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**DIVERSIFICATION BY DISPERSAL OUT OF THE ANDES REVEALED BY A
NEWLY DISCOVERED HUMMINGBIRD CLADE, THE ‘TRUE BRILLIANTS’**

BY

MARIALEJANDRA CASTRO-FARÍAS

B.A., Biology, Universidad Central de Venezuela, 2017

THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Master of Science

Biology

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DEDICATION

A María Josefa. No se muere quien se va, solo se muere el que se olvida y yo a ti no te olvido. Gracias por el fuego, la terquedad y la resiliencia. Honrada me siento de llevar tu nombre.

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To the ones that showed up for me. To the ones that always believe, even when I was lost in my own forest. Thank you.

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To my mentor, Jorge Pérez-Emán. Bienaventurada el alma noble que riega y ama su fruto sin esperar recompensa de su sabor.

**DIVERSIFICATION BY DISPERSAL OUT OF THE ANDES REVEALED BY A
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ABSTRACT

We identified a novel clade with striking biogeographic implications. Unsourced genera, *Hylonympha* and *Sternoclyta*, were found to be close to the genus *Heliodoxa* within the Brilliants. *Heliodoxa* tend to occur in lower montane habitats, such as the tropical, upper tropical, and subtropical elevational zones of the Andes and the Neotropics. Analysis of geographic and elevational zones showed that genus *Heliodoxa* and related genera diversified by out-of-Andes dispersal to mountain ranges of Central America, coastal Venezuela, the Pantepui, and southeastern Brazil, since the mid-Miocene. Within the Brilliants, reductions in elevation preceded these geographic expansions. Secondary colonization of the lowlands from the mountains appears to be rare in hummingbirds, with only one occurrence across the phylogeny of the two major Andean clades of hummingbirds, the Coquettes and the Brilliants. The ‘True Brilliants’, a newly recognized clade comprising the *Heliodoxa* and its close relatives, provides an example of hummingbird evolution toward lower elevations.

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Diversification by dispersal out of the Andes revealed by a newly discovered hummingbird clade, the ‘True Brilliants’.

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SUMMARY

Aim: To elucidate the relative roles of montane-lowland transitions and inter-mountain range dispersal in the diversification of hummingbirds.

Location: Neotropics, including: eastern Central America, the tropical Andes, the Coastal Cordillera and Paria Peninsula of Venezuela, the Pantepui Region, the Amazon lowlands, and southeastern Brazil.

Taxon: ‘Brilliant’ tribe (Coeligenini), a diverse clade of hummingbirds (54 species and more than 100 subspecies), mostly distributed in the Andes Mountains, with a focus on two enigmatic, monotypic genera: *Sternoclyta* and *Hylonympha*.

Methods: Molecular phylogenomic and biogeographic analyses including sampling of previously unsampled genera of unknown affinities.

Results: We identified a novel clade with striking biogeographic implications. Previously unsampled genera, *Hylonympha* and *Sternoclyta*, were found to be close to the genus *Heliodoxa* within the Brilliant tribe. *Heliodoxa* and closely related genera tend to occur in lower montane habitats, such as the tropical, upper tropical, and subtropical elevational zones of the Andes or other mountainous areas of the Neotropics. Bayesian biogeographical analysis of geographic and elevational zones showed that *Heliodoxa* and related genera diversified by out-of-Andes dispersal to mountain ranges of Central America, coastal Venezuela, the Pantepui, and southeastern Brazil, respectively, since the mid-Miocene. Within the larger clade of Brilliant, successive reductions in elevation preceded these geographic expansions.

Main conclusions: Secondary colonization of the lowlands from the mountains appears to be rare in hummingbirds, with only one unambiguous occurrence evident across the phylogeny of the two major Andean clades of hummingbirds, the Coquettes and the Brilliant. Here we

introduce the ‘True Brilliants’, a newly recognized clade comprising the genus *Heliodoxa* and its close relatives, which provides the most definitive example of hummingbird evolution toward lower elevations. In the true brilliants, downward evolution was accompanied by dispersal to montane areas of the Neotropics that are now isolated from the Andes by vast swaths of lowland habitats. Colonization of outlying mountain ranges of tropical-latitude South America does not appear to have occurred in higher-elevation subclades of the Brilliants or Coquettes. We conclude that, in hummingbirds, downward elevational shifts were a necessary precursor to range expansion out of the Andes; but once the True Brilliants occupied the pre-montane, foothill zone, expansion to distant mountain systems repeatedly occurred during cooler climate periods, leading to speciation.

Keywords: Trochilidae, hummingbirds, Brilliants, Andes, Neotropical biogeography, species pump, BioGeoBears, *Sternolcyta*, *Hylonympha*, *Heliodoxa*.

INTRODUCTION

The Neotropical Region is one of the most biodiverse areas in the world. The exuberance of its vegetation and richness of species was highlighted by early naturalists (Bates, 1863; Wallace, 1854). Exceptional species richness in the Neotropics has been demonstrated for many organisms, including plants, invertebrates and vertebrates (Antonelli & Sanmartín, 2011; Buckley & Jetz, 2007; Jenkins, Guénard, et al., 2013; Jenkins, Pimm, et al., 2013; Robbins & Opler, 1997). Explaining the origin and maintenance of such large diversity has been the focus of many studies (Antonelli et al., 2015, 2018), and a large amount of attention has been given lately to mountain regions due to their exceptional diversity and vulnerability to current anthropogenic changes (Antonelli et al., 2018; Elsen et al., 2020; Hoorn et al., 2010; Rahbek et al., 2019).

The Andes region is one of the most diverse systems in the world, hosting an exceptional diversity and endemism of its biota. Almost 30,000 species of vascular plants and more than 3,400 vertebrate species (excluding fishes) are found in this mountain region, with about half of them endemics to this system (Kessler & Kluge, 2008; Myers et al., 2000; Orme et al., 2005; Pérez-Escobar et al., 2022). The origin and maintenance of this diversity have been linked to different ecological and evolutionary processes interacting with the geological and geographical dynamics at different spatial and temporal scales (Rahbek et al., 2019a; Rahbek et al., 2019b), leaving a signature in current species assemblages that resulted from the interplay among speciation, coexistence, and persistence (Cadena et al., 2019; Rahbek et al., 2019). Spectacular cases of diversification and radiation in the Andean biota have been linked to the uplift of the Andes, its colonization, and the dispersal-vicariance dynamics generated by the interaction of climate changes and rugged topography (Cadena et al., 2020; Hughes & Eastwood, 2006; Lagomarsino et al., 2016; Vallejos-Garrido et al., 2023). In birds, one lineage

characterized by a large radiation associated with the Andes are the hummingbirds (family: Trochilidae) (McGuire et al., 2007).

Hummingbirds are characteristic birds of the Neotropics. Although fossil remains from the Oligocene of Europe have been identified as part of the stem lineage of hummingbirds (Mayr, 2005), the origin of extant hummingbirds occurred in the South American lowlands during the Early Miocene (McGuire, Witt, Renssen Jr, et al., 2014). Subsequently, an explosive diversification gave origin to almost 340 species that colonized the newly available habitats formed during a highly dynamic geological period (Hoorn et al., 2010) and colonize different biogeographic regions (Bleiweiss, 1998a; McGuire et al., 2007; McGuire, Witt, Renssen, et al., 2014). An important event in the evolution of this clade is the orogenic dynamics of the Andes, a region that holds almost 40% of the hummingbird diversity (McGuire, Witt, Renssen, et al., 2014). However, the geographic and habitat distribution of hummingbird diversity is tightly linked to its evolutionary history showing association with its phylogenetic structure (Bleiweiss, 1998b; McGuire et al., 2007; McGuire, Witt, Renssen, et al., 2014).

Hummingbirds are currently known to be grouped into nine major lineages or clades. Phylogenetic studies have provided congruent results regarding the phylogenetic structure of the family Trochilidae, with nine clades recognized by their informal names: Topazes, Hermits, Bees, Mountain Gems, Giants, Emeralds, Mangoes, Coquettes, and Brilliants (Altshuler et al., 2004; Bleiweiss et al., 1997; McGuire et al., 2009). These groups differ in their morphology, use of habitat, and geographic distribution (Bleiweiss, 1998b; Stiles, 2004, 2008), as well as in their evolutionary history (McGuire, Witt, Renssen, et al., 2014). Topazes, Hermits, and Mangoes comprise the earliest divergences since the most recent common ancestor of hummingbirds; each is characteristic of South American lowlands, with only two Hermit species and four Mango species ascending as high as the temperate zone of the tropical Andes (> ~2400 m). Bees, Mountain Gems, and Emeralds comprise the most recent radiation in the

family and are the groups that most successfully have colonized Central and North America; although they are mostly found in lowlands, numerous lineages in this diverse clade have colonized mountains, though rarely > ~3000 m elevation.

