Quaternary paleoclimatology, neotropical biodiversity, and potential effects of global warming

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Resum

Els canvis climàtics quaternaris enregistrats a l'hemisferi nord també han afectat la regió neotropical i han contribuït a definir-ne els patrons actuals de biodiversitat. Els estudis moleculars de DNA que s'han dut a terme en espècies neotropicals actuals mostren una acceleració significativa de les taxes d'especiació en els darrers 5 milions d'anys, fet que coincideix amb un refredament global durant el Pliopleistocè. A més, prop de la meitat de les espècies estudiades han aparegut durant els darrers 2,6 milions d'anys, en el marc de les glaciacions pleistocenes. La hipòtesi dels refugis es considera poc adequada pel Neotròpic i es proposen mecanismes alternatius de diversificació associats als canvis climàtics. Entre aquests, les migracions biòtiques verticals controlades per l'alternança climàtica glacial/interglacial, i les consegüents connexió i desconnexió de les biotes de terres altes i baixes, s'han considerat factors importants d'especiació. Un nombre important d'espècies endèmiques de les terres altes neotropicals estan potencialment amenaçades d'extinció per la pèrdua o fragmentació de l'hàbitat, com a conseqüència de l'escalfament global que es pronostica per a la fi de segle.

Paraules clau: paleoecologia, paleoclimatologia, Quaternari, biodiversitat, neotròpic

Abstract

The Quaternary paleoclimatic trends documented for the Northern Hemisphere also affected the neotropical region, and contributed to the shaping of its present-day biodiversity patterns. DNA molecular-clock studies on extant neotropical species have recorded a significant acceleration of speciation rates in the last 5 million years (my), coinciding with a marked Plio-Pleistocene global cooling. Furthermore, around half of the species studied originated during the last 2.6 my, in the frame of Pleistocene glaciations. The refuge hypothesis is considered inadequate for the Neotropics, and alternative diversification mechanisms linked to climate change are discussed herein. Among them, recurrent vertical migrations controlled by alternating glacial/interglacial climates, and the resulting connection and disconnection of lowland and highland biotas, have been considered important speciation factors. A significant number of endemic taxa from the neotropical highlands is potentially threatened of extinction by habitat loss/fragmentation, due to the global warming predicted by the end of the present century.

Keywords: paleoecology, paleoclimatology, Quaternary, biodiversity, neotropics

Knowledge of the ecological and evolutionary mechanisms of speciation and extinction that shaped present-day biodiversity patterns is essential to adequately manage its conservation [1]. Processes linked to paleogeographic reorganizations such as mountain building and the formation/destruction of land bridges have been relevant, especially during the Miocene and the Pliocene (23.8 to 5.3 and 5.3 to 2.6 my before present [BP]) [2]. Environmental change has also been recognized as one of the most powerful forcing factors for biotic diversification, mainly during the Quaternary (the last 2.6 my), characterized by alternating glacial/interglacial climates [3]. On the other hand, both climate change and human activities (hunting, habitat destruction, etc.) have been proposed as the main causes for biodiversity loss [4]. Therefore, climate change is intimately related to both aspects of biodiversity shaping, namely speciation and extinction, thus becoming a key issue in this context. The patterns of Quaternary climatic change and their influence on the biota are relatively well-known for the temperate regions [5]. By contrast, in the tropics, despite their comparatively huge biological diversity, this field of research is still in its infancy. This is especially true for the Neotropics, the portion of America situated between the Tropics of Cancer and Capricorn (~23° 27' N and 23° 27' S, respectively) (Fig. 1), which holds the vast Amazon and Orinoco basins and is among the most biodiverse regions in the world [6].

