

RESEARCH ARTICLE

Areas of endemism of hummingbirds (Aves: Apodiformes: Trochilidae) in the Andean and Neotropical regions

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ABSTRACT. Using track analysis and cladistic biogeography, we identified areas of endemism of hummingbirds in the Andean and Neotropical regions. Our results point out that the current areas of endemism of hummingbirds occur in the Andes, Guiana Shield, the Lesser Antilles, western Central and North America and the Chiapas Highlands. The cladistic biogeographic analysis suggests a hummingbird distribution shaped mainly by dispersal events.

KEY WORDS. Historical biogeography, cladistic biogeography, dispersal events, PAE

INTRODUCTION

Biogeography is the science that aims at explaining the distribution of life on Earth and investigating the processes behind it. It also determines the historical relationship between the occurrence areas of a given taxon based on their distribution and phylogenetic analysis (Henderson 1991). According to Crother and Murray (2011), endemism is the concept most closely associated with distribution and results from both historical factors, as vicariance, and ecological factors, which are consistent with the current limits of the taxa (Morrone 2014b).

On the other hand, an area of endemism is a geographic region that has several taxa with their distribution restricted to it (Silva et al. 2004, Szumik and Goloboff 2004, Sirgrist and Carvalho 2009). According to the theory of vicariance, an area of endemism results from the fragmentation of the ancestral biota due to the emergence of a barrier that breaks the gene flow between populations and, consequently, results in allopatric speciation (Hausdorf and Hjenning 2003).

Based on the presence of endemic taxa, Morrone (2001a, b) delimited the Neotropical and Andean regions, which are natural biogeographic units. South America can be divided in two regions and, for some time it has been known that the Andes divides the continent into two very distinct areas. The tracks of several taxa that inhabit the western portion of South America

connect this area with Australia and New Zealand; whereas the tracks of several taxa that inhabit the eastern portion of the continent connect this area to the Old World tropics. Hence, the western portion of the continent belongs to the Andean region and the rest belongs to the Neotropical region, which extends to Central America, the Antilles, and Mexico, where it limits with the Nearctic region.

Transition zones are also important elements, because they show a mixture of biotic elements of two regions (Sánchez-González et al. 2013). They are important from a biological perspective, as they represent areas of biotic interactions and can either be poor or show a considerable diversity (Morrone 2006). In the present study, we considered two transition zones: the Mexican transition zone, which comprises Neotropical and Nearctic elements, and the South American transition zone, which includes Neotropical and Andean elements (Morrone 2004, 2006, 2014a).

Both in the Neotropical and Andean regions, as well as in the transition zones, several areas of endemism have been identified for different taxa (Cracraft 1985, Vázquez-Miranda et al. 2007, Silva et al. 2004, Escalante et al. 2009, Echeverry and Morrone 2010, Prado et al. 2015).

With the objective of contributing to the knowledge of the biogeography of these regions, we undertook a track analysis and a cladistic biogeographic analysis, aimed at identifying areas

of endemism of hummingbirds (Trochilidae) in the Andean and Neotropical regions. We also describe the distribution of hummingbirds in under the light of a current molecular phylogenetic hypothesis proposed for the taxon (McGuire et al. 2014).

MATERIAL AND METHODS

The Andean and Neotropical regions are natural biogeographic units delimited by the presence of endemic taxa (Morrone 2001a, 2014a).

We used as models 265 Trochilidae species (approximately 78% of hummingbirds' richness), which comprised the following clades proposed by Bleiweiss et al. (1997): Topazes, Hermits, Mountain Gems, Bees, Mangoes, Brilliants, Coquettes, Emeralds, and the species *Patagona gigas* (Vieillot, 1824). We obtained georeferenced records from the literature, consulted vouchers deposited in the ornithological collections of the Smithsonian Institution (<http://www.si.edu/Collections>) and the American Museum of Natural History (<http://www.amnh.org/our-research/vertebrate-zoology/ornithology>), and used the georeferenced point records available by BirdLife International (<http://www.birdlife.org>). Records without geographic coordinates or of doubtful origin were discarded from the study; therefore, it was not possible to sample 100% of the species of hummingbirds. Nomenclature follows Clements et al. (2012).

Track analysis is based on three basic concepts: individual tracks, generalized tracks, and nodes (Morrone and Crisci 1995). In the present study, we plotted hummingbird locality records on maps of the Andes and Neotropics using the shapefiles of the regions of Löwenberg-Neto (2014, 2015) in the software DIVA-GIS 7.5 (Hijmans et al. 2012).

We connected each locality to the nearest one, forming individual tracks. Superimposed individual tracks formed generalized tracks, which are areas where a former ancestral biota have fragmented due to vicariance events (Morrone and Escalante 2002, Carvalho 2011). Where two or more generalized tracks overlap, a node is identified, which is considered a high diversity zone (Morrone and Escalante 2002).

For this analysis, we used a parsimony analysis of endemism (PAE) that classifies areas according to the species they share, which allows the identification of biotic relationships (Morrone and Crisci 1995, Urtubey et al. 2010). We built a presence/absence matrix (1/0) of each species based on individual tracks. We analyzed this matrix in the software WINCLADA (Nixon 1999) and built a cladogram. After the first analysis, we implemented a PAE-PCE or PAE with progressive character elimination, which consists in removing from the matrix synapomorphies (species) that define each clade, and successively carrying out parsimony analyses (Luna-Vega et al. 2000, Urtubey et al. 2010).

With this analysis, we sought to identify areas where ancestral populations of hummingbirds were fragmented by vicariance events. This analysis is possible through the generalized tracks (Morrone and Escalante 2002).

Cladistic biogeographic analysis

This analysis consists in replacing the name of the species with the area where it is distributed in the terminal branches of the taxon cladogram. The congruence between different area cladograms will allow obtaining a general area cladogram, whose sequence indicates its historical separation (Morrone and Escalante 2002). We used as a framework the molecular phylogeny of McGuire et al. (2014). The areas that replaced the species were the biogeographic provinces proposed by Morrone (2014a, 2015) for the Andean and Neotropical regions.

