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Biogeography of the Lost World (Pantepui region, northeastern South America): Insights from bryophytes

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Abstract

The 'Pantepui' region of northern South America comprises about 50 topographic islands above a lowland/upland rainforest matrix and constitutes a model of choice for testing island theory hypotheses in a continental setting. Although the Guiana Highlands are considered as the second most important center of endemism in the Neotropics for hepatics, the 10% endemism rates at the species level in liverworts, and probably even less in mosses, pale in comparison of the 42% of endemic angiosperm species. While about 60% of angiosperm endemics are distributed on a single tepui, single-tepui endemics represent only 1/3 of endemic liverworts and only one single-tepui endemic moss species has been described to date. These observations point to a higher dispersal ability of bryophytes as compared to angiosperms and may account for the contrasting rates of endemism between the two groups. In contrast to the vertical displacement hypothesis, which proposes that endemic tepui species originated from niche diversification and local adaptation during vertical migrations in the course of glacial/interglacial cycles, the Amazonian element represents only about 10% of the liverwort flora. By contrast, 1/2-2/3 of the species belong to the montane Neotropical element. The recurrent disjunctions observed between the Andes and the Pantepui region suggest that the bulk of endemic species in the Pantepui area might have originated by dispersal from cold-adapted Andean ancestors.

Key words: tepui, island biogeography, bryophyte, liverwort, moss, flora, endemism, migrations, glaciations, *Scorpidium scorpioides,* Brazil

Introduction

McArthur & Wilson's island theory (1967) proposes that the number of species on an island is a balance between immigration and extinction rates. Immigration rates are regulated by the facility with which new incomers are recruited, and hence, the distance separating the island from the nearest continental sources. Extinction rates, on the other hand, are mostly determined by island size. In the course of the two last decades, island theory has seen a revival of interest, in particular owing to its application to terrestrial ecosystems in the context of the metapopulation theory since habitat fragmentation has been identified as one of the most serious threats to biodiversity (Heywood & Iriondo 2003).

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The ‘Pantepui’ region is a biogeographic province referring to the complex of mountains mainly derived from the sandstone of the Roraima Group in southern Venezuela, northwestern Guyana and northern Brazil. The region, which includes about 50 topographic islands, called "tepuis", above a lowland/upland rainforest matrix, is a model of choice for testing the hypotheses of the island theory in a continental setting. The tepuis are tabular mountains reaching ca. 1200 to 2800 m of elevation from a surrounding lowland/upland tropical rainforest (Fig. 1, 2). They belong to the Precambrian Guiana Shield, which separated from the African Shield with the opening of the South Atlantic Ocean, 80–100 mya. The Pantepui area constitutes the remains of a gigantic erosion surface that has been dissected by the Amazon and Orinoco basins, which contain among the largest and most important rivers in terms of annual discharge on earth. Tepuis' summits are mostly flat and their surface area ranges between 0.2 and 1096.3 km^2 (McDiarmid & Donnelly 2005). In addition, unlike oceanic islands, tepuis exhibit, owing to their remoteness, almost pristine habitats, offering a unique possibility to test the predictions of the island theory in a context that is basically free of any human disturbance (Huber & Alarcón 1994).

Like oceanic islands, the continental islands of the Pantepui region include a unique flora and fauna. Owing to its extremely difficult access, the area remains, however, poorly explored. New species and genera of invertebrates, amphibians, and reptiles are still described at a rapid pace almost every year (e.g. Barrio-Amorós & Brewer-Carías 2008; Rödder & Jungfer 2008; Thompson 2008; Kok, 2008, 2009a, b; James 2009). In vascular plants, no less than 2,500 species in 630 genera—39 of which are endemic—have been recorded in the area. Among the 65% of vascular plant species that are endemic to the Guiana Shield, 33% are endemic to the Pantepui region, and around 25% to the summit of a single tepui (Berry & Riina 2005), making the Pantepui region one of the most important centers of endemism in the Neotropics. Considering that the surface of the tepuis summits only represents ca. 0.5% of the total area of the region, the density of endemics on the tepuis is, arguably, one of the highest of the biosphere.

In the present paper, we briefly summarize the main hypotheses that have been proposed to account for the evolution of the unique biota in the Pantepui region. We then document patterns of diversity and endemism in bryophytes and examine the extent to which they are comparable to those documented for higher plants. Finally, we discuss several hypotheses that may explain the differences observed in the patterning of diversity between bryophytes and angiosperms.

1. Origin and evolution of the unique biota of the Pantepui region: a review of evidence

Two major conflicting hypotheses have traditionally been proposed to account for the unique patterns of endemism observed in the flora and fauna of the Pantepui region. Maguire (1970), Steyermark (1986) and Vuilleumier & Monasterio (1986), among others, noted that the geological bedrock of the tepuis is very ancient and inherited from the break-up of Gondwana. This very ancient isolation would have given rise to the spectacular endemism rates observed today as well as the striking range disjunctions observed between the flora of the Pantepui with that of other Gondwana fragments, including western Africa, Malaysia, and Australia (Berry & Riina 1995). This theory implies that endemics currently observed on the tepuis have not had the opportunity to disperse over tens of million years and that evolution of the taxa that are disjunct among former Gondwana fragments has been extremely slow. Patterns of distribution of endemics on the tepuis tend to provide some support with this hypothesis, since about 60% of the endemic angiosperm species are single-tepui endemics (Berry & Riina 1995).