Coquettes and Brilliants are the two Andean clades, and each contains species that have ascended to the highest available habitats, > 4500 m elevation. These two Andean clades differ somewhat in their use of habitats; whereas Coquettes tend to occur in open and unforested areas, Brilliants are more tied to forested habitats. Morphology and use of flower resources also differs on average between these clades (Stiles, 2008). The Andean assemblage of hummingbirds is dominated by Coquettes and Brilliants, but includes additional species from some of the other clades and show no sign of density-dependent diversification, suggesting potential for further diversification in the region (McGuire, Witt, Renssen, et al., 2014). Such ecological and taxonomic diversity of hummingbirds in the Andes make this group amenable to study the biogeographic dynamics of some of these lineages (i.e. speciation, persistence, and dispersal), as well as to explore biogeographical hypotheses such as whether the Andes has acted as a ‘species pump’, driving speciation that contributes diversity to neighboring biogeographic regions.

To conduct formal study of the biogeography and elevation of montane hummingbirds, we need well-resolved phylogenies with thorough species sampling across diverse taxa that vary in ranges and elevations. The phylogenetic framework of the family Trochilidae is approximately 80% complete at the species level (McGuire, Witt, Renssen, et al., 2014; Ornelas et al., 2014), though substantial within-species diversity remains a frontier for hummingbird systematics (Benham et al., 2015; Chaves et al., 2011; Cowles et al., 2022; Zamudio-Beltrán et al., 2020). In the last two decades, with the increase and use of large molecular data, we have moved from a classification in which more than 50% of genera comprising the family were monotypic (Schuchmann, K.L, 1999) to a current taxonomic treatment with one-third of genera

having only one species (Gill, Frank et al., 2023). However, some genera remain to be examined. For example, the monotypic genus *Anopetia*, a hermit species found in northeastern Brazil, as well as *Sternoclyta* and *Hylonympha*, two species with small distributions in the northern South America, have yet to be studied in a phylogenetic framework using DNA sequences. These last two genera are monotypic and found almost exclusively in humid and wet premontane forests in Venezuela. *Sternoclyta* occurs in the Central Coastal Cordillera and the Merida Andes, while *Hylonympha* is restricted to the highest available elevations of the Paría Peninsula, a relictual ridge of the Andes near its northeastern most extent (Hilty, 2003).

The phylogenetic placement of the monotypic genera *Sternoclyta* and *Hylonympha* is uncertain. Although most current classification authorities place both genera with the Brilliants (Remsen, J. V., Jr. et al., 2023), no data are available to confirm such placement. *Sternoclyta* was initially described by Gould (Gould, 1846) under the Mountain Gem subgenus *Lampornis*, and later placed adjacent to the Brilliants in the linear sequence of classification, though also close to the Mountain Gem genus *Eugenes* (Cory, 1918; Elliot, 1879; Peters, 1945.) At some point, the genus *Eugenes* was even considered a species in the genus *Heliodoxa*. *Hylonympha* was initially placed adjacent to *Thalurania*, an Emerald, but soon was placed close to members of the Brilliants, including *Heliodoxa* and related genera (Boucard, 1895; Cory, 1918; Peters, 1945; Simon, 1921). Renner and Schuchmann (Renner & Schuchmann, 2004) lumped both monotypic genera into the genus *Eugenes* based on patterns of coloration, habitat, and morphological data, and disregarding DNA-DNA hybridization evidence that *Eugenes* and *Heliodoxa* were not closely related taxa (Bleiweiss et al., 1997). This hypothesis was influential for modern classifications that continue to group *Eugenes* with *Hylonympha* and *Sternoclyta* (Cracraft, 2013; McGuire et al., 2009) (but see Remsen et al. 2023 for a different arrangement). Moreover, McGuire et al. (2009), while acknowledging a lack of evidence, suggested both genera could be included in the Emeralds on the basis of their

general appearance and the fact that numerous emerald genera exist around the Caribbean rim that have anomalous phenotypes. Stiles (in Remsen et al. 2023) proposed that both genera to be placed in the Brilliants based on morphological and plumage similarities (when considering females rather than sexually-selected males), and considering the large plumage diversity in the group that led in the past to create additional genera for different species that are currently recognized as being in or close to the genus *Heliodoxa*: *Polyplancta*, *Iolaima*, *Phaiolaima*, *Lampraster*, and *Clytolaema*.

Alternative evolutionary and biogeographic scenarios are possible depending on the phylogenetic placement of the genera *Sternoclyta* and *Hylonympha*. The most likely scenario involves their placement in the Brilliants, which will provide with a lineage of hummingbirds with large diversity of geographical distributions, both elevationally (lowlands, mid-elevation and high-elevation) and regionally (Andes, Coastal Cordillera, Paria Peninsula, southeastern mountains, Amazonas and Central American mountains). Such combination of geographical traits will allow to test scenarios of upward/downward elevational movements and dispersal into/out of the Andes, contributing further to the exploration of the Andes as a species pumps, contributing diversity to other regions. It would also allow to test the proposed evolutionary and biogeographic scenario for the origin and distribution of both *Sternoclyta* and *Hylonympha* from Renner and Schuchmann (2004), stressing the role of elevational shifts in habitat distribution influenced by Pleistocene climate changes. On the other hand, a phylogenetic placement with the Emeralds and/or Mountain Gems would extend the elevational or geographical distribution of either of these lineages, as Emeralds are not common in mountains and Mountain Gems are almost exclusive to Northern and Central America (with the exception of *Heliomaster spp.*).

As a preliminary step toward this study, we obtained fresh tissue samples of *Sternoclyta* and *Hylonympha*, and we sequenced the six genes that had been used by McGuire et al. (2014)

to test their clade assignment within the hummingbirds. Those data showed unambiguously that these two genera belonged to the Brilliant tribe, were close to members of the genus *Heliodoxa*, and had no close relationship at all with the genus *Eugenes*, a Mountain-Gem. This fills one of the last remaining gaps regarding the higher-level taxonomy and phylogenetic biogeography of hummingbirds. However, the six-gene dataset did not resolve phylogenetic relationships within the Brilliant. The poor resolution at several nodes, in both Bayesian and Maximum Likelihood inference, precluded us from identifying the closest relatives of *Sternoclyta* and *Hylonympha*. Those limited data suggested a hard polytomy, leading us to conclude that the lack of phylogenetic resolution may not be associated with inadequate taxon-sampling or gene-sampling, but rather an evolutionary process of rapid or near-simultaneous diversification.

The principal goals of this study were (1) to determine the phylogenomic relationships of these two monotypic genera along with all species of the genus *Heliodoxa* and closely related genera, if it would be possible to resolve; and (2) to use the resulting time-calibrated estimates of the hummingbird tree to elucidate biogeographic patterns of diversification. We sought to describe the evolutionary and biogeographical history of this clade that is widely distributed in tropical South America and concentrated in forested montane habitats of the Andean Cordillera. Our focal clade is unique within the Andean radiation of hummingbirds because it is concentrated at relatively low, foothill elevations and it because it appears to contain the only unambiguous instance of a *bona fide* lowland species evolving from within a montane radiation.

METHODS

Taxon Sampling and Laboratory Methods

Tissue samples of three individuals each of *Sternoclyta cyanopectus* and *Hylonympha macrocerca* were obtained in the field and vouchers deposited at the Phelps Ornithological Collection (Table S1).

In addition to the samples obtained in the field, we borrowed 16 tissue subsamples from frozen tissue collections, representing vouchered museum specimens (Table S2), belonging to the *Heliodoxa* and close relatives (11), *Urochroa* (1), *Ocreatus* (1), *Coeligena* (1), *Aglaeactis* (1), and a sample from the Coquette genus *Aglaiocercus*, as an outgroup.

Library preparation and sequencing

We designed the sequence-capture probes for our study by assembling a target file of genetic loci previously used for phylogenetic inference. We extracted rapidly evolving long exons loci (RELEC) (Karin et al., 2020) from the *Calypte anna* genome (Korlach et al., 2017) using Alibaseq (Knyshev et al., 2021). Anchored tag loci (Anchored tags) (Lemmon et al., 2012) for *Archilochus colubris* were taken from (Prum et al., 2015). We also included ultra-conserved elements (UCEs) from *Promerops guryneyi* that were sequenced as additional loci that are used widely in avian phylogenetics. The resulting sequences for these phylogenetic loci, along with additional loci for other projects, were used by Nimblegen (Roche) to design a custom SeqCAP EZ HyperCap sequence-capture kit.