The aim of this paper is to review and discuss the evidence for Quaternary climatic changes in the Neotropics and their effect on biological systems, with emphasis on the origin of

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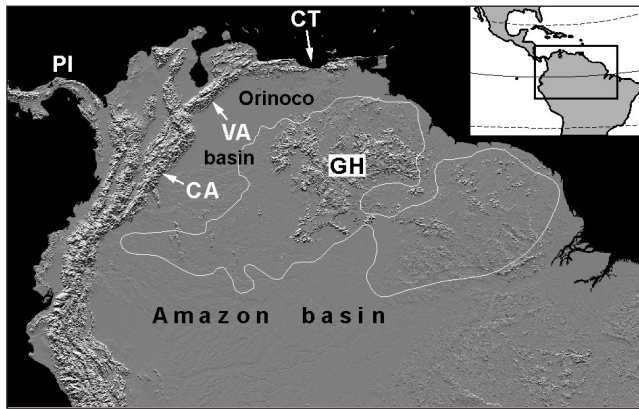
Figure 1. Map of northern South America, indicating the locations cited in the text (a reference map with the approximate extension of the Neotropics is provided at the upper right corner). The solid white line is the approximate contour of the Precambrian Guayana Shield, which roughly defines the Guayana region. CA, Colombian Andes; CT, Caricao Trough; PI, Panama Isthmus; GH, Guayana Highlands; VA, Venezuelan Andes. Radar image courtesy of NASA/JPL-Caltech.

neotropical biodiversity and its potential fate in light of the current global warming. The study is focused on the northernmost part of the Andean range and the Guayana region (Fig. 1). These regions have been preferred subjects in the author's research due to special environmental and biotic characteristics. The Venezuelan Andes reach ~5000 m in altitude, with large areas above the treeline (~3000 m), which marks the lower boundary of high-mountain environments [7]. The high-mountain biome is especially useful to document past changes, due to its elevated sensitivity to climate shifts and the presence of suitable paleoclimatic archives such as peat bogs and lake sediments [8]. Moreover, the historical human pressure on this part of the Andes has been minimal and limited to the last centuries. Prior to the European colonization (~AD 1500), the indigenous presence was restricted to small and scattered marginal populations, isolated from the main cultures of the central Andes [9]. Therefore, the archives from these environments likely hold excellent records of past, natural climatic changes. The Guayana region is sparsely inhabited and highly pristine, with around 90% of the rain forests still intact [10]. Guayana is thus considered as a natural laboratory for elucidating the role of natural environmental changes on the genesis of the living world [11]. The combination of both regions, the Andes and Guayana, will provide a thorough scenario for neotropical climate change, including highlands, midlands and lowlands.

The review is divided into three main parts. First, Quaternary climatic changes recorded so far in both study regions are summarized, and then compared with those of surrounding areas, to differentiate local from regional and global (or quasi-global) events. Unless otherwise stated, all the dates mentioned in the text are calibrated radiocarbon dates. The second section discusses the potential role of climatic changes in the origin of extant neotropical species, and a diversification model based on the glacial/interglacial alternation is proposed for the Guayana mountains. Third, a case study is presented as an example of potential extinction rates due to habitat loss in the Guayana highland flora, as a result of continued global warming in the

present century. Finally, suggestions for future studies and recommendations for conservation strategies are given.

Paleoclimatic trends

1. Quaternary neotropical paleoclimates

During the Quaternary, the Neotropics have been under the same climatic oscillations affecting the temperate and boreal regions. One of the longest continental cores obtained so far (380 m depth) was drilled in the neotropical Colombian Andes, and embraces the last ~2 my [12]. Pollen analysis of this core revealed up to 22 alternating phases of grass and arboreal pollen, corresponding to glacial/interglacial oscillations. Glacial conditions were characterized by the dominance of grasses, due to an average downward biotic displacement of about 1500 m, corresponding to a temperature dropping of 7.5 ºC with respect to the present averages [13]. Further studies on similar cores showed a close correspondence with oxygen isotope curves from marine and Antarctic cores, and confirmed that palynological cycles matched the Milankovitch cycles of 100 thousand years (ky) (eccentricity), 40 ky (obliquity) and 19-23 ky (precession) periods [14]. Accordingly, it was demonstrated that neotropical climates were linked to the rest of the globe through complex mechanisms of heat transport [12]. Further studies revealed that a typical neotropical glaciation, as exemplified by the Last Glacial Maximum (LGM), occurred around 20 ky BP, was characterized, in both highlands and lowlands, by an average temperature decline of 5-6ºC, a downward biotic migration of around 1100 m, and a decrease of 20-40% in precipitation with respect to the present values [15, 16].