For each species of the cladogram we analyzed its individual track. This way, we obtained the provinces where each species was recorded. Based on this analysis, we built a presence/absence matrix (1/0), in which the rows were biogeographic provinces and the columns, species. Based on this matrix, we obtained the general cladograms of the areas using the software WinClada. Data from this study, the species used and the location of biogeographic provinces are presented in the supplementary material (Fig. S1 and Table S1).

RESULTS

Generalized tracks

Based on the superimposition of the individual tracks, we found 17 generalized tracks (Fig. 1), with the support of species of almost all clades. *Patagona gigas* and all the species of the clade that includes Topazes did not belong to any of the generalized tracks. Some generalized tracks coincide partially with tracks found for other plant and animal groups (Table 1).

Cladistic biogeography

The general area cladogram (Fig. 2) places the Ecuadorian province as the sister group of almost all the provinces of the Neotropical region, except Galapagos Islands, Atacaman, and Prepuna (Fig. 2 and Table 2).

Considering the area cladograms for each clade, the cladogram obtained in the biogeographic analysis for Topazes supports Araucaria Forest as the sister group of ((Atlantic, Parana Forest) Cerrado (Caatinga (Xingú-Tapajós (Pará (Roraima (Guiana Lowlands (Pantepui (Imeri, Madeira)))))). The synapomorphic species of this clade, *Florisuga fusca*, was probably extinct in (Xingú-Tapajós (Pará (Roraima (Guiana Lowlands (Pantepui (Imeri, Madeira)))))) (see Fig. 2).

The Hermits clade shows a broad distribution, from the Mexican transition zone to the provinces of the Southern Brazil dominion, the South American transition zone and the Chacoan sub-region. The area cladogram implies several dispersal events and two synapomorphies, all in South America (Table 2). The first synapomorphies supports the dichotomy between the Atlantic and Parana Forest, and the second places Rondonia province as the sister group of (Ucayali (Napo (Páramo (Magdalena, Cauca)))).

Table 1. Support of the generalized track of Trochilidae and superimposition of other tracks.

Track	Species	Provinces (Morrone 2014a, 2015)	Overlapping tracks
A	<i>Eulampis holosericeus</i> and <i>Oreotrochilus estella</i>	Lesser Antilles	Echeverry and Morrone (2013) – (Animal and plants) and del Río et al. (2015) – Coleoptera
B	<i>Leucippus baeri</i> and <i>Myrmia micrura</i>	Ecuadorian + Cauca	Escalante et al. (2011) – (Nematoda)
D	<i>Atthis ellioti</i> ; <i>Campylopterus rufus</i> and <i>Doricha enicura</i>	Chiapas Highlands + Veracruz	Escalante et al. (2011) – (Nematoda)
E	<i>Chalcostigma ruficeps</i> , <i>Heliodoxa aurescens</i> , <i>H. branickii</i> and <i>Eriocnemis sapphiropygia</i>	Puna + Rondônia + Ucayali	Alzate et al. (2008) – (Alstroemeriaceae), Escalante et al. (2011) – (Nematoda) and Echeverry and Morrone (2010) – (Vascular plants)
F	<i>Adelomyia melanogenys</i> , <i>Amazilia viridicauda</i> , <i>Chalcostigma stanleyi</i> and <i>Metallura eupogon</i>	Puna + Rondônia + Ucayali	Alzate et al. (2008) – (Alstroemeriaceae) and Escalante et al. (2011) – (Nematoda)
G	<i>Aglaeactis aliciae</i> and <i>Metallura phoebe</i>	Puna	del Río et al. (2015) – Coleoptera
L	<i>Amazilia decora</i> , <i>Chlorostilbon assimilis</i> , <i>Elvira chionura</i> , <i>Eupherusa nigriventris</i> , <i>Lampornis calolaemus</i> , <i>L. hemileucus</i> , <i>Lophornis adorabilis</i> , <i>Selasphorus flammula</i> and <i>S. scintilla</i>	Guatuso-Talamanca + Puntarenas-Chiriquí	Escalante et al. (2011) – (Nematoda) and Escalante et al. (2011) – (Nematoda)
M	<i>Chaetocercus heliodor</i> and <i>Heliangelus mavors</i>	Guajira	Alzate et al. (2008) – (Alstroemeriaceae)
N	<i>Amazilia castaneiventris</i> , <i>A. saucerrottei</i> , <i>Anthocephala floriceps</i> , <i>Boissonneaua flavescens</i> and <i>Coeligena bonapartei</i>	Magdalena + Cauca	Alzate et al. (2008) – (Alstroemeriaceae)
O	<i>Heliangelus exortis</i> , <i>Heliodoxa imperatrix</i> and <i>Metallura williami</i>	Cauca	Alzate et al. (2008) – (Alstroemeriaceae)
P	<i>Eriocnemis nigriventris</i> , <i>Haplophaedia lugens</i> , <i>Heliangelus strophianus</i> and <i>Urochroa bougueri</i>	Cauca	del Río et al. (2015) – Coleoptera and Alzate et al. (2008) – (Alstroemeriaceae)
R	<i>Archilochus colubri</i> and <i>Hylocharis eliciae</i>	Guatuso-Talamanca + Pacific Lowlands + Chiapas Highlands	Escalante et al. (2011) – (Nematoda)