Comprehensive collecting, however, revealed that many taxa have a wider elevational range than previously thought, and that taxa from both highlands and lowlands merge at intermediate altitudes (Steyermark & Dunsterville 1980; Huber 1988). Also, the myth of total geographical isolation has been questioned, because large valleys and ridges effectively connect some tepui summits with the surrounding uplands (Huber 1988). The idea of evolution in isolation therefore progressively lost credibility and the Vertical Displacement hypothesis emerged. According to Steyermark & Dunsterville (1980), connection

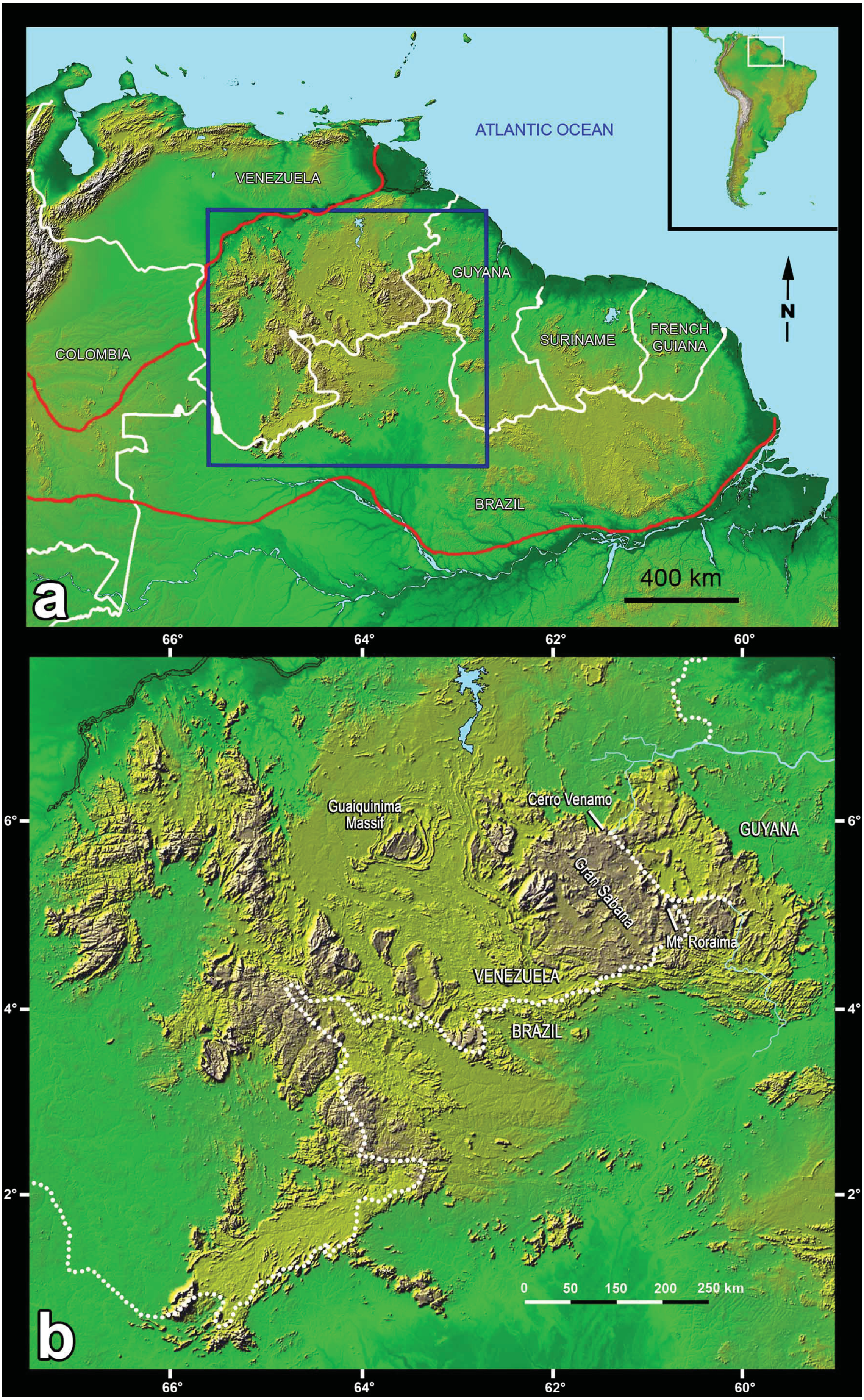

FIGURE 1. Map of the Guiana Shield (a) and the Pantepui region (b) of South America.