The climatic nature of the post-glacial interval, from the end of the LGM to the beginning of the Holocene, around 11.5 ky [17], is still being debated for the Neotropics. The more characteristic event of this interval is the Younger Dryas (YD), a quasi-global cooling (stadial) consistently recorded in temperate latitudes between about 13 and 11.7 ky BP (11 and 10 ^{14}C ky BP) [18]. In the neotropical Andes, some studies agree with a cool event synchronous with the YD while others do not [19, 20]. Perhaps the most compelling evidence for a climatic event synchronous with the YD in the Neotropics was found in the marine cores from the Cariaco basin, where a reversal in the Titanium curve was manifested between 12.6 and 11.5 ky BP [21]. However, this was not interpreted in terms of depleted temperatures but as a decrease in rainfall and runoff. During the Holocene (the last 11.5 ky), temperature variations have been negligible in the Neotropics, but moisture conditions have changed markedly. It is difficult, however, to identify general trends, due to the heterogeneity in the wet/dry oscillations created by local variations [22, 23]. For example, a recent generalization attempt proposed a regional shift to wetter conditions in the tropical South America around 4 ky BP [24], in disagreement with the Cariaco record, which favours a markedly dry phase between 4 and 2 ky BP [21]. The main proposed causes for Holocene moisture variations are latitudinal displacements of the Intertropical Convergence Zone (ITCZ) and changes in

the intensity of El Niño events, both of which control precipitation regimes. A recent and conspicuous temperature shift of global extent known as the Little Ice Age (LIA), occurred roughly between the 13th and the 19th centuries, after the so-called Medieval Warm Epoch (MWE) [25]. The cause for such oscillation remains unclear but the most accepted forcing factors are an increase in atmospheric volcanic ash, and a minimum in the sun's energy output. The neotropical evidence for the LIA comes mainly from the Andes, where high-resolution isotopic and pollen stratigraphies clearly show the cooling [26, 27]. Whether the LIA was wet or dry in the Neotropics is still an open question.

2. Venezuelan Andes and Guayana

Most of the former climatic trends and events were also documented in the Venezuelan Andes, where the record begins during the last glaciation, and Guayana, where only Holocene sediments have been found [28, 29]. Stratigraphic and palynological studies of a sedimentary sequence covering the interval ~70-50 ky BP allowed recording a general cooling phase (7°C below present-day temperatures) with several short warming events (3 °C below present and ~2 ky duration each), which were correlated with the interstadials (ISs) 11 to 20 defined in the Greenland ice cores [30-32]. This demonstrated that the northern tropical Andes followed the same climatic pattern, in both timing and magnitude, as the higher latitudes during the last glaciation, that is, an extended cooling of ca. 80 my duration, spiked by 20-25 short ISs, also known as Dansgaard-Oeschger cycles [33]. The LGM was documented between ca. 23 and 20 ky BP [34]. A typical manifestation was the El Caballo stadial (~20 ky BP), during which average temperatures were 7°C below the present ones and the downward snowline shift was of about 1200 m [35]. The deglaciation was in progress around 16 ky BP, but minor glacier readvances were recorded until about 10 ky BP [34]. The occurrence or not of the YD is an open issue. The Mucubají Cold Phase II (centered at 11.5 ^{14}C ky BP), characterized by a cooling of 2-3°C below present [36] was suggested as a potential YD equivalent [29], but this cooling was not clearly detected in other high-resolution studies [37], thus preventing a definite assessment. For the Guayana region, it was suggested that, during the last glaciation, the climate was dry enough to prevent peat accumulation [38, 39]. Arid or semi-arid conditions have been proposed also for adjacent lowlands, on the basis of assumedly Pleistocene sand dune fields in the Venezuelan Llanos and the desiccation of Lake Valencia at the end of the Pleistocene [40, 41]. The main handicaps, however, are dating uncertainties and the lack of evidence due to the absence of glacial sediments [28, 29].

