# Diversification patterns in the North Andean Block: a perspective from biogeographical hypotheses

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*To my parents, Beatriz Ortiz S. and Jose Ayus R., for their love and by its support throughout my life.*

*To my sister, Daniela Ayus O., the person who has helped me to be stronger.*

*To Edward Rueda D. by its support in difficult times.*

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# Abstract

**TITLE:** DIVERSIFICATION PATTERNS IN THE NORTH ANDEAN BLOCK: A PERSPECTIVE FROM BIOGEOGRAPHICAL HYPOTHESES*

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**KET WORDS:** DIVERSIFICATION, ANDES, BIOGEOGRAPHY, DISPERSAL-VICARIANCE ANALYSIS, HYPOTHESIS TESTS.

We used 637 species from six taxonomic classes to identify the pattern(s) of diversification, occurring in the North Andean Block estimating phylogenetic relationships, divergence times, dispersal-vicariance events, and ancestral distributions. We assessed four hypotheses that explain the diversification in the NAB. For each hypothesis we specified: three sets of unequal rates of dispersal between areas and a temporal stratification, containing four-time intervals for the Miocene. The North Andean taxa showed three ancestral distributions such as the Amazonian region, Central America, and Central Andes where we recovered the major dispersal events. The pattern from North Andean Cordilleras to lowlands fit better the diversification inside the NAB. However, according to the smaller log-likelihood deltas obtained between hypotheses, the taxa followed two patterns, from lowlands to highlands and *vice-versa*. We found seven out of 15 groups that diversified at the rhythm of the North Andean uplift showing different times to reach each Cordillera. The south-to-north pattern was supported by 80% of the groups. Furthermore, exchanges between South and Central America were identified occurring between 15 to 10 Ma. The two altitudinal patterns from lowlands to North Andean Cordilleras and *vice-versa* are plausible regardless the ancestral area estimated, and these patterns occurred multiple times in the same temporal frame (Miocene). However, the pattern from North Andean Cordilleras to lowlands fit better which might support a highlands origin inside or outside the NAB. Finally, the North Andean taxa followed the mountain building scenario, where the Central Cordillera raised first, later the Western Cordillera, and last the Eastern Cordillera.

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*Bachelor Thesis

**Facultad de Ciencias. Escuela de Biología. Director: Daniel R. Miranda-Esquivel, PhD. En Ciencias Naturales.

# Resumen

**TÍTULO:** PATRONES DE DIVERSIFICACIÓN EN EL BLOQUE NORTE DE LOS ANDES: UNA PERSPECTIVA DESDE LAS HIPOTESIS BIOGEOGRÁFICAS*

**AUTOR:** VIVIANA LIZETH AYUS ORTIZ**

**PALABRAS CLAVES:** DIVERSIFICACIÓN, ANDES, BIOGEOGRAFÍA, ANÁLISIS DE DISPERSIÓN -VICARIANZA, TEST DE HIPÓTESIS.

Utilizamos 637 especies pertenecientes a seis clases taxonómicas para identificar el/los patrones de diversificación en el Bloque Norte de los Andes (BNA), estimando relaciones filogenéticas, tiempos de divergencia, eventos de dispersión y vicarianza y distribuciones ancestrales. Evaluamos cuatro hipótesis que explican la diversificación en el BNA, cada una con tres matrices de dispersión diferentes y una estratificación temporal para el Mioceno. Como distribución ancestral obtuvimos áreas adyacentes tales como Amazonas, Centroamérica y Andes Centrales en las cuales recuperamos la mayor proporción de eventos de dispersión. El patrón de Cordilleras hacia tierras bajas ajusta mejor a la diversificación dentro del BNA. Sin embargo, de acuerdo a los deltas de log-likekihood entre hipótesis, los *taxa* siguen ambos patrones, de tierras bajas a tierras altas y viceversa. Encontramos siete grupos que diversifican al ritmo del levantamiento Andino mostrando diferentes tiempos para alcanzar cada Cordillera. El 80% de los grupos soportan el patrón Sur-Norte. Además, identificamos pasos desde y hacia Sur y Centroamérica entre 15-10Ma. Los dos patrones, tierras bajas hacia Cordilleras del BNA y viceversa, son plausibles independientemente del área ancestral estimada, y pueden encontrarse varias veces en el mismo marco temporal (Mioceno). Sin embargo, el patrón de Cordilleras del BNA hacia tierras bajas ajusta mejor, lo que podría apoyar un origen en tierras altas dentro o fuera de la NAB. Por último, los *taxa* del BNA siguieron el escenario del levantamiento Andino, donde el orden de levantamiento es: Cordillera Central, Cordillera Occidental y finalmente la Cordillera Oriental.

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*Trabajo de Grado

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# Introduction

The North Andean Block (NAB) is located in the Neotropical region and is characterised for containing a high number of species (Myers *et al.*, 2000; Pennington *et al.*, 2004). Geologically, it is defined as a tectonic microplate (Kellogg *et al.*, 1995; Bird, 2003) located between the Nazca, the Caribbean, and South American plates (Bird, 2003). The northern and southern boundaries of the NAB are subduction zones (Collot *et al.*, 2002), to the east, it is a fault system (Freymueller *et al.*, 1993; Bird, 2003), and to the west, it extends to the union of the Caribbean and Panama plates (Bird, 2003). This block extents from Ecuador to Colombia– Venezuela, and generally is subdivided into three mountain systems: the Western, Central and Eastern Cordilleras including the Merida Andes (Bird, 2003, but see Audemard and Audemard 2002). The uplift of the three Cordilleras is divided into two periods with different geological history for each time frame (Gregory-Wodzicki, 2000). The initial period took place from the Oligocene to early Miocene (~23 Ma) and the second period from the late Miocene (~12 Ma) to early Pliocene (~4.5 Ma) (Hoorn *et al.*, 2010). The first range in raise up was the Central Cordillera with an intensified uplift during the Miocene. Meanwhile, the final uplift of the Eastern Cordillera was recorded for the Pliocene-Holocene.

The geological events that occurred inside this block caused geoclimatic changes at a South American level (Hartley, 2003; Ehlers and Poulsen, 2009). Thus, the diversification in the North Andean Block has been explained based on different paleoclimatic and geological events.

The refuge hypothesis was proposed, based on paleoclimatic data, to explain the diversification during the Pleistocene (~2.5 Ma Haffer, 1967, 1969; Patton and da Silva, 1998). Geological data, as the significant mountain building of the NAB (~20-5 Ma), has been used to explain the diversification in a temporal range greater than the Pleistocene. The Andean orogeny promoted diversification in the NAB, isolating populations in the Miocene (23.03-5.33 Ma) from south-to-north (Doan, 2003; Chaves *et al.*, 2011), from west-to-east (Chapman, 1917; Kattan *et al.*, 2004), and separating lowlands and highlands (García-Moreno and Fjeldså, 2000; Ribas *et al.*, 2007; Antonelli *et al.*, 2009).

The diversification in the NAB also is studied under a temporal stratification separating the Miocene-Pliocene (23.03-2.5 Ma) time frame from the early Pliocene-Pleistocene (2.59-0.01 Ma) (Velazco and Patterson, 2008; Schweizer *et al.*, 2011; Benham *et al.*, 2014).

Chazot *et al.* 2016 proposed a framework of biogeographic scenarios containing four main evolutionary mechanisms (speciation, extinction, older colonisation times, and migration) to investigate variation in diversity between Andean and non-Andean regions using the subtribe Godyridina. Each mechanism has been the support for the cradle (Fjeldså, 1994; Hutter *et al.*, 2013), museum (Stebbins, 1974; Smith *et al.*, 2007), time-for-speciation (Stephens and Wiens, 2002) and species-attractor (Beckman and Witt, 2015) hypotheses. However, there are still not studies with this framework assessing multiple taxonomic groups. Most diversification studies were focused on a specific taxonomic group and do not use, at the same time, multiple groups classified in different taxonomic categories.

We assessed four hypotheses to identify the pattern(s) of diversification occurring in the NAB. We took the three most common hypotheses used in the literature to explain the diversification in this area and we formulated another hypothesis based on other affirmations in the literature.

***Origin: Amazonian region, Pattern: Lowlands to Highlands***: North Andean taxa originated in the Amazonian region. Taxa arrived at the valleys during the early-middle-Miocene (~15-10 Ma), and then followed the lowlands to highlands pattern in the NAB. The Amazonian region was connected to the Magdalena valley and also to the North-Caribbean zone; the Eastern Cordillera was not more than 40% of its current elevation (~15-11 Ma, Gregory-Wodzicki, 2000) Once established in the North Andean lowlands, the biota moved to highlands following the mountain-building for each Cordillera *ca*. (13-7 Ma) (~13-7 Ma) (Antonelli *et al.*, 2009; Brumfield and Edwards, 2007; Ribas *et al.*, 2007).

***Origin: Central America, Pattern: Lowlands to Highlands***: North Andean taxa originated in Central America. Taxa arrived first at valleys during the early-middle-Miocene (~15-10 Ma), and then followed the lowlands to highlands pattern in the NAB. The Amazonian region was connected to the Magdalena Valley and also to the North-Caribbean zone. Some taxa reached the Amazonian region early in time due to the final uplift of the Eastern Cordillera, which took place in the Plio-Pleistocene (~13-7 Ma, Hoorn *et al.*, 1995, 2010). Once established in North Andean lowlands, the biota arrived at the highlands following the mountain-building of each Cordillera *ca*. (13-7 Ma) (Daza *et al.*, 2010; Ornelas *et al.*, 2013).

***Origin: Central Andes, Pattern: Highlands to Lowlands***: North Andean taxa originated in the Central Andes. Taxa arrived first at the Cordilleras during the early-middle-Miocene (~15-10 Ma) and then followed the highlands to lowlands pattern in the NAB. The biota, following the south-to-north pattern, went to the Central Cordillera approximately 20-15 Ma (Initial uplift: 65

to 33 Ma; significant uplift: 23-10 Ma), then to the Western Cordillera by *ca*. 15 Ma (Significant uplift: middle Miocene (~13 Ma) to Holocene), and finally to the Eastern Cordillera (~10 Ma). From the North Andean highlands, the taxa followed the highlands to lowlands pattern towards the valleys and the Amazonian region ((Doan, 2003; Chaves *et al.*, 2011).

***Altitudinal and horizontal pattern***: The North Andean biota followed two different patterns, one altitudinal (highlands and lowlands) and the other horizontal (between Cordilleras). The altitudinal pattern, lowlands to highlands, occurred from valleys following the mountain uplift (~15-7 Ma). Once the taxa were at the highlands a differentiation occurred among flanks of the Cordilleras (after ~7 Ma). Thus, each flank was associated with lowlands, subdividing the North Andean Block in three regions such as: Pacific region (Western Cordillera), inter-Andean region (Valleys, Central Cordillera, and Western flank of the Eastern Cordillera), and Eastern region (Eastern flank of the Eastern Cordillera and the Amazonian region) (Kattan *et al.*, 2004).