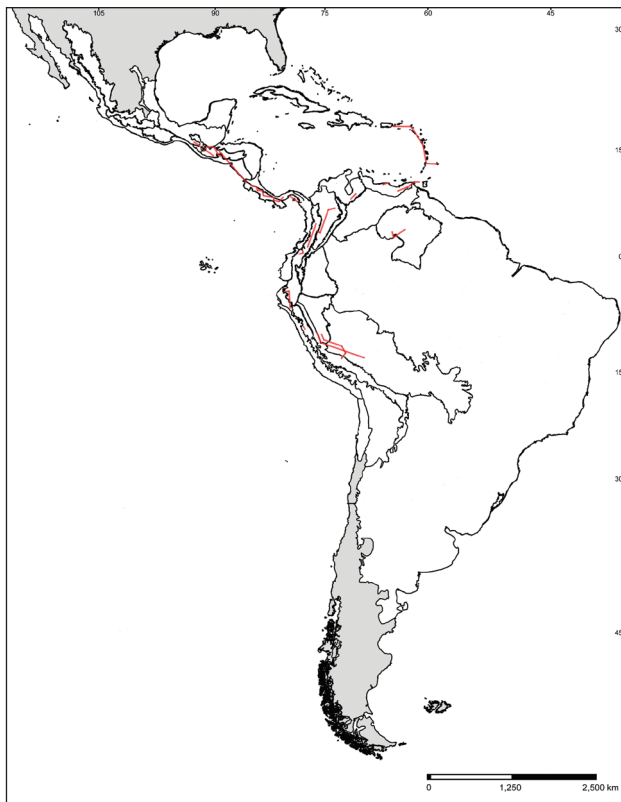


Figure 1. Generalized tracks for Trochilidae in the Neotropical and Andean regions.

The Mountain Gems clade shows a more restricted distribution than the previous clades. It occurs from the Mexican transition zone to the provinces in northern South America, in the Pacific dominion. The area cladogram supports with four synapomorphies the monophyly of the provinces Guatuso-Talamanca and Puntarenas-Chiriquí.

The distribution of the Bees clade is associated with the provinces close to the Pacific coast, in the western part of the American continent, from the Mexican transition zone to the South American transition zone. The area cladogram shows only one synapomorphy, which places the Transmexican Volcanic Belt as the sister group of (Sierra Madre del Sur, Balsas Basin). The other clade places the Desert province as the sister group of (Puna (Yungas (Rondônia (Ucayali (Napo (Paramo (Magdalena, Cauca)))))) and Rondônia as the sister group of (Ucayali (Napo (Paramo (Magdalena, Cauca)))).

The distribution of the Mangoes clade comprises the Mexican transition zone, the Antilles, all the Brazilian sub-region, part of the South American transition zone, and the Xingú-Tapajós province, in the South-eastern Amazonian dominion. The area cladogram shows groups supported by a single synapomorphy, in which the sister group of (Pará (Roraima (Guianan Lowlands (Pantepui (Imerí, Madeira)))) is followed by Pantepui of (Imerí, Madeira). In the Antilles sub-region, there is the clade Hispaniola and Puerto Rico, and in the Brazilian sub-region, the clade Guatuso-Talamanca and Puntarenas-Chiriquí.

The clade Brilliants is distributed from the Mesoamerican dominion to the South American transition zone, and some provinces of the Pacific, Boreal Brazilian and Chacoan domin-

Table 2. Events of dispersal, extinction and synapomorphies represented in the cladogram (Fig. 2). Each number represents the events described.

Number in the cladogram	Synapomorphy	Dispersal	Extinction
2	Ancestor of Brilliants, Coquettes, Montain Gems, Patagona gigas, Bees and Emeralds	Ancestor of Topazes and Hermits	-
3	Bees and Patagona gigas	-	-
4	Ancestor of Patagona gigas, Montain Gems, Bees and Emeralds	Ancestor of Brilliants, Coquettes, Montain Gems, Patagona gigas, Bees and Emeralds	-
5	-	Mangoes and ancestor of Topazes and Hermits	-
6	-	Emeralds and Mangoes	-
7	-	Coquettes, Emeralds, Hermits and ancestor of Hermits	-
8	-	Brilliants, Emeralds and Hermits	-
9	-	Brilliants, Mangoes and ancestor of Brilliants, Coquettes, Montain Gems, Patagona gigas, Bees and Emeralds	Mangoes
10	-	Brilliants, Coquettes, Mangoes, Hermits and ancestor of Coquettes	-
11	Brilliants and Coquettes	Brilliants, Coquettes, Emeralds, Montain Gems, Topazes, Patagona gigas and ancestor of Topazes and Bees	-
12	Coquettes	Brilliants and Emeralds	-
13	Brilliants, Coquettes and Emeralds	Brilliants, Coquettes, Hermits and Mangoes	-
14	Brilliants and Hermits	Bees, Brilliants, Emeralds, Hermits and Mangoes	-
15	Brilliants, Emeralds and Hermits	Emeralds and Hermits	Coquettes and Emeralds
16	Brilliants and Coquettes	Brilliants, Hermits, Mangoes and ancestor of Mangoes	Brilliants and Emeralds
17	Brilliants	Brilliants, Emeralds, Mangoes, Montain Gems and ancestor of Montain Gems and Bees	-
18	Brilliants, Coquettes and Emeralds	Coquettes, Emeralds, Hermits and Mangoes	Hermits
19	-	Ancestor of Montain Gems, Bees, Emeralds and Patagona gigas	-
20	-	Ancestor of Brilliants, Coquettes, Montain Gems, Bees, Emeralds and Patagona gigas	-
21	-	Brilliants and Mangoes	-
22	Coquettes	Brilliants	-
23	-	Ancestor of Montain Gems, Bees, Emeralds and Patagona gigas	-
24	-	Brilliants, Emeralds and Mangoes	-
25	-	-	Ancestor of Mangoes, Brilliants, Coquettes, Montain Gems, Emeralds and Patagona gigas
26	-	Emeralds	-
27	-	Emeralds	Emeralds
28	-	Emeralds	-
29	-	Emeralds	-
30	-	Emeralds	-
31	-	Coquettes, Montain Gems and ancestor of Montain Gems and Bees	Emeralds
32	-	Emeralds, Mangoes, Patagona gigas and ancestor of Bees, Brilliants, Coquettes, Emeralds, Hermits, Mangoes, Montain Gems and Topazes	-
33	-	Emeralds and Hermits	-
34	-	Bees, Coquettes, Emeralds, Mangoes, Montain Gems, Patagona gigas and ancestor of Topazes, Hermits, Coquettes, Brilliants, Mantoos, Montain Gems, Bees and Emeralds	-
35	-	Bees	-
36	-	Hermits and Montain Gems	-
37	-	Emeralds	-
38	Emeralds	Emeralds and Hermits	-
39	Ancestor of Topazes	Hermits, Topazes and ancestor of Hermits and Topazes	-
40	-	Hermits and Mangoes	-
41	Emeralds	Hermits and Emeralds	-
42	Brilliants, Emeralds and Hermits	Brilliants, Mangoes, Patagona gigas, and ancestor of Bees, Brilliants, Coquettes, Emeralds, Mangoes and Montain Gems	-
43	-	Hermits and Montain Gems	-
44	Hermits	-	-
45	-	Emeralds and Hermits	Emeralds
46	-	Hermits	-

