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How tectonic, volcanic and climatic processes in Andean 'sky islands' shaped the diversification of endemic ground beetles

Jérôme Murienne¹ | Álvaro Barragán² | Sophie Manzi¹ | Pablo Samaniego³ | Pierre Moret⁴

¹Laboratoire Evolution et Diversité Biologique (UMR5174 EDB), CNRS, IRD, Université Toulouse 3 Paul Sabatier, Toulouse, France

²Laboratorio de Entomología, Museo de Zoología QCAZ-I, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador

³Laboratoire Magmas et Volcans, Université Clermont-Ferrand Auvergne, CNRS, IRD, Clermont-Ferrand, France

⁴Laboratoire TRACES (UMR5608), CNRS, Université Toulouse 2 Jean Jaurès, Toulouse, France

Correspondence

Pierre Moret, Université Toulouse 2 Jean Jaurès, Toulouse, France.
Email: pierre.moret@univ-tlse2.fr

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Abstract

Aim: The Andean superpáramo ecosystem, above c. 4200 m a.s.l., currently forms an archipelago of isolated "sky islands" which provides a unique setting to study biogeography. However, there is still a poor understanding of how past geological events and climatic changes have shaped the distribution of life in this ecosystem. Our aim was to investigate the importance of biogeographic barriers in local diversifications and to analyze how populations have become isolated on current "sky islands".

Location: Neotropics, Andes, Páramo, Ecuador.

Taxon: Coleoptera, Carabidae, Platynini, *Dyscolus*.

Methods: We first used distributional data of 45 superpáramo specialist species to define areas of endemism in Ecuador. We then selected 34 isolated populations of 12 species to perform a high-throughput genome skimming approach encompassing the complete mitogenome and the complete nuclear ribosomal cluster. We also generated a time-calibrated estimation for the diversification of the group and compared it to geochronological data.

Results: A high proportion (60%) of the sampled species are microendemic, restricted to a single mountain summit. Three mutually exclusive areas of endemism are limited by deep transverse valleys, in relation to Pliocene speciation events. The genome-skimming approach provides a robust phylogenetic base to analyze the diversification of species and populations throughout the Plio-Pleistocene.

Main conclusions: The opening of the Interandean Valley did not play a significant role in the diversification of the group before the Pleistocene. More recently, multiple populations became isolated on the superpáramo of various volcanoes by independently colonizing it during repeated glacial-interglacial cycles. Our results highlight the joint contribution of orogeny and climatic fluctuations for explaining current distribution patterns. Each species had a different colonization history, with its populations reaching the different volcanoes at different glacial-interglacial cycles. They also provide a powerful tool to constrain the geological processes responsible for topographic changes along and across the Cordillera.

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KEYWORDS

carabids, genome-skimming, geogenomics, neotropics, phylogeography, Pleistocene climate change, volcano

1 | INTRODUCTION

Tropical Andes form a biodiversity hotspot (Myers et al., 2000) that presents a high level of species richness and endemism. Probably one of the most peculiar ecosystems of the Andes in term of species composition is the páramo (Arroyo & Cavieres, 2013), a 35,000 km² biogeographical province present above the treeline in the mountain ranges of Northern Peru, Ecuador, Colombia and Venezuela (Morrone, 2014). The province is divided into three elevational zones: the subpáramo (c. 3200–c. 3500 m), the páramo itself (c. 3500–c. 4200 m) and the superpáramo (above 4200 m). The superpáramo now forms an archipelago of the so-called 'sky islands' isolated on mountain tops (Jiménez-Rivillas et al., 2018; Peyre et al., 2018; Sklenář & Balslev, 2005; Vuilleumier, 1970), most of them being active or potentially active volcanoes, which provides a fantastic setting to study biogeography and understand how past geological and geomorphological events, in conjunction with past climatic changes, have shaped the diversification of life.

The evolution of the páramo ecosystem is intimately linked to the onset of the Andean orogeny which provided new mountainous habitats and allowed the establishment of alpine climatic conditions (Pérez-Escobar et al., 2022). Although Andean uplift started as early as 30 Ma in the Eastern Cordillera of Ecuador, a significant uplift was only reached during or after the Late Miocene (Coltorti & Ollier, 2000; Mora et al., 2011). This uplift caused exhumation rates ≥ 0.5 km/Ma in the Eastern Cordillera from the last 15 Ma (Spikings & Simpson, 2014). Between 10 and 8 Ma, prior to the formation of the Interandean Valley, volcanic formations covered the Cordillera at elevations currently ranging from 2500 to 3600 m (Lavenu et al., 1992; Steinmann et al., 1999). A 'prepáramo' open high Andean vegetation might have been present above 2000 m from the Early Pliocene onward (van der Hammen, 1974; Vuilleumier & Monasterio, 1986). Palynological records highlight that páramo vegetation had been established by the Late Pliocene (Hooghiemstra et al., 2006). The Pleistocene saw the formation of the current volcanic arc since at least 1.5 Ma (Bablon et al., 2019, 2020a). In the same period, climatic fluctuations led to dynamic shifts in the elevation of páramo habitats, creating a flickering connectivity system (Flantua et al., 2019). These repeated cycles of connections and allopatry might have set up a species-pump mechanism promoting speciation events.