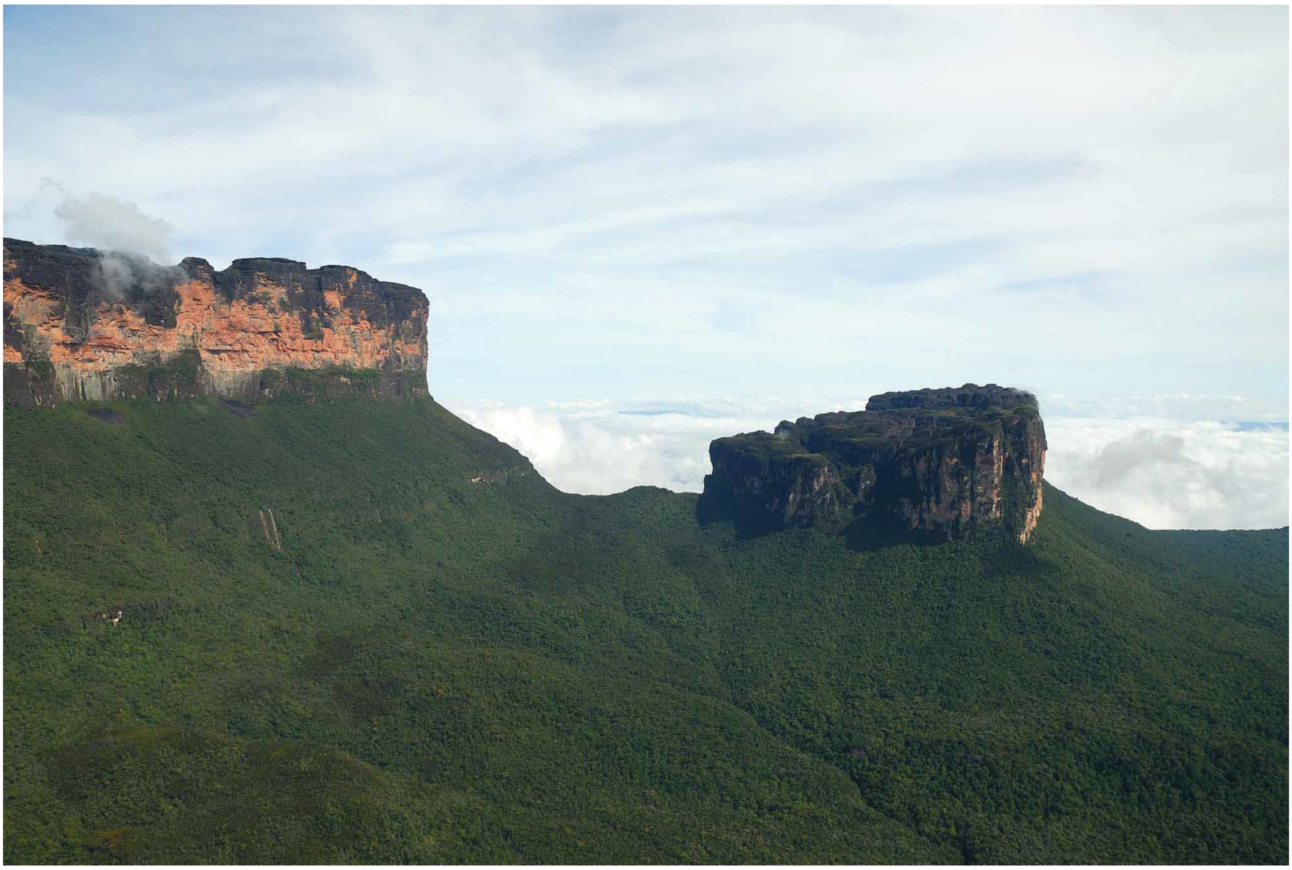

FIGURE 2. The Pantepui region: a mosaic of flat tepui summits with vertical cliffs above the upland/lowland rainforest. Here Mount Roraima (on the left) and Wei Assipu Tepui (on the right) (Photo: P. J. R. Kok).

between the ecosystems of the tepui summits is possible. They propose two mechanisms: (1) migrations using river valleys, and (2) vertical displacement during Pleistocene glacial-interglacial cycles. This model is comparable to the one invoked to describe current biotic patterns in Europe and North Africa owing to climatic changes since the upper Cenozoic era (Hewitt 2000). It emphasizes the prime importance of the tepuis as centers of speciation according to two processes associated with the glacial and interglacial periods. During the former, biota would have migrated towards lower elevations. In the course of this migration, sympatric speciation would have occurred owing to the large physiographic and microclimatic heterogeneity along the altitudinal gradient, which would have promoted niche diversification and local adaptation. As a result of those recurrent migrations, populations from different tepuis would have likely been in contact, thereby decreasing the role of allopatric speciation. During the interglacial periods by contrast, cold-adapted species would have migrated towards the summit of the tepuis, eventually resulting in the divergence of the populations on each individual tepui, but also in massive extinctions owing to the loss of habitat diversity (Rull 2005). In the course of the upper Cenozoic, glacial conditions predominated during 80% of the time (Shackleton *et al.* 1995; Willis & Whittaker 2000). Warm interglacial periods, about 40 of which occurred during the last 2.5 myrs (Hooghiemstra 1989; Raymo 1994), only occurred for a few thousand years each. A net gain of biodiversity would therefore have resulted from those climatic oscillations (Berry *et al.* 1995-2005).

