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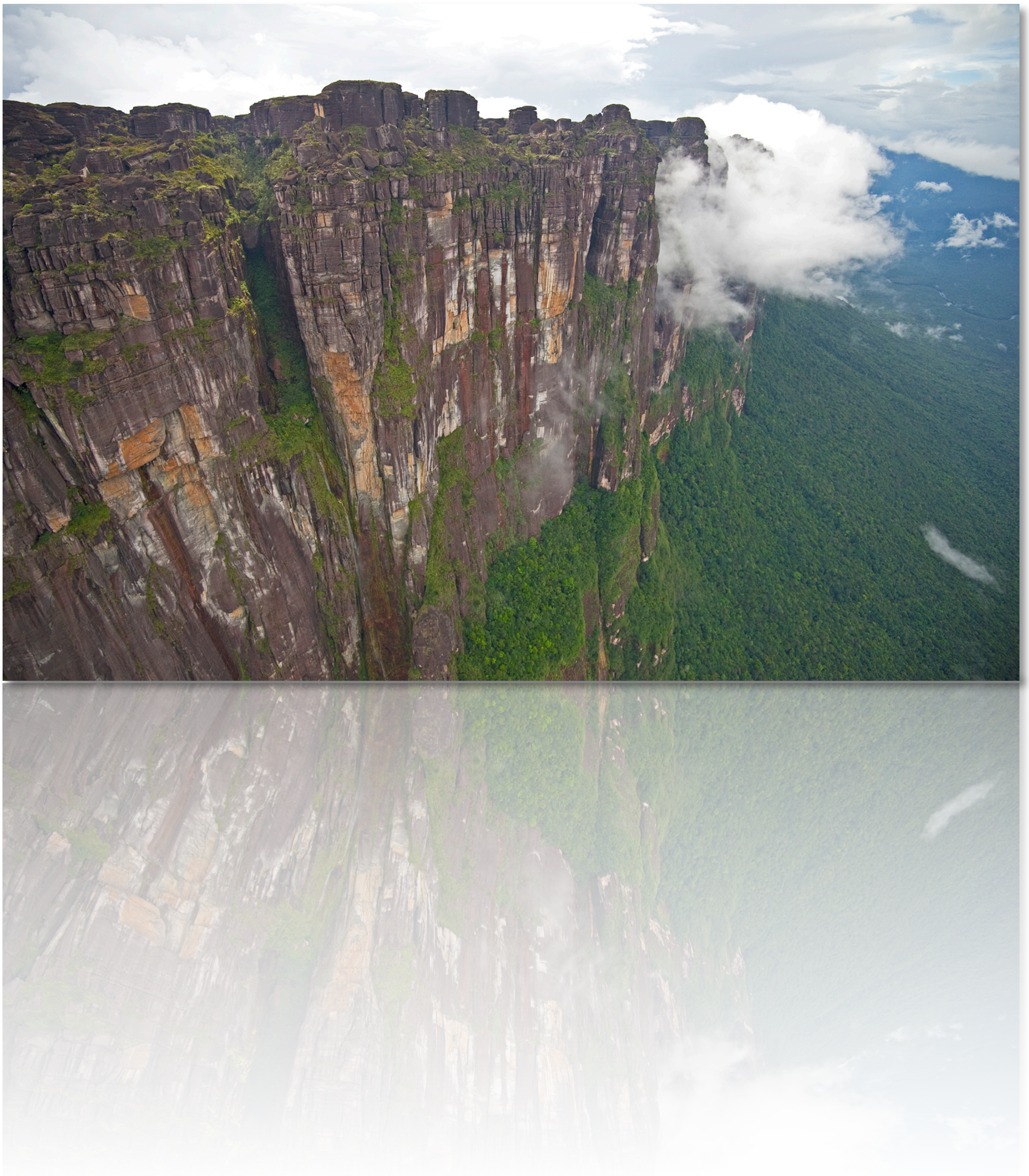
GENERAL CONCLUSION: THE “LOST WORLD” CONUNDRUM, INSIGHTS FROM PANTEPUI AMPHIBIANS AND REPTILES

“*Imagination is more important than knowledge*”
A. Einstein

“*Se non è vero, è ben trovato*”
Italian proverb



Neotropical diversification, timing and evolutionary causes

Timing of the origin and evolutionary causes of the high species diversity of many taxonomic groups in the Amazon Basin and adjacent Guiana Shield lowlands remain highly controversial (*e.g.* Hoorn *et al.* 2010, Rull 2011, Hoorn *et al.* 2011). Most explanations of diversification mechanisms have focused on the role of geographic isolation through vicariance to produce phenotypic divergence (allopatric speciation). The causes of isolation of populations have been explained by several hypotheses (briefly reviewed in Antonelli *et al.* 2010), the major ones being the Riverine Barrier hypothesis (Ayres & Clutton-Brock 1992), the Marine Transgression hypothesis (Frailey *et al.* 1988), the Disturbance-Vicariance hypothesis (Colinvaux 1993, expanded by Bush 1994), the Vanishing Refuge hypothesis (Vanzolini & Williams 1981), the Taxon Pulses hypothesis (Erwin 1979), and the Refuge hypothesis (*i.a.* Haffer 1969, Mayr & O'Hara 1986, Haffer & Prance 2001). The latter, for a long time treated as the definitive driver of the rich Amazonian biodiversity, has recently been strongly criticized on the basis of recent paleoecological and paleobotanical data (*i.a.* Bush 1994, Rull 2004a, b, Bush & de Oliveira 2006, Hoorn *et al.* 2011), tending to confirm that the high Neotropical biodiversity has been shaped by complex and more varied mechanisms (*i.a.* Bush 1994, Colinvaux 1998, Rull 2005, Rull 2011).

The so-called Refuge hypothesis argues that a series of climatic changes during the Pleistocene resulted in a drastic reduction in tropical rainforest cover of lowland South America due to aridification. Some tropical rainforest taxa would thus have been restricted to isolated, usually small areas wet enough to support evergreen forest (like hilltops, where orographic precipitation was sufficient to maintain such an ecosystem, or riverine forests). This isolation would have led to increased allopatric speciation among forest species (Haffer & Prance 2001). According to this assumption, Quaternary climatic fluctuations would have been the main factor producing the Neotropical species richness. However, as reported by several authors (*i.a.* Bush & de Oliveira 2006), paleoecological data do not support the predominance of savannah in the Amazon Basin during the Pleistocene. Another compelling argument against the Refuge hypothesis is that many Amazonian species divergence events seem to predate the Quaternary (*e.g.* Heyer & Maxson 1982, Moritz *et al.* 2000, Bush 2005, Ribas *et al.* 2005, Gamble *et al.* 2008). Rheindt *et al.* (2008), for instance, in their recent study of the evolutionary history of *Elaenia* flycatchers (Neotropical birds) highlighted the importance of savannah habitat during the Neotropical Pliocene and late Miocene biogeography, thus before the Pleistocene. Despite these criticisms, the results provided by some authors (*i.a.* Wüster *et al.* 2005a, Quijada-Mascareñas *et al.* 2007) still argue in favour of the Refuge hypothesis, whereas in particular the extent of Pleistocene tropical rainforest fragmentation remains unclear. Interpretation of data and phylogeographic analyses were sometimes subject to vibrant discussions (*i.a.* Gosling & Bush 2005, Wüster *et al.* 2005b). Complicating the matter further is the fact that some authors (*i.a.* Schneider *et al.* 1999) presented results indicating that isolation through vicariance may be insufficient to produce phenotypic divergence among populations. Habitat and elevation shifts may occur frequently and likely constitute an important diversification mechanism.

