands are especially well developed in Pantepui, both physiognomically and floristically. Most of them grow on rock outcrops, sandy soils or peat. A singular shrubland type that occurs only in the GH is the paramoid scrub, characteristic of the huge Chimantá massif (>600 km^2 of summit area), where it is restricted (Huber, 1992). These scrubs are organized around 3 species of the endemic Asteraceae genus *Chimantaea* (*C. mirabilis*, *C. humilis* and *C. lanocaulis*), with characteristic stem rosettes (caulirossulae) 1–3 m tall, develop dense and extensive colonies on organic water-saturated soils (Fig. 2). The paramoid shrublands grow on the highest summits of the Chimantá massif up to around 2600 m, showing a notable diversification and geographical segregation (Huber, 1992). The name of this formation comes from its remarkable physiographical and taxonomic resemblance with the Andean páramos, dominated by caulirossulae of *Espeletia* (Asteraceae), situated above the treeline (Luteyn, 1999). The tepui meadows are herbaceous vegetation types dominated by herbs without a gramineous morphology, mainly Rapateaceae and Xyridaceae. In the GH, the dense broad-leaved meadows are typical, especially those dominated by *Stegolepis* (Rapateaceae), which is the prevailing and most characteristic floristic element of this biome in the Guayana region (Fig. 2), with a conspicuous geographical and altitudinal differentiation (Huber, 1988; Berry *et al.*, 1995). These formations grow on deep and wet organic soils, attaining up to ~ 1 m tall, and are spiked by small stands of shrubs, mainly of Asteraceae, Cyrillaceae and Rubiaceae. Finally, pioneer formations (lithobiomes) are early colonizers of bare habitats, mostly exposed rock surfaces. There are not vascular plants, but cyanobacteria, fungi and incrustant lichens, which contribute to rock weathering. On incipient organic soils, more advanced successional stages are represented by small clusters of vascular plants also present in shrublands and meadows, mainly Bromeliaceae, Ericaceae, Xyridaceae and Rapateaceae (Berry *et al.*, 1995).

The Pantepui region is still nearly pristine. International conservation organizations have recognized the GH as a preferential subject for biodiversity preservation. They have been included in the WWF Global 2000 Project as the Ecoregion ER-45, and have been defined as one of the WWF/IUCN Neotropical Plant Diversity centres (Pantepui or SA-2), considered crucial for the evolution of the Guayanan and the Amazon biota
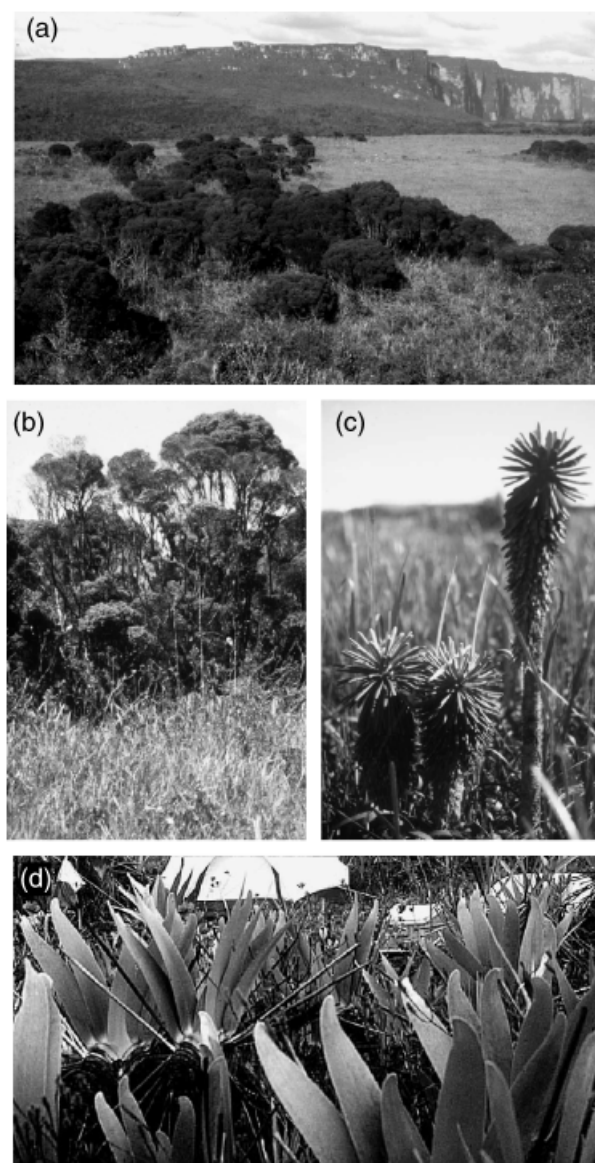
Fig. 2 Vegetation types and significant taxa mentioned in the text. (a) Summit view of the Akopán-tepui, in the Chimantá massif, showing the typical *Bonnetia* forests (in this case a gallery forest), surrounded by *Stegolepis* meadows. The cliffs of the higher Churí-tepui are at the background. (b) Closer view of a *Bonnetia* forest. (c) Specimens of *Chimantaea mirabilis* (Asteraceae) from the Amurí-tepui, in the Chimantá massif. (d) *Stegolepis ligulata* from the summit of the Akopán-tepui, in the Chimantá massif (photos V. Rull).

