DOI: 10.1111/jbi.13093

ORIGINAL ARTICLE

WILEY Journal of Biogeography

Historical biogeography of the palaeoendemic toad genus *Oreophrynella* (Amphibia: Bufonidae) sheds a new light on the origin of the Pantepui endemic terrestrial biota

Philippe J. R. Kok[1]* | Sebastian Ratz[1]* | Ross D. MacCulloch[2] | Amy Lathrop[2] | Raheleh Dezfoulian[1] | Fabien Aubret[3] | D. Bruce Means[4]

[1]Department of Biology, Amphibian Evolution Lab, Vrije Universiteit Brussel, Brussels, Belgium

[2]Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, Toronto, ON, Canada

[3]USR 2936, Station d'Ecologie Expérimentale du CNRS à Moulis, Moulis, France

[4]Coastal Plains Institute and Land Conservancy, Tallahassee, FL, USA

Correspondence
Philippe J. R. Kok, Department of Biology, Amphibian Evolution Lab, Vrije Universiteit Brussel, Brussels, Belgium.
Email: philippe.kok@vub.be

Funding information
Fonds Wetenschappelijk Onderzoek, Grant/Award Number: FWO12A7614N, FWO12A7617N

Editor: Alain Vanderpoorten

Abstract

Aim: Using the Pantepui palaeoendemic toad genus *Oreophrynella*, we explored (1) the origin of Pantepui endemism and the hypothesis of Pantepui being a source of diversity for the surrounding areas, including the geologically younger Andes; (2) whether early diversification of *Oreophrynella* conforms with that of *Stefania* (Hemiphractidae), another Pantepui endemic amphibian, which was recently shown to have vicariantly diverged from Pantepui highlands widespread Oligocene ancestors.

Location: The fractured island-like topography of the Pantepui biogeographical region in north-eastern South America.

Methods: We inferred the molecular phylogeny of *Oreophrynella* and other "basal" Bufonidae genera using three mitochondrial and two nuclear DNA sequences under Bayesian and maximum likelihood methods. We estimated divergence times using a relaxed-clock model and reconstructed ancestral areas through multiple models in a common likelihood framework.

Results: Phylogenetic analyses recovered a monophyletic *Oreophrynella* sister to *Atelopus*. Biogeographical analyses strongly suggested colonization of Pantepui via a pre-Miocene (Eocene/Oligocene) long-distance dispersal of a proto-Andean ancestor, followed by pre-Quaternary (lower Miocene) vicariant divergences of main lineages, and endemism of these main lineages to distinct biogeographical subunits.

Main conclusions: Our results suggest that at least part of the Pantepui diversity stemmed from dispersals from the proto-Andes. Three hypotheses emerge for the origin and evolution of Pantepui endemism, the Distance Dispersal theory, the Plateau theory and the Disturbance–Vicariance theory. Our results indicate that the early diversification of *Oreophrynella* conforms to that of *Stefania*, but hint at different factors responsible for the survival or extinction of different tepui summit amphibians.

KEYWORDS
ancestral areas, anuran, divergence times, long-distance dispersal, molecular phylogenetics, Pantepui, phylogeography, tepui, vicariance

---

*These authors contributed equally to this paper.

1 | INTRODUCTION

Since the first explorations of the Guiana Shield highlands and the famous novel "The Lost World" by Sir Arthur Conan Doyle (1912), the enigmatic tepuis—sandstone tabletop mountains of the Guiana Shield—have been considered to harbour phylogeographically isolated relict species (Rull, 2004a). Tepuis are the dominant landscape of Pantepui, a biogeographical region consisting of the remnants of a vast ancient sandstone plateau on the igneous-metamorphic basement of the Guiana Shield (Figure 1). The basement itself developed during several orogenetic phases during the Archaean and the Proterozoic era, starting from *c.* 3,600 Ma, and was subsequently covered by sedimentary layers 1,600 to 1,000 Ma (Huber, 1995). These sediments gradually cemented together and are today referred to as the Roraima Supergroup (Huber, 1995). Epeirogenetic uplifts and erosion by wind and weathering gradually led to the present-day geomorphology of Pantepui (Huber, 1995). Timing of the isolation of tepui summits is, however, still debated and proposed periods of uplift range from *c.* 2.6 Ma to more than 150 Ma (see Kok, 2013 for a summary). The exact timing of the initial erosion of the Roraima Supergroup surface is impossible to estimate since several thousand metres of sediments have already been eroded (Briceño & Schubert, 1990).

The Precambrian age of the rock formations and their island-like topography led to the assumption of tepuis harbouring ancient lineages, with patterns of isolation and speciation comparable to those observed among isolated oceanic islands. Although several palaeoendemic vertebrates (i.e. phylogenetically isolated relicts of old lineages) do occur in the area (see Heinicke et al., 2009; Hoogmoed, 1979), a thorough sampling and the implementation of molecular phylogenetic analyses revealed that most extant tepui summit anuran species are of relatively recent origin (Kok et al., 2012; Salerno et al., 2012). Dating estimates place the time of divergence among most of the currently isolated studied amphibian and reptile summit populations at the end of the Last Glacial Maximum (LGM) (Kok et al., 2012). The considerable vertical displacement of ecosystems during the Pleistocene-Holocene glaciation cycles, as suggested by palaeoclimatic and palynological data, makes the persistence of demographically large and biodiverse communities on the summits unlikely (Rull, 2004b). Because of these uncertainties, the origin and drivers of diversification of the Pantepui fauna and flora are still debated and multiple biogeographical hypotheses have been proposed, primarily for birds, for example, the Plateau theory (Mayr & Phelps, 1967), the Cool Climate theory (Mayr & Phelps, 1967), the Modified Cool Climate theory (Haffer, 1970), the Habitat Shift theory (Mayr & Phelps, 1967), the Distance Dispersal theory (Mayr & Phelps, 1967), the Specialized Habitat theory (Mayr & Phelps, 1967), the Mountain Bridge theory (Haffer, 1974) and the Disturbance–Vicariance theory (Colinvaux, 1998) (see Kok, 2013 for recent summaries).

In this study, we used the most comprehensive sampling of the Pantepui palaeoendemic toad genus *Oreophrynella* to explore (1) the hypothesis of Pantepui being a source of diversity for the surrounding areas, including the geologically younger Andes; (2) whether early diversification of *Oreophrynella* follows a similar timing and pattern