An alternative hypothesis to the geographical models, the Gradient hypothesis, was suggested by Endler (1977). This model does not necessarily require an isolating barrier (*i.e.* parapatric speciation) and postulates that geographic differentiation and speciation may develop with or without gene flow.

More recently, Santos *et al.* (2009) studying Amazonian poison frogs suggested that instead of being a key source of diversity (from which species dispersed to other areas), the Amazon Basin diversity stemmed from repeated dispersals from adjacent areas, especially from the Andes—but also from the Guiana Shield (from where the oldest dispersal would have occurred)—and is primarily derived from late Miocene lineages. Likewise, Hoorn *et al.* (2010) showed that the Andean uplift played a major role in Neotropical diversification and that "*current biodiversity patterns are rooted deep in the pre-Quaternary*" (Hoorn *et al.* 2010, 2011) arguing that Andean mountain building primarily shaped the remarkable Neotropical species richness, not Quaternary climatic fluctuations.

Diversification in the Pantepui region, current hypotheses

On a smaller geographic scale, there is still much debate about the origin and the diversification of the Pantepui biota (Myers & Donnelly 1996). According to Rull (2004b) and based on the latest palynological data, tepui summits likely did not serve as a biotic refuge during the Pleistocene glaciations simply because the climate on tepui tops during the Last Glacial Maximum (LGM) seems to have been unfavourable to the subsistence of extensive summit communities (although the existence of microrefugia has been postulated, *e.g.* Rull *et al.* 1988, Rull 2009a, 2010b). On the contrary, it has been hypothesized that glacial maxima would have allowed spreading of highland organisms via ecological connections between tepuis (*e.g.* Cook 1974, Rull 2004b).

Rull (2009b) considered the origin of the "*amazing levels of biodiversity and endemism*" in the Pantepui region as a still-unresolved evolutionary enigma.

Although the palaeoecologist Rull produced many publications on the subject (not without redundancy, *e.g.* Rull 2004a vs. 2004b), the same author (Rull 2010a) pointed out that very few recent contributions shed any fresh insight on this hot topic, and that all the current hypotheses are still those formulated by earlier scientists (mainly Tate 1930, 1938, 1939, Chapman 1931, Mayr & Phelps 1967, Maguire 1970, Haffer 1970, 1974, Cook 1974). Pérez-Hernandez & Lew (2001), for instance, proposed a review of six hypotheses of diversification in Pantepui (the Mountain Bridge theory, the Plateau theory, the Cool Climate theory, the Distance Dispersal theory, the Modified Cool Climate theory, and the Habitat Shift theory), but their contribution does not bring any new or additional information compared to the discussion already provided by Hoogmoed more than twenty years before (Hoogmoed 1979). In their comprehensive review of the herpetofauna of the Guiana Highlands and in the light of their compiled distributional data McDiarmid & Donnelly (2005) examined in detail four main hypotheses (Distance Dispersal, Cool Climate, Habitat Shift, and Plateau Hypothesis) that, they say, could explain the Pantepui herpetofauna origin. Concomitantly, Rull (2004a, b, 2005) rekindled the debate based on observations from the latest palaeoclimatic and palynological data. Désamoré *et al.* (2010) summarized the main hypotheses (old vicariance vs. recent dispersal) accounting for the evolution of the Pantepui biota, and documented patterns of diversity and endemism in bryophytes in the region. Marín (2010) listed the main biogeographic hypotheses and discussed the origin and diversification of Pantepui birds, providing new interpretations of previously existing information. A critical shortcoming of all these biogeographical analyses is that they only use limited sampling (and thus likely incomplete distributional data), and lack any molecular phylogenetic evidence.

Nevertheless, a few molecular phylogenetic analyses tackled, at least partly, the processes of diversification of some Pantepui organisms (*e.g.* Bromeliaceae and Rapateaceae by Givnish *et al.* 1997, 2000, 2004, 2011, and the frog genus *Tepuihyla* by Salerno *et al.* 2012), but once more sampling was limited and samples were mostly gathered from few and usually "easily" accessible tepuis (this mainly for the reasons mentioned in Chapters 1 and 10).

Below I propose a tentative reappraisal of the suggested hypotheses in the light of new molecular phylogenetic evidence based on a thorough sampling of tepui summit vertebrates including both Pantepui endemics and more widespread taxa.

Biogeographical hypotheses proposed to account for the origin and unique patterns of biotic diversification in the Pantepui region belong to two mechanisms: "old" vicariance, which invokes landscape evolution and fragmentation as the main drivers of speciation, and "recent" dispersal, which invokes migratory events leading to genetic isolation.

1) Vicariant theory:

Plateau theory

Author: Although the name was first coined by Mayr & Phelps (1967), this theory was originally formulated for birds by Tate (1930, 1938), and Chapman (1931).

Synonyms: Panbiogeography theory [in part] (Croizat 1976), Lost World hypothesis (Rull 2004a).

Assumption: The Plateau theory states that extant tepui summit species are derived from highland ancestors that occupied a large continuous plateau that was gradually eroded and dissected into several isolated tepuis. Because the tepui dissection is often reported as being very old (tepui isolation dating back to the Cretaceous, but see Chapters 1 and 10), this theory implies that tepui summit species remained isolated for millions of years, and therefore would currently harbour "relict" organisms. This model would explain the observed current high level of endemism on tepui summits and the apparent similarities between tepui top populations. The condition of "long isolation" led Rull (2004a) to rename this hypothesis the "Lost World hypothesis", based on the famous novel by Sir Arthur Conan Doyle (1912). Rivero (1970) suggested a modified version of the Plateau theory to explain the distribution of frogs of the genus *Stefania* (Hemiphractidae) in Pantepui. Rivero's modified theory implies that the Roraima Formation was a mountain range with valleys, watersheds, and depressions instead of a "*smooth and unindented plateau*" (Rivero 1970: 471).

2) Dispersal theories:

Cool Climate theory

Author: Although the name was first coined by Mayr & Phelps (1967), this theory was originally formulated by Chapman (1931) and Tate (1938).