(WWF, IUCN, 1997; Olsson *et al.*, 2000). At present, more than 70% of the Guayanan territory is under official protection through the existence of seven national parks, five natural monuments, two biosphere reserves, four forest reserves, and one world heritage area (Berry *et al.*, 1995). Nevertheless, the potential

consequences of future global change have not been fully realized so far. Only a general assessment about an assumed global warming driven decrease in available moisture, and its potential consequences, has been advanced for the Guayana region as a whole (Berry *et al.*, 1995), but the potential effects of the global warming on the summit GH biota have not been addressed to date.

Natural vs. global-warming trends and rates of change

Until recently, the GH had been considered fairly stable from an environmental point of view. Recent palaeoecological studies, however, have recorded vertical displacements of summit taxa in response to temperature shifts (Rull, 2004a). The estimated extent of these displacements is of a few hundreds of meters for the Holocene (the last $\sim 11\,500$ years), and of more than 1000 m for the last glacial epoch. Indeed, during the Last Glacial Maximum (occurred around 21 000 years before present), when average temperatures were around 5–6 °C below the present ones, the neotropical biomes have been estimated to be about 1100 m below their present altitude (Farrera *et al.*, 1999; Rull, 2004b, c). The subsequent postglacial warming pushed the biota upward again until the present-day situation. Therefore, this upward biotic shift occurred at an average rate of 5.25 m per century, accompanying a temperature increase of about 0.025 °C per century. These can be considered the natural (i.e. free from human disturbance) rates of change to which GH organisms are adapted. A significant acceleration of this warming rate has been observed during the last 250 years, when average temperatures have increased 0.6 °C, which roughly represents a 10-fold increase (0.24 °C per century). The IPCC predicted increase for the end of this century (AD 2100) is expected to occur at even higher rates of 1.5–5.8 °C per century (Houghton *et al.*, 2001). For IPCC prediction purposes, the GH lie in the so-called 'Amazonia' (AMZ) region, for which the projected warming for the end of the present century is of 2–4 °C, depending on the forecasting model and the scenario considered (Houghton *et al.*, 2001). This represents a rate 80–160 times higher than the 'normal' for the GH taxa. Using the present-day lapse rate of about -0.6 °C per 100 m altitude (Berry *et al.*, 1995), an upward shift of environmental conditions between ~ 330 and 670 m is expected for AD 2100. Therefore, many taxa adapted to the highermost parts would be in danger of habitat loss and irreversible extinction. Species with lower and/or wider altitudinal ranges might theoretically survive, but they could hardly follow the estimated rates of change.

Habitat loss estimation and potential extinction

With the limited data available so far about the GH biota, is not possible to know the exact amount of potential extinction under global warming conditions, but some illustrative estimations are possible. For example, a simple altitudinal range displacement (ARD) analysis shows that about one-third of the endemic genera, all monotypic, are endangered assuming a 2–4 °C warming (Table 1). Furthermore, several species from polytypic genera that are not under risk as a whole, are also endangered (Table 2). In summary, of the 45 species corresponding to Pantepui endemic genera, 16 ($\sim 35\%$) are threatened of habitat loss by global warming. A similar analysis on all the species of the GH is required for a definite extinction risk assessment, but this is prevented by the lack of detailed phytogeographical information. Because of their remoteness and access difficulties, not all the tepuis have been visited by scientists, and the level of exploration of those surveyed is very little to moderate (Berry *et al.*, 1995). Therefore, the knowledge of the spatial distribution and topographical arrangement of their taxa is far from being enough for a satisfactory risk assessment. However, some characteristic Pantepui taxa, such as, the formerly mentioned *Chimantaea*, *Stegolepis* or *Bonnetia*, are relatively well known and suitable for a first appraisal (Huber, 1988, 1992; Givnish *et al.*, 2000).