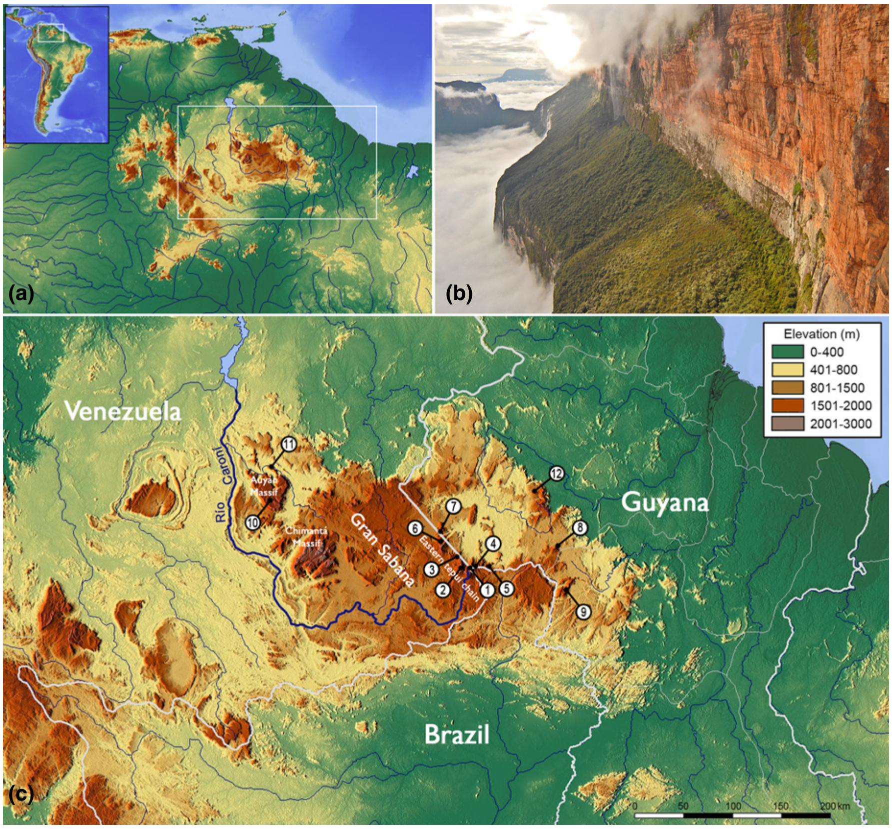


FIGURE 1 (a) Map of Pantepui and its location within South America (inset); white rectangle enlarged in (c). (b) Aerial view of the eastern wall of Mount Roraima, Guyana, showing typical tepuian sheer cliffs and lower forested slopes; Wei-Assipu-tepui is visible on the left. Photo: DBM. (c) Map of eastern Pantepui showing localities mentioned in the text: 1. Mount Roraima; 2. Kukenán-tepui; 3. Yuruaní-tepui; 4. Wei-Assipu-tepui; 5. Maringma-tepui; 6. Ilú-tepui; 7. Tramen-tepui (1–7 = eastern tepui chain); 8. Mount Ayanganna; 9. Wokomung Massif; 10. Auyán-tepui; 11. Cerro El Sol; 12. Merume Mountain

to the Pantepui frog genus *Stefania* as recently described by Kok et al. (2017), that is, divergence from widespread Oligocene tepuian ancestors.

2 | MATERIALS AND METHODS

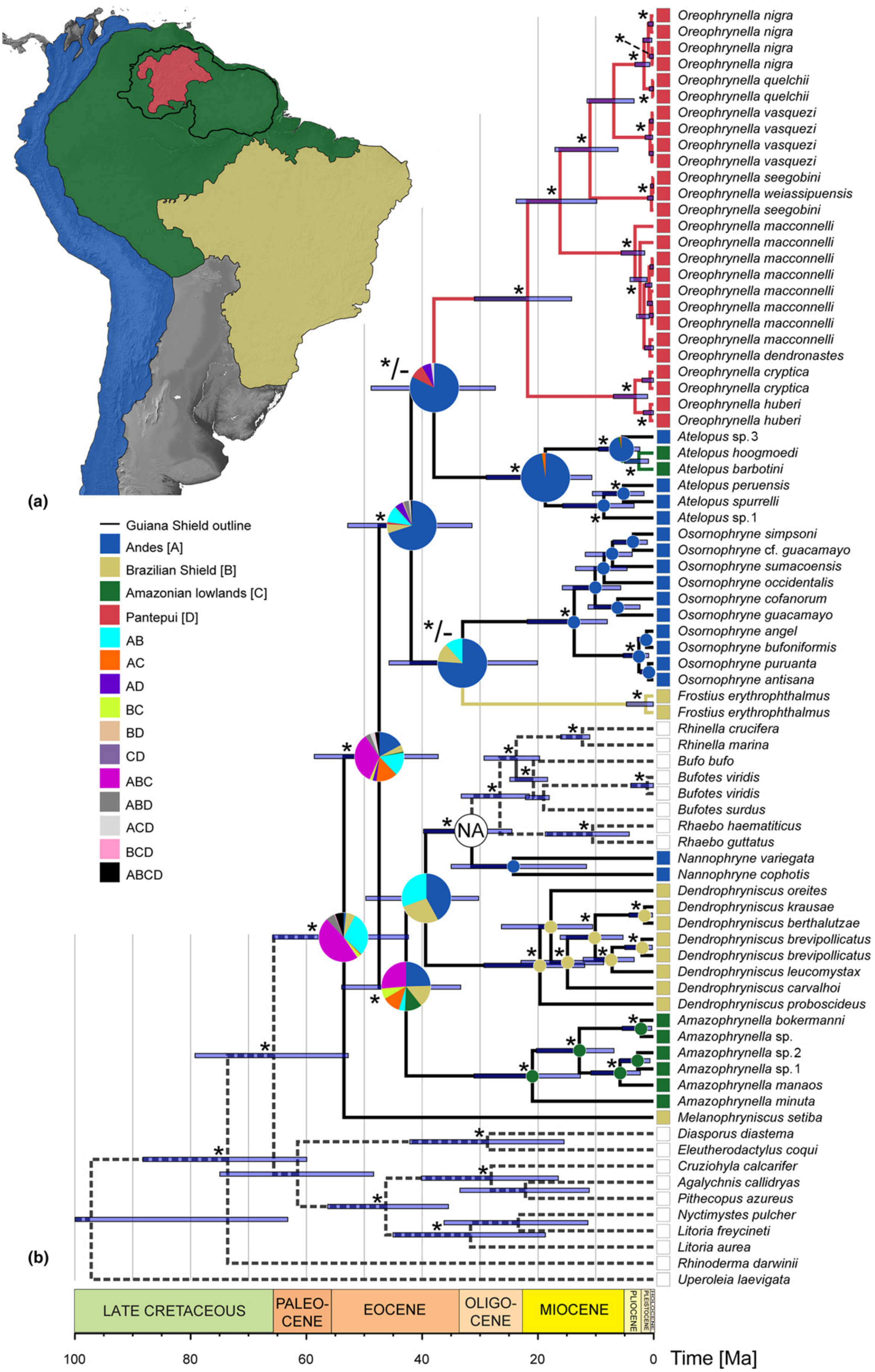
2.1 | Tissue sampling and molecular data

Our molecular dataset included samples of (1) all described *Oreophrynella* species; (2) members of all available "atelopodid" Bufonidae genera (understood here as the paraphyletic taxa branching near the base of the bufonid tree); (3) 10 species belonging to five genera of "non-atelopodid" Bufonidae; (4) members of the families Eleutherodactylidae, Pelodryadidae, Phyllomedusidae and Rhinodermatidae (Hyloidea) used for time calibration; and (5) *Uperoleia laevigata* (Myobatrachidae, sister to Hyloidea according to Roelants et al., 2007) to root our tree. Our final dataset comprised 59 species/79 individuals (see Tables S1 and S2 in Appendix S1). A combination of mitochondrial (fragments of the 16S rRNA gene [16S] and of the subunit 1 of the NADH-dehydrogenase gene [ND1]) and nuclear markers (fragments of the C-X-C chemokine receptor type 4 gene [CXCR4] and of the recombination activating gene 1 [RAG1]) was selected for phylogenetic inference because (1) it has been shown to sufficiently resolve deep and recent phylogenetic splits (e.g. Kok et al., 2017); and (2) several sequences of these genes were already available on GenBank for the targeted taxa. We additionally included a fragment of the mitochondrial 12S rRNA gene [12S], as it was available for most "atelopodid" Bufonidae vouchers. Sequences retrieved from GenBank were combined with 74 novel DNA sequences for *Atelopus*, *Amazophrynella*, *Bufotes*, *Dendrophryniscus*, *Frostius*, *Oreophrynella* and *Osornophryne*. Novel sequences have been deposited in GenBank under the accession numbers MF573819-MF573892. See Appendix S1 for technical details about DNA extraction, PCR, sequencing and sequence alignment.