Synonyms: Vertical Displacement hypothesis [in part] (Rull 2004a, b), Vertical

Migration hypothesis [in part] (Rull 2010a).
Assumption: This model, first suggested for Pantepui birds (Chapman 1931), then for Pantepui mammals (Tate 1939), assumes that a more or less important decrease in temperature in the lowlands between the Andes and the Guiana Shield (thus within the Amazon Basin) during glacial periods (ice ages) would have shifted the habitat and thus facilitated migration of cold-adapted Andean organisms. This habitat shift (or habitat expansion) would also have allowed the existence of ecological corridors between tepuis previously isolated by the warmer, environmentally distinct intervening areas. Rull lengthily discussed this theory for plants (*i.a.* 2004a, b, 2005, 2006) renaming it the "Vertical Displacement hypothesis", and revisited the model based on observations from new palaeoclimatic and palynological data. The author hypothesized that both vicariance and dispersal (biotic mixing) account for the origin and diversification of the Pantepui biota (Rull 2004a, b), a scenario already postulated by Cook (1974) and Steyermark & Dunsterville (1980). Repeated speciation and dispersal events (notably vertical displacements) instigated by numerous climatic oscillations in the Guiana Highlands throughout the Pleistocene would have caused the Pantepui region to act as a "biodiversity pump" for the lowlands (Rull 2005). This scenario is also similar to the Disturbance-Vicariance hypothesis for Amazonian lowland biodiversity (Colinvaux 1993, Bush 1994).

Distance Dispersal theory

Author: Although the name was first coined by Mayr & Phelps (1967), the ideas behind this theory were originally discussed and formally rejected by Chapman (1931).
Synonyms: "Island-Hopping" (Salerno *et al.* 2012).
Assumption: This theory was initially invoked to explain the distribution of the Pantepui avifauna. Western tepuis would have been colonized by Andean bird species (or their ancestors) flying across the intervening lowlands, and subsequently dispersing eastward by "island hopping" from a tepui to another.

Modified Cool Climate theory

Author: Haffer (1970).
Synonyms: Vertical Displacement hypothesis [in part] (Rull 2004a, b), Vertical Migration hypothesis [in part] (Rull 2010a).
Assumption: This model combines aspects of the Cool Climate theory with those of the Distance Dispersal theory (Haffer 1970, 1974, Cook 1974) and assumes that the cooling of the climate in the Amazon Basin was not sufficient to make these lowlands subtropical instead of tropical, but may have facilitated dispersal in some organisms (like birds) thanks to the shift of mountain life zones to lower altitudes. It suggests that organisms were able to disperse through "sub-optimal" habitats, using small mountains harbouring optimal habitat as "steppingstones".

Habitat Shift theory

Author: Mayr & Phelps (1967).
Synonyms: None.
Assumption: The Habitat Shift theory states that some Pantepui organisms are derived from lowland ancestors that shifted their habitat preference (Hoogmoed 1979). Some species would thus have locally diversified after invasion of the highlands by lowland ancestors, or have sufficient ecological plasticity to survive in the lowlands/uplands and on tepui summits.

Specialized Habitat theory

Author: Mayr & Phelps (1967).
Synonyms: None.
Assumption: This model has been proposed for birds living on tepui cliffs and in tepui crevices and suggests that some tepui organisms are found in the Pantepui region only because their specialized requirements are not met in the intervening lowlands or uplands.

Mountain Bridge theory

Author: Although the name was first coined by Haffer (1974), this theory was originally formulated for birds by Chapman (1917) and Todd & Carriker (1922) to explain the origin and the distribution of some Colombian birds.
Synonym: None.
Assumption: This hypothesis was invoked to explain the apparent affinities between the Andean and the Tepuian avifauna and assumes the past existence of a physical connection (a "bridge") between the Andes and the tepuis that would have allowed the bird faunas to disperse in their respective life zone.

Lessons from Pantepui amphibians and reptiles

Before examining the hypotheses outlined above, the following observations can be made, all inferred from phylogeny reconstructions and molecular dating (see Chapter 10), taxonomic study of museum specimens obtained during the course of this study (see Chapters 2–9), and review of pertinent literature. See previous chapters for material and methods.

(1) When known, divergence between each amphibian or reptile genus endemic to Pantepui—or that has multiple representatives on tepui summits—and its known sister group predates the Neogene. In all cases studied the divergence dates back to the Paleogene: Eocene/Oligocene (*ca*. 25–45 mya) for the taxa studied here (this work, Heinicke *et al*. 2007, Santos *et al*. 2009, Van Bocxlaer *et al*. 2010, Salerno *et al*. 2012), and up to the Paleocene for *Ceuthomantis* (*ca*. 60 mya according to Heinicke *et al*. 2009).

(2) When known, "basalmost" members of clades sister to Pantepui amphibian endemics are generally (i) found outside the Guiana Shield, (ii) not Amazonian,

(iii) currently geographically separated from Pantepui endemics by lowland areas that have potentially been impacted by periodic marine incursions, possibly since the Late Cretaceous (see Lovejoy *et al.* 1998, Hernández *et al.* 2005, Antonelli *et al.* 2009, Bloom & Lovejoy 2011).

(3) Although most genera endemic to Pantepui are early-branching lineages, they are always more recent than the oldest supposed age of tepui dissection, which is stated to date back to the Cretaceous, *ca.* 70–90 mya in some recent biological studies (*e.g.* Salerno *et al.* 2012).

(4) Several extant species or populations from individual tepui summits were only recently isolated (isolation as recent as the Holocene/Pleistocene; see Chapter 10), including species in genera that diverged from their known sister group in the Eocene (*e.g. Oreophrynella*).

(5) Pantepui currently harbours one endemic amphibian family (Ceuthomantidae), eight endemic amphibian genera (*Ceuthomantis*, *Dischidodactylus*, *Metaphryniscus*, *Minyobates*, *Myersiohyla*, *Oreophrynella*, *Stefania*, and *Tepuihyla*) and four endemic reptile genera (*Adercosaurus*, *Kaieteurosaurus*, *Pantepuisaurus*, and *Riolama*). This does not include some still undescribed putative genera of frogs and lizards (McDiarmid & Donnelly 2005, R. McDiarmid, pers. comm.).

(6) Among the genera endemic to Pantepui studied here, the highest genetic divergences between species and oldest diversification events are found in the genus *Stefania* and date back to the late Eocene/Oligocene (see Chapter 10, Salerno *et al.* 2012).

(7) Some populations from different summits form monophyletic clades (see Chapter 10).

(8) Genera having representatives both in the Andes and on tepui summits are scarce.

(9) In the region investigated (which represents only a fraction of Pantepui), single-tepui endemism does not seem as common as previously suggested. Some tepui summit species described as being single-tepui endemics turned out to be synonyms of more widespread taxa (*e.g.* in the genera *Anomaloglossus* and *Tepuihyla*, see also Chapters 8–9). On the one hand, species reported as highly restricted often also occur on nearby tepuis, or in some cases in the surrounding uplands. On the other hand, some populations occurring on different tepui summits and identified as a single species turned out to be a complex of distinct taxa (*e.g.* in the genus *Stefania*).

(10) In spite of very low genetic distances arguing in favour of conspecificity, some tepui summit populations recognized as distinct species show striking phenotypic differences (Fig. 1). Conversely, some tepui summit populations show identical morphology in spite of high genetic divergences (Fig. 2).