The case of *Chimantaea* is especially significant in the present context because of its narrow geographical range and its preference for highermost summits. *Chimantaea* has nine described species with two subspecies, all of them restricted to the Chimantá massif and three adjacent tepuis (Auyán, Aprada and Murisipán) (Huber, 1992). As mentioned, they live in the uppermost parts, with a lowermost distribution limit (LDL) around 1900 m, except for two, *C. lanocaulis* and *C. rupicola* (Table 2). The maximum altitude of the tepui summits in which *Chimantaea* occurs is around 2650 m (Huber, 1992), some 750 m above the LDL of most of its species. Therefore, using the present-day lapse rate, ARD analysis predicts that all the *Chimantaea* species would be under risk of habitat loss by a warming of 4.5 °C, which is very close to the maximum predicted. The estimated temperature increases for *C. lanocaulis* and *C. rupicola* to loose its altitudinal habitat fall within the risk region (Table 2). Therefore, these two species are in high risk of habitat loss while the others, although less endangered, might be pushed up to small uppermost summit areas, with the consequent habitat reduction and fragmentation. For example, an intermediate increase of 3 °C, would remove the habitat of *C. lanocaulis* and *C. rupicola*, and restrict the remaining species to altitudes above 2400 m, which are attained only on reduced,

Table 1 Altitudinal range displacement (ARD) analysis for the endemic genera of the Guayana Highlands in relation to the risk of habitat loss by upward displacement of environmental conditions

Genus	Family	LDL	HPH	UDHL	THL	Species
Saccifolium	**Saccifoliaceae**	**2700**	**3014**	**314**	**1.9**	**1**
Marahuacea	**Rapateaceae**	**2400**	**2800**	**400**	**2.4**	**1**
Comoliopsis	Melastomataceae	2300	3014	714	4.3	1
Tyleropappus	**Asteraceae**	**2200**	**2358**	**158**	**0.9**	**1**
Neblinantha	Gentianaceae	2200	3014	814	4.9	2
Huberopappus	**Asteraceae**	**2000**	**2400**	**400**	**2.4**	**1**
Mallophyton	**Melastomataceae**	**2000**	**2650**	**650**	**3.9**	**1**
Coccochondra	**Rubiaceae**	**2000**	**2400**	**400**	**2.4**	**1**
Achnopogon	Asteraceae	1800	2650	850	5.2	2
Pyrrorhiza	Haemodoraceae	1800	3014	1214	7.3	1
Coryphothamnus	Rubiaceae	1700	2450	750	4.5	1
Achlyphilla	Xyridaceae	1700	3014	1314	7.9	1
Chimantaea	Asteraceae	1600	2650	1050	6.3	9
Glossarion	Asteraceae	1600	3014	1414	8.5	2
Quelchia	Asteraceae	1600	2650	1050	6.3	4
Rutaneblina	Rutaceae	1600	3014	1414	8.5	1
Brewcaria	Bromeliaceae	1500	2800	1300	7.8	2
Tepuia	Ericaceae	1500	2650	1150	6.9	7
Celiantha	Gentianaceae	1500	3014	1514	9.1	3
Adenarake	Ochnaceae	1500	3014	1514	9.1	1
Aracamunia	**Orchidaceae**	**1500**	**1600**	**100**	**0.6**	**1**
Adenanthe	Ochnaceae	1300	2650	1350	8.1	1

LDL, lower distribution limit of the genus; HPH, highest potential habitat represented by the highest tepui summit within the present geographical range of the genus; UDHL, upward displacement required for total habitat loss (HPH−LDL); THL, temperature required for total habitat loss (as derived from UDHL, using the present-day lapse rate of −0.6 °C 100/m). Altitudes in metres above sea level. Genera threatened of total habitat loss are in bold. The endemic genus *Ochthephilus* (Melastomataceae) has not been included because of the lack of appropriate data. Raw data from Berry *et al*. (1995).