In the present study, we used multiple taxonomic groups and combining historical biogeography, we assessed the four hypotheses presented above to identify the pattern(s) of diversification occurring in the NAB and to assess two main questions: What is the hypothesis that best fits the diversification of the North Andean taxa? and what are the biogeographical and temporal scenarios of the Andean uplift?

# 2. Materials and Methods

## 2.1 Taxon and DNA sequence sampling

Following Sanmartín *et al.* (2001) and Sanmartín and Ronquist (2002), we established two compatible rules for choosing the study groups. The first rule was to use taxa that had at least three species distributed in the NAB, and the second rule was to select groups with sister clade(s) distributed in adjacent areas. We found 15 monophyletic groups belonging to six taxonomic classes (Magnoliopsida, Insecta, Amphibia, Reptilia, Aves, Mammalia) that agree with these rules. The total sample included 637 species representing 13 families and 65 genera (see Table 1. Appendix A). We downloaded the corresponding DNA sequences from GenBank (NCBI, Benson *et al.*, 2012). The number of available genes ranges from two (*Leptodeira* 1764 bp, Tanagers 2184 bp Sedano and Burns, 2010) to ten (Centroleninae 6160 bp).

## 2.2 Phylogenetic analyses and divergence time estimations

For each phylogeny, we aligned the DNA sequences under the multiple-sequence-alignment-algorithm implemented in MUSCLE (v.3.8.31, Edgar, 2004), and calculated the best evolutionary model using the Akaike Information Criterion (Akaike, 1974) as implemented in the R package Phangorn (v.2.1.1, Schliep, 2011). Phylogeny and divergence times were estimated for partitioned data set using Bayesian Inference approach. Preliminary analyses were performed using MrBayes (v.3.2.2, Ronquist *et al.*, 2012), with 10 million generations, four Markov Monte Carlo chains, temperature set as 0.2, and sampling every 10000 generations; for each analysis, we used the Robinson and Foulds distance (RF) (Robinson and Foulds, 1981) to compare the reconstructed phylogeny with the trees reported in the literature. Phylogenetic and divergence times estimations were conducted in BEAST (v.1.8.2, Drummond and Rambaut, 2007; Drummond *et al.*, 2012) using an uncorrelated relaxed lognormal clock (Drummond *et al.*, 2006) with a Speciation Yule Process set as tree prior because we did not take into account extinction and we assessed different genera and species but not populations (Yule, 1924; Aldous, 2001). We performed two runs of 30 million generations, sampling every 1000 generations. We checked the convergence using Tracer (v.1.6, Rambaut *et al.*, 2014) considering an acceptable effective sample size (ESS) greater than 200 (Drummond *et al.*, 2009) and standard deviations below $1x10^{-3}$. We conducted for each group a calibration prior exploration, assessing uniform and normal distributions, and selecting between them by Bayes factors (Kass and Raftery, 1995).

We used fossil information or secondary calibrations (estimated from previous studies) depending on the availability for each group (see Table 1. Appendix A). Thus, we estimated, for groups with secondary calibrations, relative divergence times and not absolute node ages due to the lack of fossil information for a specific group or its relative sister clades.

## 2.3 Historical biogeography

We obtained the distributional data from the Global Biodiversity International Facility (GBIF) up to February, 2017 (Removing duplicates and points in the sea), as well as records in literature. We used a set of nine biogeographic areas based on two models of regionalisation (Cabrera and Willink, 1973; Morrone, 2014) (Areas out of the NAB; Central Andes, Central America, and the

Amazonian region; we considered the North Andean Cordilleras, as a whole, labeled as “highlands", while the North Andean valleys and the North-Caribbean region were labeled as “lowlands" [0-800 m]). We modified graphically some of these areas with respect to the paleo maps of Hoorn *et al.* (1995, 2010) in order to adjust the areas according to the temporal scale of the hypotheses. We removed the area that corresponds to Chocó-Darien province (Morrone, 2014) and to represent the North Andean highlands we used the mixed area formed by Altoandean and Páramo provinces (Cabrera and Willink, 1973). We selected nine areas in order to avoid over-parameterisation and to limit the number of possibles states in the analyses (Ree and Smith, 2008; Matzke, 2012) (e.g. with ten areas and a maximum range size of four, there are 382 possible states, while with nine areas there are 256 possible states).

**2.3.1 Ancestral area analyses.** To estimate historical patterns of dispersal and cladogenesis within each genus, we performed an ancestral area analysis. We estimated the ancestral distributions following two models, the dispersion-extinction-cladogenesis model (DEC, Ree and Smith, 2008) and the DIVALIKE model implemented in the R package BioGeoBEARS (v.0.2.1, Matzke, 2013*a*). We established a specific maximum range size for each group in order to constrain the number of states in the matrix an avoid the over-parameterisation (Matzke, 2012).

To test whether both methods, DEC and DIVALIKE, produce the same results we performed a Pearson correlation analysis between the likelihoods obtained. We compared the resulting areas by each method and quantified the percentage of composite or non-composite reconstructions, where composite estimations are a set of two or three possible areas (Castroviejo-Fisher *et al.*, 2014).

**2.3.2 Event analyses.** We conducted the event analysis as implemented in TreeFitter (v.1.3, Ronquist, 2001), using the default set of costs to maximize vicariance and duplication (Ronquist, 1997*b*). To assess the stability of the resulting cladogram we generated 300 pseudo-replicates re-sampling with no replacement using each time up to nine out of the 15 phylogenies as input data. We quantified the percentage of dispersal events towards lowlands (inter-Andean valleys and the North-Caribbean region) and/or highlands (North Andean Cordilleras).

## 2.4 Diversification Hypothesis Tests

As a result of the bibliometric analysis made from January, 1900 to December, 2016, we took into account the most common hypotheses used to explain the diversification of the North Andean taxa, as we described previously. Under a Maximum Likelihood approach we performed hypothesis tests for each taxonomic group using the dispersal-extinction-cladogenesis model (Ree and Smith, 2008) implemented in BioGeoBEARS (v.0.2.1, Matzke, 2013*a*). We specified for each hypothesis three sets of unequal rates of dispersal between areas ([1] 1 - 0.5 - 0, [2] 1 - 0.7 - 0.3 - 0, and [3] 1 - 0) and a temporal stratification containing four-time intervals ([1] 0 - 7, [2] 7 - 10, [3] 10 - 15, and [4] 15 - 20 Ma) (see Dispersal multipliers Appendix B). The stratification and the dispersal multipliers were designed to account for the major geological events such as the south-to-north uplift of the Andes, the uplift of each Cordillera in the NAB and the closure of the Western Andean Portal(Gregory-Wodzicki, 2000; Hungerbühler *et al.*, 2002; Hoorn *et al.*, 2010). According to the reconstructions obtained, we quantified the percentage of nodes that followed each pattern in different temporal intervals. We compared the resulting maximum likelihood among dispersal multipliers and between hypotheses. We generated a lineage-through-time plot (Nee *et al.*, 1995) in the R package ape (v.4.1, Paradis *et al.*, 2004), as a graphical representation for the diversification over time for all groups.

We matched the changes along the curve with the geological events that could occur in each temporal stratification of the hypotheses. Simultaneously, we compared the reconstructions obtained after the hypothesis tests with the previous ancestral area estimations, in order to verify if after the hypothesis test the ancestral distribution(s) were different in the analyses and assess the influence of dispersal multipliers on the estimation of ancestral distribution. Besides, we compared the reconstructions of the hypothesis tests with the results of the events analysis. For this instance, we seek in the hypothesis test reconstructions, nodes that shown the same dispersal events and/or vicariance obtained under the events analyses. Finally, we dated each event found according to the date in the phylogenies.

We conducted all R analyses using the version 3.4.1 (R Core Team, 2017).

## 3. Results

### 3.1 Phylogenetic analyses and divergence times

The resulting Robinson and Foulds distance (RF) between the reconstructed phylogeny and the trees reported in the literature was less than or equal to 0.5 in 90% of the comparisons (min=0.04, max=0.55, median=0.35, see RF Appendix C).

Our results indicated that for eight out of 15 phylogenies the basal node corresponded to the Miocene (23.03-5.3 Ma), three out of 15 phylogenies corresponded to the Oligocene (~33.9-23.03 Ma), and four out of 15 groups corresponded to the Eocene (~56-33.9 Ma). The groups classified in the Magnoliopsida class started to diversify in the late Eocene-Oligocene, between 35 to 25 Ma. We found that insecta taxa started to diversify in the Miocene between 15 to 10 Ma. In terms of specific groups, *Platyrrhinus* was the youngest group assessed (5.4 Ma, CI(95%)= 4.1-9.6 Ma), while *Pristimantis* was the oldest group assessed (42.3 Ma, CI(95%)= 34.5-50.4 Ma).

## 3.2 Ancestral distribution

The estimated ancestral distributions were similar between models. We obtained the same distributions in 53% of the basal nodes (see Table 3. Appendix D) but in 47% of the analyses the models reconstructed different but congruent set of areas. Meanwhile in 43% of the cases under the DEC model we obtained single areas while for the same node DIVALIKE recovered two areas (hereafter considered as composite reconstruction) (see Table 3. Appendix D). When the estimation differs among models, we found that the smallest set of areas is contained inside the largest set of areas (eight out of 15 groups, see Table 3. Appendix D).

We recovered, under DEC and DIVALIKE, equal reconstructions in the internal nodes that varied from 67% to 100% and we obtained a high correlation value of DEC and DIVALIKE log-likelihoods (R= 0.998; CI(95%)= 0.996-0.999), even when the set of areas were not exactly the same (see Table 3. Appendix D).

We recovered single areas in 43.3% of the reconstructions, varied from 62% for the Amazonian region (I) to 15% for Central Andes (A) (Fig. 1). Nevertheless, we obtained composite reconstructions along the groups showing a set of two areas as ancestral distribution (23.3%, e.g. Centroleninae: CI, *Napeogenes*: AI) or three areas as ancestral distribution (33.3%, e.g. *Pteronymia*: CHI (De-Silva *et al.*, 2017), *Pristimantis*: BCI). We found that in 29% of the composite reconstructions showing two areas, the Central Cordillera appeared together with the Amazonian region (C and I) (Fig. 1, see Table 4. Appendix D). The composite reconstruction obtained between the Eastern and Central Cordillera, the Central Andes and the Amazonian region (BCI and CI) represented 71% of the reconstructions showing two and three areas. Central America appeared in 23.5% of the composite reconstructions (e.g. HI *Amazilia*, CHI *Pristimantis*, and CHI *Pteronymia*).