(11) The "astonishing" biodiversity and endemism reported by some authors (*e.g.* Rull 2009b) on tepui summits are not observed in amphibians and reptiles, at least not at the species level and in the area studied. Tepui summit herpetofaunas are typically depauperate (Myers & Donnelly 2001, MacCulloch *et al.* 2007), and as noted earlier, single-tepui endemism has probably been overestimated. Likewise, the postulate of the Pantepui region acting as a Pleistocene "biodiversity pump" for the lowlands (Rull 2005) cannot be demonstrated for amphibians and reptiles.

Figure **1.** Striking example of phenotypic differences between currently isolated tepui summit populations in absence of significant genetic divergence (0.0% in 16S and max. 0.4% in ND1). All specimens of *Oreophrynella quelchii* (left; found only on the summits of Wei-Assipu-tepui and Mount Roraima) have a possibly aposematic ventral colouration consisting of large yellow to orangish red markings on a black background, while all specimens of *O. nigra* (right; found only on the summits of Kukenan-tepui and Yuruani-tepui) have a completely black ventral face. See Fig. 10 in Chapter 1 for location of these tepuis (#7, 8 and #9, 10, respectively). Photos by the author.

Figure **2.** Striking example of morphological stasis between currently isolated tepui summit populations in presence of significant genetic divergence (4.0% in 16S and 16.7% in ND1). Left: a still undescribed *Stefania* species endemic to the summit of Wei-Assipu-tepui. Right: *Stefania riveroi* found only on the summit of Yuruani-tepui. Both species are intraspecifically variable in colour pattern and morphology and no morphological character has been found to discriminate between them, although molecular phylogenies indicate that they are not sister species (see Suppl. Fig. 2 in Chapter 10). See Fig. 10 in Chapter 1 for location of these tepuis (#7 and #10, respectively). Photos by the author.

Test of hypotheses: towards a phylogenetically supported diversification model?

Current hypotheses aiming at explaining the origin and diversification of the Pantepui biota are mostly based on “mobile” organisms that are able to disperse through the air (*e.g.* birds, flying insects, plants). Because of their assumed better dispersal abilities, these organisms are perhaps not the best models to resolve the Pantepui conundrum. Small terrestrial vertebrates with narrow elevational limits, like amphibians and reptiles, should be, unless proved otherwise, much more reliable models for phylogeographic studies in such highly dissected landscapes. In any case, as pointed out by Hoogmoed (1979) and Duellman & Hoogmoed (1984), it is not surprising that differences in dispersal abilities and in geological ages of these groups led to different conclusions.

Although this work provides new insights on the origin and the diversification of Pantepui amphibians and reptiles (see previous chapters), we are still far from a complete understanding of all the mechanisms involved in the diversification of the Pantepui biota, which will probably require additional sampling outside the region studied here (*i.e.* west of the Río Caroní), and additional meta-analyses.

Plateau theory

Phylogenetic and temporal predictions: (1) early lineage splits are linked with geological events; (2) the origins of Pantepui endemic genera are rooted in the Paleogene; (3) multiple phylogenetic lineages are restricted to Pantepui and endemism at higher ranks than species; (4) Pantepui distributions are shared by taxa having different ecology.

Discussion: It is generally accepted that the tepuis are remnants of an enormous sedimentary landmass dating from the Precambrian that remained buried for millions of years before being sporadically uplifted, possibly since the early break-up of Gondwana. That landmass was broken up by tectonic forces; wind and weathering gradually led to the present-day appearance of the tepuis (see Chapter 1).

The Plateau theory gives rise to two fundamental questions (1) are extant Pantepui endemic species “relict” organisms derived from highland ancestors that once occupied that large plateau (in other words, is the “Lost World hypothesis” sustainable?); (2) was the magnitude of the Plateau uplift(s) sufficient to cause vicariance between the Plateau and the surrounding areas?

According to Hoogmoed (1979) and McDiarmid & Donnelly (2005) (based on morphological data), some herpetofauna distribution patterns seem to support the Plateau theory. Discussing the genus *Stefania*, Hoogmoed (1979) and Duellman & Hoogmoed (1984) invoked the Plateau theory as an explanation of the distribution pattern of the genus, and Duellman & Hoogmoed (1984) argued that

> *“Some aspects of the phylogenetic arrangements of the species of* Stefania *are consistent with the hypothesis that the tepuis are erosional remnants of a former plateau that eroded more rapidly in the west than in the east”* (1984: 34).

As suggested by McDiarmid & Donnelly (2005), the genera *Oreophrynella* and *Metaphryniscus* (Anura, Bufonidae), and *Riolama* (Squamata, Gymnophthalmidae) are other serious candidates for such a “relict hypothesis”.

The Plateau theory has also been more or less implicitly invoked in the evolution of some other groups, as shown in the following selected examples:

- Maguire (1970) discussing some families of the flora of the Guiana Highlands suggested that a highly autochthonous flora had evolved in the Guiana Highlands region before a Miocene uplift.
- Berry & Riina (2005), studying the flora of the Guiana Shield, suggested an important role of the Pantepui region in the early evolution of a number of plant families, and pointed out the need of dating the evolution of Pantepui lineages.
- De Marmels *et al.* (2003) studying the butterfly genera *Pereute* and *Pseudopieris*, and De Marmels (2007) studying the endemic Guianan damselfly genus *Tepuibasis* argued that prior to Andean orogeny, the ancient Guiana Shield region was populated by their ancestors. The authors postulated that local ancestral populations were raised to considerable height as a result of the Andean uplift, which would have triggered a simultaneous isostatic rise of large parts of the Guiana Shield. That population hence became vicariant from the surrounding lowland populations and progressively adapted to high elevation conditions. Further dissection by erosion of the Guiana Shield Plateau would have caused secondary vicariance and speciation events explaining the current distribution of the genera in Pantepui.
- Brumfield & Edwards (2007) studying two thamnophilid bird species, one from the Andes and the other from the Pantepui region, suggested that *Thamnophilus divisorius* (currently restricted to a small area in the Peruvian Andes) could represent a relict of the avifauna having inhabited an extensive ancient sandstone system that produced the present-day Pantepui region.

Until very recently, the Plateau theory had never been empirically tested owing to a lack of phylogenetic studies. Based on phylogenetic analyses and estimations of divergence time of an endemic Pantepui frog genus (*Tepuihyla*), Salerno *et al.* (2012) suggested the rejection of the Plateau hypothesis. Salerno *et al.* (2012) reinforced their point by stating that the "Lost World hypothesis" (another name for the Plateau theory, see above) was not satisfied by data for the Pantepui frog genus *Stefania* either, because *Stefania*, like *Tepuihyla*, radiated more recently than the dissection of the plateau in isolated tepuis, which according to these authors (although not based on unequivocal geological evidence) occurred in the Cretaceous, 70–90 mya. A truism since all frogs currently having stable populations on tepui summits belong to the superfamily Hyloidea, which only began to diversify in the Paleogene (Roelants *et al.* 2007), thus well after the hypothetical tepui isolation suggested by Salerno *et al.* (2012). The sampling of Salerno *et al.* (2012) only covers a single Pantepui genus, including only four (of seven known) species from three tepui summits only, and is therefore probably too limited to draw far-reaching conclusions. In addition, the Cretaceous age of tepui isolation assumed by Salerno *et al.* has not been demonstrated satisfactorily and is not widely accepted (as earlier discussed in Chapter 1). Interestingly, none of the three references given by Salerno *et al.* (2012) for a Cretaceous age of tepui isolation contains such a statement (see Chapter 1).