Table 2 Altitudinal range displacement (ARD) analysis for the endangered species of polytypic endemic genera of Table 1

Species	LDL	HPH	UDHL	THL
Achnopogon steyermarkii	1800	2450	650	3.9
Chimantaea lanocaulis	2300	2650	350	2.1
C. rupicola	2100	2650	550	3.3
Glossarion bilabiatum	2600	3014	414	2.5
Quelchia conferta	2200	2723	523	3.1
Q. eriocaulis	2100	2650	550	3.3
Brewcaria marahuacae	2500	2800	300	1.8
Tepuia vareschii	2300	2450	150	0.9
T. intermedia	1800	2450	650	3.9

See Table 1 for codes and details. Raw data from Steyermark *et al*. (1997, 1998, 1999).

disjunct areas from the north of the massif (Huber, 1992). In such a situation, besides habitat loss, intense competition for space and resources between the seven eventually surviving *Chimantaea* species is expected to be an important additional extinction factor.

Bonnetia and *Stegolepis* are more diversified and widely distributed, both geographically and topographically. *Bonnetia* is represented in Guayana by 26 species, of which 24 are part of the GH flora and 14 are restricted to it (Huber, 1988). ARD analysis shows that half of *Bonnetia* species living on the tepui summits, almost all local endemics, are under risk of habitat loss (Table 3). Among these threatened species, one of the most conspicuous elements is *B. wurdackii* one of the dominants of *Bonnetia* forests, which taxonomic composition might be significantly affected in this way. In addition, the projected warming would threaten the own existence of the uppermost belt of these forests, situated above 2000 m (Berry *et al*., 1995), because the uppermost habitat available is only 600 m upslope, attainable with a warming of ∼ 3.6 °C, which is within the predicted range. Concerning *Stegolepis*, 25 of the 28 Guayanan species occur on the GH, and 15 are restricted to these summits, most of them to one single tepui (Huber, 1988). In this case, only 4 species are threatened of ARD habitat loss, but a similar amount is very close to the threshold (Table 4), as in the case of

Table 3 Altitudinal range displacement (ARD) analysis for *Bonnetia* species in relation to the risk of habitat loss by upward displacement of environmental conditions

Species	LDL	HPH	UDHL	THL	LE
Bonnetia bolivarensis*	**2400**	**2400**	**0**	**0.0**	+
B. wurdackii	**2100**	**2650**	**550**	**3.3**	+
B. chimantensis	**2090**	**2650**	**560**	**3.4**	
B. toronoensis	**2030**	**2650**	**620**	**3.7**	+
B. roseifolia	**1922**	**2250**	**328**	**2.0**	+
B. roraimae	1900	2723	823	4.9	
B. huberiana	1850	2650	800	4.8	+
B. maguireorum	1800	3014	1214	7.3	+
B. celiae	**1800**	**2400**	**600**	**3.6**	+
B. tepuiensis ssp. *minor*	1800	2650	850	5.1	+
B. duidae	**1700**	**2358**	**658**	**3.9**	+
B. neblinae	1700	3014	1314	7.9	+
B. multinervia	1650	2700	1050	6.3	
B. steyermarkii	1600	2450	850	5.1	

See Table 1 for codes and details. LE, local endemics. Raw data from Huber (1988).

*Represented by one single locality at the top of Ptari-tepui.

Table 4 Altitudinal range displacement (ARD) analysis for *Stegolepis* species in relation to the risk of habitat loss by upward displacement of environmental conditions

Species	LDL	HPH	UDHL	THL	LE
Stegolepis terramarensis	**2600**	**2800**	**200**	**1.2**	+
S. maguireana	1950	2650	700	4.2	+
S. vivipara	1925	2650	725	4.4	+
S. grandis ssp. *jauaensis*	**1900**	**2250**	**350**	**2.1**	+
S. ligulata	1850	2650	800	4.8	+
S. pauciflora	**1820**	**2358**	**538**	**3.2**	+
S. jauaensis	**1800**	**2250**	**450**	**2.7**	+
S. neblinensis	1700	3014	1314	7.9	+
S. parvipetala ssp. *chimantensis*	1660	2650	990	5.9	
S. wurdackii ssp. *wurdackii*	1600	3014	1414	8.5	+
S. gleasoniana	1520	2358	838	5.0	+
S. cardonae	1500	2650	1150	6.9	
S. hitchcockii ssp. *hitchcockii*	1500	2200	700	4.2	+
S. grandis ssp. *phelpsiae*	1500	2200	700	4.2	+
S. membranaceae	1500	2800	1300	7.8	

See Table 1 for codes and details. LE, local endemics. Raw data from Huber (1988).