### 3.3 Relationship of areas in the North Andean Block

We obtained two area cladograms where the main difference between them was the number of dispersal events and the frequency of vicariance. The Robinson and Foulds distance between cladograms was 0.71 but the relations obtained are similar in terms of the resulting relationship of North Andean lowlands. Vicariance events were evidenced in all internal nodes but the highest frequencies were obtained in five of the seven nodes of each cladogram (Fig. 2). The areas involved in vicariance events are the Amazonian region, Central Andes, and Central America (AHI), the Central and Eastern Cordilleras (BC), the Western Cordillera and Cauca valley (DF).

The lowlands in the NAB did not appear related to the highlands (Fig. 2). The North-Caribbean area and the Magdalena valley were related in the same node in both cladograms, probably because the connection of these areas predated the mountain building. Besides, the high frequencies of vicariance obtained in the node formed by the Western Cordillera and the Cauca valley, we obtained two dispersal events towards Central America (Table 1). There were more dispersal events towards highlands (Cordilleras in the NAB) (47%) than to lowlands (inter-Andean valleys) (22%) (Table 1). There were areas such as the Amazonian region, the Central Andes, and Central America that presented dispersal events towards both, North Andean lowlands and highlands. When comparing the percentage of dispersal events from areas that disperse to both, North Andean lowlands and North Andean highlands, we obtained a major dispersion towards highlands (62%; Table 1. See also Table 5. Appendix E). We also obtained more dispersal events (41%) between Cordilleras in the NAB (Eastern, Central and Western Cordilleras). Inside the NAB 24% of the dispersal events were from North Andean Cordilleras to North Andean lowlands (Table 1).

### 3.4 Diversification pattern

We found that the hypothesis with origin: Central Andes and pattern: Highlands to Lowlands fitted best to the diversification of 73.3% of the groups showing in different time frames a highlands-to-lowlands pattern (Fig. 3). Nonetheless, the hypothesis of origin in the Amazonian region with a pattern from Lowlands to Highlands and the hypothesis based on horizontal and altitudinal pattern, fitted the diversification of taxa such as the Annonaceae and *Pristimantis* groups, respectively.

The hypotheses with different origin, Amazonian region or Central America and pattern from Lowlands to Highlands presented the lowest log-likelihood differences in five out of 15 groups. We found log-likelihood differences, between dispersal matrices, that varied from 111 to 0.01 likelihood units (Median= 8). Distinctive dispersion matrices (with different dispersal rates) did not generate larger changes in relation to the resulting maximum likelihood. The largest differences were obtained between the dispersal multipliers of the hypothesis origin: Central

Andes, pattern: Highlands to Lowlands (see Table 6. Appendix F). The minimal differences (41%) were among the results obtained by the dispersal matrices of the hypothesis origin: Central America and pattern: Lowlands to Highlands (see Table 6. Appendix F).

We recovered a different ancestral distribution when comparing with the distributions inferred in the ancestral area analyses. Thus, following the hypothesis that fitted best, the Central Andes appeared as the ancestral distribution, either in composite reconstructions (53%) or as a single area (33%).

The lowlands to highlands or *vice-versa* pattern were observed in different temporal ranges between groups. Thus, the same pattern was evidenced multiple times during the time of diversification of a specific group (Fig. 3). Considering four temporal intervals, each one of 5 million years, the percentage of nodes showing the lowlands to highlands pattern in the 5 to 0 Ma interval was 31.58%. From 15 to 10 Ma and from 10 to 5 Ma the percentage was 21.05% (Table 2). The highlands to lowlands pattern was found with a percentage of 26.32% in the 10 to 5 Ma interval. We found that both patterns fitted the diversification of the groups, even when the pattern highlands to lowlands fitted best.

We obtained the maximum and minimum percentages of nodes involved in changes from one area to another in the time intervals from 10 to 5 Ma (41.4%) and from 20 to 15 Ma (10.3%) (Table 2). We observed an increment in the number of lineages (Fig. 3) from the late-Miocene which coincides with the time interval with more evidence of both patterns highlands to lowlands and *vice-versa* (~10 to 5 Ma). We found the south to north pattern in 80% of the groups and the principal areas involved were: Central Andes, Eastern and Central Cordilleras in the NAB.

# 4. Discussion

## 4.1 Ancestral area

The correlated maximum likelihood of both models, DEC and DIVALIKE, show high similarity in the numerical calculation even when the areas estimated were not completely equal. In terms of likelihood, similar values can be obtained when some areas in composite reconstructions do not contribute to the overall likelihood obtained. Although under the DEC model we obtained more single areas than in DIVALIKE, both estimations were influenced by the history of the group and their sister clades (Castroviejo-Fisher *et al.*, 2014; Antonelli *et al.*, 2009). The parameters and distributions play a key role in the differentiation of both models, thus vicariance only differs between them when a maximum range size is greater than or equal to four (Matzke, 2013*b*). Even when both models focused in different processes, we might have the same results under specific parameters. Additionally, the distribution of sister species influences the resulting probabilities adding or decreasing the number of possible events (Matzke, 2013*b*). With our data set, we can infer that the DEC model reduces the ambiguity at basal nodes and it recovers single ancestral distribution in reconstructions with clades that have widespread organisms.

Our results showed three possible ancestral distributions for North Andean taxa (Fig. 1) presenting the largest number of dispersal events according to the event analyses. These ancestral areas are congruent with the ones proposed previously in different hypotheses (e.g. Doan, 2003; Brumfield and Edwards, 2007; Ornelas *et al.*, 2013). This indicates that the resulting ancestral distribution is maintained under different parameters and area scenarios used to address ancestral area analysis. The set of two areas (composite reconstruction), composed by the Central Cordillera in the NAB and the Amazonian region, is similar to the ancestral distribution obtained in previous studies (Castroviejo-Fisher *et al.*, 2014; Antonelli *et al.*, 2009). We may suggest that composite reconstructions are related to the history of the group because these types of reconstructions appear when the sister clade of the groups is Amazonian and most of the internal nodes are North Andean. Still, the presence of a strictly Amazonian node in the phylogeny influence the ancestral area estimation (Fig. 3) as seen in Centroleninae, *Pristimantis*, and *Stenocercus* (Teixeira *et al.*, 2016).

## 4.2 Relationship of areas in the North Andean Block

Andean uplift and the asynchronous Andean formation (Case *et al.*, 1990; Hoorn *et al.*, 1995; Gómez *et al.*, 2003) are the major events involved in taxa separation between lowlands and highlands, as seen in our area relationships, and between southern and northern latitudes (Elias *et al.*, 2009; Doan, 2003). Authors such as Chaves *et al.* (2011) and García-Moreno and Fjeldså (2000), suggest that the North Andean taxa are originated from adjacent areas that are older than the North Andean Block, such as Central Andes and the Amazonian region. The node conformed by adjacent areas as Central Andes, Central America, and the Amazonian region support the previous idea. These areas were the same obtained in single reconstructions in the ancestral area analyses and presented the largest number of dispersions towards the NAB. The resulting relationship between the highlands is supported by the observed dispersions from highland to highland (Table 1; see also Table 5. Appendix E) within the NAB, which could be related to the idea of sister flanks and divergence between Cordilleras (Kattan *et al.*, 2004). Dispersal events towards and from Central America supported connection between Central and South America.

## 4.3 Geological scenario

The connection of the Amazonian region and the North-Caribbean area has been hypothesised due to the southern part of the Eastern Cordillera started to rise along with the Central Cordillera (Hoorn *et al.*, 1995, 2010), separating the Magdalena and Amazonas Basins, however, this was not perceived with our data set. According to Gregory-Wodzicki (2000), the Eastern Cordillera was at no more than 40% of its modern elevation by 4 Ma and an intensified uplift (circa 4-5 to 3 Ma) has been associated with the South American-Panama collision (Farris *et al.*, 2011). However, *Podocnemis* (Vargas-Ramirez *et al.*, 2008) showed a vicariant node involving two species separated around 15 Ma and the Annonaceae family presented a Caribbean node separated from the Amazonian node between 20 to 15 Ma. Therefore, we establish that the Eastern Cordillera played a role as a barrier for the studied taxa distributed in these areas.

An earlier start for the formation of the Panamanian Isthmus, taking into account the hypothesis tests, was supported by groups such as *Amazilia* 15-10 Ma, *Pristimantis* 15-10 Ma, *Ithomia* 10-5 Ma, and *Leptodeira* 5-0 Ma (Fig. 3). Our results are congruent with some findings of Bacon *et al.* (2015), who obtained in their analyses organisms that probably passed through the Panama isthmus circa 20 Ma. Recent models suggest an early start for the isthmus formation in the Oligocene (Montes *et al.*, 2012) or near to 25 to 23 Ma (Farris *et al.*, 2011). Studies based on biological evidence indicate a formation between 3.5 to 3 Ma, while bathimetric evidence supports a formation approximately between 14 and 12 Ma (Duque-Caro, 1990; Coates *et al.*, 1992, 2004).

The North Andean block presented an initial significant uplift by late Oligocene to early Miocene (*ca*. 23 Ma) and the most intense peaks of mountain building followed during the late Miocene (*ca*. 12 Ma) and early Pliocene (*ca*. 4.5 Ma) (Hoorn *et al.*, 2010). Alongside, the asynchronous mountain building is supported by our results. Central Andean taxa first colonised the Central Cordillera (Initial uplift: Late Cretaceous to Paleogene, Intensified uplift: Miocene. Cooper *et al.*, 1995; Gómez *et al.*, 2003; Hoorn *et al.*, 2010) within the 20 to 15 Ma time interval. Two groups with Central Andes as ancestral distribution colonised the Eastern Cordillera, probably the southern part of this range in the 20 to 15 Ma time interval. A major colonisation of the Eastern Cordillera occurred between 10 to 5 Ma because the initial mountain building was by 12 Ma and a high uplift rate was recorded during the Pliocene-Holocene (after *ca*. 5 Ma). When the ancestral distribution was the Amazonian region, the first range colonised was the Central Cordillera in the North Andean Block. The early colonisation of the Central Cordillera is congruent with the model of mountain building previously proposed.

## 4.4 Diversification pattern

Although the hypothesis with origin: Central Andes and pattern: Highlands to Lowlands did not fit all groups, it always presented lower likelihood differences in comparison with the hypothesis that fit better to each group (see Table 6. Appendix F) and implying that the major part of the groups could follow the highlands to lowlands pattern over time, however, based on the likelihood differences between hypotheses, we could state that the taxa followed multiple patterns as highlands to lowlands, lowlands to highlands and south to north in different time frames during their diversification.

The node reconstructions recovered after the hypothesis tests are not the same as the ones inferred in the ancestral area analyses because the dispersal matrix influenced the results. However, the hypothesis with an origin in the Amazonian region and lowlands to highlands pattern fitted better the diversification of the Annonaceae family showing the Amazonian region as the ancestral distribution in all tests and reconstructions. Annonaceae was not the only group that shared the ancestral area in both analyses (ancestral area and hypotheses tests). We found that even when the hypothesis that fit better was origin: Central Andes and pattern: Highlands to Lowlands, the area obtained in the ancestral area analyses was recovered by the hypotheses tests in *Amazilia* and *Leptodeira*.