2.2 | Molecular phylogenetic analyses

Preliminary alignments of the genes of interest were obtained using MAFFT 7 (http://mafft.cbrc.jp/alignment/server/), under the iterative G-INS-i refinement method and default parameters. We used MESQUITE 3.11 (Maddison & Maddison, 2016) for minor alignment correction, like exclusion of gaps and ambiguously aligned regions, and estimation of codon positions under the respective genetic code models (standard or vertebrate mitochondrial). Protein-coding sequences were translated into amino acids to check for stop codons, which would be indicative of pseudogenes or misalignments. A partition homogeneity test performed in PAUP 4.0b150 (Swofford, 2002) with 1,000 replicates confirmed the homogeneity of the gene fragments (p = .94), which were thus treated as a single concatenated dataset. Concatenation of the dataset was performed in MESQUITE, using the export formats "Conservative NEXUS" for the alignment and "Fused matrix export (NEXUS)" for the annotations and definitions (gene positions, codon positions). We used PAUP 4.0b150 (Swofford, 2002) to combine alignments and annotations in a final interleaved NEXUS file. The 12S + 16S + ND1 + RAG1 + CXCR4 dataset contained 2,981 base pairs (bp) after exclusion of 371 ambiguously aligned bp from the 12S and 16S sequences. The myobatrachid frog *Uperoleia laevigata* was selected as outgroup (see above). Best fitting partition schemes and substitution models were estimated using PARTITIONFINDER 1.1.1 (Lanfear, Calcott, Ho, & Guindon, 2012) implementing the "greedy" algorithm and the "mrbayes" model. We tested partitions by gene and partitions by codon position, using the partition resulting in the best supported Bayesian phylogeny for the final analyses (see Appendix S2 for best partitioning schemes). A Bayesian analysis was conducted in MRBAYES 3.2.6 (Ronquist et al., 2012) on the CIPRES Science Gateway 3.3 (Miller, Pfeiffer, & Schwartz, 2010; https://www.phylo.org/). Clade credibility was estimated using Bayesian posterior probabilities (PP) under the best partitioning schemes, and other settings were left default with flat Dirichlet priors for base frequencies and substitution rate matrices and uniform priors for among-site rate parameters. Four parallel Markov chain Monte Carlo (MCMC) runs of four incrementally heated (temperature parameter = 0.2) chains were performed, with a length of 2.10^7 generations, a sampling frequency of 1 per 1,000 generations, and a burn-in of the first 1,000 saved trees. Convergence of the parallel runs was confirmed by split frequency SDs (<0.01) and potential scale reduction factors (*c.* 1.0) for all model parameters, as reported by MRBAYES. TRACER 1.6 (Rambaut & Drummond, 2009) was used to confirm convergence of all analyses by plotting the log-likelihood values against the generation time for each run. Effective sample sizes (ESS) of all parameters were largely over 200, which indicated stationarity and adequate sampling sizes. A maximum likelihood (ML) analysis was conducted in RAxML-HPC2 8.1.11 (Stamatakis, 2006) on the CIPRES Science Gateway 3.3 (https://www.phylo.org/, Miller et al., 2010) under the GTR+I+G substitution model. The dataset was not partitioned for the analysis

FIGURE 2 Time-calibrated phylogeny of "atelopodid" Bufonidae showing ancestral range reconstructions. (a) Map of northern South America showing the biogeographical regions as understood here. (b) Dated phylogeny obtained from the BEAST analysis, with ancestral range estimates of BIOGEOBEARS under the DEC + J model. Node support values of PP > 0.95 (MrBayes) and BS > 75 (RAxML) are depicted by an asterisk, */- indicates PP > 95 and BS < 75 (only shown for two critical nodes). Light blue bars indicate the 95% HDP interval of the inferred branching dates (bar on root truncated to 100 Ma). Coloured branches indicate proposed dispersal events with p = 1 for the corresponding range; inferred ranges of other branches are indicated by small circles (p = 1) or pie charts (proportion of probabilities for multiple scenarios, see Table S6 in Appendix S3). Labels at branch tips indicate range of extant species. Caption refers to colours of areas in (a) and branches, tips + pie charts in (b). Taxa not included in the biogeographical analyses are depicted by grey hatched branches; (NA) = not used in the biogeographical analysis


(a)
Guiana Shield outline
Andes [A]
Brazilian Shield [B]
Amazonian lowlands [C]
Pantepui [D]
AB
AC
AD
BC
BD
CD
ABC
ABD
ACD
BCD
ABCD
(b)
*/-
NA
Oreophrynella nigra
Oreophrynella nigra
Oreophrynella nigra
Oreophrynella nigra
Oreophrynella quelchii
Oreophrynella quelchii
Oreophrynella vasquezi
Oreophrynella vasquezi
Oreophrynella vasquezi
Oreophrynella vasquezi
Oreophrynella seegobini
Oreophrynella weiassipuensis
Oreophrynella seegobini
Oreophrynella macconnelli
Oreophrynella macconnelli
Oreophrynella macconnelli
Oreophrynella macconnelli
Oreophrynella macconnelli
Oreophrynella macconnelli
Oreophrynella macconnelli
Oreophrynella macconnelli
Oreophrynella dendronastes
Oreophrynella cryptica
Oreophrynella cryptica
Oreophrynella huberi
Oreophrynella huberi
Atelopus sp. 3
Atelopus hoogmoedi
Atelopus barbotini
Atelopus peruensis
Atelopus spurrelli
Atelopus sp. 1
Osornophryne simpsoni
Osornophryne cf. guacamayo
Osornophryne sumacoensis
Osornophryne occidentalis
Osornophryne cofanorum
Osornophryne guacamayo
Osornophryne angel
Osornophryne bufoniformis
Osornophryne puruanta
Osornophryne antisana
Frostius erythrophthalmus
Frostius erythrophthalmus
Rhinella crucifera
Rhinella marina
Bufo bufo
Bufotes viridis
Bufotes viridis
Bufotes surdus
Rhaebo haematiticus
Rhaebo guttatus
Nannophryne variegata
Nannophryne cophotis
Dendrophryniscus oreites
Dendrophryniscus krausae
Dendrophryniscus berthalutzae
Dendrophryniscus brevipollicatus
Dendrophryniscus brevipollicatus
Dendrophryniscus leucomystax
Dendrophryniscus carvalhoi
Dendrophryniscus proboscideus
Amazophrynella bokermanni
Amazophrynella sp.
Amazophrynella sp. 2
Amazophrynella sp. 1
Amazophrynella manaos
Amazophrynella minuta
Melanophryniscus setiba
Diasporus diastema
Eleutherodactylus coqui
Cruziohyla calcarifer
Agalychnis callidryas
Pithecopus azureus
Nyctimystes pulcher
Litoria freycineti
Litoria aurea
Rhinoderma darwinii
Uperoleia laevigata
LATE CRETACEOUS
PALEO-CENE
EOCENE
OLIGO-CENE
MIOCENE
PLIOCENE
PLEISTOCENE
100
80
60
40
20
0
Time [Ma]

as partitioning is not straightforward in RAxML and trials with partitions yielded poor results. Nevertheless, the topologies obtained from unpartitioned alignments were congruent with the Bayesian phylogenies. Nodal bootstrap values (Felsenstein, 1985) were estimated using 1,000 pseudoreplicates. The resulting phylogenies were visualized and edited in FigTree 1.4.3 (Rambaut, 2016).

2.3 | Divergence time estimation

We used a Bayesian multi-gene relaxed-clock approach (Battistuzzi, Filipski, Hedges, & Kumar, 2010) implemented in beast 1.8.3 (Drummond, Suchard, Xie, & Rambaut, 2012). The input file was created in BEAUTi 1.8.3 (bundled with beast 1.8.3). The dataset was divided into four partitions as identified by PartitionFinder 1.1.1 (Appendix S2). The MCMC sampling algorithm implemented in beast was used under an uncorrelated lognormal relaxed-clock model, allowing variation of evolutionary rates along the tree branches (Drummond, Ho, Phillips, & Rambaut, 2006). The “Birth–death process with incomplete sampling” was selected as tree prior because in contrast to the “Yule” prior, it allows extinction events (which are likely to have occurred considering the complex palaeoclimatic history of the study area). The ingroup was calibrated with a normally distributed prior on the node representing the most recent common ancestor of Hyloidea (i.e. the split between Rhinodermatidae and the remaining Hyloidea) with a mean of 65.5 Ma and a standard deviation of 10 Ma, following Roelants et al. (2007). In addition, five shallow nodes were calibrated using fossil and geographical information (see Appendix S2 for details). Other priors were left default. The beast analysis was run on the CIPRES Science Gateway V 3.3 (Miller et al., 2010) with one MCMC chain of 50.10^6 generations; trees and parameters were sampled every 1,000 generations. Convergence was confirmed for all analyses using Tracer 1.6 (Rambaut & Drummond, 2009). The first 5,000 generations were discarded as burn-in; the ESS of estimated posterior parameter estimates were largely above 200. The resulting trees were summarized in TreeAnnotator 1.8.3 (part of the beast package), and results were visualized and edited in FigTree 1.4.3 (Rambaut, 2016).