Chimantaea. All these species are local endemics. *S. terramarensis* dominates the upper meadows of one single tepui, the Marahuaka (Berry *et al.*, 1995); hence, its disappearance would determine the indirect extinction of other ecologically related taxa. A similar situation is found for *S. squarrosa*, which is not part of the present analysis because it is not strictly a GH species, but is equally endangered of habitat loss. This species occurs
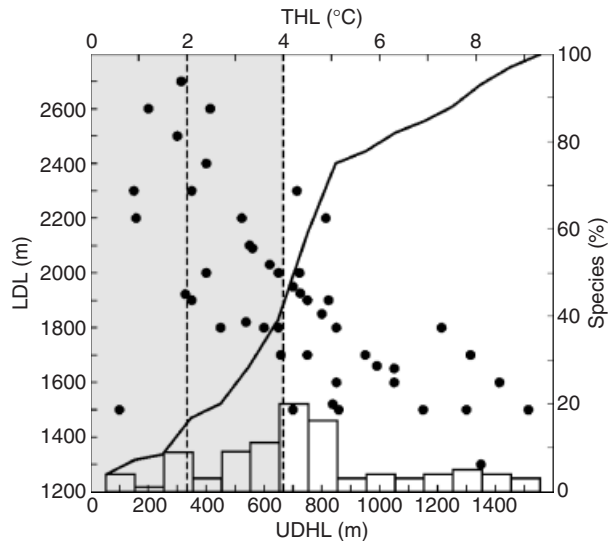
Fig. 3 Graphical altitudinal range displacement (ARD) analysis for all the species analysed. Acronyms as in Table 1. Black dots are the species' arrangement according to their upward displacement required for total habitat loss (UDHL) temperature required for total habitat loss(THL) and lower distribution limit of the genus (LDL) values. Solid line represents the cumulative habitat loss in percentage, and empty bars are the rate of change of this parameter. Broken lines indicate the range of the IPCC-predicted temperature increase for the end of the present century, and the risk region is in grey. *Bonnetia bolivarensis* has been excluded from the analysis (see Table 3).

between 1200 and 1600 m altitude, as the absolute dominate of the extensive meadows of the Guaiquinima massif (Rull, 2005a), one of the largest Guayanan table mountains, with more than 1000 km^2 of summit area (Steyermark & Dunsterville, 1980). Because the maximum altitude of this massif is of about 1600 m (Berry *et al.*, 1995), an upward shift of 400 m, equivalent to a warming of 2.4 °C, would be enough for *S. squarrosa* to entirely loose its habitat.

The results of gross ARD analysis for the endemic species considered here are summarized graphically for a better general risk appraisal and prediction (Fig. 3). Overall, seven to 27 of the 76 species considered (∼ 9–35%) are in danger of habitat loss by a predicted warming of 2–4 °C. All of them are GH endemics, so they are at risk of worldwide extinction. However, the ARD framework of Fig. 3 should not be viewed as static. Indeed, IPCC predictions are periodically revised, and continued botanical fieldwork eventually enhances the known range for certain involved species. If so, only temperature thresholds and selected LDLs should be modified to obtain the new prediction framework. In this way it is possible, for example, to evaluate the expected habitat loss under a progressive warming trend. For the species studied here, habitat loss is