Although my results show a similar pattern of recent isolation in many extant tepui summit species (see Chapter 10), they do not necessarily refute the Plateau hypothesis. On the contrary several elements seem to support that hypothesis for the early origin of the Pantepui fauna. Many lineages of amphibians and reptiles, but also in other zoological groups such as birds (*e.g.* Mayr & Phelps 1967), invertebrates (*e.g.* Breure 2009), and in plants (*e.g.* Steyermark 1986, Berry & Riina 2005) are currently endemic to the remnant of that ancient plateau. As highlighted in Chapter 10, several of the taxa studied here (*Oreophrynella*, *Stefania*, *Tepuihyla*, *Riolama*) represent phylogenetically distinct lineages restricted to the Pantepui region, and the area as a whole seems to act as a reservoir of endemism at the genus and species levels, but also at the family level (*e.g.* the recently discovered frog family Ceuthomantidae), which is remarkable given the current relatively reduced size of the region.

Endemic taxa are more likely to develop in isolated areas (oceanic islands being probably the most iconic example), and areas of endemism are often assumed to be the result of non-stochastic processes, such as vicariance caused by geological or climatologic events (Evans *et al.* 2004). A concordant pattern of distribution and endemism observed in other Pantepui groups than amphibians and reptiles (both in plants and animals) seems to further support the Plateau hypothesis. However, what actually caused the isolation of Pantepui and what were, and probably still are, the barriers to dispersal (biotic and abiotic) of some Pantepui organisms remain puzzling.

As pointed out in Chapters 1 and 10, time estimates for the isolation of individual tepuis range roughly from the Cretaceous to the Quaternary. If we re-evaluate the age of tepui isolation assumed by Salerno *et al.* (2012) of *ca.* 45 million years downward (which does not disagree with time estimates for geological events suggested by *e.g.* Gansser 1954, Simpson 1979, Gómez *et al.* 2003, Orme 2007, and Hoorn & Wesselingh 2010), and thus remove the assumption of "very long" (*i.e.* Cretaceous) isolation of Pantepui, the Plateau theory appears to be congruent with phylogenetic data. Preliminary observations seem to indicate a link between early lineage splits and timing of possible uplift(s) (and/or subsidence of surrounding areas, *e.g.* the Takutu Rift), as well as timing of marine incursions (in which case the foothills of the Andes and Pantepui could have served as "ancient" refuges), but confirmation of this requires extensive additional analyses.

The occurrence of "young" taxa on tepui summits and the Plateau theory are thus not mutually exclusive and in my opinion the Plateau theory cannot be unequivocally refuted, most Pantepui amphibian and reptile endemics appearing to be the result of long-term survival and evolution on an isolated plateau since the Paleogene rather than "recent" founder dispersal from the surrounding areas. Despite probable extinction events (see below), some metapopulations of Pantepui organisms have preserved patterns of endemism and vicariance that seem to reflect the geological history of the region.

The following (still highly speculative) scenario could tentatively be deduced from phylogenetic results, estimates of divergence time, and literature data. The exact role of uplift(s) in Pantepui isolation still needs to be elucidated:

1) Pantepui, which was submerged until the Lower Triassic, experienced a (first?) epeirogenic uplift during the Lower Cretaceous, possibly contemporaneously with the break-up of Gondwana and the opening of the South Atlantic Ocean. The extent of this uplift is difficult to assess, but erosional denudation was probably extensive and could have substantially lowered the plateau, keeping it low and accessible to the paleofauna [according to geologists (H. Briceño pers. comm.), about 3,000 m of sediments would have been removed from the top of the present-day tepuis due to erosion, but no exact dating of this event is available (see Chapter 1)].
2) A second significant (?) epeirogenic uplift began in the Upper Cretaceous/Paleocene, close to the K-T boundary, as the first signs of the Amazon Basin became visible

(Haffer 1974, Duellman 1979, Simpson 1979); erosion was probably accelerated. That uplift slightly predates (and possibly promoted?) the split between the frog genus *Ceuthomantis* (Ceuthomantidae) and its sister taxon (all other Terraranans). Again, the extent of the uplift is difficult to appreciate, but vertical isolation from the surrounding areas of the—already partly eroded[1]—plateau would have likely reached its apogee in the Middle Eocene/Oligocene, with some major massifs (*e.g.* Chimantá and Auyantepui) disconnected from each other, but several tepuis and tepui massifs still linked to each other and to the uplands by more or less extensive ridges (remnants of which are still visible today, see Fig. 3). That epoch (Middle Eocene/Oligocene) roughly corresponds to the split between most known endemic Pantepui genera and their respective sister group, as well as to the earliest diversification in *Stefania*. That episode of high fragmentation and rapid vertical isolation corresponds in part to the Andean orogeny, but also to the Oligocene uplift of the Sierra de Perijá, an extension of the eastern Andean chain in northern Venezuela (*ca.* 25 mya according to Kellogg 1984).

3) Rate of erosion and weathering, although not constant, gradually led to the present-day appearance of the tepuis, but some connectivity between tepui summits within a same massif or "tepui chain" (like in the Eastern tepui chain) could have remained at least until a potential third uplift and its erosional response in the late Miocene/Pliocene, concomitant with the emergence of the Central American Isthmus and the climax of Andean tectonism (Hoorn & Wesselingh 2010). That period roughly corresponds to the earliest diversification of several Pantepui endemics (except *Stefania*). Valleys between some nearby tepuis could have been less deep than today, a topography maintained until fairly recently (*e.g.* Pleistocene/Holocene).

In summary, patterns of distribution and endemism of several Pantepui amphibians and reptiles seem to argue in favour of the Plateau theory. When the timing of the geomorphological evolution of the tepuis and the timing of amphibian and reptile species diversification inferred from molecular phylogeny reconstructions and estimates of divergence time are considered as a whole, the Plateau theory turns out to seem appropriate to explain the early origin of several Pantepui taxa (*e.g.* *Oreophrynella*, *Stefania*, *Tepuihyla*) and several diversification events. But vicariance alone fails to explain the distribution and diversification of all extant tepui summit taxa. As mentioned in Chapter 1, the Andean main uplift (starting *ca.* 25–30 mya, with a peak around 10 mya) and the emergence of the Central American Isthmus (final closure *ca.* 3 mya) are major regional mountain-building episodes that drastically modified the hydrologic regime and the climate in South America and probably played a major role during the following period, which is described below under the Disturbance-Vicariance theory.