We used the Qiagen DNeasy extraction kit, following the manufacturer's protocol, to extract DNA from each tissue sample. DNA concentrations were quantified using Qubit 4.0 fluorometer (ThermoFisher Scientific). From 0.3 - 2 μg of DNA was diluted with 1x low TE

(10mM Tris, 0.1 mM EDTA) into a final volume of 110 μ L in a sonicator tube. The DNA was sonicated in a qSonica machine typically with the following conditions: pulse = 15 seconds on, 15 seconds off; amplitude = 40%; time = 2.5 minutes of sonication, after which the tube was vortexed and spun down, and then followed by 2.5 minutes more sonication (5 minutes total). The sonication time was reduced for samples with degraded DNA. We then performed a doubled sided bead cleanup (first 0.5x and then 0.65x beads) with low-ratio formula SPRI (Sera-Mag) beads to preferentially select for DNA within the size range of 300-500 bp. Libraries were constructed with a KAPA (Roche) library prep kit using a one quarter reaction size. The libraries were dual indexed with 8 bp indexes. We combined 200 ng of each indexed library into a common pool along with additional hummingbird libraries for other projects. We hybridized 1.1 - 1.3 ug of the pooled DNA to the capture probes for 19 - 72 hours and then performed the capture reaction according the SeqCAP EZ HyperCap protocol. The captured DNA for most of the samples was sequenced on a NovaSeq S1 150 PE lane, with a few samples sequenced on two NovaSeq S4 150 PE lanes along with other samples.

Sequence alignment

We used HTStream v 1.3.3 (HTStream version 1.3.3. <https://github.com/s4hts/HTStream>) to: 1) remove phiX sequences, 2) remove PCR duplicates, 3) remove adapter sequences and merge any overlapping reads, 4) screen out any remaining adapter contamination using a file containing the Illumina adapter sequences, 5) remove low quality bases with a window size of 10 bp and a quality threshold of 20, 6) trim off sequences containing N characters, 7) remove any reads that were smaller than 20 bp, and 8) calculate statistics about the reads and data quality. The cleaned reads were mapped to our target file of sequences using the BWA-MEM 0.7.17-r1188 mapper (Li & Durbin, 2009) Samtools was used to merge, sort, and index the bam files of the mapped reads (Danecek et al., 2021) Picard v. 2.23.4

(<http://broadinstitute.github.io/picard/>) was used to add read groups and GATK v3.6 (McKenna et al., 2010) was used to realign the reads surrounding indels. ANGSD v. 0.933-79-gda26ba4 (Korneliussen et al., 2014) was used to export a consensus sequence in Fasta format for each locus (145 RELEC loci, 239 anchored tag loci, and 2314 UCEs) with a minimum base quality of 20, a minimum mapping quality of 30, a minimum depth of coverage of 3, a maximum depth of coverage of 10000, and an iupacRatio of 0.2. We used FastQC v 0.11.8 (Andrew, 2010) for conducting quality control on the unmapped reads, Qualimap v.2.2.1 (Okonechnikov et al., 2016) to assess the mapped reads, and MultiQC version 1.1 (Ewels et al., 2016) to summarize the results of these programs.

Phylogenetic Analyses

The phylogenetic analyses were conducted at the Center for Advance Research Computing (CARC) at the University of New Mexico.

Phylogenetic hypotheses for the three independent data sets, Anchored tags, RELEC and UCEs, were estimated by Maximum Likelihood using IQ-TREE 2 v.2.2.0 (Minh et al., 2020). The support of the nodes of the resulting tree was obtained by means of an ultrafast bootstrap (UFBoot) with 1000 pseudo-replicas (Hoang et al., 2018).

The partition scheme of the genes and the specific molecular substitution models that best describe the evolutionary scenario of each partition, were selected using ModelFinder in IQ-TREE 2 (Kalyaanamoorthy et al., 2017). For the selection of the models, we used the corrected Bayesian information criterion (BIC) and the relaxed hierarchical clustering algorithm (*rcluster* = 20) to find the best partitions schemes and reduce computation time. To conduct the selection of the models and partitions scheme, the three data matrices were divided into a number of partitions (Anchored Tags = 239; RELEC = 145; UCEs = 2314). To select the tree with the best log likelihood, and higher bootstrap support, we also ran analyses using

concatenated matrices and compare the results with the best partitions scheme and model selected by IQ-TREE.

Molecular Dating Analysis

For the Bayesian phylogenetic inference, we used the three independent data sets, Anchored tags (239 genes), RELEC (245 genes) and for the UCEs data set, we selected randomly two subsets of 100 genes samples each, to reduce computational time and estimation.

The chronology of diversification of true Brilliants, and, in particular, the time of divergence for the genera *Sternoclyta* and *Hylonympha*, were estimated with BEAST 2.5.2 (Bouckaert et al., 2019). We used a lognormal relaxed molecular clock model (UCLN) and default substitution rates (mean and standard deviation) with a normal distribution for a concatenated matrix for each of the data sets. This method was successful for McGuire et al. (2014) who used it to generate times of divergence that were nearly perfectly concordant with the rigorous phylogenomic time-tree of modern birds of (Jarvis et al., 2014); the latter tree used both clock-like substitution rates for exons and 19 fossil calibrations. As selection of time information for the calibration of nodes can increase the accuracy of divergence time estimation (Mello & Schrago, 2014), we added three calibration nodes in the tree based on the phylogenetic hypothesis and divergence times of McGuire et al. (2014); the most recent common ancestor for *Urochroa* and *Heliodoxa*, the most recent common ancestor of the Brilliants, and the most recent common ancestor of the Coquettes and Brilliants (Table 1).

We ran two independent analyses for 50 million generations each, taking samples every 10,000 generations, obtaining a total of 5,000 final trees per run. To evaluate the convergence and stability of the analysis, we used the Tracer v.1.7 (Rambaut et al., 2018). We combined the two independent runs using LogCombiner (Bouckaert et al., 2019) and we discard the first

1000 trees (10% burn-in) and summarize our results in a tree of maximum credibility using the TreeAnnotator program v.2.5.2 (Bouckaert et al. 2019).

Ancestral Elevation Estimates

To estimate the evolutionary history of elevational ranges across the brilliants clade, we spliced our maximum clade credibility trees for the true brilliants and relatives together with the more comprehensively sampled time tree of McGuire et al. (2014), and we did so for both strongly supported topological variants from our phylogenomic results. We compiled minimum and maximum elevation ranges from field guides discarding uncommon or rare observations (Hilty, 2003; McMullan & Donegan, 2014; Renner & Schuchmann, 2004; Schulenberg et al., 2010). We input elevational range data and the maximum clade credibility trees into the *fastAnc()* function from the R package Phytools (Revell, 2017) to estimate the ancestral minimum and maximum elevation ranges of the Brilliants. This function performs ancestral state estimation using maximum likelihood by re-rooting the tree at each internal node and computing the contrasts for the new root following Felsenstein 1985. We generated phenograms for lower and upper range limit reconstructions in Phytools from their respective ancestral state reconstructions (Revell, 2017). Phenograms distort phylogenetic trees by constraining node position along a reconstructed character axis of a continuous trait.

Ancestral Biogeographic Estimates

We compiled the range descriptions from field guides (Hilty, 2003; McMullan & Donegan, 2014; Renner & Schuchmann, 2004; Schulenberg et al., 2010). which we vetted and adjusted with expert knowledge (personal communication, J. Pérez & C. Witt) to bin each Brilliant taxa into one or more of eight biogeographic regions defined for our analyses: Amazonia, Brazilian Shield + Atlantic Forest, Central America, Low Andes (< 1500 m), High Andes (> 1500 m),

Pantepui, Cordillera de la Costa, and Peninsula de Paria. We estimated the ancestral biogeographic states on maximum clade credibility trees with minor topological conflicts (RELEC & UCEs) using the R packages BioGeoBEARS (Matzke, 2013). Because previous work has shown that BioGeoBEARS default null range can underestimate local extinction and lead to unrealistic ancestral range estimates (Massana et al., 2015), we chose to prohibit transitions into the null range in our model sets. We ran a total of six models (DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, and BAYAREALIKE+J), and present the best models based on model comparisons with AICc (Tables 3 and 4). The +J models allow instantaneous transitions into previously unoccupied ranges. Though some work criticizes the ‘j’, or jump models (specifically DEC+J), for unrealistically representing founder event speciation and artificially inflating the contribution of the j parameter while underestimating dispersal and extinction parameters (Ree & Sanmartín, 2018), we opted to include models with the parameter, as it is the only available way to model range switching in this framework. Furthermore, it is not unreasonable to assume hummingbird lineages could speciate following long distance dispersal events or evolutionarily rapid vicariance events not captured on the timescales of the phylogenies.