2.4 | Ancestral range reconstruction

The historical biogeography of *Oreophrynella* was inferred on the dated phylogeny using the BioGeoBEARS package (Biogeography with Bayesian [and Likelihood] Evolutionary Analysis in R Scripts) (Matzke, 2013) in R 3.1.1 (R Core Team, 2014). The package implements several likelihood-based models of ancestral range reconstruction and explicitly allows for statistical testing of model fit against the data. Of special interest is the recruitment of the free parameter *j*, allowing for founder-event speciation, which was shown to play a significant role in island biogeography (Matzke, 2014). Following the approach of Kok et al. (2017), we applied and compared six biogeographical models implemented in BioGeoBEARS: (1) the dispersal–extinction–cladogenesis (DEC) model as implemented in Lagrange (Ree, Moore, Webb, & Donoghue, 2005); (2) DEC + J (DEC allowing for founder-event speciation); (3) DIVALIKE, a ML version of dispersal–vicariance analysis (DIVA; Ronquist, 1997); (4) DIVALIKE + J (DIVALIKE allowing for founder-event speciation); (5) BAYAREALIKE, a ML version of the Bayesian inference of historical biogeography (BayArea) by Landis, Matzke, Moore, & Huelsenbeck (2013); and (6) BAYAREALIKE + J (BAYAREALIKE allowing for founder-event speciation). Model fit was evaluated with the statistical tools implemented in BioGeoBEARS, using likelihood ratio test (LRT) and comparing weighted Akaike’s information criterion (AIC) scores (Matzke, 2013). Distribution data of the species of interest are provided in Table S3 in Appendix S1. Two ancestral range estimations were performed on different taxonomical scales. For the genus-level analysis, non-atelopodid Bufonidae were removed from the dated tree, which was pruned to include only one terminal per species. For the detailed analysis of the genus *Oreophrynella*, all other taxa were removed from the dated tree, with *Oreophrynella* being pruned to include only one terminal per population. Pruning of trees was performed in R, using the APE package (Paradis, Claude, & Strimmer, 2004). The maximum number of areas per node was left unconstrained because the geomorphological history of the Pantepui region and the past distribution of Pantepui biota are highly speculative (Kok et al., 2017). Likewise, no constraint was set on potential ancestral distributions and on dispersal probabilities (Kok et al., 2017). For the genus level analysis, we defined four biogeographical areas based on the current distribution of the included taxa: (1) the Andes and peripheral lowlands; (2) the Brazilian Shield and peripheral lowlands; (3) Amazonia, including lowlands of the Guiana Shield; and (4) Pantepui (Figure 2a). For the detailed analysis of *Oreophrynella*, we defined the following biogeographical areas: (5) the summits of the Auyán-Massif (including Auyán-tepui and Cerro El Sol); (6) the eastern uplands and highlands (400–2,000 m elevation, including the slopes of the Wokomung Massif, Merume Mountains, Mount Ayanganna, Maringma-tepui and Mount Roraima); (7) the summit of Maringma-tepui; and (H) the summits of the eastern tepui chain (>2,000 m elevation; including the summits of Mount Roraima, Wei-Assipu-tepui, Ilú- and Tramen-tepui, Kukenán- and Yuruaní-tepui) (Figure 3). Although a better assessment of the relationship among the summits of the eastern tepui chain would have been relevant, oversplitting without further information on possible dispersal routes could not resolve ancestral ranges.

3 | RESULTS

3.1 | Phylogenetic relationships

The topologies inferred by MrBayes using the dataset partitioned by gene and by codon were fully congruent, only differing by slightly higher node support in the latter case. Therefore, only support values from the partition by codon are discussed below. Both Bayesian and ML phylogenies (Figures S1 and S2 in Appendix S2) recovered *Atelopus* as the sister clade of *Oreophrynella*, with strong support in the Bayesian phylogeny (PP = 0.95) but lower support in the ML phylogeny (ML bootstrap [BS] = 69). *Frostius* was found sister to

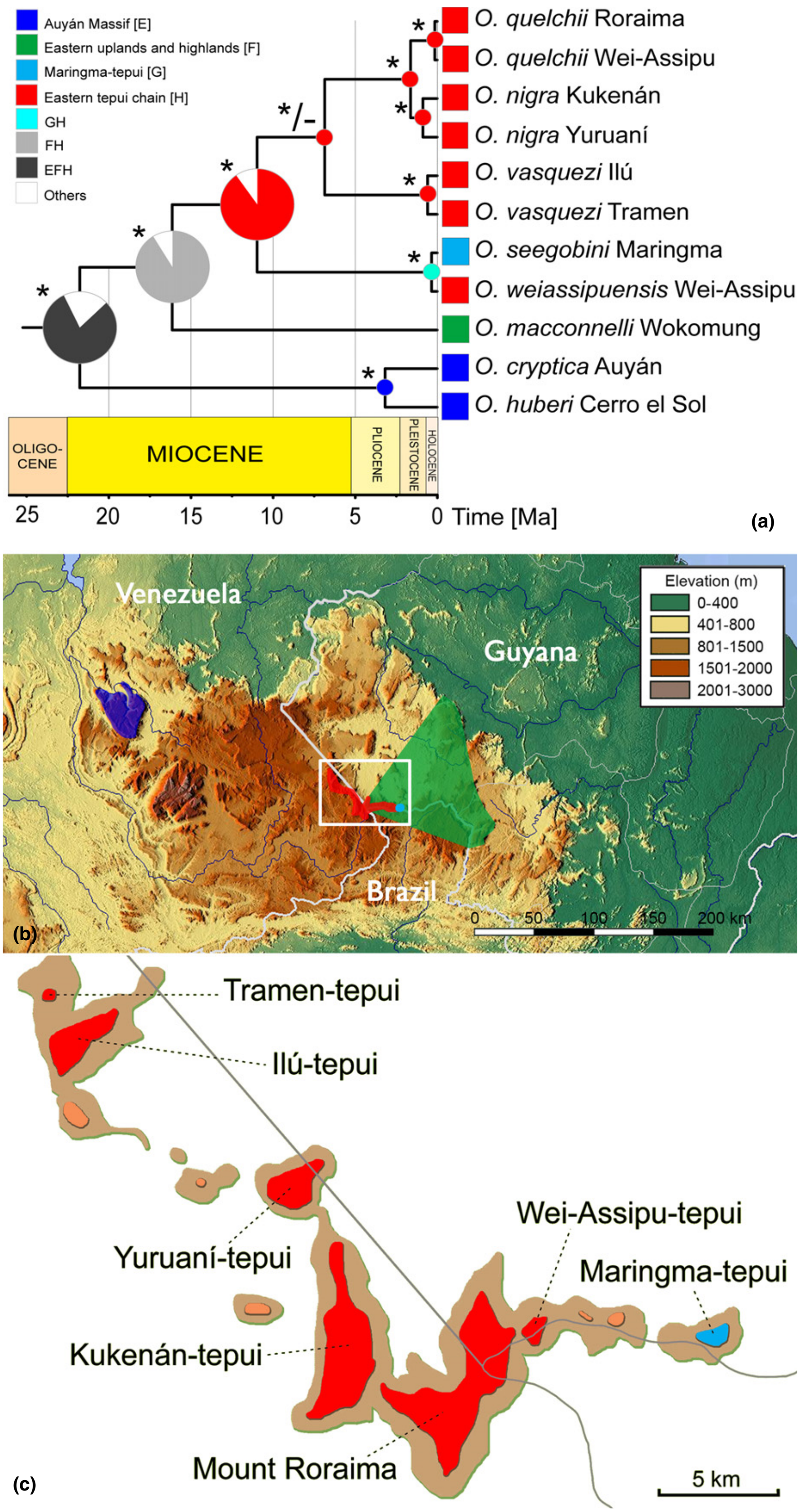


FIGURE 3 Time-calibrated phylogeny of *Oreophrynella* and estimated ancestral ranges. (a) Dated phylogeny of *Oreophrynella*, pruned from the phylogeny shown in Figure 2b, with ranges inferred by a BIOGEOBEARS analysis under the DIVALIKE model (Table S10 in Appendix S3). Asterisks indicate node supports of PP > 0.95 and BS > 75, */- indicates PP > 95 and BS < 75 (Figures S1 and S2 in Appendix S2). Small circles referring to the areas delineated in (b) and (c) indicate $p = 1$ for the corresponding age. Black in pie chart indicates a joint range of E + F + H, $p = .80$; grey in pie chart indicates a joint range of F + H, $p = .91$. Labels at branch tips indicate range of extant species. (b) Map of the eastern Pantepui district, depicting the areas implemented in the ancestral range estimates. (c) Detailed map of the eastern tepui chain, showing summits inhabited by *Oreophrynella*