The idea proposed by Pirie *et al.* (2006), dispersal events during the North Andean orogeny, to explain the diversification of the Annonaceae family could fit also other Amazonian groups and supports the lowlands to highlands pattern. Apart from the affirmation above, mountain-building could influence the diversification of different groups acting as a barrier or as a dispersal corridor (Ribas *et al.*, 2007; Elias *et al.*, 2009) and it might generate a single or multiple patterns over time (Fig. 3).

The movement from the Central Andes to the Cordilleras in the NAB represented the major percentage of changes from one area to another over time (Fig. 3; Table 3). This idea supports the south-to-north diversification pattern (Doan, 2003; Goicoechea *et al.*, 2012; Chaves *et al.*, 2011) that fit groups such as *Stenocercus* Torres-Carvajal, 2007), *Pristimantis* (Pinto-Sánchez *et al.*, 2012), and *Tournefortia* (Luebert *et al.*, 2011), as has been seen in *Adelomya* or *Proctoporus* (Doan, 2003; Chaves *et al.*, 2011). Diversification at the rhythm of the Andean uplift as it is proposed in the south-to-north speciation hypothesis (Doan, 2003; Goicoechea *et* *al.*, 2012; Chaves *et al.*, 2011) may explain the fit of the hypothesis with origin: Central Andes and pattern: Highlands to Lowlands. However, regardless the origin, the North Andean taxa might follow a South to North pattern of diversification inside the NAB at different periods of time (Fig. 3). *Amazilia* reinforces the previous statement because its ancestral area was Central America and it presented nodes that followed the south-to-north pattern. For this genus, the major divergence in Central America was during the formation of mountain systems in the area (Ferrari1999). Our results showed two patterns in two major clades, from Mesoamerica to North Andean highlands and other from Mesoamerica to lowlands in South America. We suggest that these two patterns fit the diversification in two separate clades simultaneously (Fig. 3).

Given the hypothesis fit, groups such as Centroleninae, *Pristimantis*, and *Stenocercus* support a south-to-north pattern between 15 to 10 Ma (Fig. 3; Table 2) and the principal areas involved in this pattern are the Central Andes and the Eastern and Central Cordilleras, following Doan (2003), who states that the Andean taxa followed the Andean orogeny. However, Castroviejo-Fisher *et al.* (2014) did not find a south-to-north pattern of diversification in Centrolenidae. Based on their results, they found few dispersals from the Central Andes to the NAB. The age when this south-to-north pattern fit coincides with a period of intensified uplift (circa 20-10 Ma) and let us suggest that colonisation of the North Andean highlands started nearly 10 Ma (Hoorn *et al.*, 2010). According to our results, the 10 to 5 Ma interval presented most of the evidence for both patterns, highlands to lowlands and lowlands to highlands and also is the temporal range that showed an increment in the number of lineage through time (Fig.3). For this reason, we propose that it does not exist a unique pattern within the NAB. These patterns did not begin at the same time (Fig. 3) and in many cases these patterns overlapped, comprising different nodes in the same taxon.

Bearing in mind the fit of each pattern, it is more plausible the highlands to lowlands pattern (Fig. 3; Table 3). This pattern could be associated with the major dispersal events obtained towards highlands before the 10 to 5 Ma interval. This result also explains that these patterns could be independent and a result of multiple colonisations of the Andes (Chazot *et al.*, 2016) and, as in *Mionectes* (Miller *et al.*, 2008), did not exhibit the lowlands to highlands pattern or *vice-versa* over time.

Correspondingly, we can suggest, based on our results, the evidence of “attraction" towards the Andes from adjacent areas likely followed the species-attractor hypothesis (Beckman2015). The species from the Amazonian region could have dispersed to the Andes multiple times following the assumption of multiple colonisations (Chazot *et al.*, 2016). Thus, it is possible to infer, based on the proportion of North Andean lineages *versus* Amazonian or Central American lineages, that taxa such as Annonaceae, *Leptodeira* and the *Tournefortia* clade support this idea.

We can deduce that highland taxa from the Central Andes had more time to diversify than those from adjacent lowlands, this way, those taxa from the Central Andes probably colonised North Andean lowlands first. Here we found clades (e.g *Ithomia*, *Napeogenes*, *Stenocercus*) with Central Andes as ancestral distribution that probably fit the time-for-speciation hypothesis (Stephens and Wiens, 2002). The highlands to lowlands pattern could be explained by the mechanism of older colonisation times involved in this hypothesis. García-Moreno and Fjeldså (2000) state that the highland biota diversified from the lowlands because they are older than the highlands, while opposite to this Chazot *et al.* (2016) state that highland biota came from older highlands.

Chazot *et al*. (2016) proposed a high speciation rate in the Andes as the main mechanism of diversification. Even when the speciation rate was not evaluated, we observed groups such as Centroleninae, Cinchoneae, *Ithomia*, *Napeogenes*, *Pristimantis*, and *Stenocercus* containing nodes where the Andean Cordilleras acted as a barrier for the diversification (Fig. 3). The number of lineages in adjacent Andean highlands was larger than the number of lineages in adjacent lowlands (Fig. 3, Centroleninae and *Pristimantis*). We suggest that these groups could fit the cradle hypothesis (Fjeldså, 1994; Hutter *et al.*, 2013). As proposed by Graham *et al.* (2004) and Hughes and Eastwood (2006), the geographical heterogeneity favoured the geographic diversification where the Cordilleras acted as a barrier, although, the asynchronous North Andean uplift (Case *et al.*, 1990; Cooper *et al.*, 1995; Hoorn *et al.*, 1995) also generated the opportunity for diversification at different times.

## 5. Conclusions

In terms of likelihood differences and the fit of each hypothesis, the two altitudinal patterns are plausible no matter the ancestral area estimated, and we could evidence these patterns overlapping and occurring multiple times in the same temporal frame (Miocene). However, the highlands to lowlands pattern fit better for the North Andean taxa which might support a highlands origin inside or outside the NAB.

Our analyses showed that the closing of the Panamanian Isthmus is not as recent as has been hypothesized. This supports an earlier start of the Isthmus formation. We found that diversification of North Andean taxa followed the Andean uplift and match to the times previously proposed. The taxa followed the orogeny scenario, where the Central Cordillera starts its uplift first, later the Western Cordillera, and then the Eastern Cordillera.

Finally, we proposed that two evolutionary mechanisms, the speciation rates and older colonisation times, could be involved in the diversification of North Andean taxa. This needs to be assessed in future studies using multiple taxa taxonomically differentiated and following or varying the scenario proposed recently by Chazot *et al*. (2016) and thus, compare whether under this scenario is recovered as a single pattern.

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# Tables

## Table 1.

*Dispersal events obtained in the events analyses.*

| Area | Switch to | Lowlands | Highlands | From ancestral areas to Highlands & Lowlands | |
|---|---|---|---|---|---|
| | | | | To Lowlands | To Highlands |
| **I 18.37%** | H | | | 38% | 62% |
| | C | | 1 | | |
| | D | | 1 | | |
| | B | | 1 | | |
| | A | | | | |
| | E | 1 | | | |
| | G | 1 | | | |
| | FD | 1 | 1 | | |
| | EG | 1 | | | |
| | | **0.44** | **0.44** | | |
| **H 14.29%** | I | | | | |
| | C | | 1 | | |
| | B | | 1 | | |
| | D | | 1 | | |
| | G | 1 | | | |
| | BC | | 1 | | |
| | EG | 1 | | | |
| | | **0.28** | **0.57** | | |
| **A 8.16%** | C | | 1 | | |
| | D | | 1 | | |
| | F | 1 | | | |
| | E | 1 | | | |
| | | **0.5** | **0.5** | | |
| **AI 10.20%** | H | | | | |
| | C | | 1 | | |
| | D | | 1 | | |
| | E | 1 | | | |
| | BC | | 1 | | |
| | | **0.17** | **0.6** | | |
| **AIH 4.08%** | D | | 1 | | |
| | BC | | 1 | | |
| | | | **1** | | |

| Area | Switch to | Lowlands | Highlands | From Highlands | |
|---|---|---|---|---|---|
| | | | | To Lowlands | To Highlands |
| **D* 6.12%** | H | | | 24% | 41% |
| | C | | 1 | | |
| | A | | | | |
| | | | **0.33** | | |
| **C* 12.24%** | I | | | | |
| | D | | 1 | | |
| | B | | 1 | | |
| | A | | | | |
| | FD | 1 | 1 | | |
| | AI | | | | |
| | | **0.17** | **0.33** | | |
| **B* 16.33%** | I | | | | |
| | C | | 1 | | |
| | D | | 1 | | |
| | F | 1 | | | |
| | A | | | | |
| | E | 1 | | | |
| | FD | 1 | 1 | | |
| | AI | | | | |
| | | **0.375** | **0.375** | | |
| **FD 4.08%** | H | | | | |
| | C | | 1 | | |
| | | | **0.5** | | |
| **F 4.08%** | H | | | | |
| | A | | | | |
| **BC 2.04%** | H | | | | |
| **Total of dispersions to highlands or lowlands** | | **22%** | **47%** | | |

* Highlands

Note: Percentage of dispersal events from ancestral areas towards highlands and/or lowlands. The percentage of dispersion from highlands to lowlands and between highlands is shown on the right part of the table. Highlands are marked with an asterisk (*). A: Central Andes, B: Eastern Cordillera, C: Central Cordillera, D: Western Cordillera, E: Magdalena valley, F: Cauca Valley, G: North-Caribbean, H: Central America, and I: Amazonian region.

**Table 2.**

*Patterns observed over time.*

| **Changes in nodes over time** | | **Temporal intervals in Ma** | | | |
|---|---|---|---|---|---|
| **From node →** | **→To node** | **20-15** | **15-10** | **10-5** | **5-0** |
| Lowlands | Lowlands | – | – | – | 4 |
| Highlands | Highlands | – | 4 | – | 6 |
| Lowlands | Highlands | – | 4 | 4 | 6 |
| Highlands | Lowlands | – | – | 5 | – |
| Highlands & Lowlands | Highlands | – | – | 4 | – |
| Amazonian region | Lowlands | – | 5 | 7 | – |
| Central America | Lowlands | – | – | 4 | 4 |
| Central Andes | Lowlands | – | – | – | – |
| Amazonian region | Highlands | – | 4 | – | – |
| Central America | Highlands | – | – | – | 4 |
| Central Andes | Highlands | 6 | 9 | 11 | 4 |
| Central Andes | Highlands & Lowlands | – | – | 6 | – |
| Highlands | Amazonian region | – | 4 | 5 | 4 |
| Lowlands | Central America | – | – | 4 | – |
| Highlands | Central America | – | 4 | 4 | 6 |
| Amazonian region & Central Andes | Central America | – | – | – | 4 |
| Central Andes | Amazonian region | 4 | – | – | – |
| | **TOTAL** | 10 | 34 | 54 | 42 |
| | **Percentage by time bin** | 7.14% | 24.29% | 38.57% | 30.00% |
| | **Percentage of the Lowlands to Highlands pattern** | | 21.05% | 21.05% | 31.58% |
| | **Percentage of the Highlands to Lowlands pattern** | | | 26.32% | |
| **Percentage of each area proposed as ancestral area in the hypotheses** | **Amazonian region** | | 15.52% | | |
| | **Central America** | | | 18.97% | 13.79% |
| | **Central Andes** | 10.34% | 15.52% | 18.97% | 6.90% |

Note: Four intervals analysed. Changes in nodes over time observed after the hypotheses fit.