We performed model selection using AICc on the six models for each topology. From the top supported model for each topology, we calculated ML state probabilities for each biogeographic range at each internal node on both topologies in BioGeoBEARS (Matzke 2013).

RESULTS

We obtained a total of 2,320,940 base pairs for each of the 18 taxa included in this study. The sequences representing 2698 loci for each taxon were organized in three data sets: Anchored tag loci (Anchored tag) with 239 nuclear genes, rapidly evolving long exons loci (RELEC) with 145 exons, and 2314 ultra-conserved elements (UCEs) (Table 2).

For the Maximum Likelihood tree estimation, the number of partitions estimated by IQ-TREE for each data set, were: Anchored tags, from 239 original partitions to 19 final partitions. For RELEC were 21 partitions from 145, and for the UCEs were 22 final partitions from 2314. The average best-fit model for Anchored tags was HKY + F + R2. The most common model selected as a best-fit for the RELEC loci was TVM + F + R3 and TM2 + F + R3. For the UCEs was HKY + F + R2 and TVM + F.

The monotypic genera *Sternoclyta* and *Hylonympha* were confirmed to be *Brilliantis* and formed a monophyletic group with the members of the larger *Heliodoxa* clade, to the exclusion of *Urochroa*, with high bootstrap support (100%) and posterior probabilities (1.00). This was true regardless of the methods of phylogenetic reconstruction (Figure 1–2) and the data set used. The genus *Urochroa* was strongly supported (100% bootstrap and a posterior probability equal to 1) as the sister taxon of the *Heliodoxa* clade in all the trees, regardless of the phylogenetic approach used. Considering that the name of the tribe, *Brilliantis*, arose from the common name of the species that belong to the genus *Heliodoxa* (Bleiweiss et al. 1997), we will call this clade that contains the common ancestor of *Urochroa* and *Heliodoxa* and all of its descendants the *True Brilliantis* to differentiate them from the remainder of the species in the *Brilliantis* tribe.

The reconstruction of the phylogenetic relationships among the species that comprise the clade of the *True Brilliantis* was generally consistent across methods and datasets. However,

the nodes associated with the clade comprised by *H. imperatrix*, *H. rubinoides*, and *H. leadbeateri* with *H. jacula*, were inconsistently resolved (Figures 1–2) because the UCE data, in comparison with other data subsets, supported a topology that flipped the relative positions of *H. imperatrix* and *H. rubinoides*.

Bayesian analyses strongly supported three subclades within the True Brilliants clade using RELEC Anchored tags and UCEs data set (Figure 2). One clade comprised by *Heliodoxa rubricauda* and *H. aurescens* with a posterior probability of 1 for all data sets. A second clade comprised by *H. xanthogonys*, *H. branickii* and *H. gularis* as a sister clade of *Sternoclyta cyanopectus*, with a posterior probability of 1, with the species *Hylonympha macrocerca* as the sister taxon for all of the complete data sets; only the first subset of 100 UCEs resulted in a different topology, in which *Hylonympha* was the sister taxa to rest of the true Brilliants with a posterior probability of 1. The third clade was comprised of *H. schreibersii*, *Heliodoxa rubricauda*, *H. aurescens*, *H. rubinoides*, *H. imperatrix*, *H. leadbeateri*, *H. jacula*, where the topology and posterior probability differed only subtly between the data sets. With Anchored tags and RELEC, *Heliodoxa imperatrix*, was the sister taxa to the clade comprised by *Heliodoxa leadbeateri* and *Heliodoxa jacula*, and *Heliodoxa rubinoides* was the sister taxon to this group. With the two UCEs subsets, *Heliodoxa rubinoides* was the sister taxa of the clade *Heliodoxa leadbeateri* and *Heliodoxa jacula*, and *Heliodoxa imperatrix* was the closest related taxon to this group; however, the posterior probability of the nodes involved in this alternative arrangement was lower than 1 in both subsets; with such a large dataset, low nodal support suggests conflicting signals within the data, and possibly low phylogenetic signal overall in subsets of only 100 conserved loci.

With a Maximum Likelihood approach, we found a similar topology to that which we found with Bayesian analyses (Figure 1). We found support for the three main clades (higher than 98%) using each of the three data sets. The relationships among *Hylonympha macrocerca*,

Sternoclyta cyanopectus, *Heliodoxa gularis*, *Heliodoxa branickii*, and *Heliodoxa xanthogonys* were consistent in all topologies recovered. With all of the UCE loci in the same analysis (2314), *Heliodoxa rubinoides* was the sister taxon of the clade *Heliodoxa leadbeateri* and *Heliodoxa jacula*, and *Heliodoxa imperatrix* was the sister taxon to this group, albeit with a bootstrap support lower than 95%, similar to the results obtained with UCEs under the Bayesian analysis. The best-fit substitution models for the concatenated matrices, based on the BIC (Bayesian inference criteria) were: Anchored tags, TVM+F+I+R3; RELEC, GTR+F+I+R3 and for UCEs, TVM+F+I+R7.

The node that linked *Hylonympha macrocerca* and the group comprised of *Sternoclyta cyanopectus*, *Heliodoxa gularis* and *Heliodoxa branickii*, also had a relatively low agreement among the topologies of individual gene trees for each data set. A partition including these four species appeared in 14.2% of the Anchored tags loci (34 out of 239 genes), in 29.7% of the RELEC exons (43 out of 145 genes) and in 1.69% of all UCEs (39 out of 2314 genes).

The estimation of the divergence times was relatively consistent in all data sets (Figure 2; Figure S1, Figure S2). The most recent common ancestor of the True Brilliants clade occurred ~9 Mya. The *Sternoclyta* genus has been evolving independently for ~7 Ma., and *Hylonympha* for ~8 Ma. Most of the early divergence times within the true Brilliants clade were within the Late Miocene (Figure 2). The nodes ages estimated using the subset 2 of the UCEs differed only slightly from those of the other data sets.

Ancestral state reconstructions estimated that a downward range expansion of ~350-449 meters occurred near the base of the True Brilliants excluding *Urochroa*. Reconstructions estimated the ancestor of the Brilliants to inhabit a minimum elevation of between 1170 (671-1668 m 95% CI, RELEC) and 1248 meters (722-1773 m 95% CI, UCE); but this minimum elevation evolved downward to between 799 meters (346-1253 m 95% CI, UCE) and 820

meters (390 -1250 m 95% CI, RELEC) at the base of the True Brilliants excluding *Urochroa*. The common ancestor of True Brilliants including *Urochroa* was estimated to inhabit elevations above 919 meters (436-1403 m 95% CI) and below 2332 meters (1695-2969 m 95% CI).

Model selection using AICc unanimously selected the BAYREALIKE model as the best fit for MCC trees (Tables 3, Table 4). The top model for both MCC topologies estimated that the MRCA of the Brilliants inhabited the high Andes (above 1500 m) with a probability of > 0.99 (Figures 3-4). The model for both topologies estimated dispersal at 0.01 events per million years and extinction, or range contraction, much higher at 0.146 (RELEC) and 0.148 (UCE) events per million years. Both topologies and models supported an abrupt downslope expansion at the split between *Urochroa* and the remaining members of the True Brilliants clade. At this node the estimated probability the ancestor to the True Brilliants inhabited the low Andes increased from 0.14 (RELEC) and 0.09 (UCE) to 0.39 (RELEC) and 0.22 (UCE), while the probability of inhabiting the high Andes remained strong at approximately 0.99 for both topologies. The probability of inhabiting a low Andean range dramatically increases after again *Urochroa* split from the remaining True Brilliants to ~ 0.93 (RELEC & UCE). Following the downslope shift of True Brilliants excluding *Urochroa*, the model supports an out-of-Andes colonization pattern with independent colonizations of the Pantepui, Peninsula de Paria, Brazilian Shield/Atlantic Forest, Amazonia, and Central American regions (Figure 3).

DISCUSSION

The phylogenetic hypothesis of the clade of the true Brilliants resulting from this study, together with the current distribution of each of its species and the reconstructions of the historical South American landscape, allows elaboration of an evolutionary and biogeographic

scenario for this group of species. Our phylogenetic hypothesis suggests a rapid diversification between the end of the Middle Miocene and the beginning of the Late Miocene (11–5 Mya). In fact, the first few cladogenic events within this clade, including those that led to the genera *Sternoclyta* and *Hylonympha*, were estimated to have occurred between 6 and 8 Ma. During this time, the uplift of the Andes occurred at its highest pace, creating new montane habitats throughout the regions bordering the Amazon, Orinoco, and Magdalena basins, along the flanks of the Andes, including the northeastern-most outlying Andean ridges.