Osornophryne (PP = 1; BS = 63). The clades formed by *Atelopus* + *Oreophrynella* and *Frostius* + *Osornophryne* were recovered in a well-supported sister group to the remaining Bufonidae excluding *Melanophryniscus* (PP for *Frostius* + *Osornophryne* being sister to *Atelopus* + *Oreophrynella* = 1; BS = 80). *Melanophryniscus* was recovered as “basal” to all other Bufonidae (PP = 1; BS = 92).

Amazophrynella was recovered sister to the non-atelopodid Bufonidae + *Dendrophryniscus* (PP = 1; BS = 79), the latter being, with moderate support, recovered sister to the non-atelopodid Bufonidae (PP = 0.78; BS = 71).

The monophyly of *Oreophrynella* was highly supported (PP = 1; BS = 100). The basalmost split within *Oreophrynella* separated a highly supported clade consisting of *Oreophrynella cryptica* and *Oreophrynella huberi* (PP = 1; BS = 100) from the remaining species of the genus (PP = 1; BS = 80). The next split separated the highly supported clade *Oreophrynella macconnelli* + *Oreophrynella dendronastes* (PP = 1, BS = 100) from a highly supported clade containing *Oreophrynella nigra*, *Oreophrynella quelchii*, *Oreophrynella vasquezi*, *Oreophrynella weiassipuensis* and *Oreophrynella seegobini* (PP = 0.96; BS = 83). *Oreophrynella dendronastes* was nested within *O. macconnelli* (genetic distance in 16S ≤ 1). *Oreophrynella quelchii* and *O. nigra* were sister species (PP = 1; BS = 100), albeit with very short branches. Our analyses recovered *O. vasquezi* sister to *O. quelchii* + *O. nigra* (PP = 0.99; BS = 66) and *O. weiassipuensis* + *O. seegobini* sister to that clade (PP = 0.96; BS = 83, see Figures 2 and 3).

3.2 | Divergence times within atelopodid Bufonidae and *Oreophrynella*

The BEAST analysis yielded a topology congruent with that obtained by the MrBayes and RAxML analyses (Figure 2b, see also Figure S3 in Appendix S2). The age of the most recent common ancestor of extant Bufonidae was estimated at 53.48 Ma in the early Eocene (95% HDP: 42.33–65.78 Ma) when *Melanophryniscus* diverged from all other bufonids. Relatively shortly after the initial split, still during the Eocene, the clade containing *Atelopus*, *Oreophrynella*, *Frostius* and *Osornophryne* diverged from all remaining Bufonidae (47.40 Ma; 95% HDP: 37.19–58.60 Ma). The divergence between the clades *Atelopus* + *Oreophrynella* and *Frostius* + *Osornophryne* was estimated at 41.87 Ma in the middle Eocene (95% HDP: 31.34–52.81 Ma). Approximately at the same time, *Amazophrynella* diverged from the remaining Bufonidae, shortly followed by *Dendrophryniscus* (42.73 Ma; 95% HDP: 33.31–53.85 Ma and 39.35 Ma; 95% HDP: 30.20–49.69 Ma, respectively), the latter node being moderately supported (Figures S1, S2 and S3 in Appendix S2). The most recent common ancestor of *Atelopus* and *Oreophrynella* was inferred to date back to 37.91 Ma in the late Eocene (95% HDP: 27.31–48.76 Ma), whereas the divergence of *Frostius* and *Osornophryne* was estimated to be slightly younger (32.96 Ma; 95% HDP: 20.04–45.67 Ma). Within *Oreophrynella*, five pre-Quaternary diversification events could be observed (Figures 2b and 3a). The initial divergence of the extant *Oreophrynella* species was estimated at 21.73 Ma during the lower Miocene (95% HDP: 14.14–30.95 Ma), separating *O. cryptica* and *O. huberi* from the remaining *Oreophrynella* species. This was followed by a split between *O. macconnelli* (including *O. dendronastes*) and the remaining species during the Miocene (16.12 Ma; 95% HDP: 9.79–23.72 Ma). The clade containing *O. weiassipuensis* and *O. seegobini* diverged from the clade containing *O. nigra* + *O. quelchii* and *O. vasquezi* during the late Miocene around 10.95 Ma (95% HDP: 6.11–17.01 Ma). The split between *O. nigra* + *O. quelchii* and *O. vasquezi* was estimated at 6.84 Ma in the late Miocene (95% HDP: 3.34–11.46 Ma). All extant tepui summit species are of rather recent origin (Figures 2b and 3a): *O. cryptica* and *O. huberi* likely diverged from each other during the Pliocene around 3.17 Ma (95% HDP: 1.01–6.90). The divergence between *O. quelchii* and *O. nigra* was estimated to have occurred around 1.62 Ma during the Pleistocene (95% HDP: 0.62–3.17 Ma). The divergence between *O. seegobini* and *O. weiassipuensis* was estimated to have taken place at the end of the Pleistocene or even in the Holocene (0.10 Ma; 95% HDP: 0–0.44 Ma). However, these nodes are probably too shallow to provide reliable estimates (see Kok et al., 2012).

3.3 | Historical biogeography of atelopodid Bufonidae and *Oreophrynella*

In analysing the atelopodid Bufonidae at the genus level, the DEC + J model fitted the data significantly better than the DEC model (LRT, $p = .0005$; Table S4 in Appendix S3). It also received the highest likelihood score among the six tested models (AIC = 53.56; Table S4 in Appendix S3). However, the DIVALIKE + J model's likelihood is not substantially lower (Tables S4 and S5 in Appendix S3). Because the ancestral ranges inferred for the clade of interest (including *Frostius*, *Osornophryne*, *Atelopus* and *Oreophrynella*) differed only marginally between these two models (Figure S4, Tables S6 and S7 in Appendix S3), we, hereafter, refer only to DEC + J. The ancestral areas of the most recent common ancestor of all Bufonidae and the most recent common ancestor of all Bufonidae except *Melanophryniscus* were unresolved, as was the ancestral area of the clade consisting of *Amazophrynella*, *Dendrophryniscus* and the non-atelopodid Bufonidae (Figure 2b). Considering *Osornophryne*, *Frostius*, *Atelopus* and *Oreophrynella*, the most recent common ancestor was most likely distributed in the Andean region (A: probability of distribution prior speciation [*p*] = .70; AB: $p = .11$; B: $p = .06$; see Figure 2b, Figure S4, Table S6 in Appendix S3). For the clade containing *Osornophryne* and *Frostius*, an Andean origin with dispersal of *Frostius* to the Brazilian Shield was recovered as the most likely scenario (A: $p = .76$; B: $p = .12$; AB: $p = .12$; see Figure 2b, Figure S4, Table S6 in Appendix S3). Likewise, an Andean distribution of the most recent common ancestor of *Atelopus* and *Oreophrynella* was recovered most likely (A: $p = .82$; D: $p = .09$; AD: $p = .06$; see Figure 2b, Figure S4, Table S6 in Appendix S3), followed by a jump dispersal of the ancestor of *Oreophrynella* to the Pantepui region around 38 Ma (95% HDP: 27.31–48.76 Ma), and then around 2.5 Ma (95% HDP: 0.84–4.95 Ma) dispersal of some *Atelopus* lineages to the lowlands of the Guiana Shield (Figure 2b, Figure S4 in Appendix S3).