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[1] Thus in agreement with Rivero's (1970) postulate that the Roraima Formation could have been already partly broken by some valleys and watersheds instead of being each time uplifted as a totally smooth peneplane surface. Erosion and weathering are not sudden events, and there were probably long periods in the Pantepui history during which the tepuis, as we know them today, were better connected by shallow valleys.

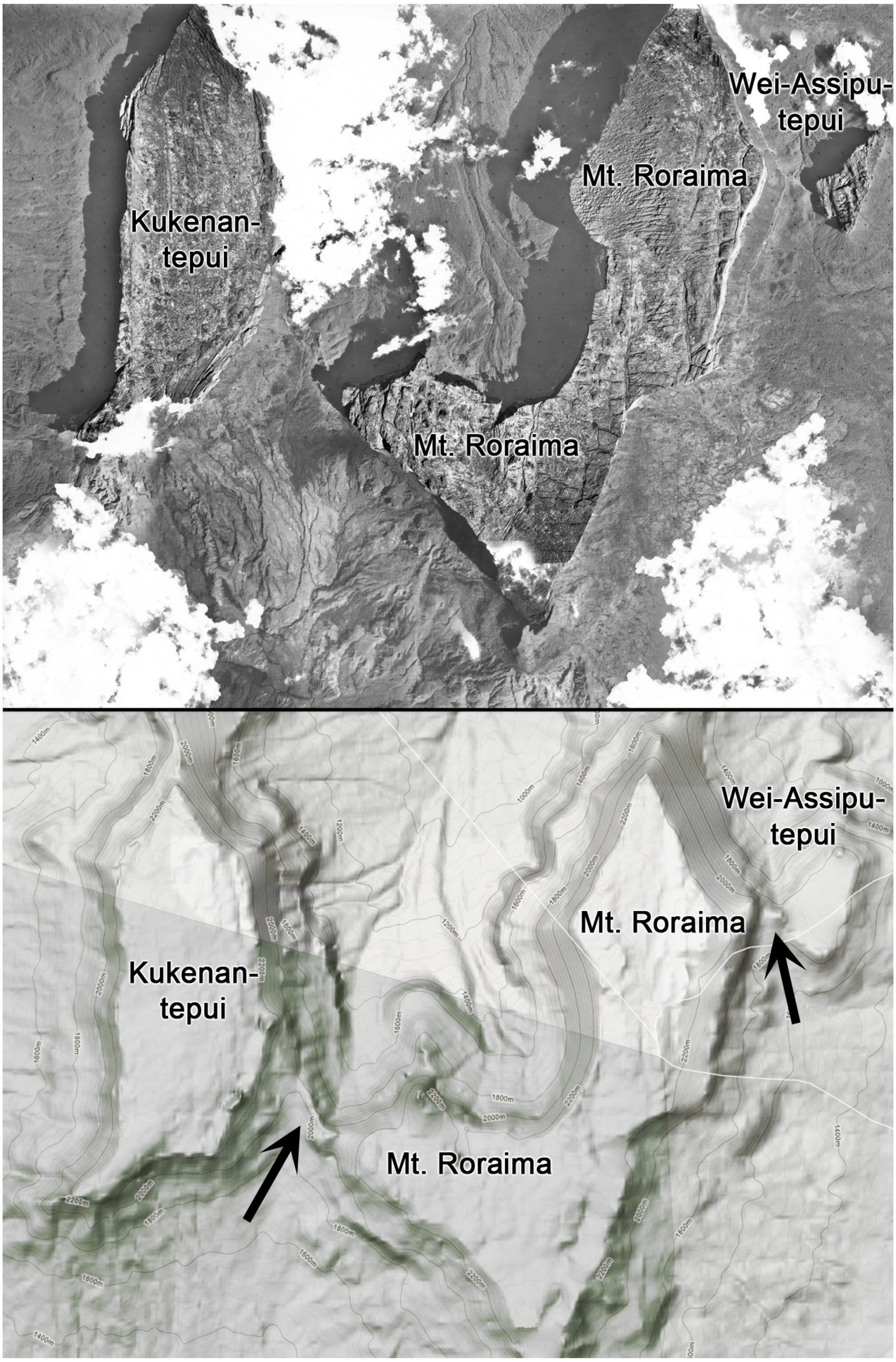

Figure **3.** Radar map (above) and relief map (below) showing examples of current tepui summits isolation and remnants of connective “bridges” (black arrows) that are barely visible on the radar map, but well noticeable on the relief map. These ridges frequently occur between tepuis. Radar map courtesy of C. Brewer-Carías, relief map © Google Maps.

Cool Climate and Modified Cool Climate theories

Phylogenetic and temporal predictions: (1) diversification events are linked to climatic instability, and (2) early lineage splits are linked to ice ages if the theory applies to the origin of the Pantepui biota (which *per se* implies Quaternary colonisation from the Andes).
Discussion: As we have seen before, early splits between Pantepui endemics and their sister taxa largely predate the Quaternary, therefore the "Cool Climate" and the "Modified Cool Climate" theories do not seem to fit the data for the early origin of the Pantepui amphibians and reptiles (which as seen earlier is probably the result of vicariance).

I reject the hypothesis of Pantepui endemic taxa being derived from "cold-adapted" Andean invaders because Andean colonisers would have had to reached Pantepui during the Paleogene by crossing large lowland areas that were (1) possibly submerged by marine incursions, (2) likely ecologically considerably different.

Climate-induced migrations could however explain diversification within Pantepui, but were probably not limited to "long" migrations caused by temperature fluctuations (as stated in the Cool Climate and the Modified Cool Climate hypotheses), or to vertical displacements (as suggested in the Vertical Displacement/Vertical Migration hypothesis). Although hypothesized migration events could have been promoted by climate, they are not necessarily linked to cooler temperatures, but could also be related to aridification, reduced atmospheric CO_2, and/or habitat modification. Similarly, migration events were likely not limited to the vertical plane. The "Disturbance-Vicariance" theory proposed by Colinvaux (1993) to account for the species richness and endemism in the Amazonian lowlands seems appropriate to describe the major processes involved in diversification within Pantepui. Under the name "Disturbance-Vicariance", I group part of the Cool Climate theory of Mayr & Phelps (1967), and the Modified Cool Climate theory of Haffer (1970, 1974), and thus the Vertical Displacement/Migration hypothesis of Rull (2004a, b, 2010a) that pertain to Pantepui local diversification.

Disturbance-Vicariance theory

Phylogenetic and temporal predictions: (1) diversification events are linked to climatic instability; (2) most species diversifications occurred in the Neogene.
Discussion: The Disturbance-Vicariance hypothesis was first formulated by Colinvaux (1993), who proposed that, under this model, speciation is triggered by temperature fluctuations, local changes in precipitation or seasonality, and habitat heterogeneity. Colinvaux (1993) underlined that the principle of Disturbance-Vicariance is also applicable on a smaller scale (thus *contra* the Cool Climate theory, which requires long distance dispersal).