The uplift of the Central Andean Plateau was most intense during the Middle Miocene and Early Miocene; and Pliocene uplift also proceeded, particularly in the Northern Andes (Garzzone et al., 2008; Gregory-Wodzicki, 2000). The final stage of these changes was at the end of the Pliocene with the final elevation of the Eastern Andes of Colombia and the Venezuelan Andes (Bermúdez et al., 2017). The increase in the elevation of this mountain chain resulted in environmental, topographic changes, restructuring of drainage systems and greater erosion and sediment deposition in the Amazon basin, changes that led to the disappearance of a large lake system (Lake Pebas), and later fluvial (Acre system) that represented a potential barrier for the movement of organisms between the Andes and montane systems of Guyana and southeastern Brazil (Mata Atlántica) (Hoorn et al., 2010; Fouquet et al., 2014). This era was also characterized by environmental changes (subsequent to the Middle Miocene climate optimum, MMCO) described by climate cooling and periods of seasonality, potentially associated with extinction events (Fouquet et al., 2014; Zachos et al., 2001). These geographic and climatic events in the region may have increased the processes of diversification, extinction, and dispersal associated with the isolation of widely distributed populations (Elias et al., 2009), in addition to the dispersion associated with the availability of new resources and habitats.

The temporal and spatial framework of the evolution of the Trochilidae family coincided with the orogenic dynamics of the Andes. Hummingbirds were already present (around 22 Ma ago) in South America at the time of the largest uprising in the Central and Northern Andes (McGuire et al., 2014). In fact, it is hypothesized that the ancestor of hummingbirds was associated with lowland environments and that, from there, it colonized montane environments, which promoted their diversification during the Late Miocene (Bleiweiss, 1998; McGuire et al., 2007; McGuire et al., 2014).

Based on our results, the common ancestor of the True Brilliants, could have occupied foothill areas in the Andes, diversify out of the Andes, and colonize adjacent regions. The rising of the Andes and the disappearance of the Amazon lacustrine/ fluvial system could have promoted the dispersion of populations of a common ancestor of the group, either throughout the Andes or through the Amazon basin, colonizing areas on the periphery of its distribution (Mata Atlántica in Brazil, high areas of Guyana). Phylogenetic and distribution patterns in plants (Antonelli et al., 2009) and butterflies (Elias et al., 2009) are consistent with this biogeographic scenario. The previous connectivity of the Atlantic forests and Amazon forests during the Middle Miocene, suggested for several groups of organisms, including birds (Batalha-Filho et al., 2013) may have facilitated the dispersal of the common ancestor of *Heliodoxa rubricauda* and *Heliodoxa aurescens* and their subsequent differentiation associated with environmental changes at the global and regional level during the Late Miocene (Fouquet et al., 2014). A similar biogeographic scenario can be considered for the common ancestor of the *H. xanthogonys* species (present in the Pantepui Region) and the sister species, *H. gularis* and *H. branicki*. The disjointed distribution pattern exemplified by these species is similar to that found for the sister anthill species (Thamnophilidae) of the genus *Thamnophilus*, *T. divisorius*, endemic to the Sierra del Divisor on the border between Acre (Brazil) and Peru, and *T. insignis*, endemic to the Pantepui Region (Brumfield & Edwards, 2007).

In light of the new phylogenetic evidence, the origin of the current distribution of *Sternoclyta cyanopectus* and *Hylonympha macrocerca* can be inferred. The elevation and expansion of the Andes during the Late Miocene could allow dispersal (and potential differentiation) to the north of Venezuela. However, although the eastern Andes of Colombia and Venezuela finished rising during the late Miocene and Pliocene, the Cordillera de la Costa (Central and Oriental) seems to have had an earlier origin (Hoorn et al., 1995; Hung, 2005) since the Oligocene to Miocene.

Therefore, a first hypothesis would be the colonization of the north of Venezuela along the Andes corridor. A second possibility would be a dispersal throughout the Amazon basin (considering the changes in the circulation patterns of the main rivers, including the Orinoco; Hoorn et al., 1995; Hoorn et al., 2010). Renner and Schuchmann (2004) favor the first hypothesis by suggesting that Pleistocene climate changes were responsible for generating the dispersal and vicariance opportunities that generated the current diversity in this group of Brilliantes. However, this hypothesis fails in its time frame, considering that our results suggest that the origin of *Sternoclyta* and *Hylonympha* is during the Miocene, which offers a totally different landscape as a spatial context of group differentiation, in addition to considering an erroneous phylogenetic hypothesis.

Heliodoxa schreibersii and *Heliodoxa whitelyana* presents a distribution in the Andean foothills and low areas close to the Amazonas region, that could have had a similar origin to the ancestor of *H. aurescens* and *H. rubricauda*. This species complex presents a fragmented distribution in the Andes with a pattern similar to *H. gularis* and *H. branicki*. This distribution pattern, on the same slopes of the Andes, can be the product of historical changes in habitat conditions throughout its distribution, so we suggest evaluating the genetic differentiation of these populations.

The group that occupies the highest elevation areas, which includes the species *H. leadbeateri*, *H. jacula*, *H. rubinoides* and *H. imperatrix* would occupy the available habitats due to the new latitudinal extension of the Andes (as well as altitudinal) and would see its fragmentation potentially populations once those from the North completed their uprising at the end of the Pliocene. A pattern of south to north colonization is represented in the evolutionary history of *Adelomyia*, as well as the treeline clade of *Metallura*, hummingbird clades from the Coquette tribe whose diversification occurred over a similar time frame to the one we are evaluating here (Benham et al., 2015; Chaves et al., 2011). On the other hand, the rising of the Andes could cause the fragmentation of the populations of the ancestor of *H. rubinoides* and *H. imperatrix* and of *H. leadbeateri* and *H. jacula*, leaving a population with greater representation on the Pacific slope of the Andes (Chocó) and another mainly in the central and eastern chains of the Andes. This biogeographic scenario should be evaluated with an exhaustive sampling of the phylogeographic patterns of these species, given their wide distribution and the sympatric patterns that characterize them in some areas of their distribution.

CONCLUSIONS

The True Brilliants are nested within a large radiation of Andean hummingbirds, but they represent a secondarily low elevation clade, whose center of abundance is in the foothill, or upper tropical zone. The assignment of two enigmatic northern South American genera to this clade reaffirms this pattern and illustrates how phylogenetic connections link disparate mountain ranges of the Neotropics, hinting at previously continuous highland habitats, or trans-lowland dispersal during cold climate periods. The True Brilliants clade exhibits a relictual, circum-Andean distribution, with its only true lowland species, *H. aurescens*, a true anomaly

among hummingbirds: a secondarily lowland species that has succeeded in the megadiverse tropical rainforests of the Amazon Basin.