Number in the cladogram	Synapomorphy	Dispersal	Extinction
47	–	Hermits	Emeralds and Hermits
48	–	Emeralds	Hermits
49	Mangoes	Mangoes, Patagona gigas and ancestor of Bees, Brilliants, Coquettes, Emeralds, Mangoes and Montain Gems	Topazes
50	–	Emeralds and Hermits	Emeralds and Hermits
51	–	Mangoes	Ancestor of Hermits and Topazes
52	–	Emeralds, Hermits and Mangoes	–
53	Coquettes	Brilliants, Emeralds, Mangoes, Patagona gigas and ancestor of Bees, Brilliants, Coquettes, Emeralds and Montain Gems	–
54	–	–	Hermits and Mangoes
55	Mangoes	Mangoes	Emeralds
56	Emeralds	Emeralds	Hermits
57	Hermits	Brilliants, Emeralds, Hermits, Topazes and ancestor of Brilliants	Emeralds
58	–	Brilliants, Coquettes and Hermits	Mangoes and Topazes
59	–	Emeralds and Mangoes	Brilliants, Coquettes, Hermits, Patagona gigas and ancestor of Bees, Brilliants, Coquettes, Emeralds, Montain Gems
60	Emeralds and Mangoes	Emeralds	–
61	Mangoes	Emeralds	–
62	–	Emeralds	–
63	Emeralds and Mangoes	Mangoes	–
64	Emeralds and Mangoes	Bees, Emeralds, Mangoes and Montain Gems	–
65	–	Emeralds, Mangoes	–
66	–	Emeralds, Hermits and Montain Gems	Mangoes
67	Emeralds	Emeralds and Mangoes	–
68	–	Emeralds and Hermits	Coquettes and Hermits
69	–	Bees, Emeralds, Hermits, Mangoes and Montain Gems	–
70	–	–	Hermits
71	–	Bees, Emeralds and Mangoes	–
72	–	Emeralds	–
73	–	Emeralds, Hermits and Montain Gems	Emeralds
74	–	Brilliants, Emeralds, Hermits and Mangoes	Emeralds, Patagona gigas and ancestor of Bees, Brilliants, Coquettes, Emeralds, Hermits, Mangoes, Montain Gems and Topazes
75	–	Coquettes, Emeralds, Mangoes, Montain Gems and ancestor of Bees and Montain Gems	–
76	–	Brilliants, Coquettes, Emeralds and Hermits	Brilliants
77	–	Emeralds, Hermits and Mangoes	–
78	Emeralds	Brilliants, Coquettes, Emeralds, Hermits and Mangoes	–
79	Emeralds	Emeralds, Hermits and Mangoes	Brilliants and Coquettes
80	Brilliants	Brilliants, Coquettes, Emeralds and Montain Gems	Brilliants, Coquettes and Emeralds
81	–	Brilliants, Coquettes and Emeralds	Mangoes
82	Emeralds	Brilliants and Emeralds	Emeralds and Mangoes
83	Emeralds, Mangoes and Montain Gems	Bees, Emeralds, Mangoes and Montain Gems	Brilliants
84	Emeralds	Bees and Hermits	Montain Gems
85	Montain Gems	Emeralds and Montain Gems	Emeralds
86	Bees	Bees and Hermits	Emeralds
87	–	–	Patagona gigas, Emeralds and Montain Gems
88	Brilliants	Emeralds and Hermits	Brilliants and Coquettes
89	–	–	Brilliants and Patagona gigas
90	–	–	Coquettes and Brilliants
91	–	Bees	Emeralds and Hermits