These two competing theories are still debated. Willis & Niklas (2004) argued that the time scale involved by the dispersal theory is far too short to account for the rates of endemism observed. Recent molecular dating analyses suggest, however, that the origin of key endemic genera such as *Stegolepis* Klotzsch ex Körnicke (1872: 480) dates back to the upper Miocene to the Pliocene (Givnish *et al*. 2004). In the same way, by suggesting that the Guianan *Atelopus* (Amphibia, Bufonidae), a group of lowland/upland taxa distributed eastward of the Pantepui region, derive from a common ancestor that migrated from the Andes through the Amazon Basin thanks to the Pleistocene cooling, Noonan & Gaucher (2005) confirm the importance of Pleistocene climatic events, at least in the eastern Guiana Shield. These observations appear consistent with the persistence of bush vegetation on some tepui summits, which is roughly similar to those of páramos (Rull 2005). Furthermore, palynological data support the idea that altitudinal migrations over hundreds of meters occurred during the glacial/interglacial cycles (Rull 2004a). Palynological studies notably on *Chimantaea* Maguire, Steyermark & Wurdack (1957: 428) and *Stegolepis* have shown that vertical flora displacements have occurred during glacial and interglacial cycles (Rull 2004a). However, the vertical displacement hypothesis was developed for a low to intermediate tepui summit (Guaiquinima, ranging from about 700–1650 m), where connections with the surrounding lowlands are evident and extensive. The situation could be different for other, higher elevation tepuis. In fact, physiographic analyses suggest that half of them are too high, preventing their flora from the possibility to colonize the lowland areas during the glacial periods (Rull 2004b), suggesting that dispersal alone cannot account for the observed floristic distribution patterns. It therefore seems that the vicariant and dispersal hypotheses are not mutually exclusive and that both may contribute to describe the evolution of the Pantepui flora.

2. Bryophytes from the Pantepui region: diversity, distribution, and endemism

Mosses are the most conspicuous elements of the bryophyte layer of the tepuis. For instance, two *Campylopus* Bridel (1919: 71) and one *Leucobryum* Hampe (1839: 42) species dominate the terrestrial vegetation on Mount Roraima at 2000-2300 m. Moss diversity is, by contrast, much lower than that of hepatics accompanying the moss cushions (Gradstein & Florschütz-de Waard 1989). Moss diversity in the Guiana Highlands is relatively low, probably not exceeding 95 genera and 200 species. Endemism seems to be lower than in hepatics and, as noted by Buck (1989), moss diversity on the summits is low, probably not much beyond 70 species. There are two endemic genera, *Holomitriopsis* Robinson (1965: 75) and *Steyermarkiella* Robinson (1965: 75), both belonging to the Leucobryaceae, and both monotypic. Furthermore, the neotropical genus *Eucamptodontopsis* Brotherus (1924: 202) (2 species) is centered in the tepuis according to Robinson (1986). Total species endemism in the tepuis is not known, but is anticipated to be lower than in hepatics (Gradstein *et al.* 2001).

In terms of diversity in fact, liverworts are the predominant bryophytes in the scrubby, endemism- and carnivorous-plant rich vegetations on the extremely poor, moist sandstone soils, such as *Bonnetia* von Martius (1824: 114) woodlands and bogs, which characterize higher elevations of the tepuis. The total number of hepatic genera and species recorded is not very high (89 genera, ca. 250 species), and endemism reaches ca. 10% at the species level. All the endemic species are leafy liverworts (Jungermanniidae) (Table 1). The Guiana Highlands are the second most important center of endemism in the Neotropics for hepatics, with 7 endemic or sub-endemic genera, including morphologically highly specialized taxa such as *Haesselia* Grolle & Gradstein (1988: 327) and *Trabacellula* Fulford (1967: 86), *Vanaea* (Inoue & Gradstein 1988: 88) Gradstein & Florschütz-de Waard (1989: 33), and *Odontoseries* Fulford (1968: 364) (Gradstein *et al.* 2001; Schuster 2002). All of them, except *Haesselia* (2 species), are monotypic. The main hepatic genus of the tepuis is *Micropterygium* Lindenberg, Nees & Gottsche (1845: 233) (Lepidoziaceae), a neotropical genus of ca. 18 species, half of which are endemic to the Guiana Highlands. The region is also the center of diversity of subfamily Trabacelluloideae (*Trabacellula, Haesselia*), a morphologically specialized group of Cephaloziaceae.

About one third of the endemic liverworts occur on a single tepui. In mosses, only a single endemic, namely *Sphagnum boomii* Crum (1990: 185), is restricted to a single tepui, whereas 10 others have a distribution range that encompasses at least two tepuis (Table 1).