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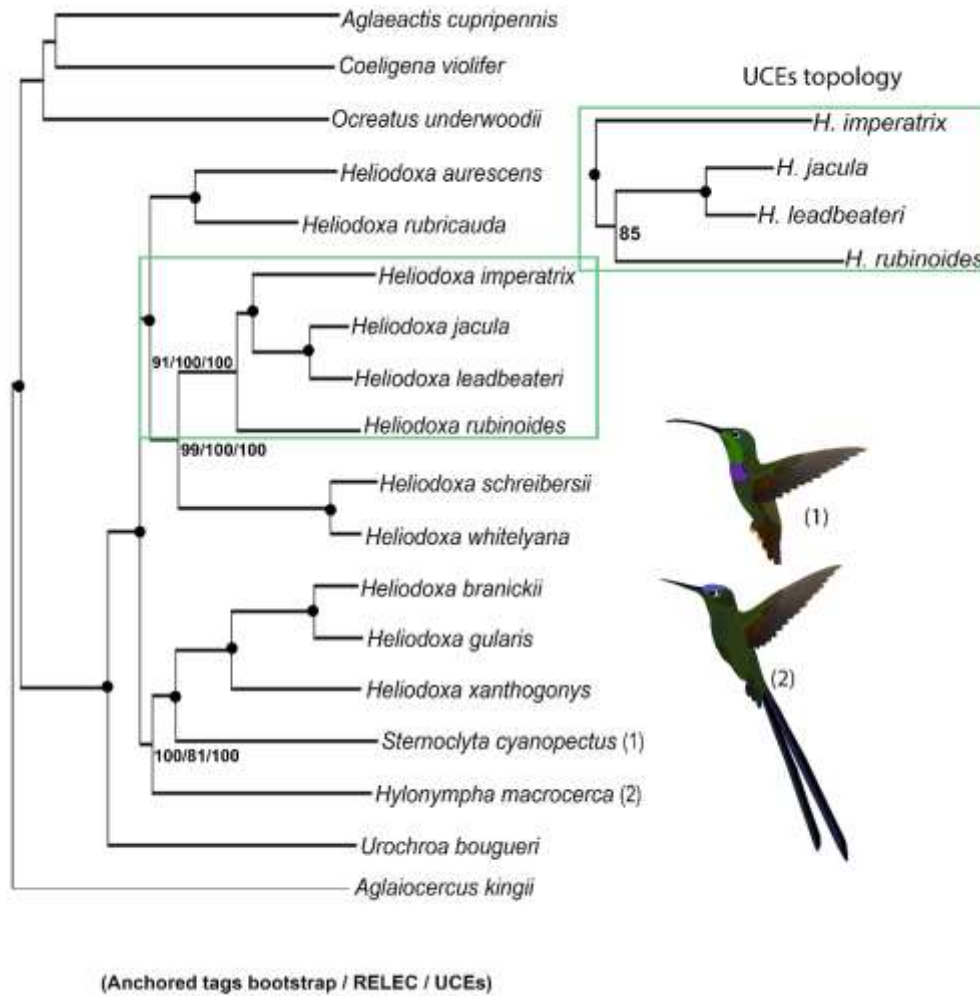


Figure 1. Phylogenetic hypotheses obtained in the maximum likelihood analysis using IQ-TREE 2 using the three data sets: Anchored tags, RELEC and UCEs. Black circles at the nodes correspond to the bootstrap values equal to 100. Values associate to the nodes represent bootstrap values lower than 100. The zoom-in clade, is the only difference in the topology of the tree reconstructed using the UCEs data set. In the figure, the illustrations of the males of *Sternoclyta cyanopectus* and *Hylonympha macrocerca*. The topology of the tree recovers the split of three groups: *H. aurescens* and *H. rubricauda*. *Sternoclyta cyanopectus*, *H. branickii*, *H. gularis*, *H. xanthogonys* and *Hylonympha macrocerca* clade and the group conform by *H. rubinoides*, *H. imperatrix*, *H. leadbeateri*, and *H. jacula*. The three data sets support the monophyly of the the novel clade true Brilliants, with the inclusion of the monotypic genera *Sternoclyta cyanopectus* and *Hylonympha macrocerca*

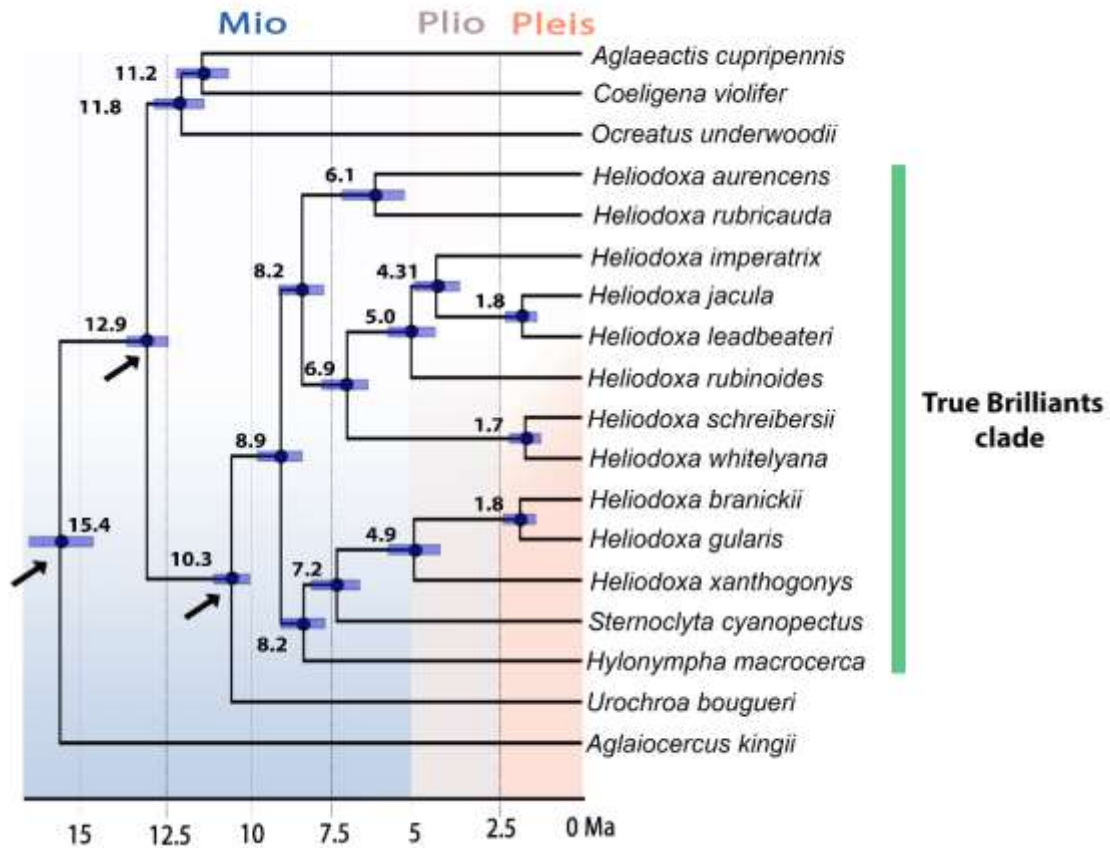


Figure 2. Divergence times tree and phylogenetic relationships with Anchoed tags and RELEC obtained by BEAST. The bars in the nodes represent the 95% highest posterior density (HPD) confidence intervals of the divergence time and the values associate with the nodes are the divergence times obtained by the Anchoed tags data set (the divergence times were relative consistent for all data set, see supplemental Figure S1 and Figure S2 for more details). Black circle in the nodes of the trees, represent the posterior probabilities = 1. The scale shows the time (and geological periods) in millions of years (Ma): Mio: Miocene; Plio: Pliocene; Pleis: Pleistocene. Arrow in the tree, represent the three calibration point nodes.