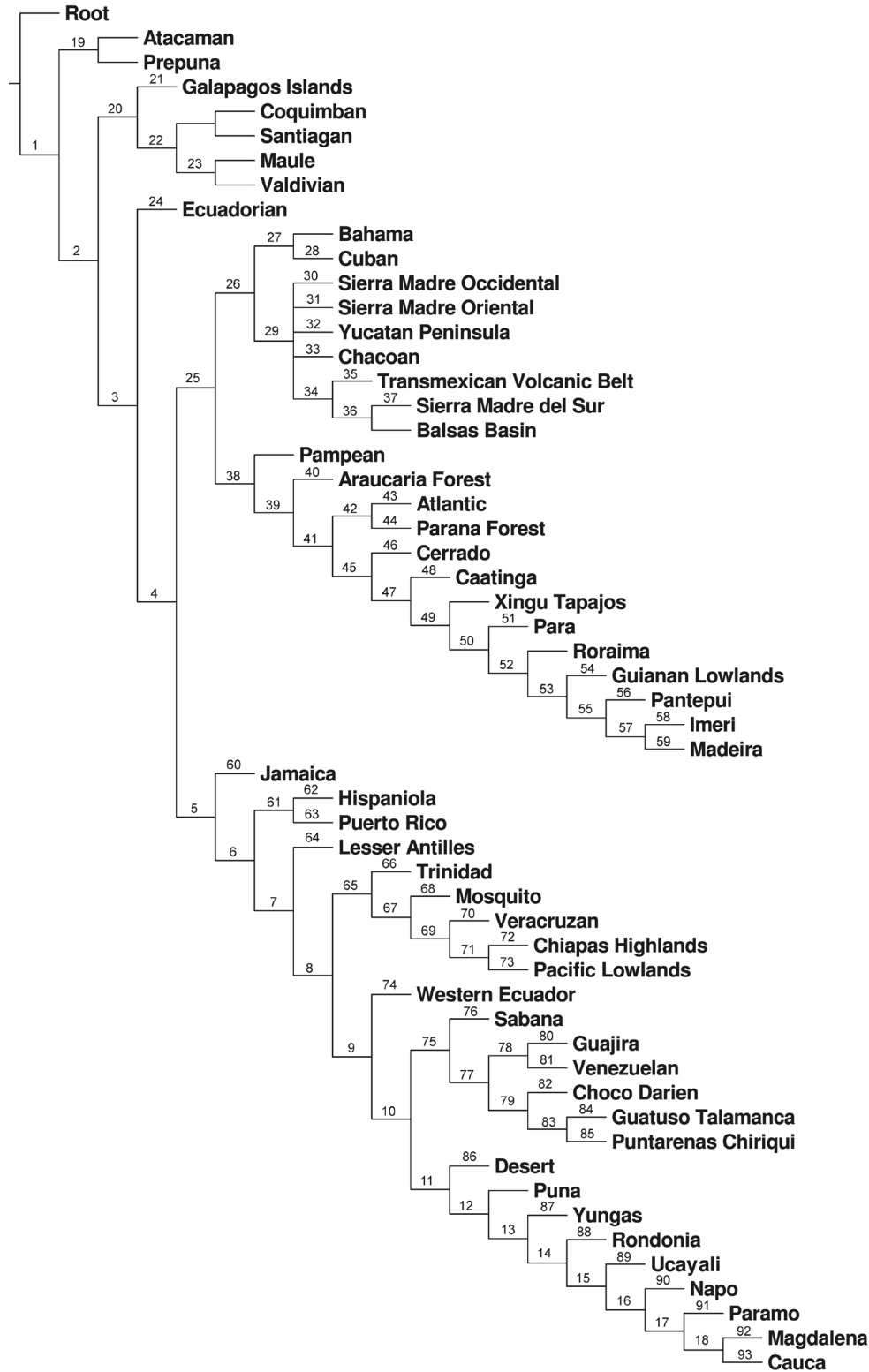


Figure 2. General area cladogram for Trochilidae. Events of dispersal, extinction, and synapomorphies detailed in the Table 2.

ions. The area cladogram shows nine synapomorphies; the best was supported by Yungas as the sister group of (Rondônia (Ucayali (Napo (Páramo (Magdalena, Cauca))))), Ucayali as the sister group of (Napo (Páramo (Magdalena, Cauca))), and Páramo as the sister group of (Magdalena, Cauca).

The clade Coquettes is distributed in western Neotropical provinces and some provinces of the Andes and South American transition zone. The area cladogram shows the extinction of the entire clade in the provinces Chocó-Darién, Guatuso-Talamanca, and Puntarenas-Chiquirí and strongly supports three groups. The first places Desert as the sister group of (Puna (Yungas (Rondônia (Ucayali (Napo (Páramo (Magdalena, Cauca)))))), the second places Puna as the sister group of (Yungas (Rondônia (Ucayali (Napo (Páramo (Magdalena, Cauca))))), and the third supports the clade Magdalena + Cauca.

The clade Emeralds showed the largest number of records and also the largest distribution, which comprises the Mexican transition zone, the Antilles, and almost all the Neotropical provinces of South America, as well as part of the South American transition zone. The area cladogram showed 11 synapomorphies. The first places the Ecuadorian province as the sister group of the provinces in the Neotropical region and the Mexican transition zone except (Atacaman, Prepuna) and Galapagos Islands and Pampean as the sister group of (Araucaria forest (Atlantic, Parana forest) (Cerrado (Caatinga (Xingu-Tapajós (Pará (Roraima (Guianan Lowlands (Pantepui (Imeri, Madeira))))))), also in the same clade between Atlantic and Parana forest, Pantepui and (Imeri, Madeira). In addition, Mosquito is the sister group of (Veracruzian (Chiapas Highlands, Pacific Lowlands)), Guajira and Venezuelan, Choco-Darién is the sister area of (Guatuso-Talamanca, Puntarenas-Chiquirí), Yungas is the sister group of (Rondônia (Ucayali (Napo (Paramo (Magdalena, Cauca))))), Ucayali is the sister group of (Napo (Paramo (Magdalena, Cauca))). The clade Magdalena + Cauca is supported, though weakly.

DISCUSSION

Generalized tracks

The track analysis suggests that current areas of endemism of hummingbirds occur in the Andes, Guiana Shield, Lesser Antilles, western Central and North America. In southern Mexico, more precisely in the Chiapas Highlands province, there is a biogeographic node: a zone of complex diversity for the family (Fig. 1). It is likely that vicariance events, especially of geological nature, occurred in these areas and involved all clades. In addition, the areas of endemism of Trochilidae in South America are within or partially superimpose the areas identified by Cracraft (1985) for the bird fauna. The generalized tracks corroborate some current hypotheses about the phylogeography of the family and reflect the geological, climatic, and tectonic events that occurred in the Neotropical and the Andean regions (McGuire et al. 2007, 2009, 2014, Bleiweiss et al. 1997, Bleiweiss 1998, 2008, Fogden et al. 2014).

Track "A" comprises the entire province of Lesser Antilles and part of Hispaniola, and is supported by Mangoes (*Eulampis holosericeus* (Linnaeus, 1758)) and Coquettes (*Oreotrochilus estella* (d'Orbigny & Lafresnaye, 1838)). This track suggests the fragmentation of the hummingbird population as had already occurred for other taxa (Ricklefs and Bermingham 2008), due to the effects of the geological history of Lesser Antilles. This track partially superimposes with the tracks obtained by Echeverry and Morrone (2013) and Del Río et al. (2015).