Several studies have focused on analysing species distribution data in the páramo, either through a bioregionalization approach (Jiménez-Rivillas et al., 2018; Peyre et al., 2018; Sklenář & Balslev, 2005) or looking for climatic determinants of species richness (Peyre et al., 2019). While those studies provide interesting insights into the patterns of biodiversity in the páramo, only evolutionary studies can settle the foundation for deciphering

the underlying processes responsible for current patterns of species distribution and richness. In this regard, the last decade has seen a plethora of phylogenetic studies largely focusing on plants (Hughes & Atchison, 2015; Luebert & Weigend, 2014; Madriñán et al., 2013) with charismatic examples such as frailejones (Cortés et al., 2018; Diazgranados & Barber, 2017; Pouchon et al., 2018) and lupins (Drummond, 2008; Drummond et al., 2012; Hughes & Eastwood, 2006; Nevado et al., 2016, 2018).

In this context, the emerging field of geogenomics can provide meaningful insights into the biogeographical processes as it is based on the use of phylogenetic data to test geological hypotheses, and vice versa, in an integrated approach (Baker et al., 2014; Dolby et al., 2022). The case studies presented so far address broad regional or continental problems (Bacon et al., 2015). Here, we show that a geogenomics approach can also help understand local processes at the species and population level. We focus on the ground beetle genus *Dyscolus* (Carabidae, Platynini) which represents a major predatory component of insect communities in the tropical alpine páramo ecosystem above 3500 m. As many mountain-specialized ground beetle lineages (Brandmayr, 1991; Staunton et al., 2016), all the *Dyscolus* species living in the páramo are flightless, due to wing reduction (brachyptery). The dispersal ability of flightless ground beetles is drastically reduced, enhancing their sensitivity to isolation processes, which can explain their high level of endemism (Weng et al., 2020). More than 40 *Dyscolus* species are restricted to the superpáramo above 4200 m a.s.l., and within some of these species, isolated populations are distributed on currently isolated sky islands (Moret & Murienne, 2020). This group thus represents an ideal model to establish a biogeographical reconstruction of the diversification processes that led to the present-day distribution of species and isolated populations, taking advantage of recent geochronological advances in the dating of the Ecuadorian volcanic arc.

We first address the speciation process of high-altitude ground beetles in the framework of past tectonic, volcanic and valley incision processes. We hypothesize that at least some of the species might be originating from allopatric speciation processes related to the formation of the Interandean Valley and of transverse valleys across the Andes, which would have acted as orogenic barriers. In this case, we would expect to find a congruence between cladogenetic events and tectonic, volcanic and palaeogeographical events.

At the intraspecific level, that is, that of populations currently isolated on volcano summits, we postulate that two different processes could explain the observed pattern (Figure 1). In the first hypothesis, a number of species are present in the páramo. As a consequence of volcanoes' growth, new habitats become available at higher elevations and the various species of the páramo colonize



these newly available spaces. Following the upward shift of the páramo populations during the next warm interglacial period, populations become isolated on each volcano. Under this hypothesis, we expect to see the age of each population matching the age of each volcano, but also the ages of populations to be congruent between species.

In the second hypothesis, a number of species are present in the páramo but not evenly distributed in all locations. Following volcanoes' growth and the emergence of high-altitude habitats, the páramo species colonize these available spaces in the nearby locations. Further to the extinction of the ancestral populations, the isolated superpáramo populations become connected during each glacial–interglacial cycle and can migrate to colonize a new volcano before becoming isolated again. The colonization process is therefore dependent on the local topographic constraints as well as on the location of the original population. Under this hypothesis, we expect that the ages of each population do not necessarily correspond to the volcanoes' ages. In addition, because the colonization process is not deterministic, the ages of populations are not expected to be congruent between the different species. To test these hypotheses, we used a phylogenomic approach based on complete mitogenomes and complete ribosomal clusters to provide a dated phylogeny of the *Dyscolus* species endemic to the superpáramo.