Climates at the onset of the Holocene were 2-3°C colder and wetter than at present in Guayana [42]. The Holocene is characterized by local heterogeneity in climatic trends. The more significant events recorded in the Andes were the La Culata dry phase (~6 ^{14}C ky BP) and the Miranda warm and humid phase (2.5 ^{14}C ky BP) [36]. In Guayana, two dry phases around the middle and late Holocene were documented from depleted lake levels [43], the second coinciding with a trend of maximum

levels of Lake Valencia [44]. Therefore, it is difficult to extract regional patterns with the data available so far. The LIA was clearly recorded in the Venezuelan Andes using both palynology (Piedras Blancas cold phase) and glaciological analyses [44, 45]. It extended from the 13th to the 19th centuries, with four cold peaks around AD 1180-1350, 1450-1590, 1640-1730 and 1800-1820. These match perfectly with four maxima of solar irradiance as deduced from [10]Be and Δ^{14}C fluctuations in lake sediments [46]. A pollen-altitude calibration based on modern analogues [47] allowed estimation of temperature decrease of 3.2°C below the present one. During the same interval, lake levels were high in Guayana and the Lake Valencia, and the European colonization began [29].

Climatic change and biodiversity

1. On the origin of neotropical biodiversity

The debate about the origin of neotropical biodiversity is intimately linked to the Quaternary glaciations, as the defenders of the Quaternary (Q) hypothesis believe that the main bulk of extant species originated during this period. In contrast, opponents defend an earlier, Tertiary (T) origin. A strong component of the Q hypothesis has been the refuge hypothesis, according to which glacial climates were dry, and the tropical forests were fragmented and their species refugiated into islands within a sea of savannas and deserts, which covered the Amazon and Orinoco basins. During the interglacials, the islands expanded and coalesced, thus creating an alternation between glacial vicariance and interglacial gene flow that promoted speciation [48]. The refuge hypothesis, however, is not consistent with the currently available paleoecological evidence [49] and is now under serious criticism in the Neotropics [50]. Therefore, it is not appropriate to equate the Q and the refuge hypotheses, a common but confusing practice. Other diversification mechanisms linked to climate change have been proposed; these emphasize the need for more complex models based on the coupling of different mechanisms [51, 52]. The main forcing factors involved in biological diversification according to the T hypothesis are related to paleogeographic reorganizations mainly driven by continental drift, and hence to the building and vanishing of barriers and bridges that modify the migration and isolation patterns of species [53]. The best-known reorganizations in the Neotropics are the uplift of the Andes, the closure of the Panamá Isthmus, the flooding of the Amazon basin by epicontinental seas, and the barrier effect of large rivers [54-56].