Tracks "B", "E", "F", "G", "M", "N", "O", and "P" are related to the uplift of the northern, southern, and central parts of the Andes and are supported by Bees (*Chaetocercus heliodor* (Bourcier, 1840) and *Myrmia micrura* (Gould, 1854)), Emeralds (*Amazilia castaneiventris* (Gould, 1856)), *A. saucerrottei* (Delattre & Bourcier, 1846), *A. viridicauda* (von Berlepsch, 1883), *Anthocephala floriceps* (Gould, 1853) and *Leucippus baeri* (Simon, 1901), Coquettes (*Adelomyia melanogenys* (Fraser, 1840), *Chalcostigma ruficeps* (Gould, 1846), *C. stanleyi* (Bourcier, 1851), *Heliangelus exortis* (Fraser, 1840), *H. mavors* Gould, 1848, *H. strophianus* (Gould, 1846), *Metallura eupogon* (Cabanis, 1874), *M. phoebe* (Lesson & Delattre, 1839) and *M. williami* (Delattre & Bourcier, 1846)) and Brilliants (*Aglaeactis aliciae* Salvin, 1896, *Boissonneaua flavescens* (Loddiges, 1832), *Coeligena bonapartei* (Boissonneau, 1840), *Eriocnemis mirabilis* Meyer de Schauensee, 1967, *E. nigrivestris* (Bourcier & Mulsant, 1852), *E. sapphiropygia* Taczanowski, 1874, *Haplophaedia lugens* (Gould, 1852), *Heliodoxa aurescens* (Gould, 1846), *H. branickii* (Taczanowski, 1874), *H. imperatrix* (Gould, 1856) and *Urochroa bougueri* (Bourcier, 1851) and comprise the Ecuadorian, Cauca, Desert, Ucayali, Rondônia, Yungas, Guajira, Magdalena, and Chocó-Darién provinces. The importance of the Andes for hummingbirds has been highlighted in several studies (Schuchmann et al. 2001, Weller and Schuchmann 2002, Schuchmann et al. 2003, Parra et al. 2009, Chaves et al. 2011) and corroborated by generalized tracks. According to Bleiweiss (1998), the main reason for the spectacular radiation of hummingbirds is their ecological capacity of colonizing high altitude habitats formed by the orogeny of the Andes, this fauna comprising several lineages with lowland origin. Moreover, the high potential for coevolution between hummingbirds and plants probably facilitated the success of the Andean taxa. On the other hand, McGuire et al. (2014) highlight the opening of new niches with the uplift of the Andes for well-succeeded colonization in that environment. Some species stand out in this habitat, especially the members of the clades Brilliants and Coquettes (McGuire et al. 2009). The tracks partially superimpose those obtained by Alzate et al. (2008), Echeverry and Morrone (2010), Escalante et al. (2011) and Del Río et al. (2015).

Tracks "H" and "J" comprise the Venezuelan and Trinidad provinces, in the Cordillera de La Costa and are supported by Emeralds (*Campylopterus ensipennis* (Swainson, 1822) and *Chalybura buffoni* (Lesson, 1832)), Bees (*Chaetocercus jourdani* (Bourcier, 1839)) and Hermits (*Phaethornis longuemareus* (Lesson, 1832)).

Most of track “Q” is located in the Pantepui and part of Imerí, and is supported by Brilliants (*Heliodoxa xanthogonys* Salvin & Godman, 1882) and Emeralds (*Amazilia cupreicauda* Salvin & Godman, 1884). The area comprises a mountain complex whose importance and formation will be discussed later.

Track “I” is supported only by Emeralds (*Lepidopyga coeruleogularis* (Gould, 1851)) and *Juliamyia julie* (Bourcier, 1843) and comprises the provinces of Chocó-Dárien and Guatuso-Talamanca. Therefore, we hypothesize that the closing of the Isthmus of Panama, at approximately 3-5 million years ago, affected the distribution of Trochilidae in the area.

Tracks “C”, “D”, “L” and “R” are supported by Mountain Gems (*Heliomaster constantii* (Delattre, 1843), *Lamprolaima rhami* (Lesson, 1839), *Lampornis calolaemus* (Salvin, 1865) and *L. hemileucus* (Salvin, 1865)), Bees (*Archilochus colubris* (Linnaeus, 1758), *Atthis ellioti* Ridgway, 1878, *Doricha enicura* (Vieillot, 1818), *Selasphorus flammula* Salvin, 1865, *S. scintilla* (Gould, 1851), *Tilmatura dupontii* (Lesson, 1832)), Emeralds (*Amazilia decora* (Salvin, 1891), *Campylopterus rufus* Lesson, 1840, *Chlorostilbon assimilis* Lawrence, 1861, *Elvira chionura* (Gould, 1851), *Eupherusa nigriventris* Lawrence, 1868 and *Hylocharis eliciae* (Bourcier & Mulsant, 1846) and Coquettes (*Lophornis adorabilis* Salvin, 1870). In the same area, there is also a biogeographic node. It comprises the provinces located in the Mexican transition zone and the Mesoamerican dominion. All tracks are located in provinces of the western coast, close to the Pacific Ocean. The tracks partially superimpose with those obtained by Escalante et al. (2011).

Paleogeographic events

Some important events that occurred in the Andean and Neotropical region during the Neogene equally influenced different clades of Trochilidae: uplift of the Andes (Gregory-Wodzicki 2000, Ramos 2009), the change of course of large rivers (Hoorn et al. 1995, Gamero 1996, Lovejoy et al. 1998, Lundberg et al. 1998, Nie et al. 2010, Sacek 2014), the closing of the Amazonian and Paranaense seas (Webb 1995), the closing of the Isthmus of Panama (Fortunato 2008, Farris et al. 2011), tectonic, volcanic, and climatic events in Central and North America (Pregill 1981, Briggs 1987, Pindell and Barret 1990, Hedges 1996, Ricklefs and Bermingham 2008), the Last Glacial Maximum (LGM) and, consequently, the rise in sea level and climate changes (Pregill and Olson 1981, Bourgouis et al. 1984, Codignotto et al 1992, Ferreira 2002, Filho et al. 2002), forest expansion and retraction (Filho et al 2002), volcanism (Fortunato 2008), and tectonism (Ramos 2009), and demonstrated in biogeographic analyses. Hence, we notice that the current distribution of Neotropical and Andean hummingbirds reflects the complex geological history of the region, which influenced the clades differently as we discuss as follows.