expected to be null below $\sim 1\,^{\circ}\mathrm{C}$ warming, with a first slight increase between $1\,^{\circ}\mathrm{C}$ and $2\,^{\circ}\mathrm{C}$, followed by a drop just after this value, and a subsequent increase between $3\,^{\circ}\mathrm{C}$ and $4\,^{\circ}\mathrm{C}$ (Fig. 3). The maximum rates of habitat loss occur around 4–$5\,^{\circ}\mathrm{C}$, which is beyond the maximum warming predicted for the AMZ region by AD 2100 (Houghton *et al.*, 2001). Such a warming, which is very unlikely and would involve altitudinal displacements up to $\sim 1000\,\mathrm{m}$, would remove the habitat of $>70\%$ of the GH species studied. Beyond $5\,^{\circ}\mathrm{C}$, rates of habitat loss show a conspicuous drop, because most species have been already affected previously. From these estimations, the high vulnerability of the endemic vascular flora and, by extension, the biota of the GH is manifest and surprising. Furthermore, ARD calculations involve only total habitat loss, and an unknown amount of potential extinction because of habitat reduction below critical size and/or fragmentation should be added.

From a biogeographical/evolutionary point of view, it is interesting that a displacement similar to that recorded since the Last Glacial Maximum to the present because of natural causes ($>1000\,\mathrm{m}$), would cause a biodiversity loss of around 80% of the endemic species considered here. This agrees with the still untested hypothesis about the existence of unknown enigmatic communities lacking modern analogues on the summits of the tepuis during the last glaciation, and their post-glacial extinction (Rull, 2005b). A similar situation has been widely recognized in northern temperate areas but, whereas in them the major source of dissimilarity between past and modern communities rely upon differences in the geographical array and the relative abundance of taxa (Jackson & Williams, 2004), in the GH, the occurrence of a significant amount of species with no extant representatives has been suggested (Rull, 2005b). The existence of these assumed unknown glacial communities at the top of the tepuis, and the consequent interglacial extinction, would be also extended to past glacial cycles. Since the beginning of late-Cenozoic glaciation of the Northern Hemisphere, about 2.5 million years ago, roughly 40 cycles of glacial extent have occurred (Raymo, 1994), hence, the cumulative extinction of GH taxa since then would have been remarkable. Such extinctions are most probably irreversible because of the lack of source areas, i.e. terrains higher than 3000 m altitude, able to preserve populations and provide propagules for recolonization (Rull, 2005b). The present-day, global-warming scenario is analogous to a typical postglacial warming trend, the difference being a matter of rate of change. Indeed, the extinction magnitude is expected to be similar, but it will occur in a century instead of $\sim 20\,000$ years.

It should be stressed that ARD results do not necessarily involve straightforward extinction. They are arguments for both lower and higher extinction amounts than expected from ARD analysis alone. For example, some studies show that temperate high-mountain species migrate upwards at lower rates than predicted using solely lapse rate estimations (Grabherr *et al.*, 1994), thus, reducing their effective risk of habitat loss and extinction. On the other hand, not only habitat loss, but also critical habitat size and fragmentation, are important extinction-risk factors for mountain taxa (Dinrböck *et al.*, 2003). In this way the excessive habitat reduction may lead to the existence of small and isolated populations, insufficient to guarantee the continuity of the involved species (Clubbe, 1996). In the tepui summits, given its characteristic stepped topography, it is expected that habitat reduction by upward displacement will be even more drastic than in other mountains with a more conical shape. In addition, the extinction of a keystone species, that which is critical for the existence of a community (Heywood & Iriondo, 2003), can have a magnifying effect. This would be the case for the paramoid-forming *Chimantaea* species and those of *Bonnetia* and *Stegolepis* that dominate the forests and meadows, respectively. Indeed, their extinction would promote the disappearance of other species not directly threatened by environmental change, but highly dependent on the existence of these communities. Another element that can enhance extinction is the successful establishment of introduced and/or invasive species (Clubbe, 1996), which in this case would arrive from lower altitudes pushed up by the warming trend. Therefore, profound changes are expected to occur in the composition of GH uppermost communities under climate forcing, as it has been recorded in the past (Bush, 2002).