When the genus *Oreophrynella* is analysed separately, both the DIVALIKE and the DIVALIKE + J models fitted best the data (Figure S5, Tables S8 and S9 in Appendix S3). The likelihoods of these two models did not significantly differ, and the ancestral ranges estimated under both models were congruent, except for the most recent common ancestor of *O. weiassipuensis* and *O. seegobini* (Figure S5 in Appendix S3). For clarity purpose, only the likelihoods conferred by the DIVALIKE model are mentioned below. Both models retrieved the most recent common ancestor of all extant *Oreophrynella* as most likely being distributed throughout the areas (except Maringma-tepui) currently inhabited by extant species (E + F + H: $p = .80$; Figure S5, Table S10 in Appendix S3). This ancestral population diverged into three vicariant lineages corresponding to the tested areas, with a joint origin of the eastern uplands and summits for the most recent common ancestor of *O. macconnelli* (including *O. dendronastes*) and a summit radiation of the eastern tepui chain (F + H: $p = .91$; Table S10 in Appendix S3). This radiation expanded to the summit of Maringma-tepui, where *Oreophrynella seegobini* is retrieved as a vicariant population of *O. weiassipuensis* ($p = 1$). Under the DIVALIKE + J model, *O. seegobini* was found to have likely dispersed very recently from Wei-Assipu-tepui to Maringma-tepui ($p = .88$; Figure S5, Table S11 in Appendix S3).

4 | DISCUSSION

Our results strongly suggest that the most recent common ancestor of *Oreophrynella* and *Atelopus* was living in the proto-Andean region, probably during the late Eocene, therefore—in this case—rejecting the hypothesis of the geologically older Pantepui region being a source of diversity for the surrounding areas. Post-Miocene Andean origins of Pantepui endemic species were demonstrated in groups with better dispersal abilities than anuran amphibians (e.g. Bonaccorso & Guayasamin, 2013; based on shared distribution of birds), and range disjunctions between the Andes and the Pantepui region have been observed, for example, in bryophytes (Désamoré, Vanderpoorten, Laenen, Gradstein, & Kok, 2010), and recently in the frog genus *Tepuihyla* (Ron, Venegas, Ortega-Andrade, Gagliardi-Urrutia, & Salerno, 2016). However, a pre-Miocene Andean origin of a Pantepui endemic vertebrate genus is here demonstrated for the first time.

The timing of divergence between *Oreophrynella* and *Atelopus* (likely caused by a jump dispersal event, see above) comes after a major phase of mountain building in the Andean region (the "Incaic II," *c.* 44 Ma; Noble, McKee, Mourier, & Mégard, 1990), although at that time the proto-Andes were considerably lower than today (Gregory-Wodzicki, 2000). A similar timing is observed in *Stefania* (Kok et al., 2017), and this period, for which Kok (2013) proposed the vertical isolation of the Pantepui plateau being at its apogee, could correspond to the split between most tepui-endemic amphibian and reptile genera and their sister taxa (Kok, 2013). Divergence between the clade comprising *Osornophryne* + *Frostius* and the clade consisting of *Atelopus* + *Oreophrynella* as well as the split between *Amazophrynella* + *Dendrophryniscus* from the non-atelopodid Bufonidae also roughly correspond to that period (Figure 2b). This could be indicative of major ecological reorganizations across the continent as indicated by a cooling phase that started during the late Eocene (37–29 Ma), possibly corresponding to the establishment of the Antarctic Circumpolar Current (Fouquet et al., 2012; Orme, 2007). Fouquet et al. (2012) suggested a correlation between the split *Amazophrynella*/*Dendrophryniscus* and climate change induced by the Andean uplifts and the opening of the circum-Antarctic sea, likely fostering the spread of open vegetation types and possibly already establishing the dry corridor separating Amazonia from the Atlantic forest (Fouquet et al., 2012). More importantly, palaeoenvironmental data indicate that marine incursions have separated the northern Andes and the Guiana Shield between the Eocene and the middle Miocene, but the extent and connectivity of these embayments remain uncertain (e.g. Antonelli, Nylander, Persson, & Sanmartín, 2009; Roddaz et al., 2010). Our results suggest that the proto-Andean ancestor of *Oreophrynella* crossed inhospitable areas and jump-dispersed to Pantepui. Further research is needed to determine the respective roles of jump dispersal and vicariance in the origin of the Pantepui endemic herpetofauna, but our results indicate that vicariance alone (as hypothesized by, e.g. Croizat, 1976) is not sufficient to explain the origin of the Pantepui endemic herpetofauna.

Our results also revealed that the early historical biogeography of *Oreophrynella* follows a similar pattern to the Pantepui endemic frog genus *Stefania* (Kok et al., 2017): splits among the tested biogeographical areas were strongly indicative of vicariant events (i.e. lineages occupied subsets of their ancestors' range). The first speciation event, separating a widespread ancestor into a clade endemic to the summits of the Auyán-Massif and a clade occurring on the summits of the eastern tepui chain and the eastern uplands and highlands, was estimated to have taken place during the lower Miocene, indicating the emergence of a dispersal barrier between the two areas today separated by the Gran Sabana. Kok et al. (2017) inferred a vicariant split between the lineages of *Stefania* endemic to the Auyán-Massif (and to the western Pantepui district) and a large eastern radiation within a similar time frame. These vicariant events predate the global increase of savanna biomes starting from the late Miocene (Orme, 2007). We, therefore, hypothesize that a connection between the Auyán-Massif and the eastern tepui chain existed before the end of that epoch. That "ridge" was probably lowered by the ongoing erosion of the Gran Sabana (i.e. the Kamarata surface, which likely initiated in the Mesozoic; Schubert, Briceño, & Fritz, 1986), until it became too low and hence probably inhospitable for cool-adapted summit endemics. The next divergence between the tested areas happened shortly after, during the Miocene, when the upland/highland species *O. macconnelli*/*O. dendronastes* diverged from the summit endemics of the eastern tepui chain. Although the timing roughly matches divergence events in *Stefania* in the same region, our analyses recovered the split between summits and highlands caused by a vicariant event, whereas in *Stefania*, the summits most likely were colonized via two subsequent dispersal events (Kok et al., 2017). The hypothesized vicariant event separating the present-day arboreal upland/highland *O. macconnelli*/*O. dendronastes* from the clade comprising the eastern summit endemics could have been triggered by the general climate change in South America due to the ongoing Andean uplift throughout the Miocene, leading to less humid conditions and the emergence of savanna biomes towards the late Miocene (Kok, 2013; Orme, 2007), possibly isolating populations of *Oreophrynella* (and other amphibians like *Stefania*) in areas with higher precipitation. The climatic scenario seems more probable than vicariance through physical landscape dissection in a species today restricted to tepui slopes. The subsequent divergence of the clade *O. weiassipuensis* + *O. seegobini* (late Miocene), and shortly after of *O. vasquezi*, from the other members of the eastern chain summits clade seem to be related to the ongoing erosion dissecting the tepuis. The divergence between *O. cryptica* and *O. huberi*, dated in the Pliocene, seems to be related to erosional dissection of the central Auyán-tepui from its satellite tepuis. As mentioned before, the timing and extent of erosion in the Pantepui region remains highly speculative, and it is credible to assume the isolation of tepui summits starting from the Pliocene (Schubert et al., 1986; Schubert & Briceño, 1987; see also Kok, 2013 for a summary). Erosion was possibly accelerated during the glaciation cycles of the Pleistocene (Kok, 2013).