# Figures

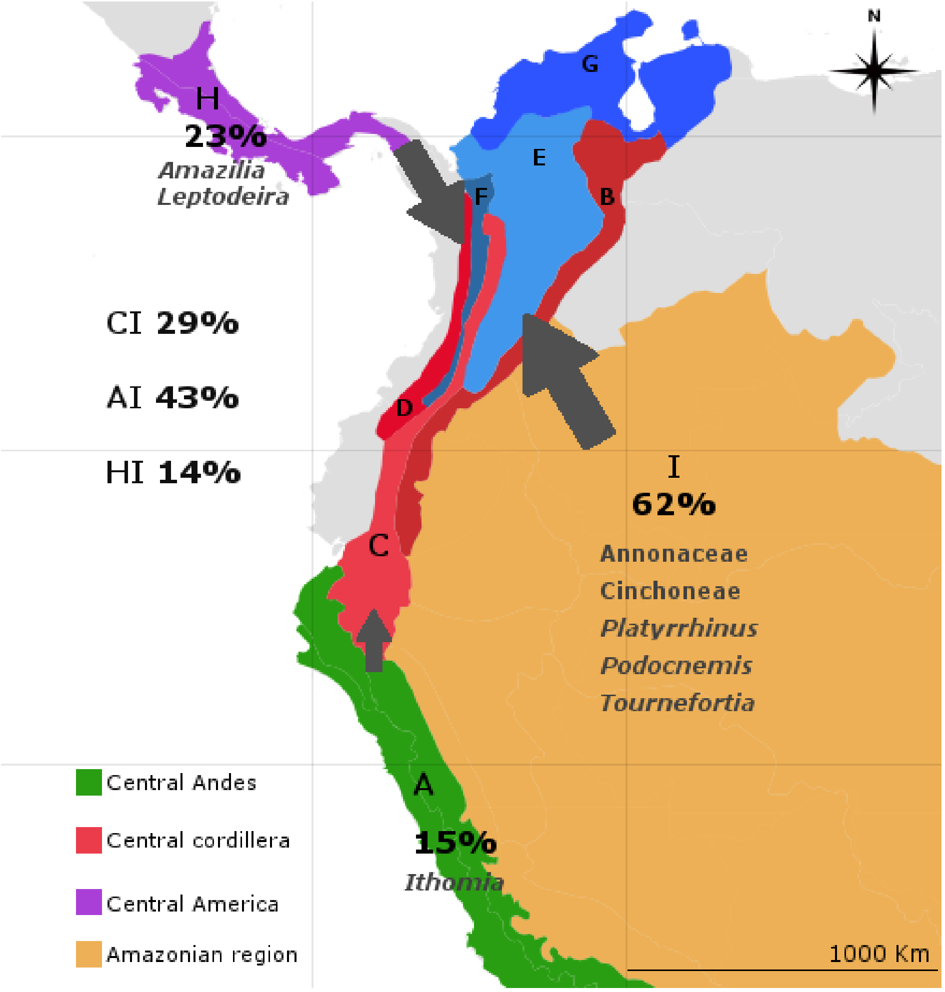


***Figure 1.* Summary of the ancestral area and events analyses.** Map of the North Andean Block (NAB) and adjacent areas**.** We show the percentage of different areas in composite (two areas 23.33%) and, non-composite (single areas 43.33%) reconstructions. The Amazonian region represents the 62% of the single areas obtained while Central America and Central Andes represented the 23% and 15%, respectively. AI and CI presented the major percentage within composite areas. Central Andes, Central America and the Amazonian region formed the node with highest dispersal events (41%). The arrows size is proportional to the number of dispersal events of each area. A: Central Andes, North Andean highlands (red) labeled as, B: Eastern Cordillera, C: Central Cordillera and, D: Western Cordillera. North Andean lowlands (blue) labeled as, E: Magdalena Valley, F: Cauca Valley, G: North-Caribbean. H: Central America and I: Amazonian region.

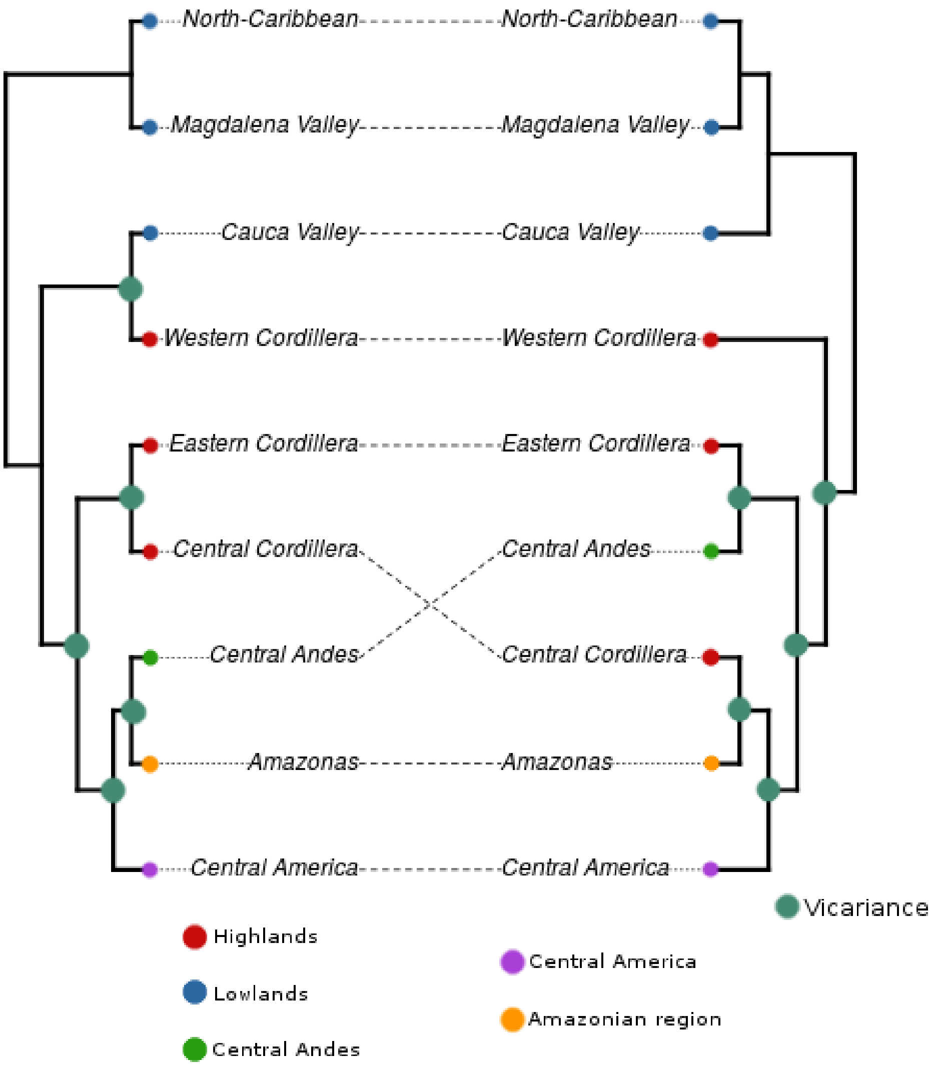


***Figure 2.*** **Cladograms of areas obtained after the stability test in the event analyses.** Vicariant nodes showed as circles. Lowlands in the NAB appeared related in a single node, blue tip label. The Robinson and Foulds distance for both cladograms was 0.71.