Future studies, final remarks and some conservation insights

Although the results of the present study should be considered preliminary and their extrapolation still premature, the numbers are striking and stress the importance of a more detailed study on the potential consequences of the predicted global warming in the Pantepui region. Such study should be based on detailed field observations using satellite-positioning systems, and high-resolution techniques of spatial/topographical data analysis such as GIS tools. Fortunately, the tepuian localities studied so far are relatively well documented (Berry *et al.*, 1995), and some of these measures are still possible, but an extensive research program including new field surveys oriented towards specific objectives within the climate change framework is needed. A useful complementary tool would be the extrapolation of observed upward migration rates in recent times, namely the last century, a method

successfully used in other mountains (Grabherr *et al.*, 1994; Dinrböck *et al.*, 2003). In the GH, in spite of the long history of their exploration (Berry *et al.*, 1995), these historical records seem, at first sight, insufficient, but a more careful consideration of this possibility is needed. A better basic phytogeographical knowledge using these advanced techniques would allow substitution of simple ARD analysis by more sophisticated prediction tools, for example, spatially constrained models able to simulate the expected distribution area of any species at any possible future warming scenario (e.g. Halloy & Mark, 2003). This would enable more realistic and accurate predictions, given the complex GH topography and environmental variability. Finally, not only temperature shifts, but also changes in available moisture are known to be important climatic forcings for living communities, especially in the tropics. However, the IPCC-projected precipitation change for the AMZ region by AD 2100 is roughly -5% to 5% with respect to the present (Houghton *et al.*, 2001), which is negligible as compared with temperature change.

The global warming scenario suggested for this study is surprising, given the present healthy and apparently safe aspect of the GH biomes. This is especially true if the comparison is made with the climatically stressed high-mountain environments immediately below the snowline of the highest mountain ranges. Uppermost taxa from highermost mountain ranges might have the possibility to accommodate future warming by colonizing higher altitudes presently under permanent snow because of increased, warming-induced, snow ablation. For example, it is estimated that 50–90% of the European alpine glaciers will be melted by the end of the century (Watson & Haeberli, 2004). Furthermore, northward migration would be also theoretically possible in those mountain ranges with latitudinal continuity. In the GH, both latitudinal and altitudinal migration ways are hindered by physical isolation and the absence of a nival stage, thus habitat loss and potential extinction seems unavoidable and irreversible for many atop taxa. Therefore, future climate change is expected to reverse the present-day stress conditions on mountaintop biotas, so 'the last shall be the first, and the first last'. Given the large amount of endemism in the GH, the projected extinction directly hits global biodiversity, a situation that is not expected for mountains of lower endemicity levels as, for example, many temperate ranges. In addition, the potential for future biodiversity generation in the Guayana and neighbouring regions would be also compromised, because the GH have been considered as neotropical 'diversity pumps', because of their salient role in biotic diversification processes (Rull, 2005b).

The case of the GH is an issue of global concern. Many other mountain top biotas with characteristics similar to the GH (high endemism, geographical isolation, absence of a nival stage) exist elsewhere, especially on tropical and subtropical islands, and in the Mediterranean and circum-Mediterranean region. They should be urgently considered for conservation policies if the warming-driven global biodiversity loss has to be mitigated. Strategies for the preservation of these menaced biotas are challenging, as *in situ* policies (Heywood & Iriondo, 2003) are difficult to undertake. One possibility is to declare these areas as biodiversity 'hotspots' (Myers *et al.*, 2000) in relation to global warming, which would help delineating temporary and local protection actions. This proposal is supported by studies of worldwide bird diversity patterns (Orme *et al.*, 2005). Emphasis should be placed on conservation of individual taxa rather than communities. Palaeoecological studies support the view of communities as transient states of species' aggregation, which repeatedly form and vanish because of differential individualistic responses of their components to environmental forcing, a situation that is expected to be true also in the future (Bush, 2002). However, effective environmental protection to prevent habitat loss seems unattainable under continued global warming. Alternatively, some *ex situ* strategies could be considered. They should be based on a combined ecological and palaeoecological surveys oriented to: (1) identify all the potentially vulnerable species, (2) accurately estimate and compare the magnitude and rates of their upward migration under natural and global warming conditions, (3) assess the extinction risk for each species and (4) define conservation priorities accordingly. With this information, several *ex situ* actions to preserve genetic material (botanical gardening, seed/pollen/gene/DNA storing, etc.) might be evaluated. It would be asked if it is ethical to preserve such taxa considering the low probability of a short/medium-term environmental recovery needed to eventually reintroduce them under natural conditions. A reasonable answer to this question seems to be that preservation is the only way of keeping this possibility alive, while leaving endangered taxa to extinction means to make a decision of irreversible consequences.

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