TABLE 1. Bryophyte species strictly endemic to the tepuis: extent of occurrence in the Pantepui region.

Single tepui endemics

Liverworts (8)

Haesselia acuminata Gradstein (1989: 30)

Haesselia roraimensis Grolle & Gradstein (1988: 327)

Vanaea plagiochiloides (Inoue & Gradstein 1988: 88) Inoue & Gradstein (1989: 33)

Cheilolejeunea neblinensis Ilkiu-Borges & Gradstein (2008: 522)

Drepanolejeunea papillosa Arnell (1953: 170)

Pictolejeunea piconii Pócs (2007: 110)

Pictolejeunea reginae Ilkiu-Borges (2002: 318)

Odontoseries chimantana Fulford (1968: 364)

Mosses (1)

Sphagnum boomii Crum (1990: 185)

Tepui endemics occurring on more than 1 tepui

Liverworts (14)

Adelanthus squarrosus Grolle (1989: 243)

Mnioloma venezuelanum (Fulford 1968: 287) Schuster (2000: 509)

Iwatsukia bifida (Fulford 1967: 80) Schuster (1968: 314)

Iwatsukia spinosa (Fulford 1972: 840) Schuster (1990: 249)

Trabacellula tumidula Fulford (1967: 86)

Blepharolejeunea chimantaensis Kruijt & van Slageren (1985: 126)

Micropterygium bialatum Fulford (1966: 268)

M. bolivarense Fulford (1966: 263)

M. conchifolium Reimers (1933: 155)

M. duidae Reimers (1933: 147)

M. grandistipulum Stephani (1901: 98)

M. steyermarkii Fulford (1966: 270)

M. tatei Reimers (1933: 150)

M. tumidulum Fulford (1966: 272)

Mosses (10)

Holomitriopsis laevifolia (Brotherus 1901: 90) Robinson (1965: 76)

Leucomium steerei Allen & Veling (1987: 674)

Renauldia paradoxica Allen (1987: 678)

Octoblepharum tatei (Williams 1931: 502) Bartram (1960: 4)

Sematophyllum maguireorum Buck (1990: 194)

Sphagnum ornatum Crum (1985: 181)

Sphagnum sanguinale Warnstorf (1898: 385)

Steyermarkiella anomalodictya Robinson (1965: 75)

Syrrhopodon rupestris Mitten (1869: 124)

Syrrhopodon steyermarkii Robinson (1972: 390)

Hypnella guayanensis Allen & Buck (1990: 190)

Biogeographic patterns in the liverwort flora established for two selected tepuis indicate that the bulk of the species belong to the montane Neotropical element, which represents one half of the flora on Cerro Venamo and two thirds on Mount Roraima (Fig. 3). From those, 6% and 24% are restricted to the Andes and the tepuis, respectively, including rare taxa such as *Aureolejeunea paramicola* (Herzog) Schuster (1987: 446), *Pleurozia heterophylla* Stephani ex Fulford (1972: 842), *Riccardia algoides* (Taylor 1846: 410) Meenks (1987: 168), *R. calcarea* (Stephani) Meenks (1987: 170) and *R. smaragdina* Meenks & de Jong (1985: 20). The lowland Amazonian elements only represent about 10% of the flora. Among those, *Protocephalozia ephemeroides* (Spruce 1982: 24) Goebel (1893: 83), *Pycnolejeunea papillosa* He (1999: 55), *Pteropsiella*