Remarkably, *Oreophrynella* is absent from the Chimantá Massif although Chimantá is geographically much closer to the Auyán Massif than to the eastern tepui chain (Figure 1). In strong contrast to *Oreophrynella*, there is a radiation of at least seven microendemic species of *Stefania* (i.e. the "*ginesi*-clade") occurring in the Chimantá Massif and peripheral tepuis (Kok, Russo, Ratz, & Aubret, 2016; Kok et al., 2017). *Oreophrynella* might have gone extinct in the Chimantá Massif, due to factors that are better tolerated by *Stefania*. Only two species of *Stefania* occur on isolated summits in the eastern tepui chain (Kok et al., 2017), where *Oreophrynella* is widespread. Again, this hints at different factors being responsible for the extinction or the survival of different tepui summit amphibians.

5 | CONCLUSION

Historical biogeography of *Oreophrynella* supports three hypotheses for the origin and evolution of Pantepui endemism. The colonization of Pantepui via a long-distance dispersal of a proto-Andean ancestor matches the Distance Dispersal theory of Mayr and Phelps (1967); except Mayr and Phelps (1967), most authors considered long-distance dispersal (LDD, also known as jump dispersal) as rather implausible for the origin of the Pantepui biota, especially for non-flying organisms (e.g. Chapman, 1931; Hoogmoed, 1979; McDiarmid & Donnelly, 2005). However, although LDD is probably a rare phenomenon, there is ample evidence of such events, including in terrestrial vertebrates (see Lomolino, Riddle, Brown, & Brown, 2010 for a summary). The original dispersal was likely followed by in situ diversification, which is best explained by the Plateau theory (Mayr & Phelps, 1967). Although the Plateau theory has commonly been rejected due to the apparent time discrepancy between (presumably) ancient landscape and relatively recent taxa (e.g. Salerno et al., 2012; Voss, Lim, Díaz-Nieto, & Jansa, 2013), it fits best the biogeographical patterns of several Pantepui endemic amphibians (Kok, 2013; Kok et al., 2017). In *Oreophrynella*, like in *Stefania* and other Pantepui endemic lineages (Kok, 2013), pre-Quaternary branching of main clades is observed, most likely due to vicariance, followed by endemism of these main lineages to distinct biogeographical subunits. Low genetic diversity among extant tepui summit *Oreophrynella* populations suggests a drastic reorganization during the glaciation cycles of the Pleistocene, fitting the Disturbance–Vicariance theory of Colinvaux (1998), although, for endemic tepui summit terrestrial vertebrates like *Oreophrynella*, Pleistocene climate oscillations most likely depleted biodiversity instead of fostering it (Kok, 2013). The scenario hypothesized by Kok et al. (2017) could thus be refined as follows for Pantepui endemic genera: (1) Palaeogene vicariance (possibly caused by marine incursions) and long-distance dispersals (from the proto-Andes, and possibly from the Brazilian Shield) led to the isolation of Pantepui endemic genera, possibly starting from the Eocene. Isolation of these lineages might have been further strengthened by the gradual vertical isolation of the Pantepui plateau; (2) late Oligocene/lower Miocene vicariance (caused by erosion of the Roraima Supergroup) of main lineages, and endemism to distinct biogeographical subunits; (3) reorganization of species diversity during periods of climatic instability in the Pleistocene, which caused massive local extinctions and induced low genetic divergence among most extant species. It will be interesting to determine the respective roles of jump dispersal and vicariance in the origin of the Pantepui endemic biota by comparing the historical biogeography of all Pantepui endemic taxa.

ACKNOWLEDGEMENTS

P.J.R.K.'s work is supported by postdoctoral fellowships from the Fonds voor Wetenschappelijk Onderzoek Vlaanderen (FWO12A7614N/FWO12A7617N). Fieldwork was supported by the Belgian Directorate-General for Development Cooperation, the King Léopold III Fund for Nature Exploration and Conservation, the Smithsonian Institution, the Royal Ontario Museum (ROM) Reproductions and Acquisitions Fund, the ROM Foundation, the ROM Department of Natural History, Goldstone Resources, Conservation International, National Geographic Society, and the Coastal Plains Institute and Land Conservancy. Permission to conduct research in indigenous lands in the Pakaraima Mountains of Guyana was granted by the Guyanese Ministry of Amerindian Affairs. Research and export permits were issued by the Guyana Environmental Protection Agency and the DIREN Guyane (French Guiana). We thank Miguel T. Rodrigues and Bruna Batista (Universidade de São Paulo, Brazil) for providing tissue samples, and Arturo Berti (Kamarata, Venezuela) and Brad Wilson (Atlanta, USA) for excellent company and assistance in the field.

ORCID

Philippe J. R. Kok http://orcid.org/0000-0001-9743-9738

REFERENCES

Antonelli, A., Nylander, J. A., Persson, C., & Sanmartín, I. (2009). Tracing the impact of the Andean uplift on Neotropical plant evolution.

Proceedings of the National Academy of Sciences of the United States of America, *106*, 9749–9754.

Battistuzzi, F. U., Filipski, A., Hedges, S. B., & Kumar, S. (2010). Performance of relaxed-clock methods in estimating evolutionary divergence times and their credibility intervals. *Molecular Biology and Evolution*, *27*, 1289–1300.

Bonaccorso, E., & Guayasamin, J. M. (2013). On the origin of Pantepui montane biotas: A perspective based on the phylogeny of *Aulacorhynchus* toucanets. *PLoS ONE*, *8*, e67321.

Briceño, H. O., & Schubert, C. (1990). Geomorphology of the Gran Sabana, Guayana Shield, Southeastern Venezuela. *Geomorphology*, *3*, 125–141.

Chapman, F. M. (1931). The upper zonal bird-life of Mts. Roraima and Duida. *Bulletin of the American Museum of Natural History*, *63*, 1–135.

Colinvaux, P. (1998). A new vicariance model for Amazonian endemics. *Global Ecology & Biogeography Letters*, *7*, 95–96.

Croizat, L. (1976). Biogeografía analítica y sintética (“panbiogeografía”) de las Américas. Academia de Ciencias Físicas, Matemáticas y Naturales, Caracas (two volumes).

Désamoré, A., Vanderpoorten, A., Laenen, B., Gradstein, G., & Kok, P. J. R. (2010). Biogeography of the lost world (Pantepui region, northeastern South America): Insights from bryophytes. *Phytotaxa*, *9*, 254–265.

Doyle, A. C. (1912). *The lost world*. London: Hodder & Stoughton.

Drummond, A. J., Ho, S. Y., Phillips, M. J., & Rambaut, A. (2006). Relaxed phylogenetics and dating with confidence. *PLoS Biology*, *4*, e88.

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973.

Felsenstein, J. (1985). Confidence limits on phylogenies: An approach using the bootstrap. *Evolution*, *39*, 783–791.

Fouquet, A., Recoder, R., Teixeira, M., Cassimiro, J., Amaro, R. C., Camacho, A., . . . Rodrigues, M. T. (2012). Molecular phylogeny and morphometric analyses reveal deep divergence between Amazonia and Atlantic forest species of *Dendrophryniscus*. *Molecular Phylogenetics and Evolution*, *62*, 826–838.

Gregory-Wodzicki, K. M. (2000). Uplift history of the Central and Northern Andes: A review. *Geological Society of America Bulletin*, *112*, 1091–1105.

Haffer, J. (1970). Entstehung und Ausbreitung nordandiner Bergvögel. *Zoologische Jahrbücher Systematik*, *97*, 301–337.

Haffer, J. (1974). Avian speciation in tropical South America, with a systematic survey of the toucans (Ramphastidae) and jacamars (Galbulidae). *Publication of the Nuttall Ornithological Club*, *14*, 1–390.

Heinicke, M. P., Duellman, W. E., Trueb, L., Means, D. B., MacCulloch, R. D., & Hedges, S. B. (2009). A new frog family (Anura: Terrarana) from South America and an expanded direct-developing clade revealed by molecular phylogeny. *Zootaxa*, *2211*, 1–35.