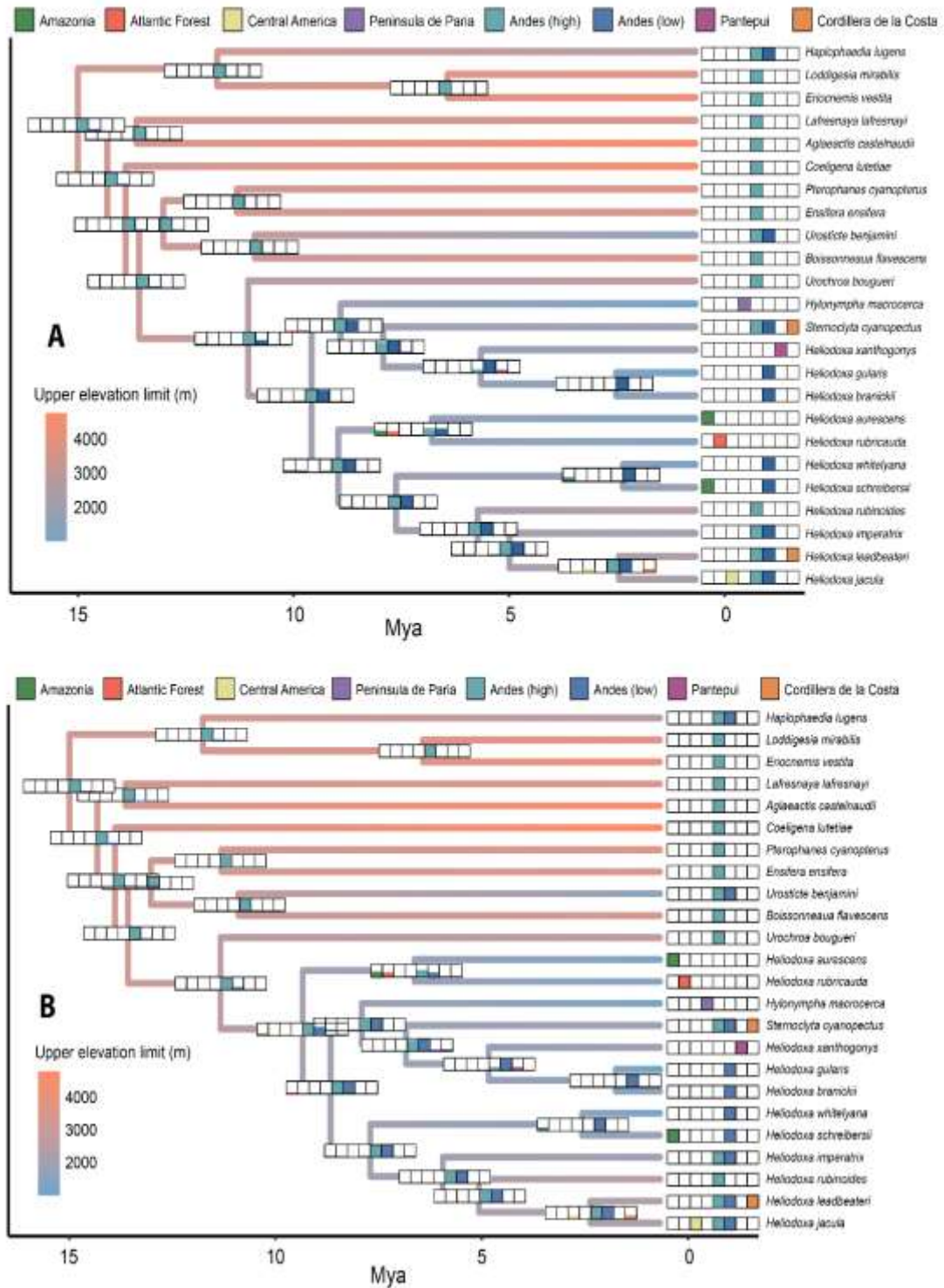


Figure 3. Biogeographic and elevational reconstructions of the Brilliants from top-supported BAYAREALIKE models for two topologically inconsistent MCC trees generated from RELEC (A) and UCE (B) markers. Boxes at internal nodes show probability of occupancy in a given range as proportion of squares filled with corresponding range color. Boxes at the tips of the tree show current distribution in eight biogeographic areas. The tree is colored by reconstructed upper elevation limit using the Phytools functions *fasAnc()* and *contMap()*.

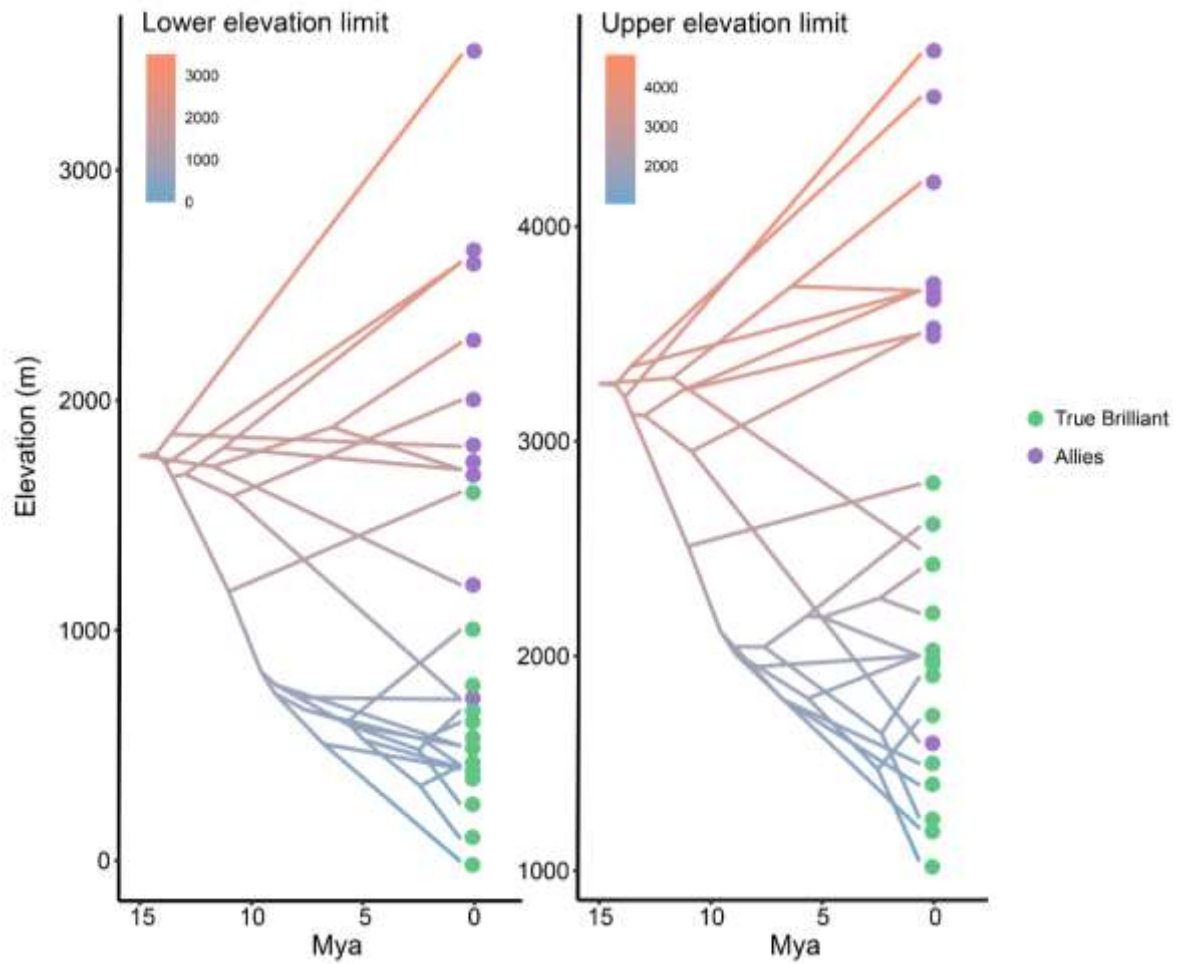


Figure 4. Phenograms mapping modern and reconstructed lower (left panel) and upper (right panel) elevation limits through time on the RELEC tree using the Phytools function *fastAnc()*, and the *ggtree* plotting function, *ggtree()*, which distorts the tree shape by anchoring nodes at their modern or reconstructed trait values along a trait axis. The trees are also colored by elevation limit to emphasize elevation changes through time. The tips are colored to show the elevation conservatism and shift of the True Brilliants (green) relative to broader Brilliants (purple).

Table 1. Values (parameters) and their distributions used as calibration points to estimate the divergence times.

Node	Parameters	Reference
Common ancestor of <i>Urochroa</i> and <i>Heliodoxa</i> species	Normal distribution Mean = 11 SD = 0.35 Range = 11 - 13 Mya Distribution center in 11.6 Mya	McGuire et al., 2014.
Common ancestor of the <i>Brilliant</i> s.	Normal distribution Mean = 12 SD = 0.5 Range = 11.23- 13.7 Mya Distribution center in 12.3 Mya	McGuire et al., 2014.
Common ancestor of the <i>Brilliant</i> s and the <i>Coquette</i> s.	Normal distribution Mean = 15 SD = 0.5 Range = 14.4 - 16 Mya Distribution center in 14.6 Mya	McGuire et al., 2014.

Table 2. Total genes, base pairs, and matrices used in this study. The parameters were estimated using IQ-TREE 2 as part of the phylogenetic estimation of Maximum Likelihood.

Matrix	Genes	Base pairs (bp)	Constant	Constant (%)	Variable	Variable (%)	Number of Parsimony informative sites (Pinf)	Pinf (%)	Number of distinct site patterns
Anchored tags	239	361956	344338	95.13	17618	4.8	5087	1.14	6778
RELEC	145	498234	458304	91.98	39930	8.01	11072	2.22	10296
UCEs	2314	1460750	1439700	98.56	21050	1.44	4429	0.30	27206

Table 3. Model Selection using AICc for the biogeographic model of diversification, based on the Relec-loci, time-calibrated topology estimated in Beast.

Model	Log likelihood	Number of parameters	Dispersal	Extinction	Jump	AICc	AICc weight
BAYAREALIKE	-58.82	2	0.010	0.146	0.000	122.216	0.765
BAYAREALIKE+J	-58.70	3	0.007	0.106	0.007	124.599	0.232
DEC	-64.92	2	0.017	0.204	0.00	134.414	0.002
DEC+J	-64.92	3	0.017	0.204	1.00E ⁻⁰⁵	137.044	0.000
DIVALIKE	-66.58	2	0.018	0.227	0.000	137.733	0.000
DIVALIKE+J	-66.58	3	0.018	0.227	1.00E ⁻⁰⁵	140.362	0.000

Table 4. Model Selection using AICc for the biogeographic model of diversification, based on the UCE-loci, time-calibrated topology estimated in Beast.