About two decades ago, the few dated fossils and scarce paleoecological evidence were the only support for either one or another hypothesis. At present, the number of DNA-based phylogenetic studies with dated divergence times for extant species is increasing, and may provide more direct evidence for testing hypotheses on the origin of present-day neotropical biodiversity. A thorough review of this evidence shows that both Q and T hypothesis should be rejected, as the >1400 neotropical species dated so far appeared in a continual fashion beginning in the early Miocene (~24 my BP), with an expo-
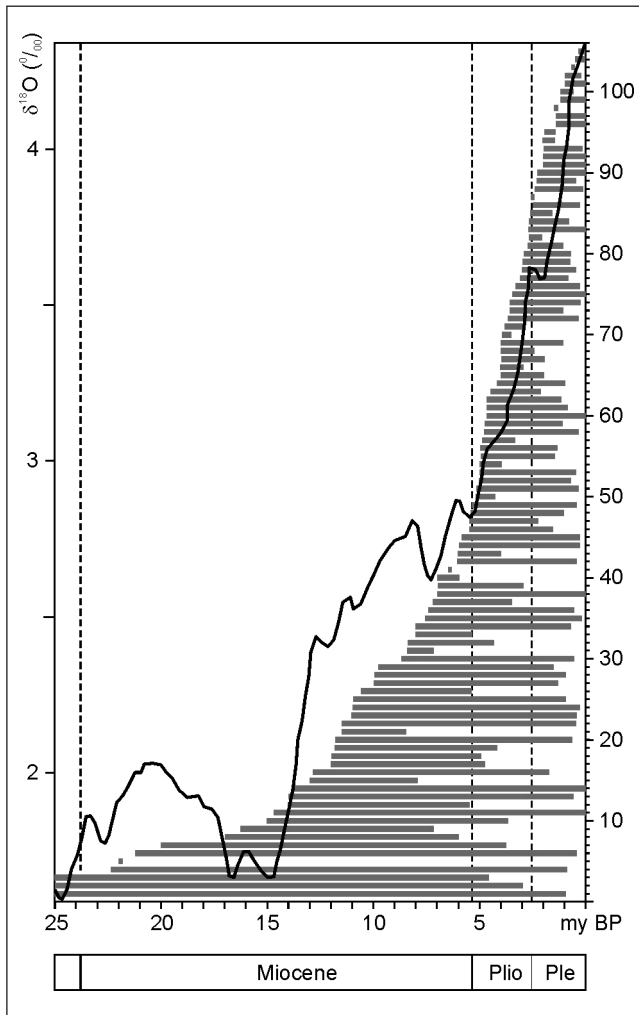
Figure 2. Time range of species divergence for the 105 groups (1404 species) of neotropical organisms studied using DNA molecular analysis. Each bar represents the range between the oldest and the youngest species for each group, including amphibians (8 groups), arachnids (1), birds (31), corals (1), echinoderms (2), fishes (15), insects (9), mammals (18), mollusks (3), reptiles (6), and vascular plants (11). Time in my BP: Plio, Pliocene; Ple, Pleistocene. The solid line represents the smoothed oxygen-isotope deep-sea curve (in $\delta^{18}O$ units [58]), which is largely controlled by the ice volume of Antarctica and the Northern Hemisphere and, hence, correlated with the intensity of continental glaciation.

nential increase in the last 5 my or the Pliocene-Pleistocene (Fig. 2) [57]. During the Miocene, one of the more influential forcing factors seem to have been the formation of the Andes, which separated coastal Pacific from inner Amazon populations, and promoted the emergence of novel adaptations to the newly formed high-mountain habitats. The final closure of the Panama Isthmus during the Pliocene also contributed to diversification by creating a passage for continental taxa and, at the same time, isolating Caribbean and Pacific marine populations. Other Tertiary paleogeographic reorganizations such as the emergence of new islands (for example the Galápagos), the isolation of large land masses by epicontinental seas or the effect of tectonically driven changes in drainage patterns, also influenced neotropical speciation [54-56]. However, the marked Plio-Pleistocene acceleration of diversification strikingly parallels the global cooling that led to Quaternary glaciations

and present-day climates. In addition, around 50% of the dated species originated during the Pleistocene 'glacial epoch' (the last 2.6 my) [57]. Therefore, although a causal relationship may not be proved solely from chronological coincidence, the influence of Plio-Pleistocene climatic changes on the origin of extant neotropical species, and hence on the origin of present-day biodiversity patterns, seems unequivocal.

Speciation processes and mechanisms linked to paleogeographical changes are relatively well known [2, 53], but those related to climate change are still poorly understood. The problematic refuge hypothesis proposed that allopatric speciation was the main speciation method during glaciations, when the assumed aridity favoured rainforest fragmentation and physical disconnection among forest patches [59]. Accordingly, present areas of endemism were considered past speciation centers and, as a consequence, the more probable locations for stable glacial refuges [48]. The critics of the refugial 'theory' demanded a more complex diversification model based on glacial age cooling, reduced atmospheric CO_2, and moderate reductions in precipitation [51, 60]. Rainforest fragmentation is no longer accepted by these researchers; instead, a continuous forest cover with no modern analogues is proposed for the Amazon basin during the glacial maxima. Under this scenario, endemism centers are not considered areas of glacial stability –wet refugia-in a dominant arid environment, as proposed by the refuge hypothesis– but of maximal disturbance, which promoted diversification [51]. Elevated areas adjacent to the Amazon basin have been considered especially active diversification centers [52], serving as biodiversity 'pumps' for the rest of the basin [61]. The Guayana Highlands are especially well suited in this respect [11], and have been used to develop complementary hypotheses on speciation linked to the Plio-Pleistocene cooling and the Pleistocene glaciations.