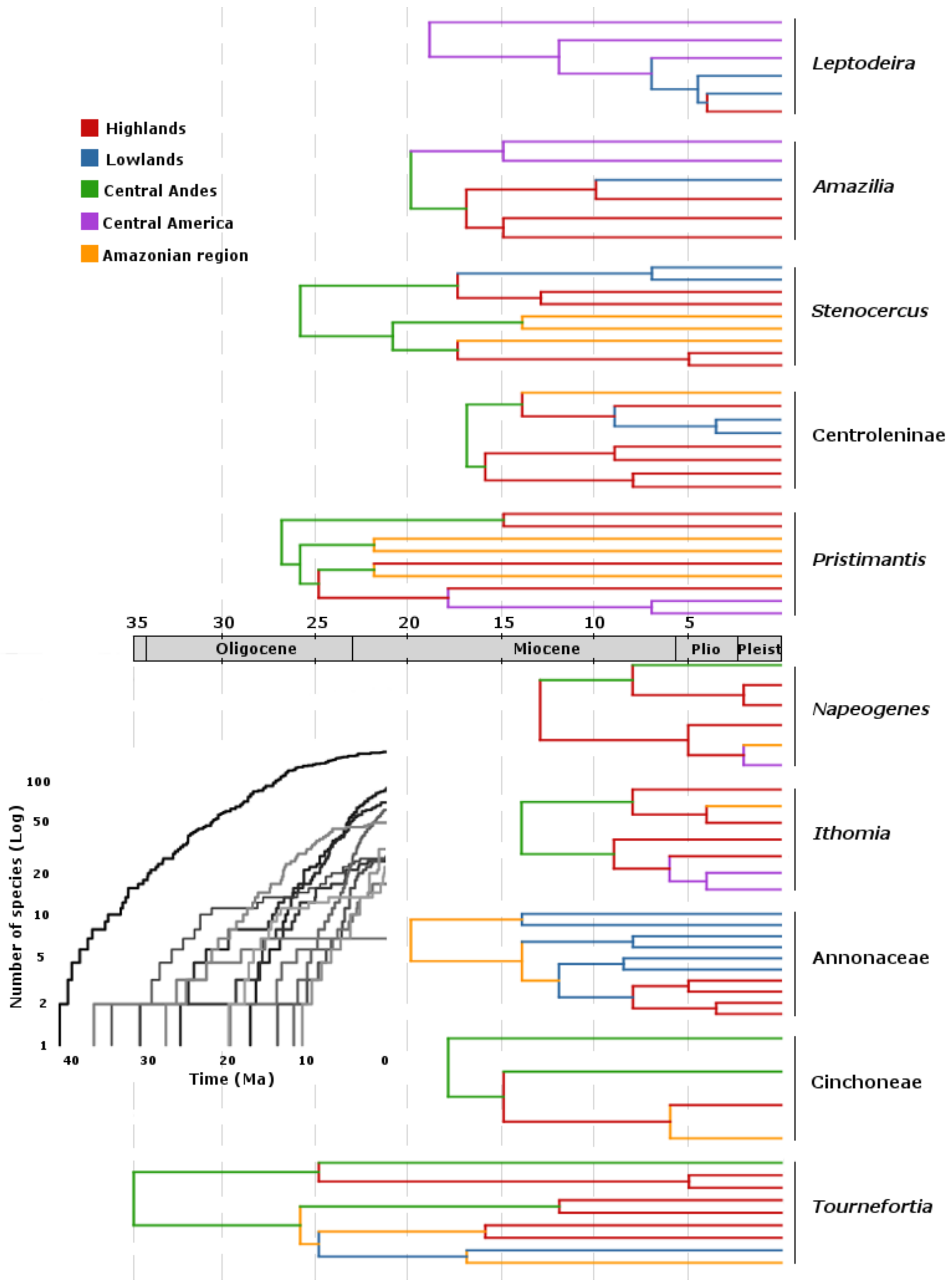


***Figure 3*. Summary of ages and diversification patterns by related taxonomic groups.** In the phylogenies, the lowlands lineages are indicated in blue, and highlands in red based on our hypotheses test. Lineages from adjacent areas are indicated in green: Central Andes, orange: Amazonian region and purple: Central America. A Lineage through time plot for all groups is showed on the left. To see *Platyrrhinus*, *Podocnemis*, *Pteronymia*, and *Thamnophilus* results see Fig. 1 Appendix F.

# Appendix

## Appendix A. Number of genes and calibration points used in this analysis

### Table 1.

*Number of genes and calibration points used in this analysis for each group.*

| Group | Taxonomic level | Class | Order | Ingroup | Outgroup | N° of genes | Nuclear genes | Mitochondrial genes | Chloropastic genes | N° of bp | Authors | Calibration points | Age | Authors |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Annonaceae | Family | Magnoliopsida | Magnoliales | 59 | 3 | 4 | 0 | 0 | 4 | 2700 | Pirie *et al*. (2006) | Maastrichtian seeds of Nigeria | 98 Ma | Richardson *et al*. (2004)<br>Doyle *et al*. (2004) |
| Cinchoneae | Tribe | Magnoliopsida | Gentianales | 22 | 4 | 4 | 0 | 0 | 4 | 1700 | Antonelli *et al*. (2009) | Fossil fruits and seeds of *Cephalanthus*. Late Eocene Gentianales | 33 Ma | Mai & Walther (1985) |
| *Tournefortia* clade |  | Magnoliopsida | Lamiales | 23 | 4 | 3 | 0 | 0 | 3 | 2340 | Luebert *et al*. (2011) | Fossil pollen of *Tournefortia*, Early Oligocene Puerto Rico | 30 Ma | Graham & Jarzen (1969)<br>Graham (1996, 2003b) |
| *Ithomia* | Genus | Insecta | Lepidoptera | 24 | 1 | 4 | 3 | 1 | 0 | 3200 | Elias *et al*. (2009) | Split of *Napeogenes* and *Ithomia*. Butterflies fossils for Nymphalidae | 21 Ma | Wahlberg *et al*. (2008) |
| *Napeogenes* | Genus | Insecta | Lepidoptera | 24 | 4 | 3 | 2 | 1 | 0 | 3160 | Elias *et al*. (2009) | Split of *Napeogenes* and *Ithomia*. Butterflies fossils for Nymphalidae | 21 Ma | Wahlberg *et al*. (2008) |
| *Pteronymia* | Genus | Insecta | Lepidoptera | 52 | 5 | 5 | 2 | 3 | 0 | 4350 | De Silva *et al*. (2017) | Time of shared nodes with the phylogeny of Nymphalidae | 15 Ma | Wahlberg *et al*. (2008) |
| Centroleninae | Subfamily | Amphibia | Anura | 75 | 5 | 10 | 7 | 3 | 0 | 6160 | Castroviejo-Fisher *et al*. (2014) | Oldest fossil of *Hyla sp*. Early Miocene. 50 Ma based on previous divergence time estimates of Hylinae | 50 15.97Ma | Rage & Rocek (2003)<br>Wiens *et al*. (2006)<br>Roelants *et al*. (2007) |
| *Pristimantis* | Genus | Amphibia | Anura | 138 | 4 | 5 | 2 | 3 | 0 | 2270 | Pinto-Sanchez *et al*. (2012) | Node representing the common ancestor of Terrarana and hylid Frogs | 60-50 Ma | Heinicke *et al*. (2007)<br>Roelants *et al*. (2007)<br>Wiens (2007, 2011)<br>Wiens *et al*. (2011) |
| *Leptodeira* | Genus | Reptilia | Squamata | 15 | 2 | 2 | 0 | 2 | 0 | 1760 | Daza *et al*. (2010) | Based on the oldest colubrid fossil known as the root of the tree | 40 Ma | Rage *et al*. (1992)<br>Head *et al*. (2005) |
| *Podocnemis* | Genus | Reptilia | Testudines | 6 | 2 | 5 | 3 | 2 | 0 | 3990 | Vargas-Ramirez *et al*. (2008) | Paleocene record of an Erymnochelys-like fossil | 65 Ma | Gaffney & Forster (2003) |
| *Stenocercus* | Genus | Reptilia | Squamata | 42 | 2 | 3 | 0 | 3 | 0 | 1740 | Torres-Carvajal (2007) Teixeira *et al*. (2016) | The most recent common ancestor of *Stenocercus* , *Uranoscodon* and *Plica* | 49 Ma | Prates *et al*. (2015) |
| *Amazilia* | Genus | Aves | Apodiformes | 20 | 10 | 3 | 0 | 3 | 0 | 1180 | Ornelas *et al*. (2013) | *Eurotrochilus inexpectatus*<br>*E. noniewiczi* | 30.5 Ma | Mayr (2004, 2007)<br>Bochenski & Bochenski (2008) Louchart *et al*. (2008) |
| Tanagers |  | Aves | Passeriformes | 96 | 14 | 2 | 0 | 2 | 0 | 2200 | Sedano & Burns (2010) | Origin of the Thraupidae family | 12.6 Ma | Cracraft & Barker (2009) |
| *Thamnophilus* | Genus | Aves | Passeriformes | 27 | 3 | 3 | 0 | 3 | 0 | 2460 | Brumfield & Edwards (2007) | *Thamnophilus bernardi* Late Pleistocene | ~15,000–18,000 yrs | Oswald & Steadman (2015) |
| *Platyrrhinus* | Genus | Mammalia | Chiroptera | 14 | 3 | 4 | 1 | 1 | 0 | 3260 | Velazco & Patterson (2008) | Pleistocene records of *P. incarum* and *P. lineatus* Eastern Brazil | 0.126 Ma | Czaplewski & Cartelle (1998)<br>Fracasso & Salles (2005) |

Note: Classification of each group, number of the ingroup sequences, type of genes, number of base pairs, and reference authors.

# Appendix B. Dispersal multipliers

## Unequal rates of dispersal between areas for each hypothesis.

[1] Origin: Amazonian region, Pattern: Lowlands to Highlands: 1 – 0.5 – 0.

7-0 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.5 | 0.5 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0.5 | 0.5 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0.5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 1 |

10-7 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0.5 | 0.5 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0.5 | 0.5 | 0 | 1 |

15-10 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0.5 | 0.5 | 0 | 1 |

20-15 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0.5 | 0.5 | 0 | 1 |

[2] Origin: Amazonian region, Pattern: Lowlands to Highlands: 1 – 0.7 – 0.3 – 0.

7-0 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.7 | 0.7 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0.7 | 0.7 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0.3 | 0.3 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0.3 | 0 | 0.3 | 0 | 1 |

10-7 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0.3 | 0.3 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0.3 | 0.7 | 0 | 1 |

15-10 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0.3 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0.3 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0.7 | 0.7 | 0 | 1 |

20-15 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0.3 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0.3 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0.7 | 0.7 | 0 | 1 |

[3] Origin: Central America, Pattern: Lowlands to Highlands: 1 – 0.5 – 0.
7-0 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.5 | 0.5 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0.5 | 0.5 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0.5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

10-7 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0.5 | 0.5 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0.5 | 1 | 0.5 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

15-10 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0.5 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

20-15 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0.5 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

[4] Origin: Central America, Pattern: Lowlands to Highlands: 1 – 0.7 – 0.3 – 0.
7-0 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.7 | 0.7 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0.7 | 0.7 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0.3 | 0.3 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

10-7 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0.3 | 0.3 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0.3 | 0.7 | 0.3 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

15-10 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0.3 | 1 | 0.7 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

20-15 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0.3 | 1 | 0.7 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

[5] Origin: Central Andes, Pattern: Highlands to Lowlands: 1 – 0.5 – 0.
7-0 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0.5 | 0.5 | 0 | 0.5 | 0 |
| 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.5 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

10-7 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.5 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0.5 |
| 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0.5 | 0 |
| 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0.5 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0.5 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0.5 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

15-10 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.5 | 1 | 0.5 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

20-15 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.5 | 1 | 0.5 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

[6] Origin: Central Andes, Pattern: Highlands to Lowlands: 1 – 0.7 – 0.3 – 0.
7-0 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0.7 | 0 | 0.3 | 0 | 0.3 |
| 0 | 0 | 1 | 0 | 0.7 | 0.7 | 0 | 0.3 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0.7 | 0 | 0.7 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0.3 | 1 | 0.3 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0.3 | 0.7 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.3 | 0.3 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

10-7 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.3 | 0.7 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0.3 |
| 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0.3 | 0 |
| 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0.7 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0.3 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0.3 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

15-10 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.3 | 1 | 0.3 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

20-15 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.3 | 1 | 0.3 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

[7] Altitudinal and horizontal pattern: 1 – 0.5 – 0.

20-15 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |
| 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0.5 |
| 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0.5 |
| 0 | 0 | 0 | 0 | 0 | 0.5 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 |

15-10 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.5 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.5 | 1 | 0 | 1 | 0.5 | 1 | 0 | 0.5 |
| 0 | 0 | 1 | 0.5 | 0.5 | 1 | 1 | 0.5 | 0 |
| 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0.5 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 1 |

10-7 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.5 | 1 | 0 | 1 | 0 | 1 | 0 | 0.5 |
| 0 | 0 | 1 | 0.5 | 0 | 1 | 0.5 | 0.5 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0.5 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

7-0 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| 0 | 0.5 | 1 | 0.5 | 1 | 1 | 1 | 0 | 0 |
| 0 | 0 | 0.5 | 1 | 0 | 1 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 0 | 0 | 0 | 0.5 | 0 | 0.5 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

[8] Altitudinal and horizontal pattern: 1 – 0.7 – 0.3 – 0.