Hummingbirds and northern South America

Tectonic processes of the Andean orogeny reshaped South America nearly to the current form (Ramos 2009, Revollo 2015)

and were crucial for the conformation of the current distribution of the family Trochilidae through vicariant events and the subsequent opening of new niches (McGuire et al. 2007, 2014). In addition, according to the generalized tracks, these tectonic processes divided the ancestral populations of hummingbirds. Uplift processes and all their resulting modifications in South America affected the populations of Emeralds, which can be corroborated by the presence of a generalized track (Fig. 1). Based on a molecular clock, the minimum age of hummingbirds has been postulated to be 65 Ma (Pacheco et al. 2011), at the K/T boundary.

The tectonism involved with the uplift of the central and northern parts of the Andes changed the drainage of large rivers, such as the Amazon, Orinoco, and Magdalena, and established the connection of the Amazon River with the Atlantic Ocean, completing the Amazon-Caribbean connection through the “Amazonian sea or Caribbean sea” (Hoorn et al. 1995, Webb 1995, Lundberg et al. 1998 Hernández et al. 2005, Nie et al. 2010, Sacek 2014, Revollo 2015). Trochilidae populations, in particular Hermits, may have been affected during this north-east movement of the Amazon River. The presence of a generalized track (Fig. 1) indicates that ancestral populations have been fragmented by vicariance events in this area. Our hypothesis is that the movement of the river has fragmented the population of hummingbirds.

Still in the context of the Andes, with the uplift of the Cordillera Oriental (East Andes) there was the formation of an arid valley (Magdalena Valley) and change in the drainage of the Magdalena River (Hoorn et al. 1995, Lundberg et al. 1998, Egbue and Kellogg 2012, Muñoz-Ortiz et al. 2015), which affected other taxa (Muñoz-Ortiz et al. 2015) and hummingbirds, in particular the clades Brilliants and Coquettes, as indicated by the presence of a generalized track (Fig. 1). This event may have acted in a similar way to the Amazon River, that is, this change in the course of the river may have fragmented ancestral hummingbird populations.

In addition to the Andes, the Pantepuis, located in northern South America also showed a significant relevance for Trochilidae, as a generalized track occurs in the region (Fig. 1). The Pantepuis are a mountain complex that belongs to the Precambrian Guiana Shield, which was separated from the African Shield by the opening of the South Atlantic. It contains the largest rivers in the world in terms of annual discharge (Désamoré et al. 2010, Costa et al. 2013). This area is particularly important for Mangoes, Brilliants, and Emeralds.

Generalized tracks indicate ancestral populations that have been fragmented by vicariance events (Morrone and Escalante 2002). Therefore, events involving Andean orogenic processes, changes in the Amazon and Magdalena Rivers, and the formation of the Pantepuis may have acted as barriers that fragmented the ancestral population of hummingbirds.

The relevance of the Andean orogeny for Trochilidae was pointed out by McGuire et al. (2014) and highlights the impor-

tance of the Neogene for the radiation of several taxa, including hummingbirds (Bleiweiss 1998). Our work corroborates the postulate by the authors, highlighting the importance of the upward “pulses” and all the geological changes that have taken place, the forms in South America, as the molding processes of the current distribution of the group in the continent.

Hummingbirds and the Last Glacial Maximum

Another important event in the Neotropical region was the Last Glacial Maximum, which produced profound changes in the physical geography of Earth (Hoorn et al. 1995, Ferreira 2002). Climatic fluctuations during the last million years led to long periods of global cooling, which changed the distribution of many species (Hewitt 2000). During the glacial period in the Pleistocene, the southern part of the Atlantic Forest became climatically unstable in comparison with its central part and served as refuge for several Neotropical species (Carnaval et al. 2009). The region also underwent with a drop in rainfall during the Mid-Holocene, when its climate was drier than today (Melo and Marengo 2008). The current Araucaria forest underwent a significant retraction during the Last Glacial Maximum, and it is thought to have been rare in high altitude areas (Behling 1998). The climatic gradient created by this event in the Neotropics, more precisely in the Atlantic Forest, was significant for Topazes, Brilliants, Emeralds, and Hermits.

Hummingbirds, North America and Mesoamerica

The closing of the Isthmus of Panama occurred at 3-5 million years ago and brought severe climatic and geological changes (Briggs 1987, Kellogg and Veja 1995, Coates et al. 2004, Fortunato 2008, Farris et al. 2011, Bacon et al. 2015). It comprised the tectonic collision between South America and Panama, which closed the connection between the Pacific Ocean and the Caribbean Sea and formed an important bridge for the exchange of fauna and flora (Farris et al. 2011, O’Dea et al. 2012). There was also a floristic diversification, which facilitated the dispersal of some birds, including hummingbirds (Ornelas et al. 2014). Concomitantly, there was an uplift of the Andes in northern Colombia (Kellogg and Veja 1995, Farris et al. 2011). The presence of generalized tracks (Fig. 1 and Suppl. material 1) demonstrates that this event was important for Mangoes, Mountain Gems, and Emeralds.

The origin of the Caribbean area is connected to the breakup of Pangea, when Laurasia began to separate from Gondwana (Hedges 1996). Current islands are classified as the Greater Antilles, which comprise old fragments of the continental crust, and the Lesser Antilles, which were formed by a volcanic arc and the current islands (Hedges 1996, Pindell and Barret 1990, Ricklefs and Bermingham 2008), where vicariant events could have generated endemism (Hedges 2017). During the Last Glacial Maximum, the Bahamas were the most affected islands of the Antilles due to the sea level rise, which caused the loss of

several habitats and a drier climate (Pregill and Olson 1981). In the period of a low sea level, the Lesser Antilles were probably connected, forming three large islands and their combination showed a different topography (Pregill and Olson 1981). This region stands out as a very important area for Trochilidae, in particular for Mangoes. The Lesser Antilles stand out due to the presence of a generalized track, which suggests the fragmentation of ancestral hummingbird populations (Fig. 1).

The Mexican transition zone and the provinces of the Mesoamerican dominion are equally important for hummingbirds, where, in addition to the generalized tracks that indicate endemism, there is a biogeographic node. Geological events that may have shaped the current Trochilidae distribution are volcanism (Mora et al. 2007) and tectonism (Bourgouis et al. 1984).