Model	Log likelihood	Number of parameters	Dispersal	Extinction	Jump	AICc	AICc weight
BAYAREALIKE	-58.90	2	0.010	0.148	0.000	122.4	0.751
BAYAREALIKE+J	-58.70	3	0.007	0.101	0.009	124.6	0.246
DEC	-64.70	2	0.016	0.189	0.000	134.0	0.002
DEC+J	-64.70	3	0.016	0.185	1.00E ⁻⁰⁵	136.6	0.001
DIVALIKE	-66.41	2	0.018	0.215	0.000	137.4	0.000
DIVALIKE+J	-66.41	3	0.018	0.215	1.00E ⁻⁰⁵	140.0	0.000

SUPPLEMENTARY MATERIALS

Table S1. Specimen ID, localities and collection's name for the samples collected for this study. LBCA = Laboratorio de Biología y Conservación de Aves, Instituto de Ecología y Zoología Tropical. COP = Colección Ornitológica Phelps. Samples collected under the project "Distribución e historia natural de aves del Macizo Montañoso del Turimiquire y de la Península de Paria", permission number 578, October, 2016. Mark in bold the samples selected specifically for this study.

Species	ID	Locality	Collection
<i>Sternoclyta</i>	JM69	P.N. Henri Pittier; Estación Biológica Rancho Grande; Vía	LBCA
<i>cyanopterus</i>		La Toma; Aragua; Venezuela.	
<i>Sternoclyta</i>	JM28	P.N. Tigua; Carretera Nirgua-La Florida; Yaracuy-Cojedes;	LBCA
<i>cyanopterus</i>	9	Venezuela.	
<i>Sternoclyta</i>	IC98	P.N. Sierra de San Luis; Cerro Galicia; Falcón; Venezuela	COP
<i>cyanopterus</i>	4		
<i>Hylonympha</i>	HM0	P.N. Península de Paria; Las Melenas; Sucre; Venezuela.	COP
<i>macrocerca</i>	1		
<i>Hylonympha</i>	HM0	P.N. Península de Paria; Las Melenas; Sucre; Venezuela.	COP
<i>macrocerca</i>	2		
<i>Hylonympha</i>	HM0	P.N. Península de Paria; Las Melenas; Sucre; Venezuela.	COP
<i>macrocerca</i>	3		

Table S2. Specimen ID, localities and collection's name for the samples selected for this study. FMNH = Field Museum of Natural History; LSU = Louisiana Museum of Natural History; MSB = Museum of Southwestern Biology; ZMUC = Zoological Museum University of Copenhagen; MVZ = Museum of Vertebrate Zoology.

Species	ID	Locality	Collection
<i>Heliodoxa rubricauda</i>	395405	Sao Paulo; Boraceia, Brasil	FMNH
<i>Heliodoxa jacula</i>	B11940	Esmeralda Province, Ecuador.	LSU
<i>Heliodoxa leadbeateri</i>	36134	Alto Biavo, 2.7 km south of Plataforma; Bella Vista; San Martin, Peru.	MSB
<i>Heliodoxa rubinoides</i>	B01651	Pasco Department, Peru.	LSU
<i>Heliodoxa whitelyana</i>	B2009	Pasco Department; Puellas; Km 41 on Villa Rica - Puerto Bermudez highway, Peru.	LSU
<i>Heliodoxa schreibersii</i>	B05440	San Martin Department, Peru.	LSU
<i>Heliodoxa xanthogonys</i>	B7415	La Neblina, Estado Amazonas, Venezuela.	LSU
<i>Heliodoxa aurescens</i>	36386	Cusco; Quespicanchis; Camanti, Peru.	MSB
<i>Heliodoxa branickii</i>	B1996	Pasco Department, Peru.	LSU
<i>Heliodoxa gularis</i>	B5428	San Martin Department, Peru.	LSU
<i>Heliodoxa imperatrix</i>	B12088	Pichincha Province, Ecuador.	LSU
<i>Urochroa bougueri</i>	128083	Near Junin; Imbabura, Ecuador.	ZMUC
<i>Aglaeactis cupripennis</i>	183221	1.1 km W Puente Carrizales, Junin, Peru.	MVZ
<i>Coeligena violifer</i>	183228	1.1 km W Puente Carrizales, Junin, Peru.	MVZ

<i>Ocreatus</i>	B22594	La Paz Department, Bolivia.	LSU
<i>underwoodii</i>			

<i>Agelaiocercus kingii</i>	183274	2.3 km W Calabaza, Junin, Peru.	MVZ
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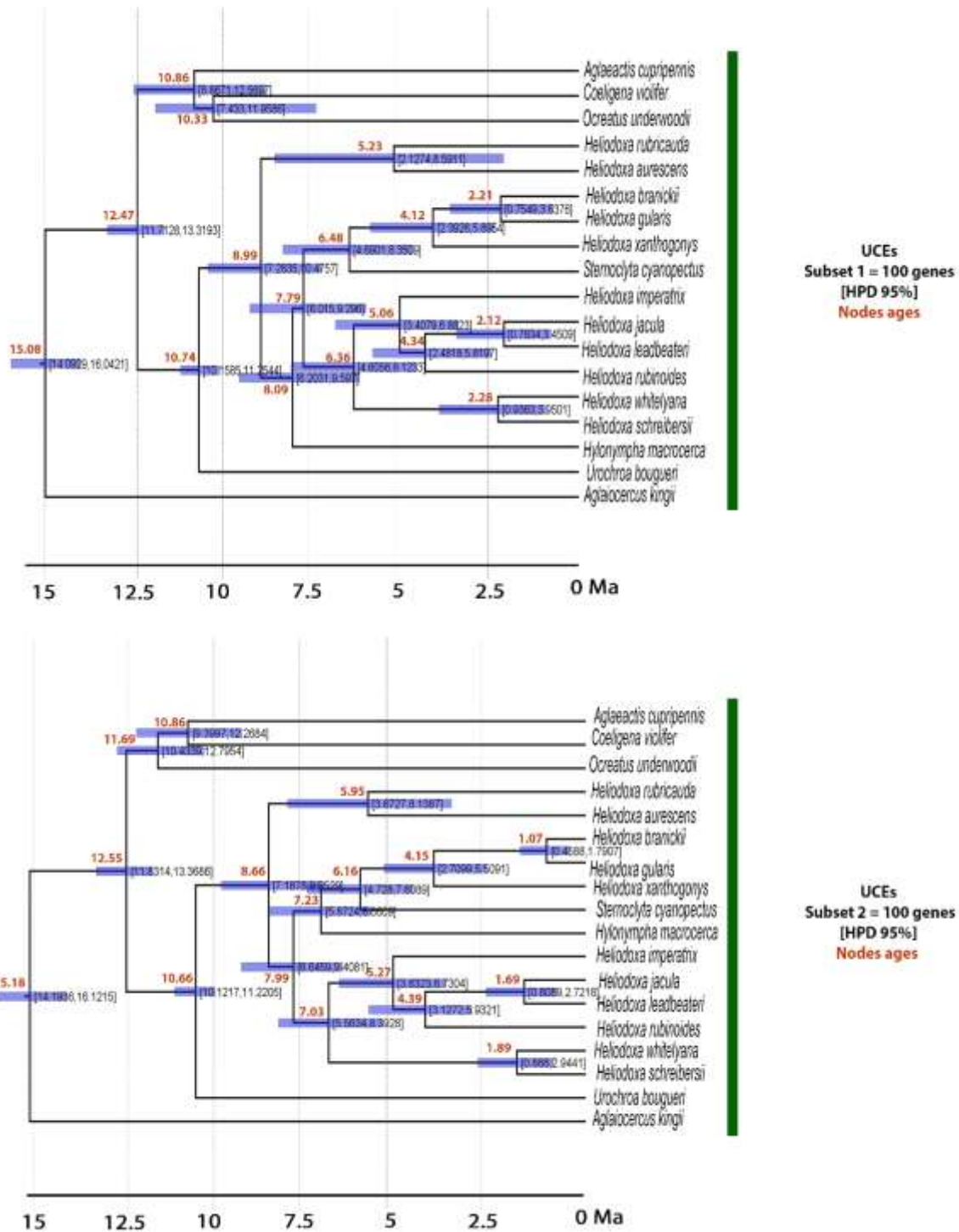


Figure S1. Divergence times tree and phylogenetic relationships with Anchored tags and RELEC obtained by BEAST. The bars in the nodes represent the 95% highest posterior density (HPD) confidence intervals of the divergence time and the values associate with the nodes are the divergence.