20-15 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 1 | 1 | 0.7 | 0 | 1 |
| 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0.3 |
| 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0.3 |
| 0 | 0 | 0 | 0 | 0.7 | 1 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0.7 | 0.3 | 0 | 1 |

15-10 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0.3 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.3 | 1 | 0 | 1 | 0.3 | 1 | 0 | 0.3 |
| 0 | 0 | 1 | 0.7 | 0.7 | 1 | 1 | 0.3 | 0 |
| 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0.3 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0.3 | 0 | 0.5 | 0 | 1 |

10-7 Ma

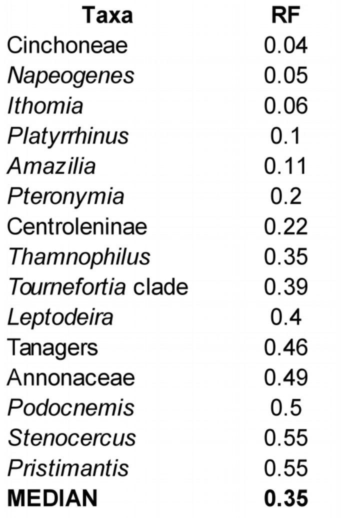
| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0.7 | 1 | 0 | 1 | 0 | 1 | 0 | 0.3 |
| 0 | 0 | 1 | 0.7 | 0 | 1 | 0.7 | 0.3 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0.7 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0.3 | 0 | 0.3 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

7-0 Ma

| A | B | C | D | E | F | G | H | I |
|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 1 | 0 | 0 | 1 | 0 | 0.7 | 0 | 1 |
| 0 | 0.7 | 1 | 0.7 | 1 | 1 | 1 | 0.3 | 0 |
| 0 | 0 | 0.7 | 1 | 0 | 1 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0.3 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| 0 | 0 | 0 | 0.3 | 0 | 0.3 | 0 | 1 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0.3 | 0 | 1 |

## Appendix C. Robinson and Foulds distance

Comparisons between the reconstructed phylogeny with the trees reported in the literature.



| **Taxa** | **RF** |
|---|---|
| Cinchoneae | 0.04 |
| *Napeogenes* | 0.05 |
| *Ithomia* | 0.06 |
| *Platyrrhinus* | 0.1 |
| *Amazilia* | 0.11 |
| *Pteronymia* | 0.2 |
| Centroleninae | 0.22 |
| *Thamnophilus* | 0.35 |
| *Tournefortia* clade | 0.39 |
| *Leptodeira* | 0.4 |
| Tanagers | 0.46 |
| Annonaceae | 0.49 |
| *Podocnemis* | 0.5 |
| *Stenocercus* | 0.55 |
| *Pristimantis* | 0.55 |
| **MEDIAN** | **0.35** |

## Appendix D. Ancestral area analyses

**Table 3.**
*Log-likelihood values and area(s) estimated by DEC and DIVALIKE models for each taxonomic group.*

| **Group** | **Area estimated** | | **Log-Likelihood** | |
|---|---|---|---|---|
| | **DEC** | **DIVALIKE** | **DEC** | **DIVALIKE** |
| *Amazilia* | HI | H | -95.05 | -114.48 |
| Annonaceae | I | I | -186.51 | -186.97 |
| Centroleninae | CI | CI | -300.17 | -306.56 |
| Cinchoneae | I | I | -113.27 | -116.99 |
| *Ithomia* | A | A | -109.91 | -115.1 |
| *Leptodeira* | H | H | -73.94 | -76.96 |
| *Napeogenes* | AI | ACI | -108.24 | -109.36 |
| *Platyrrhinus* | I | BCI | -58.83 | -59.01 |
| *Podocnemis* | I | I | -11.6 | -10.92 |
| *Pristimantis* | BCI | CHI | -485.48 | -499.15 |
| *Pteronymia* | CHI | CHI | -274.45 | -280.31 |
| *Stenocercus* | ACI | AI | -88.4 | -97.03 |
| Tanagers | ACI | ACI | -250.89 | -260.21 |
| *Thamnophilus* | CGI | GI | -83.98 | -79.75 |
| *Tournefortia* clade | I | AI | -87.74 | -98.11 |

Note: *Composite reconstructions refers to a set of 2 or 3 areas. A: Central Andes, B: Eastern Cordillera, C: Central Cordillera, D: Western Cordillera, E: Magdalena valley, F: Cauca Valley, G: North-Caribbean, H: Central America, and I: Amazonian region.

**Table 4.**

*Number of single and composite reconstructions obtained by model.*

| | **DEC** | **DIVALIKE** | **TOTAL** | **Proportion of each set of areas** | | | |
|---|---|---|---|---|---|---|---|
| **Single area** | 7 | 6 | 13 | **I**<br>8 | **A**<br>2 | **H**<br>3 | |
| **% Single areas** | 0.47 | 0.40 | 43.33% | 0.62 | 0.15 | 0.23 | |
| **Two areas** | 3 | 4 | 7 | **HI**<br>1 | **CI**<br>2 | **AI**<br>3 | **GI**<br>1 |
| **% Two areas** | 0.20 | 0.27 | 23.33% | 0.14 | 0.29 | 0.43 | 0.14 |
| **Three areas** | 5 | 5 | 10 | **ACI**<br>4 | **BCI**<br>2 | **CHI**<br>3 | **CGI**<br>1 |
| **% Three areas** | 0.33 | 0.33 | 33.33% | 0.40 | 0.20 | 0.30 | 0.10 |

Note: *Composite reconstructions refers to a set of 2 or 3 areas. The proportion of each set within the reconstructions is shown on the right. A: Central Andes, B: Eastern Cordillera, C: Central Cordillera, D: Western Cordillera, E: Magdalena valley, F: Cauca Valley, G: North-Caribbean, H: Central America, and I: Amazonian region.

## Appendix E. Event analyses

### Table 5.

*Dispersal events obtained in the events analysis.*

| Area | Switch to | Lowlands | Highlands | From ancestral areas to Highlands & Lowlands | |
|---|---|---|---|---|---|
| | | | | To Lowlands | To Highlands |
| **I 25%** | H | | | **41%** | **59%** |
| | C | | 1 | | |
| | D | | 1 | | |
| | B | | 1 | | |
| | A | | | | |
| | E | 1 | | | |
| | G | 1 | | | |
| | BA | | 1 | | |
| | | **0.25** | **0.5** | | |
| **H 22%** | C | | 1 | | |
| | B | | 1 | | |
| | A | | | | |
| | G | 1 | | | |
| | EG | 1 | | | |
| | BA | | 1 | | |
| | FEG | 1 | | | |
| | | **0.43** | **0.43** | | |
| **A 19%** | I | | | | |
| | C | | 1 | | |
| | D | | 1 | | |
| | F | 1 | | | |
| | E | 1 | | | |
| | CI | | 1 | | |
| | | **0.33** | **0.5** | | |

| Area | Switch to | Lowlands | Highlands | From Highlands | |
|---|---|---|---|---|---|
| | | | | To Lowlands | To Highlands |
| **D* 13%** | H | | | **0%** | **54%** |
| | A | | | | |
| | BA | | 1 | | |
| | CI | | 1 | | |
| | | | **0.5** | | |
| **C* 9%** | H | | | | |
| | A | | | | |
| | BA | | 1 | | |
| | | | **0.33** | | |
| **B* 3%** | CI | | 1 | | |
| | | | **1** | | |
| **CI 6%** | B | | 1 | | |
| | A | | | | |
| | | | **1** | | |
| **CIH 3%** | BA | | 1 | | |
| | | | **1** | | |
| **Total of dispersions to highlands or lowlands** | | **21%** | **46%** | | |

* Highlands

Note: Percentage of dispersal events from ancestral areas towards highlands and/or lowlands. The percentage of dispersion from highlands to lowlands and between highlands is shown on the right part of the table. Highlands are marked with an asterisk (*). A: Central Andes, B: Eastern Cordillera, C: Central Cordillera, D: Western Cordillera, E: Magdalena valley, F: Cauca Valley, G: North-Caribbean, H: Central America, and I: Amazonian region.

## Appendix F. Hypothesis tests

### Table 6.

*Log-likelihood of each hypothesis test and comparisons between hypotheses and dispersal matrices.*