Hummingbirds and marine transgressions

During the Miocene, the rise in sea level and tectonic processes in South America produced a significant marine incursion into the continent (Lovejoy et al. 1998). These events contributed to the appearance of the Amazonian and Paranaense seas, which separated the north and south of the continent at 16 and 13 million years ago. Associated with Andean tectonic processes, these seas altered drastically the drainage of South American rivers (Lundberg et al. 1998, Hernández et al. 2005, Sacek 2014). Fossil evidence showed the existence of paleogeographic corridors formed by two large marine transgressions (Lundberg et al. 1998, Hernández et al. 2005). The area cladogram for hummingbirds shows signals of these events for the clades Emeralds and Coquettes.

Cladistic biogeography

Bleiweiss (1998) and McGuire et al. (2007, 2014) highlighted dispersal as a striking characteristic in hummingbird history, with some vicariance events. Considering the area cladogram of Trochilidae, dispersal is confirmed to be important in the family. However, this trend is not the same for all clades, i.e., some clades have a more restricted distribution, support several generalized tracks, and are synapomorphies of groups of some provinces. This divergence occurred mainly in the “Clade of the Andes”.

The first synapomorphy found places the Ecuadorian province as the sister group of nearly all the other Neotropical provinces, except Galapagos Island, Prepuna, Atacaman (in the South America transition zone) and Coquimban, Santiagan, Maule and Valdivian. Prepuna and Atacaman would be more related to the provinces of the Andes than the Neotropical ones, as would be Galápagos (Fig. 2). Emeralds also support the group in which the Pampean province is the sister group of the provinces of the Chacoan, Parana, South-eastern, and Boreal Brazilian dominions, which occupy nearly the entire plains of South America, or the mid-northern area of the continent. The dichotomy between the Atlantic and Parana Forests is well supported by Brilliants, Emeralds, and Hermits. This result can

be related to the floristic similarity between these two provinces, which are within the Atlantic Forest in southeastern and northeastern Brazil, respectively. These provinces have similar geological histories since the Last Glacial Maximum, which altered flora and fauna. The grouping of the provinces Guatuso-Talamanca and Puntarenas-Chiriquí is equally well supported by Mangoes, Mountain Gems, and Emeralds. Brilliants, Coquettes, and Mountain Gems appear as synapomorphies of the clade in which Desert is the sister group of the provinces of the South American transition zone and the South Brazilian and Boreal Brazilian dominions. In the cladogram, the same provinces are rearranged, with Puna as the sister group, followed by Yungas, Rondonia, Ucayali, Napo, and Paramo as sister groups of the provinces located to the west of South America on both sides of the Andes (Central and South). Provinces from different dominions were grouped, which reinforces the striking dispersal of the group. It is worth highlighting that, geographically, the cladogram reflects the grouping of provinces at the east and west of the continent (related to the Andes) and Central America.

Our results corroborate the hypothesis that the more basal group (Topazes clade) of Trochilidae was distributed in the plains of South America, and the dispersal to the Andes and North America were posterior events, before the Neogene phase of uplift of the Cordillera (McGuire et al. 2014). As shown in the area cladogram (Fig. 2), most grouped provinces belong to the Brazilian Shield and have the Araucaria forest region as sister group.

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Supplementary material 1

Table S1. Neotropical and Andean provinces (Morrone 2014, 2015). Legend: SM, Sierra Madre Occidental; SMO, Sierra Madre Oriental; TM, Transmexican Volcanic Belt; SMS: Sierra Madre del Sur; CH, Chiapas Highlands; BH, Bahama; CB, Cuban; CI, Cayman Islands; JM, Jamaica; HP, Hispaniola; PR, Puerto Rico; LA, Lesser Antilles; PL, Pacific Lowlands; BB, Balsas Basin; VC, Veracruz; YP, Yucatan Peninsula; MQ, Mosquito; QT, Guatuso-Talamanca; PC, Puntarenas-Chiriqui; CD, Choco-Darien; GJ, Guajira; VN, Venezuelan; TR, Trinidad; MG, Magdalena; SB, Sabana; CA, Cauca; GI, Galapagos Islands; WE, Western Ecuador; EC, Ecuadorian; NP, Napo; IM, Imerí; PT, Pantepui; GL, Guianan Lowlands; RR, Roraima; PR, Pará; UC, Ucayali; MD, Madeira; RD, Rondonia; YG, Yungas; XT, Xingu-Tapajós; CAA, Caatinga; CRR, Cerrado; CC, Chacoan; PP, Pampean; AT, Atlantic; PF, Parana; AF, Araucaria Forest; PM, Paramo; DT, Desert; PU, Puna; AM, Atacama; PRP, Prepuna; MT, Monte.

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Supplementary material 2

Figure S1. Neotropical and Andean provinces (Morrone 2014, 2015). Legend: SM, Sierra Madre Occidental; SMO, Sierra Madre Oriental; TM, Transmexican Volcanic Belt; SMS: Sierra Madre del Sur; CH, Chiapas Highlands; BH, Bahama; CB, Cuban; CI, Cayman Islands; JM, Jamaica; HP, Hispaniola; PR, Puerto Rico; LA, Lesser Antilles; PL, Pacific Lowlands; BB, Balsas Basin; VC, Veracruz; YP, Yucatan Peninsula; MQ, Mosquito; QT, Guatuso-Talamanca; PC, Puntarenas-Chiriqui; CD, Choco-Darien; GJ, Guajira; VN, Venezuelan; TR, Trinidad; MG, Magdalena; SB, Sabana; CA, Cauca; GI, Galapagos Islands; WE, Western Ecuador; EC, Ecuadorian; NP, Napo; IM, Imerí; PT, Pantepui; GL, Guianan Lowlands; RR, Roraima; PR, Pará; UC, Ucayali; MD, Madeira; RD, Rondonia; YG, Yungas; XT, Xingu-Tapajós; CAA, Caatinga; CRR, Cerrado; CC, Chacoan; PP, Pampean; AT, Atlantic; PF, Parana; AF, Araucaria Forest; PM, Paramo; DT, Desert; PU, Puna; AM, Atacama; PRP, Prepuna; MT, Monte.

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