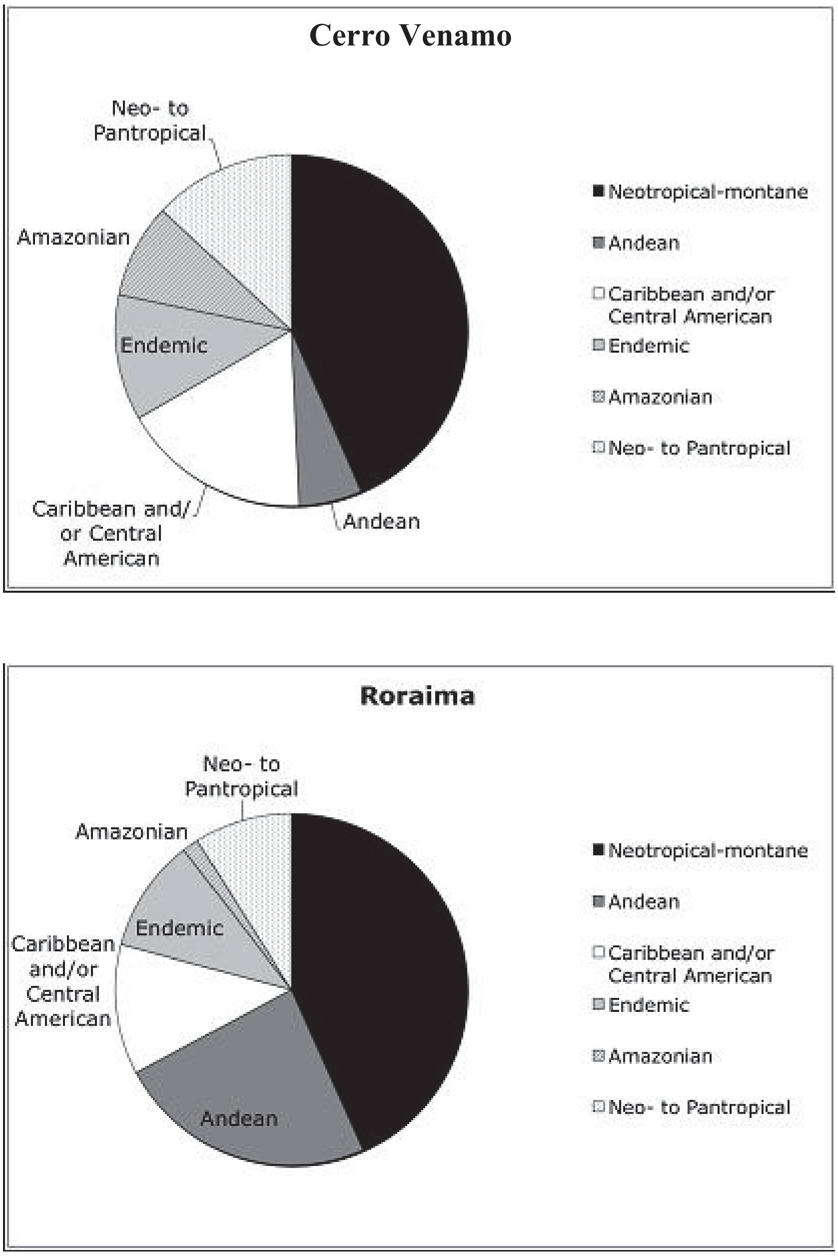

FIGURE 3. Biogeographic spectrum of the liverwort flora of two selected tepuis: Cerro Venamo (1000-1890 m) and Mount Roraima (2000-2800 m). Data from Dauphin & Ilkiu-Borges (2002) for Cerro Venamo and Gradstein & Florschütz-de Waard (1989), Rico & Pócs (2004) for Mount Roraima. 'Neotropical montane' includes species that occur commonly and widely throughout the mountains (above 500 m) of tropical America, including those of Mexico and Central America (Am2), the Caribbean (Am3), Brazil and the Guianas (AM5) and the tropical Andean countries (AM4). 'Andean' refers to species that are restricted to the high mountains of the backbone of tropical America (the Cordilleran track: see Schuster 1983 and Gradstein & Vaña 1987), from Mexico to Bolivia.

frondiformis Spruce (1876: 1), *P. serrulata* Spruce ex Stephani (1908: 276), *Telaranea pecten* (Spruce 1882: 85) Engel & Merrill (2004: 178), *Plagiochila gymnocalyx* Inoue (1989: 34), *Radula gradsteinii* Yamada (1989: 37), and *R. guyanensis* Yamada (1989: 38) are endemic to the lowland areas of the Guiana Shield (Gradstein *et al*. 2001), while four species exhibiting a range disjunction between the foot of the tepuis and lowland rainforests outside of the Guiana Shield: *Mnioloma nephrostipum* (Spruce 1885: 412) Schuster (1995: 847) and *Zoopsidella serra* (Spruce 1882: 32) Robinson (1969: 666) from Chocó, *Bromeliophila helenae* Gradstein (1997: 218) from Dominica and Colombia, and *Micropterygium reimersianum* Herzog (1943: 225) from Bahia. In mosses, exhaustive data for single tepuis are not available but, from the species lists already published for Mount Roraima, a clear Andean connection is evidenced through the presence of typical Andean species including *Atractylocarpus longisetus* (Hooker 1816) Bartram (1946: 110), *Campylopus richardii* Bridel (1819: 73), *Ctenidium malacodes* (1869: 509), *Hypnum amabile* (Mitten 1869: 513) Hampe (1869: 869), *Rhacocarpus purpurascens* (Bridel 1812: 121) Paris (1900: 29), and *Rhizogonium lindigii* (Hampe 1865: 345) Mitten (1869: 328). Further Andean connections are indicated by the recent discovery of *Scorpidium scorpioides* (Hedwig 1801: 295) Limpricht (1899: 571) on Wei-Assipu (LG, *Kok s.n*., 25.11.2009, 5°N13'03" and 60°W42'25"). A circumpolar boreo-artic montane species, *S. scorpioides* was previously reported from South America only from the Andes (Hedenäs 2003). The new locality documented here represents a disjunction of more than 1000 km (Fig. 4) and a new record for the moss flora of Guyana and Brazil. Two species, *Dicranoloma brittoniae* Bartram (1928: 69) and *Macromitrium ulophyllum* Mitten (1869: 206), are rare endemics to the disjunction formed by the tepuis and the Andes.