| | | | Hypotheses LogL | | | | Comparisons in terms of maximum likelihoods between hypotheses | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Taxon** | **ALL equal scenario** | **Matrix** | **Origin: Amazonian region, pattern: Lowlands to Highlands** | **Origin: Central America, pattern: Lowlands to Highlands** | **Origin: Central Andes, pattern: Highlands to Lowlands** | **Altitudinal and horizontal pattern** | △ 1&2 | △ 1&3 | △ 1&4 | △ 2&3 | △ 2&4 | △ 3&4 |
| *Annonaceae* | **156.86** | 2_1 | 285.71 | 394.49 | 333.59 | **328.18** | 108.28 | **4.94** | 46.27 | 103.34 | 62.01 | 41.33 |
| | | 3_1 | **281.91** | 390.93 | 334.36 | 337.59 | | | | | | |
| | | 4_1 | 282.67 | **390.19** | **286.85** | 328.60 | | | | | | |
| | | **Min △** | 0.76 | 0.74 | 46.74 | 0.42 | | | | | | |
| | | **Max △** | 3.80 | 4.30 | 47.51 | 9.41 | | | | | | |
| Cinchoneae | **113.28** | 2_1 | 215.21 | 323.34 | 214.38 | **223.36** | 33.14 | 54.35 | **14.58** | 87.49 | 18.56 | 68.93 |
| | | 3_1 | **208.78** | 353.63 | 214.72 | 233.67 | | | | | | |
| | | 4_1 | 238.54 | **241.92** | **154.43** | 230.28 | | | | | | |
| | | **Min △** | 6.43 | 81.42 | 59.95 | 6.92 | | | | | | |
| | | **Max △** | 29.76 | 111.71 | 60.29 | 10.31 | | | | | | |
| *Tournefortia* clade | **87.74** | 2_1 | 189.54 | 213.18 | 150.41 | **154.04** | **26.44** | 61.70 | 30.47 | 88.14 | 56.91 | 31.23 |
| | | 3_1 | **184.51** | **210.95** | 154.19 | 159.21 | | | | | | |
| | | 4_1 | 199.01 | 233.33 | **122.81** | 157.77 | | | | | | |
| | | **Min △** | 5.03 | 2.23 | 27.60 | 3.73 | | | | | | |
| | | **Max △** | 14.50 | 22.38 | 31.38 | 5.17 | | | | | | |
| *Ithomia* | **117.35** | 2_1 | 219.69 | 219.34 | 153.74 | **253.58** | **4.57** | 85.49 | 47.01 | 90.06 | 42.44 | 132.50 |
| | | 3_1 | **206.57** | 214.14 | 154.07 | 255.88 | | | | | | |
| | | 4_1 | 218.33 | **211.14** | **121.08** | 255.47 | | | | | | |
| | | **Min △** | 13.12 | 3.00 | 32.66 | 1.89 | | | | | | |
| | | **Max △** | 11.76 | 8.20 | 32.99 | 2.30 | | | | | | |
| *Napeogenes* | **108.24** | 2_1 | 228.31 | 242.85 | 153.38 | **200.86** | **5.34** | 91.62 | 19.33 | 96.96 | 24.67 | 72.29 |
| | | 3_1 | **220.19** | **225.53** | 155.40 | 206.30 | | | | | | |
| | | 4_1 | 238.57 | 228.18 | **128.57** | 202.54 | | | | | | |
| | | **Min △** | 8.12 | 2.65 | 24.81 | 1.68 | | | | | | |
| | | **Max △** | 18.38 | 17.32 | 26.83 | 5.44 | | | | | | |
| *Pteronymia* | **276.45** | 2_1 | 300.71 | 374.49 | 343.19 | **288.90** | 79.45 | 3.72 | **1.77** | 83.17 | 81.22 | 1.95 |
| | | 3_1 | 311.91 | 370.93 | 333.38 | 305.40 | | | | | | |
| | | 4_1 | **290.67** | **370.12** | **286.95** | 300.67 | | | | | | |
| | | **Min △** | 10.04 | 0.81 | 46.43 | 11.77 | | | | | | |
| | | **Max △** | 21.24 | 4.37 | 56.24 | 16.50 | | | | | | |
| Centroleninae | **300.55** | 2_1 | **435.42** | 472.54 | 403.88 | **514.42** | **30.42** | 97.73 | 79.00 | 128.15 | 48.58 | 176.73 |
| | | 3_1 | 445.27 | 466.73 | 399.95 | 524.91 | | | | | | |
| | | 4_1 | 463.92 | **465.84** | **337.69** | 516.13 | | | | | | |
| | | **Min △** | 9.85 | 0.89 | 62.26 | 1.71 | | | | | | |
| | | **Max △** | 28.50 | 6.70 | 66.19 | 10.49 | | | | | | |
| *Pristimantis* | **485.58** | 2_1 | 761.93 | 813.94 | 676.28 | **611.49** | **29.96** | 78.73 | 131.04 | 108.69 | 161.00 | 52.31 |
| | | 3_1 | **742.53** | 813.28 | 670.99 | 670.67 | | | | | | |
| | | 4_1 | 755.10 | **772.49** | **663.80** | 670.02 | | | | | | |
| | | **Min △** | 12.57 | 40.79 | 7.19 | 58.53 | | | | | | |
| | | **Max △** | 19.40 | 41.45 | 12.48 | 59.18 | | | | | | |
| *Leptodeira* | **73.94** | 2_1 | **123.79** | 238.06 | 134.16 | 110.24 | 108.51 | 75.99 | 19.83 | 184.50 | 128.34 | **56.16** |
| | | 3_1 | 132.58 | 232.62 | 120.08 | **103.96** | | | | | | |
| | | 4_1 | 155.55 | **232.30** | **47.80** | 109.90 | | | | | | |
| | | **Min △** | 8.79 | 0.32 | 72.28 | 5.94 | | | | | | |
| | | **Max △** | 31.76 | 5.76 | 86.36 | 6.28 | | | | | | |
| *Podocnemis* | **11.6** | 2_1 | 20.80 | 16.28 | 7.78 | 10.30 | 3.98 | 12.51 | 2.73 | 8.53 | 7.31 | **1.38** |
| | | 3_1 | 20.24 | 16.27 | **7.57** | 10.42 | | | | | | |
| | | 4_1 | **11.68** | **16.26** | 7.73 | **8.95** | | | | | | |
| | | **Min △** | 8.56 | 0.01 | 0.16 | 1.35 | | | | | | |
| | | **Max △** | 9.12 | 0.02 | 0.21 | 1.47 | | | | | | |
| *Stenocercus* | **88.9** | 2_1 | 170.25 | 157.47 | 121.29 | 128.01 | 37.30 | 46.64 | 40.13 | 9.34 | **2.83** | 6.51 |
| | | 3_1 | **167.34** | **130.04** | **120.70** | 129.01 | | | | | | |
| | | 4_1 | 168.55 | 138.64 | 121.11 | **127.21** | | | | | | |
| | | **Min △** | 1.21 | 8.60 | 0.41 | 0.80 | | | | | | |
| | | **Max △** | 2.91 | 27.43 | 0.59 | 1.80 | | | | | | |
| *Amazilia* | **95.08** | 2_1 | 148.62 | 183.37 | 145.95 | 144.30 | 37.15 | 30.08 | **0.37** | 67.23 | 37.52 | 29.71 |
| | | 3_1 | **142.14** | 187.17 | 145.60 | **141.77** | | | | | | |
| | | 4_1 | 167.19 | **179.29** | **112.06** | 146.00 | | | | | | |
| | | **Min △** | 6.48 | 4.08 | 33.54 | 2.53 | | | | | | |
| | | **Max △** | 25.05 | 7.88 | 33.89 | 4.23 | | | | | | |
| Tangaras | **450.01** | 2_1 | 661.93 | 713.94 | 576.28 | **630.49** | 29.96 | 101.73 | **12.04** | 131.69 | 42.00 | 89.69 |
| | | 3_1 | **642.53** | 713.28 | 570.99 | 635.67 | | | | | | |
| | | 4_1 | 655.10 | **672.49** | **540.80** | 638.02 | | | | | | |
| | | **Min △** | 12.57 | 40.79 | 29.48 | 5.18 | | | | | | |
| | | **Max △** | 19.40 | 41.45 | 30.19 | 7.53 | | | | | | |
| *Thamnophylus* | **83.98** | 2_1 | 169.47 | 193.18 | **170.41** | **174.04** | 26.37 | 5.83 | 9.46 | 20.54 | 16.91 | **3.63** |
| | | 3_1 | **164.58** | **190.95** | 174.29 | 179.29 | | | | | | |
| | | 4_1 | 170.01 | 193.33 | 171.81 | 177.97 | | | | | | |
| | | **Min △** | 4.89 | 2.23 | 1.40 | 3.93 | | | | | | |
| | | **Max △** | 5.43 | 2.38 | 3.88 | 5.25 | | | | | | |
| *Platyrrhinus* | **58.83** | 2_1 | **132.79** | 158.06 | 130.16 | 110.95 | 19.51 | 23.99 | 27.83 | 43.50 | 47.34 | **3.84** |
| | | 3_1 | 133.58 | 152.62 | 110.08 | **104.96** | | | | | | |
| | | 4_1 | 166.55 | **152.30** | **108.80** | 109.20 | | | | | | |
| | | **Min △** | 0.79 | 0.32 | 2.00 | 4.24 | | | | | | |
| | | **Max △** | 33.76 | 5.76 | 22.08 | 5.99 | | | | | | |

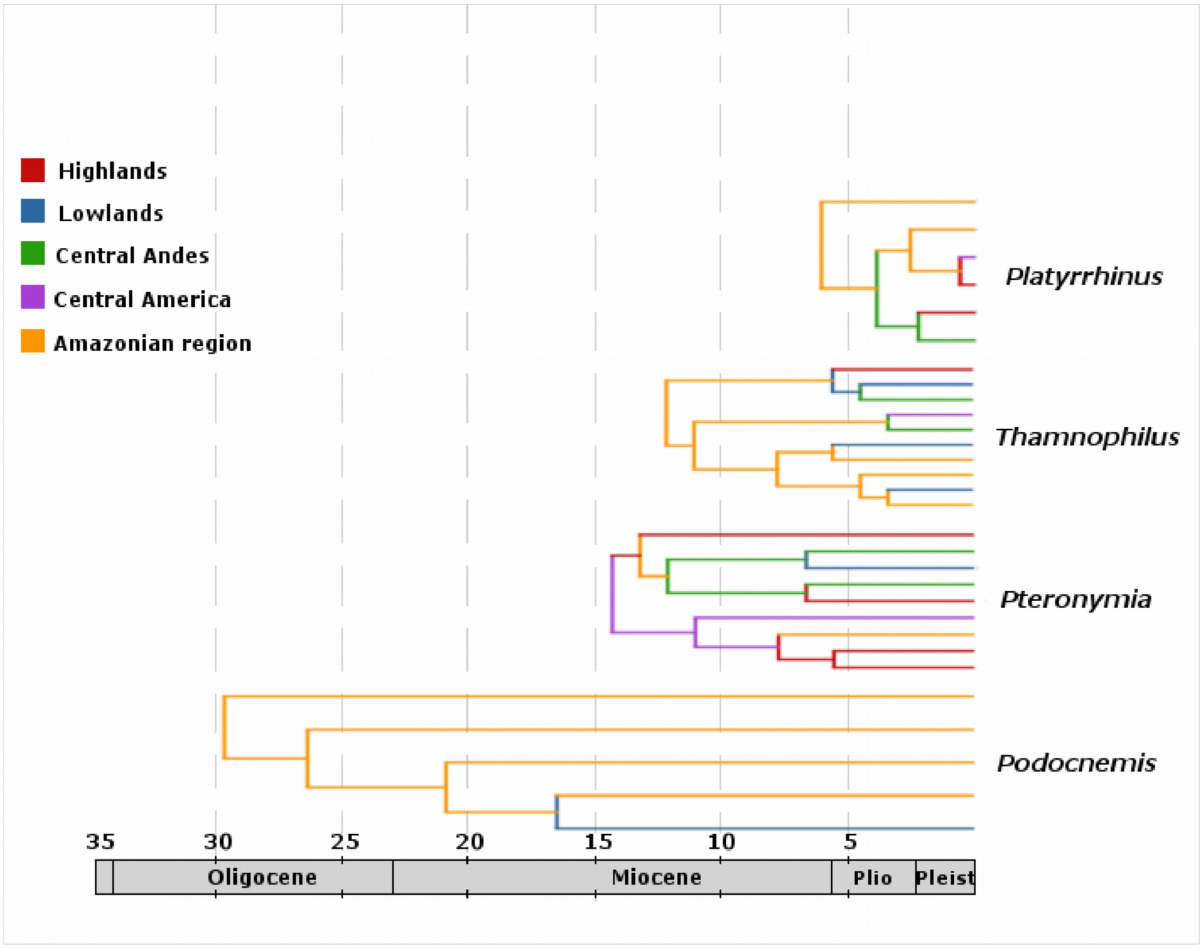


***Figure* 1.** Summary of ages and diversification patterns of *Platyrrhinus*, *Podocnemis*, *Pteronymia,* and *Thamnophilus*.