My results mostly agree with Haffer (1970, 1974), Cook (1974), Steyermark (1986), and Rull (*i.a.* 2004a, b, 2005), showing that dispersal promoted by climate instability probably actively contributed to the diversification of most Pantepui amphibians and reptiles at a local scale (*i.e.* within Pantepui). Rull (2005) also stated that niche fragmentation and climatic instability are the main forces driving the timing and the extent of evolutionary processes in the Guiana Highlands.

However my analysis diverges from Rull's (2004a) model because, as explained below, my results seem to indicate that climate instability caused, in several cases, a depletion of ancestral Pantepui amphibian and reptile populations instead of promoting a so-called "biodiversity pump" for the surrounding areas.

Data strongly suggest that most herpetofaunal diversity patterns in Pantepui were shaped before the Pleistocene, probably in the Oligocene or even earlier (here hypothesized as pre-Neogene vicariance), but tend to indicate that species diversity was substantially reorganized during or shortly after periods of climate instability that occurred in the area from the late Miocene until today (as shown by the recent isolation of several extant species or populations from individual tepui summits). The data suggest that some genera that apparently originated in the Pantepui region (the best example being *Oreophrynella*) suffered significantly from climate change and its probable corollary habitat modification at those high elevations, forcing them to move (probably altitudinally) and find alternative suitable habitat. Climate change could have considerably reduced their populations causing local extinctions and bottlenecks. This could explain an early-lineage branching and a recent origin of most extant species.

I hypothesize that the causes of these extinctions and bottlenecks in several groups were the climate instability promoted by (1) the climax of the Andean orogeny, (2) the emergence of the Central American Isthmus, and (3) Quaternary climate oscillations. Climate change most likely was not an *opportunity* for all Pantepui organisms to locally disperse, but instead it was a *constraint* for most of them to move. Only reduced populations of these Pantepui taxa would have been able to survive in small "dispersal centres" (*sensu* Steyermark 1979), possibly at slightly lower elevations, and subsequently reinvaded their original range (theoretically tepui summits) constrained again by ecological factors induced by climate oscillations (implying that lower elevation populations went extinct). This scenario is still highly speculative, but could explain the observed low genetic diversity among many extant tepui summit populations.

Box 1 – Ecological preferences of Pantepui organisms

We should be cautious in our speculations about ecological preferences of Pantepui ancestors. A shift in ecological preferences may have taken place in the evolution of some taxa, and a putative good example in Pantepui is *Oreophrynella*. All *Oreophrynella* species have opposable toes, but only two known species (*O. macconnelli* from the Eastern Pantepui uplands, and *O. weiassipuensis* known only from a deep canyon on Wei-Assipu-tepui) are mainly arboreal (pers. obs., D.B. Means pers. comm.), whereas strict tepui summit species are terrestrial. Although the opposable toes condition is plesiomorphic in the genus, we do not know whether the *Oreophrynella* ancestor was arboreal or terrestrial (see also Chapter 4). It is tempting to assume the *Oreophrynella* ancestor as being arboreal, but opposable toes could also be an adaptation to rock climbing (or be involved in unknown functions), that was subsequently co-opted by two extant taxa for tree climbing ("exaptation" *sensu* Gould & Vrba 1982). It should be noted that among the many extant arboreal anuran taxa, only a very few have opposable toes (to my knowledge only species of the hylid genus *Phyllomedusa*), so the selective advantage of opposable toes for arboreality in anurans is not obvious.

Reinvasions of original ranges, supposedly tepui summits, were probably easier among tepuis that were still physically connected (though even poorly) to the Pantepui uplands and/or between each other, for instance by shallow valleys. Reinvasions were probably restrained by major watercourses. Tepuis and tepui massifs that were already strongly isolated from the relictual populations could not be reinvaded by some groups, which may

Box 2 – The case of *Stefania*

Under the Disturbance-Vicariance theory, the only taxon here studied that *seems* to have less significantly suffered from climatic instability is *Stefania*. Genetic divergences between *Stefania* species are relatively high and single-tepui endemism seems less uncommon in the genus (Chapter 10). Although this could be linked to the structure of the genome of ancestral species (*e.g.* ancestral polymorphism), a possible interpretation lies in a different response to environmental challenge compared to other tepui organisms. *Stefania* is the only taxon currently found on tepui summits that is not dependent on water or on at least semi-permanent moist places to deposit its eggs. Indeed, *Stefania* females carry eggs and metamorphs on their back until juveniles are fully formed and independent (Duellman & Hoogmoed 1984, Jungfer & Boehme 1991), and they can actively procure the right conditions for the eggs to successfully develop. Other tepui summit amphibians have either a biphasic life cycle (eggs being laid in water, *e.g.* *Tepuihyla*), or are direct-developers (*e.g.* *Oreophrynella*, *Pristimantis*) laying eggs in places remaining sufficiently moist for a minimal period of time (several months in some cases). Reptiles also are dependent on such relatively moist places to deposit their eggs. *Stefania* could have better survived on individual tepui summits by using *in situ* microrefugia like deep fractures and canyons, but on the other hand could have been extirpated when suitable microrefugia were absent (*e.g.* no *Stefania* are known to occur on the summits of Mt. Roraima, Kukenan-tepui, Ilu and Tramen-tepuis, Ptari-tepui, etc.).

explain why some taxa like *Oreophrynella* and *Riolama* are now absent from the Chimantá Massif and from its western satellite tepuis (*e.g.* Upuigma, Angasima, Aprada).

Interestingly, this scenario seems to be further supported by botanical studies suggesting that tepui summits had no or very limited organic soils, during the LGM. Environmental conditions were therefore probably too inhospitable for the maintenance of viable floral and faunal populations (*i.a.* Schubert *et al.* 1986, Huber 1995, Rull 2004b, H. Briceño pers. comm.).

Vertical migration promoted by recent climatic instability was reported as not realistic for plant taxa occurring on the highest tepuis (mountains having a base-summit difference exceeding 1,100 m) because, according to Rull (2005), the maximum downward vertical shift estimated for the last glaciation in the region was 1,100 m. This is not in contradiction with the available evidence for the herpetofauna in the studied area and could explain why (1) some populations in certain groups (*e.g.* *Stefania*) show higher genetic divergences between summit populations; (2) some typical Pantepui taxa are absent from some tepui tops (probably due to extinction). Nevertheless we must be aware that current tepui isolation does not necessarily reflect the situation in the area a few million years ago.