2. The Guayana Highlands

The origin of the elevated biodiversity and the high degree of endemism at the summits of the Guayana table mountains or *tepuis* (indigenous term meaning 'stone buds') has been largely debated. Pantepui is a discontinuous biogeographic province of around 5000 km[2] that comprises all the tepui summits from the Guayana Highlands, at an altitude of 1500-3000 m [62]. The best-known organisms from Pantepui are, by far, vascular plants [63]. These include around 2450 species, of which 42% are endemic to Pantepui and 25% are endemic to a single tepui [64]. The origin of such rare and peculiar biota was previously explained by evolution in isolation since the Late Cretaceous (>65 my BP) [65], similar to the imaginary 'Lost World' of A. C. Doyle, for which the Guayana Highlands provided inspiration [66]. Further research, including paleoecological and phylogeographic evidence, favoured a different view and a more recent origin for Pantepui extant species [67]. While molecular clocks gave a Miocene age (6-12 my BP) for the emergence of significant Pantepui genera, suggesting a Plio-Pleistocene origin for their species [68], paleoecological and physiographical evidence support the possibility of biotic connection and gene flow among tepuis through the surrounding lowlands [69-71].

Evolutionary mechanisms and forcing factors are still a matter of discussion, but some proposals are worth mentioning. The combined effect of the Plio-Pleistocene cooling and Pleistocene glaciations is used to explain the present biogeography of harlequin toads of the genus *Atelopus*. After a phylogeographic survey that included DNA molecular dating, it was proposed that the Guayanan species of this genus derived from a common ancestor that migrated from the Andes between about 4.7 and 1.5 my BP. Migration was due to cooling during the Pliocene, which promoted a downward slope displacement and subsequent migration across the Amazon basin [72]. Extant *Atelopus* species originated on mountaintops from this ancestor during the last 0.5 my, favored by climatic changes and physical isolation of highland summits [73].

However, topographic isolation of tepuian summits and (allopatric) speciation is not a straightforward relationship, due to the nature of Quaternary climatic changes. As stated above, biotic connection and gene flow among summits took place during glacial phases, when cold climates promoted spreading of populations by downward migration [67]. This was the dominant scenario during the Pleistocene, as glacial conditions remained during 80% of that period [60]. Real isolation of summit biotas occurred only during interglacials, or short warmings of around 10-15 ky duration, which sensitive organisms endured by upward migration to find their suitable environments [74]. Therefore, the 'normal' scenario for Quaternary evolution of extant species has been characterized by glacial biotic spreading and connection instead of isolation of summit taxa [75]. It is assumed that glacial mixing favors sympatric speciation, hybridization, adaptative radiation in the lowlands and mountain slopes, and vicariance in highland-adapted taxa unable to reach the lowlands. During interglacials, despite summit isolation, timing is probably not sufficient to achieve significant evolutionary change, and extinction by habitat loss due to the upward displacement of environmental conditions is the more likely outcome. In this framework, the nature of summit communities during glacial phases, and the potential long-term consequences of the assumed interglacial extinctions have been topics of speculation, but new hypotheses are emerging [76].

The downward biotic displacement recorded for the Neotropics during the LGM [15] are manifested in the Guayana Highlands in a downslope migration of about 1000-1100 m with respect to present conditions [77]. Therefore, the tepuian summits, most of them situated between 2400 and 2700 m [78], would have been theoretically occupied by taxa nowadays lying between 3400 and 3800 m. Since the maximum Guayanan altitude is only 3014 m (Pico Neblina) [78], these mysterious summit LGM biotas have been termed glacial 'ghosts' and tentatively associated with potential Andean analogues [75, 79]. Regarding the assumed extinction atop the tepuis during interglacials, despite the short interglacial duration, the hypothetical recurrent extinction events maintained during the ~22 glacial/interglacial cycles recorded during the Pleistocene [12] would have resulted in a significant cumulative biodiversity loss. Further paleoecological and phylogeographic research is needed to test both hypotheses.