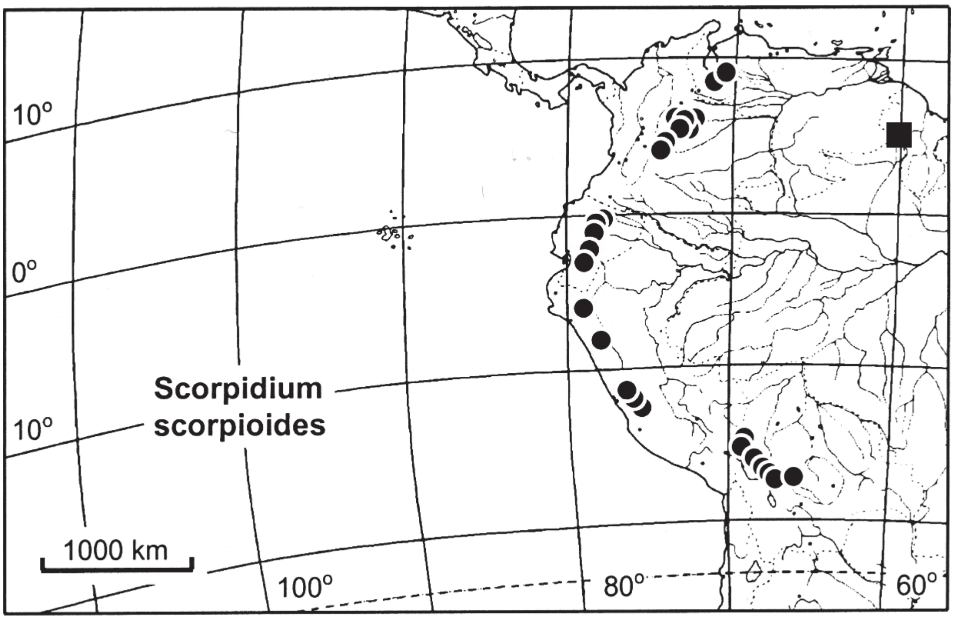

FIGURE 4. Typical range disjunction between the Andes and the Pantepui region: the moss *Scorpidium scorpioides* (data for the Andes (plain circles) from Hedenäs 2003 and for the Pantepui region (plain squares) from this study).

3. Origin and evolution of the bryophyte flora from the Pantepui region

Patterns of endemism and distribution in the bryophyte flora of the tepuis strikingly differ from those exhibited by angiosperms. First, although the Guiana Highlands are considered as the second most important center of endemism in the Neotropics for hepatics (Gradstein *et al.* 2001), the 10% endemism rates at the species level in liverworts and probably even less in mosses, pale in comparison to the 42% of endemic angiosperm species. This low endemism rate probably partly reflects the need for intensive field work that would be necessary to fully document the bryophyte flora of the area. There should be ample opportunity for discovery of new species and even genera, as evidenced by the 1985 expedition to Mount Roraima (Gradstein 1989; Gradstein & Florschütz-de Waard 1989), which yielded two striking new genera of liverworts (*Haesselia* and *Vanaea*) that were quite abundant locally and have not been found anywhere else since. The specialized morphology of these two genera, along with their monotypic condition, is suggestive of an ancient origin and an evolution characterized by many extinctions. Other stenotypic endemic genera from South America [e.g., *Zoopsidella* Schuster (1965: 24), *Pteropsiella* Spruce (1876: 161), *Schusterolejeunea* Grolle (1980: 105), and *Cephalantholejeunea* Schuster (1980: 798)] are in fact assumed to have diverged during the Tertiary owing to the long period (80 million years) of isolation since the opening of the South Atlantic and continuous tectonic activity (Schuster 1990). It is precisely such mono-or stenotypic genera that are, however, increasingly shown to have been given an inflated taxonomic rank owing to their peculiar morphology. For example, *Metzgeriopsis* Goebel (1887: 54), one of the most remarkable liverworts with a uniquely unistratose thallus that is often interpreted as an enlarged protonema and leafy sexual branches arising from thallus margins, was most recently shown to be a highly modified member of the widespread genus *Cololejeunea* (Spruce 1884: 291) Schiffner (1893: 121) (Gradstein *et al*. 2006).

Moreover, despite the need for floristic investigation, the general trend showing an at least three-fold higher endemism rate of endemism in angiosperms than in bryophytes is unlikely to be dramatically altered. Rather, the low endemism rate in the tepui bryophyte flora is very comparable to rates usually documented among island bryophytes. In the Galapagos for instance, species endemism is 13% in liverworts (Gradstein 2008) and 6% in mosses (Gradstein & Weber 1982), against about 50% in the native angiosperm flora. In the Canary Islands, the 1.5% of bryophyte species endemism pales in comparison with the 40% endemism rates observed in angiosperms (Vanderpoorten *et al*. 2010b). In the western Mediterranean, Corsica and Sardinia, which harbour nearly 10% species endemism in angiosperms, a single endemic bryophyte species has been described (Sotiaux *et al*. 2009). Even in Hawaii, one of the world's richest hot-spots of endemism, 29.4% and 48.6% of the moss and liverwort species, respectively, are considered endemic to the archipelago (Staples *et al*. 2004; Staples & Imada 2006) and, since the liverwort flora of Hawaii has not been studied taxonomically, rate of endemism are probably much lower than indicated. In angiosperms by contrast, the rate of species endemism reaches 90% (Sakai *et al.* 2002). Such low endemism rates of island bryophytes have precisely been interpreted in terms of the high dispersal ability of bryophytes, which would prevent genetic isolation among allopatric populations and hence, speciation (Vanderpoorten *et al.* 2010a).