It is noteworthy that similar observations on migration and diversification promoted by climate instability were made by Noonan & Gaucher (2005, 2006) who examined phylogeographical structure of Guianan *Atelopus* (Anura, Bufonidae) and *Dendrobates tinctorius* (Anura, Dendrobatidae) [lowland/upland taxa distributed east of the Pantepui region] and also suggested the Disturbance-Vicariance hypothesis (*i.a.* Colinvaux 1993, 1998, Bush 1994, Bush *et al.* 2002, Mayle *et al.* 2004), which "*invokes changes in temperature and atmospheric* CO_2 *levels associated with precessional cycles as the dominant factor influencing the historical continuity of Amazonian communities*" to account for their diversification (Noonan & Gaucher 2006). Noonan & Gaucher (2005) suggest that the extant Guianan *Atelopus* species derive from a common ancestor that migrated from the Andes through the Amazon Basin thanks to the Pliocene cooling, and that local diversification was promoted by Quaternary climatic instability and alternating physical isolation on hilltops. The taxa involved show very low genetic divergences between populations due to secondary contacts. At a more local scale a similar statement can be made about Pantepui.

Although climate instability probably played a major role in the recent diversification of Pantepui amphibians and reptiles, a third model must perhaps be invoked to explain diversification in groups that are not Pantepui endemics, but that are found on tepui summits like the lizards *Neusticurus* and *Arthrosaura*. This third model is the Habitat Shift theory as developed below.

Habitat Shift theory

Phylogenetic and temporal predictions: (1) occurrence of conspecific populations on tepui summits and in intervening areas, (2) tepui summit populations are derived from widespread lowland/upland taxa (*e.g.* Pan-Amazonian).

Discussion: According to Hoogmoed (1979) and McDiarmid & Donnelly (2005) several species seem to fit the Habitat Shift hypothesis, and my results concur with their observations. As noted earlier by several authors (Mayr & Phelps 1967, Myers & Donnelly 2001, McDiarmid & Donnelly 2005), tepui summits have been for long (and probably still are) available to active colonizers from the surrounding lowlands/uplands. Although sometimes surprising, it appears that some organisms are able to reach tepui tops, including some of those that seem to be currently topographically strongly isolated (*e.g.* Angasima-tepui). Invasions of tepui tops have been suggested in such groups as ants (Jaffe *et al.* 1993) or plants (Givnish *et al.* 2004).

Phylogeny reconstructions (see Chapter 10) show that, in some taxa, tepui summit populations are conspecific with upland populations and that some extant populations are derived independently from much more widespread lowland/upland taxa (*e.g. Neusticurus* and *Arthrosaura*). In the lowlands/uplands, *Neusticurus* species are primarily riparian, but on tepui summits they have been found associated with very small puddles, or were even collected under rocks far from any body of water (pers. obs.). D. B. Means (pers. comm.) reported a female *Neusticurus* with eggs in a vegetated crack about 3 m up off the top of the talus slopes at the base of Mount Roraima's cliffs. Likewise, a few species that are widespread in the surrounding uplands, or even lowlands, can be found on some tepui summits (*e.g.* the frog *Hypsiboas sibleszi*, and the snake *Leptodeira annulata,* which occurs from sea level to tepui tops). These species likely have relatively recently invaded the tepuis and have adapted to the tepui summits climate probably thanks to ecological plasticity. On the other hand, it is possible that the descendants of ancestors that could have secondarily invaded the uplands from the tepui summits are physiologically predisposed to reinvade tepui tops (*e.g. Anomaloglossus roraima*).

Distance Dispersal theory

Phylogenetic and temporal predictions: None for amphibians and reptiles since they are not able to disperse through the air.

Discussion: Although useful to explain the distribution of some flying organisms, long-distance dispersals does not appear credible for amphibians and reptiles (Hoogmoed 1979, McDiarmid & Donnelly 2005).

Specialized Habitat theory

Phylogenetic and temporal predictions: None for amphibians and reptiles.
Discussion: McDiarmid & Donnelly (2005) considered the Specialized Habitat theory of little relevance for amphibians and reptiles. As noted by these authors this hypothesis may explain the distribution of cavernicolous or "cliff dweller" birds that are more widespread in northern South America (*e.g.* the oilbird *Steatornis caripensis* a common inhabitant of tepui canyons), but it fails to explain the diversity of tepui summit amphibians and reptiles.

Mountain Bridge theory

Phylogenetic and temporal predictions: Multiple co-occurrences of congeneric species in the Andes and in Pantepui.
Discussion: Hoogmoed (1979) and McDiarmid & Donnelly (2005) rejected this model for amphibians and reptiles because no geological evidence for such connection exists [although Galvis Vergara (1994) presented new elements reported as in favour of this possibility]. My results point in the same direction as that of Hoogmoed (1979) and McDiarmid & Donnelly (2005) mostly because if a mountain bridge would have existed between Pantepui and the Andes in some recent geological time we should probably observe more genera with species distributed in the two areas, which is not the case. There are very few affinities between the Andean and the Tepuian contemporary herpetofauna. The only primarily Andean genera found on tepui summits are the lizards *Anadia* [with one tepui summit species and one upland species described so far (Chapter 7, Myers *et al.* 2009)], and *Euspondylus* [with one tepui summit species recently described (Myers *et al.* 2009)]. These species are more likely relatively recent invaders from the highlands of northern Venezuela.

Conclusion

Paraphrasing Bush (1994), speciation in Pantepui is a necessarily complex model (see also Rull 2008). Multiple nonexclusive processes implying vicariance and dispersal probably promoted the origin and the diversification in Pantepui possibly according to the following sequence based on the Plateau, Disturbance-Vicariance, and Habitat Shift theories: (1) pre-Quaternary vicariance, (2) recent reorganization of species diversity constrained by climatic instability (climate oscillations), (3) recent invasions (post-Pleistocene) of widespread upland taxa.

The diversification model hypothesized here appears congruent with the biogeographical history of taxa other than amphibians and reptiles. It is consistent with most geological data, and does not support the postulate of the tepuis being formed and already isolated in the Cretaceous (70–90 mya) as claimed by Salerno *et al.* (2012), rather suggesting a period of accelerated uplift and high fragmentation during the Eocene/Oligocene (25–45 mya), and a more recent period for complete isolation of individual tepui summits (late Miocene to Holocene). Results suggest that connective "bridges" between some tepui summits could have existed until relatively recently. Remnants of these possible past connections are detectable on relief maps (Fig. 3). These ridges are now too low and ecologically too different from the summit habitats to allow contemporary dispersion between tepui tops, but they might have been higher until the Pleistocene and used by some summit organisms during possible diasporas caused by forced migrations due to climate instability.

It is interesting to note that early scientists (*i.a.* Mayr & Phelps 1967, Cook 1974, Haffer 1974) who had "only" their taxonomic knowledge at hand already drafted the main principles of the Pantepui biogeographical history, which are here at least partially supported by molecular evidence.

The antagonism between vicarianists and dispersalists is no longer legitimate because both mechanisms apparently shaped the Pantepui biodiversity. As explained above, the stumbling block has most likely been a probably erroneous estimation/interpretation of the timing of the Pantepui orogeny and geomorphology as recently exemplified in Salerno *et al*. (2012). The extent to which this preconception of Cretaceous tepui isolation has been influenced by Sir Arthur Conan Doyle's fiction novel " The Lost World" is quite fascinating.

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