Global warming and biodiversity loss: a case study and a global warning

At present, we are in an interglacial ñtheHoloceneñ that began at 11.5 ky BP [17]. In the region under study, the temperature increase until today was of 2-3 °C during the last 10 ky, as deduced from a biotic upward migration of around 400-500 m [42]. Since the LGM, occurred around 20 ky BP, the average temperature increase has been of 5-6°C and the upward biotic migration has been estimated in 1000-1100 m [77]. Therefore, the mean natural rates of temperature change and upward biotic migration have been of 0.02-0.03 °C/century and 4-5 m/century, respectively. During the last 250 years, a global temperature increase of 0.6 °C has been measured [80], which is around ten times the natural neotropical rates of change (0.24 °C/century). For the end of the present century, the predicted temperature increase in northern South America is of 2-4 °C [80], more than 100 times the natural rates. Considering the present lapse rate of –0.6 °C/1000 m altitude [78], such a change would induce an upward biotic migration between 350 and 700 m in the Guayana Highlands. A preliminary study shows that this would be untenable for many Pantepui taxa, and 10-30% of the endemic vascular flora would become extinct by habitat loss, due to the altitudinal displacement and final vanishing of suitable environmental conditions [81]. The predictions of an ongoing, more detailed study using GIS modelling are even worse, with approximately 50% of the endemic Pantepui species becoming extinct [82]. Not only total habitat loss, but also critical habitat reduction, fragmentation, secondary extinction by disappearance of keystone species, and competitive exclusion by lowland invaders, must be taken into account [81].

The consequences of global warming on highland ecosystems have been already analyzed for temperate mountains, where habitat loss and fragmentation are considered to be critical for taxa living in extreme conditions above the treeline [83-84]. The biotic ascent associated to the warming recorded during the industrial era (since AD 1750) has been already documented [85-91]. Recently, a global project, the Global Observation Research Initiative in Alpine Environments (GLORIA), was launched to measure the effective upward displacement of the alpine flora throughout the world, imposed by global warming (http://www.gloria.ac.at/, last visited 2 Jan 2007). The neotropical Andes have been included only very recently and no published information is available so far. Most of these studies are concentrated on highland communities living in extreme conditions close to the snowline, which are believed to be the most threatened. However, the case of the Guayana Highlands challenges this view and draws attention to non-stressed biotas from lower mountain ranges without snow caps. In the case of Europe, for example, it is estimated that 50-90% of alpine glaciers will be melted by AD 2100 [92], thus relaxing potential habitat loss by creating new terrains to be colonized by highland organisms. A similar situation would be expected for the highlands of the tropical Andes, but in the Guayana mountains, mountaintop biotas cannot migrate to higher altitudes and their extinction by habitat loss is the more

likely consequence [81]. Given the high degree of endemism, such extinction will be of global significance. This is an issue of global concern, owing to the existence of many other isolated and highly endemic mountaintop biotas elsewhere in tropical and subtropical mountains without a nival stage, notably in the Mediterranean region.

Acknowledgements

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About the authors

*The research group on Tropical and High-Mountain Paleoecology (*Paleoecologia Tropical i d'Alta Muntanya: PATAM*) is based at the Autonomous University of Barcelona, in the Department of Animal Biology, Plant Biology and Ecology (BABVE). It was launched very recently (February 2006) by Valentí Rull and is still growing. Our main interests are: (1) Global change from a paleo-climatic perspective, (2) high-mountain paleoecology and paleoclimatology, and (3) the origin and conservation of neotropical biodiversity. Our proxy is pollen, and we are associated with other teams from Spain and elsewhere to develop multiproxy teams including geology, geochemistry, sedimentology, stable isotopes, diatoms, ostracodes, etc. At present, we lead three projects funded by the BBVA Foundation, the Ministry of Education and Science (MEC) and the Institute for Catalan Studies (IEC), and are involved in others of national and international scope. We have developed studies in the Pyrenees and the Mediterranean region (Europe), the northern Andes and the Guayana region (South America). We enjoy doing research and we hope to keep growing (but not too much), and become associated with other similar research groups. PATAM website: http://einstein.uab.es/_c_gr_patam/*