A second striking difference between the patterns of endemism and distribution exhibited by the bryophytes from the Pantepui region is that about one third of the endemic liverworts occur on a single tepui. In mosses, only a single endemic is restricted to a single tepui, whereas 10 others have a distribution range that encompasses at least two tepuis. In angiosperms by contrast, about 60% of the endemics are known from a single tepui (Berry & Riina 2005). This contrasting distribution patterns in the endemic flora is reminiscent of the situation observed on other island systems. In the Canary Islands for example, more than 95% of the endemic angiosperm species are single-island endemics. By contrast, the frequency distributions of regional endemic and non-endemic bryophytes is left-skewed, indicating that most species tend to be widespread across islands (Vanderpoorten *et al.* 2010b), again pointing to the greater dispersal ability of cryptogams.

Third, although an ancient vicariance hypothesis cannot be completely ruled out, the general idea today to explain the origin of endemic angiosperm species on the tepuis is the recruitment of endemics from a low-elevation rainforest species stock and their progressive adaptation to elevation gradients during vertical migrations that occurred during the warm interglacials (Huber 1988, Rull 2005). In mosses similarly, Buck (1989) emphasized evident close relationships between the moss flora of the tepuis and that of upper Amazonia, and the same relationships exist in hepatics (Gradstein & Costa 2003). Robinson (1986) further noted some relationships between the tepui moss flora and that of the Caribbean, since several species considered as endemic to the West Indies were also collected in the Guiana Highlands. The idea, that the bryophyte flora of the tepuis has been recruited from a stock of lowland rainforest species, led Buck (1989) to postulate that the relative low species diversity in the tepui moss flora is due to the ill-adaptation of

Amazonian species dispersed to the tepui summits by the prevailing winds from the south (Amazonia). Although some endemic taxa (e.g., *Micropterygium*) seem to have Amazonian relationships, biogeographic patterns in the liverwort flora suggest, however, that Amazonian species are not very prominent on the tepuis. Rather, important floristic connections exist with montane Neotropical areas, especially the Andes (Gradstein 1999), suggesting another hypothesis for the origin of endemism among the tepui bryophyte flora. That is, endemic species would originate from cold-adapted Andean ancestors that would have experienced long-distance dispersal events across the Llanos and Amazonia and evolved in allopatry on the tepui summits. In oceanic islands similarly, many endemics originate from long-distance dispersal across oceans. This is best illustrated in the Macaronesian endemic bryophyte flora, wherein endemic species evolved from Neotropical, sub-Saharan Africa, or even eastern Asian ancestors rather than from European or North African ones (Vanderpoorten *et al.* 2010b). Although landscape-scale dispersal limitations were evidenced in a few instances, possibly enhanced by local ecological specialization (Hutsemékers *et al.* 2010), one interpretation for the recruitment of endemics from geographically remote ancestors is that the dispersability of bryophytes precludes the establishment of isolation-by-distance patterns, and hence, opportunities for allopatric speciation, at the scale of tens to hundreds of kilometers.

Conclusion and perspectives

Bryophytes offer a unique model to revisit hypotheses regarding the origin and evolution of endemism among the Pantepui biota. As Schuster (1983) noted, and in contrast to the global equilibrium of higher plant species distributions with present climate (see Araujo & Pearson 2003, for review; but see Rull 2009), bryophytes are able to persist in microhabitats where a suitable microenvironment persists, long after the general climate of the region has changed. Consequently, and as Anderson (1963) suggested, 'the diminutive bryophytes, therefore, potentially offer a better clue to the solution of phytogeographical problems than do many vascular plants'. Thus, while the hypothesis of an ancient, early Tertiary origin has been almost abandoned in most cases (Rull 2005), the existence of 'living fossils' of mosses that retained a constant morphology over tens of million years has been recently evidenced (McDaniel & Shaw 2003; Aigoin *et al.* 2009), so that this hypothesis possibly remains valid in at least some elements of the bryophyte flora of the Pantepuis. Examination of the biogeographic affinities of the bryophyte flora from the Pantepui region, however, point to multiple and contrasting connections with the West Indies (Steyermark 1986), lowland Amazonia (Buck 1989), and the Andes (Gradstein *et al.* 1990), thereby de-emphasizing the myth of the completely isolated tower and pointing to a dynamic interchange model with different biogeographic regions, which is typical to other island systems, for explaining the patterns of endemism observed.

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