Hoogmoed, M. S. (1979). The herpetofauna of the Guianian region. In W. E. Duellman (Ed.), *The South American herpetofauna: Its origin, evolution and dispersal* (pp. 241–279). Lawrence: University of Kansas, Monograph, 7.

Huber, O. (1995). Geographical and physical features. In P. E. Berry, B. K. Holst & K. Yatskievych (Eds), *Flora of the Venezuelan Guayana*, Vol. 1 (pp. 1–61). St. Louis: Missouri Botanical Garden Press.

Kok, P. J. R. (2013). Islands in the sky: Species diversity, evolutionary history, and patterns of endemism of the Pantepui herpetofauna. PhD thesis, Leiden University, the Netherlands.

Kok, P. J. R., MacCulloch, R. D., Means, D. B., Roelants, K., Van Bocxlaer, I., & Bossuyt, F. (2012). Low genetic diversity in tepui summit vertebrates. *Current Biology*, *22*, R589–R590.

Kok, P. J. R., Russo, V. G., Ratz, S., & Aubret, F. (2016). On the distribution and conservation of two ‘Lost World’ tepui summit endemic frogs, *Stefania ginesi* Rivero, 1968 and *S. satelles* Señaris, Ayarzagüena, and Gorzula, 1997. *Amphibian & Reptile Conservation*, *10*, 5–12.

Kok, P. J. R., Russo, V. G., Ratz, S., Means, D. B., MacCulloch, R. D., Lathrop, A., . . . Bossuyt, F. (2017). Evolution in the South American ‘Lost World’: Insights from multilocus phylogeography of stefanias (Anura, Hemiphractidae, *Stefania*). *Journal of Biogeography*, *44*, 170–181.

Landis, M. J., Matzke, N. J., Moore, B. R., & Huelsenbeck, J. P. (2013). Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology*, *62*, 789–804.

Lanfear, R., Calcott, B., Ho, S. Y., & Guindon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology*, *29*, 1695–1701.

Lomolino, M. V., Riddle, B. R., Brown, J. H., & Brown, J. H. (2010). *Biogeography*, 4th ed.. Sunderland, MA: Sinauer Associates.

Maddison, W. P., & Maddison, D. R. (2016). Mesquite: a modular system for evolutionary analysis. Version 3.10. Retrieved from http://mesquiteproject.org (accessed 20 December 2016).

Matzke, N. J. (2013). *BioGeoBEARS: Biogeography with Bayesian (and likelihood) evolutionary analysis in R Scripts*. University of California, Berkeley, CA. Retrieved from http://CRAN.R-project.org/package=BioGeoBEARS (accessed 20 December 2016).

Matzke, N. J. (2014). Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology*, *63*, 951–970.

Mayr, E., & Phelps, W. S. (1967). The origin of the bird fauna of the south Venezuelan highlands. *Bulletin of the American Museum of Natural History*, *136*, 269–328.

McDiarmid, R. W., & Donnelly, M. A. (2005). The herpetofauna of the Guayana highlands: Amphibians and reptiles of the lost world. In M. A. Donnelly, B. I. Crother, C. Guyer, M. H. Wake, & M. E. White (Eds.), *Ecology and evolution in the tropics: A herpetological perspective* (pp. 461–560). Chicago: University of Chicago Press.

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES science gateway for inference of large phylogenetic trees. In Institute of Electrical and Electronics Engineers (Ed.), *Proceedings of the gateway computing environments workshop (GCE)* (pp. 1–8). New Orleans, LA: IEEE Xplore.

Noble, D. C., McKee, E. H., Mourier, T., & Mégard, F. (1990). Cenozoic stratigraphy, magmatic activity, compressive deformation, and uplift in northern Peru. *Geological Society of America Bulletin*, *102*, 1105–1113.

Orme, A. R. (2007). Tectonism, climate, and landscape change. In T. T. Veblen, K. R. Young, & A. R. Orme (Eds.), *The physical geography of South America* (pp. 23–44). New York: Oxford University Press.

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290.

R Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org (accessed 20 December 2016).

Rambaut, A. (2016). Figtree, a graphical viewer of phylogenetic trees. Retrieved from http://tree.bio.ed.ac.uk/software/gtree (accessed 20 December 2016).

Rambaut, A., & Drummond, A. J. (2009). Tracer v1.5. Retrieved from http://beast.bio.ed.ac.uk/Tracer (accessed 20 December 2016).

Ree, R. H., Moore, B. R., Webb, C. O., & Donoghue, M. J. (2005). A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution*, *59*, 2299–2311.

Roddaz, M., Hermoza, W., Mora, A., Baby, P., Parra, M., Christophoul, F., . . . Espurt, N. (2010). Cenozoic sedimentary evolution of the Amazonian foreland basin system. In C. Hoorn & F. P. Wesselingh (Eds.), *Amazonia, landscape and species evolution: A look into the past* (pp. 61–88). Chichester: Wiley-Blackwell.

Roelants, K., Gower, D. J., Wilkinson, M., Loader, S. P., Biju, S. D., Guillaume, K., . . . Bossuyt, F. (2007). Global patterns of diversification in the history of modern amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 887–892.

Ron, S. R., Venegas, P. J., Ortega-Andrade, H. M., Gagliardi-Urrutia, G., & Salerno, P. E. (2016). Systematics of *Ecnomiohyla tuberculosa* with the description of a new species and comments on the taxonomy of *Trachycephalus typhonius* (Anura, Hylidae). *ZooKeys*, *630*, 115–154.

Ronquist, F. (1997). Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. *Systematic Biology*, *46*, 195–203.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., . . . Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, *61*, 539–542.

Rull, V. (2004a). Biogeography of the 'Lost World': A palaeoecological perspective. *Earth-Science Reviews*, *67*, 125–137.

Rull, V. (2004b). An evaluation of the lost world and vertical displacement hypotheses in the Chimantá-Massif, Venezuelan Guayana. *Global Ecology and Biogeography*, *13*, 141–148.

Salerno, P. E., Ron, S. R., Señaris, J. C., Rojas-Runjaic, F. J. M., Noonan, B. P., & Cannatella, D. C. (2012). Ancient Tepui summits harbor young rather than old lineages of endemic frogs. *Evolution*, *66*, 3000–3013.

Schubert, C., & Briceño, H. O. (1987). Origen de la topografía tepuyana: Una hipótesis. *Pantepui*, *2*, 11–14.

Schubert, C., Briceño, H. O., & Fritz, P. (1986). Paleoenvironmental aspects of the Caroní-Paragua river basin (southeastern Venezuela). *Interciencia*, *11*, 278–289.

Stamatakis, A. (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, *22*, 2688–2689.

Swofford, D. L. (2002). *PAUP*. Phylogenetic analysis using parsimony (*and other methods). Ver. 4.b.10*. Sunderland, MA: Sinauer Associates.

Voss, R. S., Lim, B. K., Díaz-Nieto, J. F., & Jansa, S. A. (2013). A new species of *Marmosops* (Marsupialia: Didelphidae) from the Pakaraima Highlands of Guyana, with remarks on the origin of the endemic Pantepui mammal fauna. *American Museum Novitates*, *3778*, 1–27.

BIOSKETCH

Philippe J. R. Kok is a postdoctoral researcher at the Vrije Universiteit Brussel, Belgium. His main interests lie in the evolution, systematics, taxonomy and biogeography of amphibians and reptiles in the Neotropics. His work now primarily focuses on vertebrate evolution in the Pantepui region.

Author contributions: P.J.R.K. designed the research. P.J.R.K., S.R., D.B.M., R.D.M. and A.L. collected samples and contributed to interpret molecular results. P.J.R.K., S.R and R.D. performed the molecular work. P.J.R.K and S.R. analysed the data. P.J.R.K. and S.R. wrote the manuscript with input from all co-authors.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Kok PJR, Ratz S, MacCulloch RD, et al. Historical biogeography of the palaeoendemic toad genus *Oreophrynella* (Amphibia: Bufonidae) sheds a new light on the origin of the Pantepui endemic terrestrial biota. *J Biogeogr*. 2018;45:26–36. https://doi.org/10.1111/jbi.13093