2 | MATERIALS AND METHODS

2.1 | Study area

This study covers the páramo ecosystem in the northern part of the Ecuadorian Andes, from 1° N to 2°30' S (Figure 2). It is focused on the superpáramo zone that extends above c. 4200 m a.s.l., consisting of more than 20 currently isolated 'sky islands', most of them on the top of Quaternary volcanoes. The studied area exhibits the greatest extension of superpáramo patches in the tropical Andes. It is divided into two ranges, the Western Cordillera and the Eastern Cordillera, which are separated by the Interandean Valley, an approximately N–S-oriented topographic depression (Villagomez et al., 2005). Additionally, a major tectonic feature of this region is the Chingual-Cosanga-Pallatanga-Puna fault system which obliquely crosscuts the Cordilleras, forming a sharp boundary south and east of the North Andean Sliver (Alvarado et al., 2016; Nocquet et al., 2014).

2.2 | Taxon sampling

The ground beetle genus *Dyscolus* is a hyperdiverse neotropical taxon with more than 400 described species (Lorenz, 2019). It is the major component of the páramo ground beetle communities, from the tree

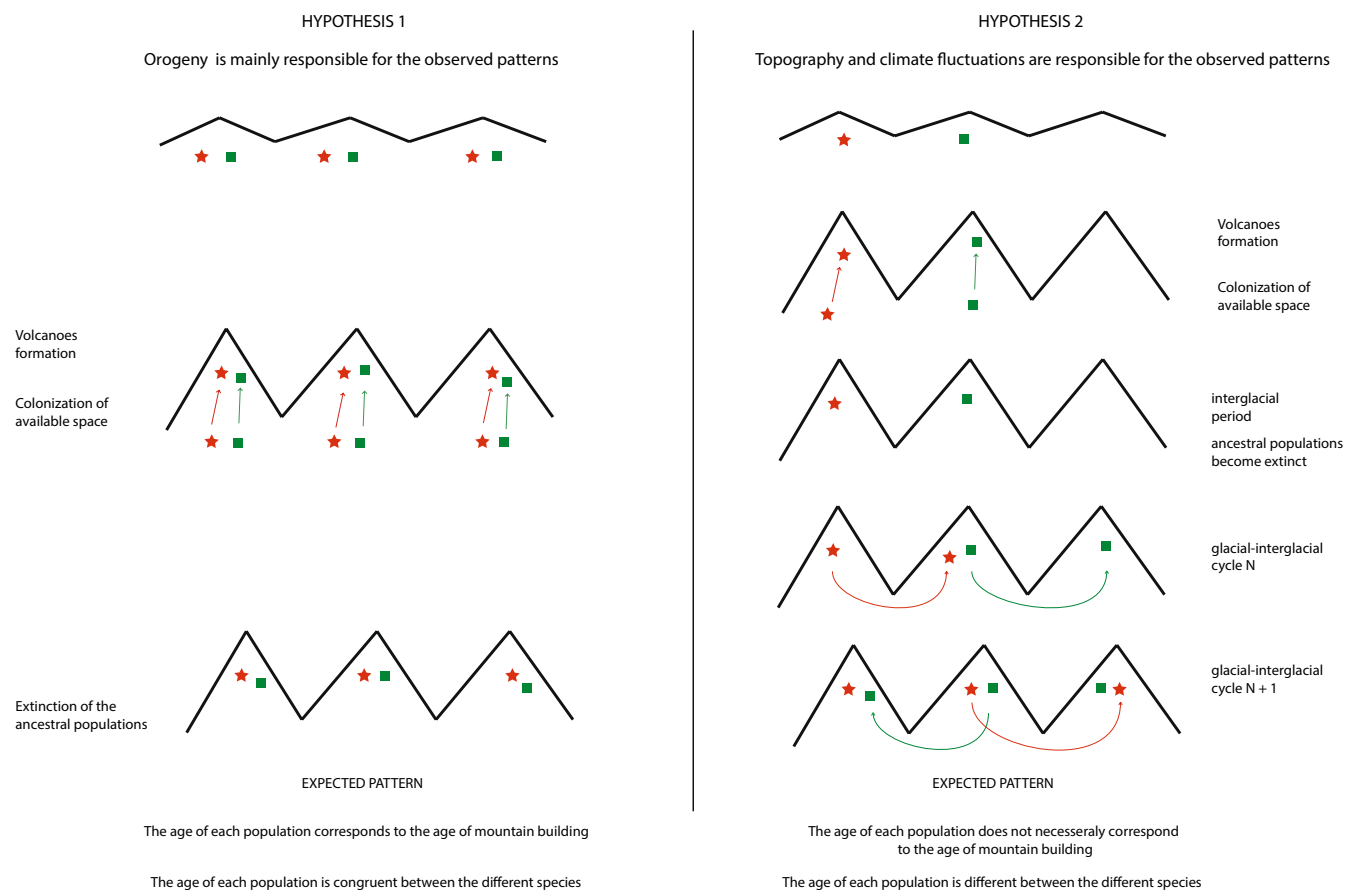


FIGURE 1 Hypotheses explaining the current patterns of repeated isolated populations on superpáramo sky-islands.

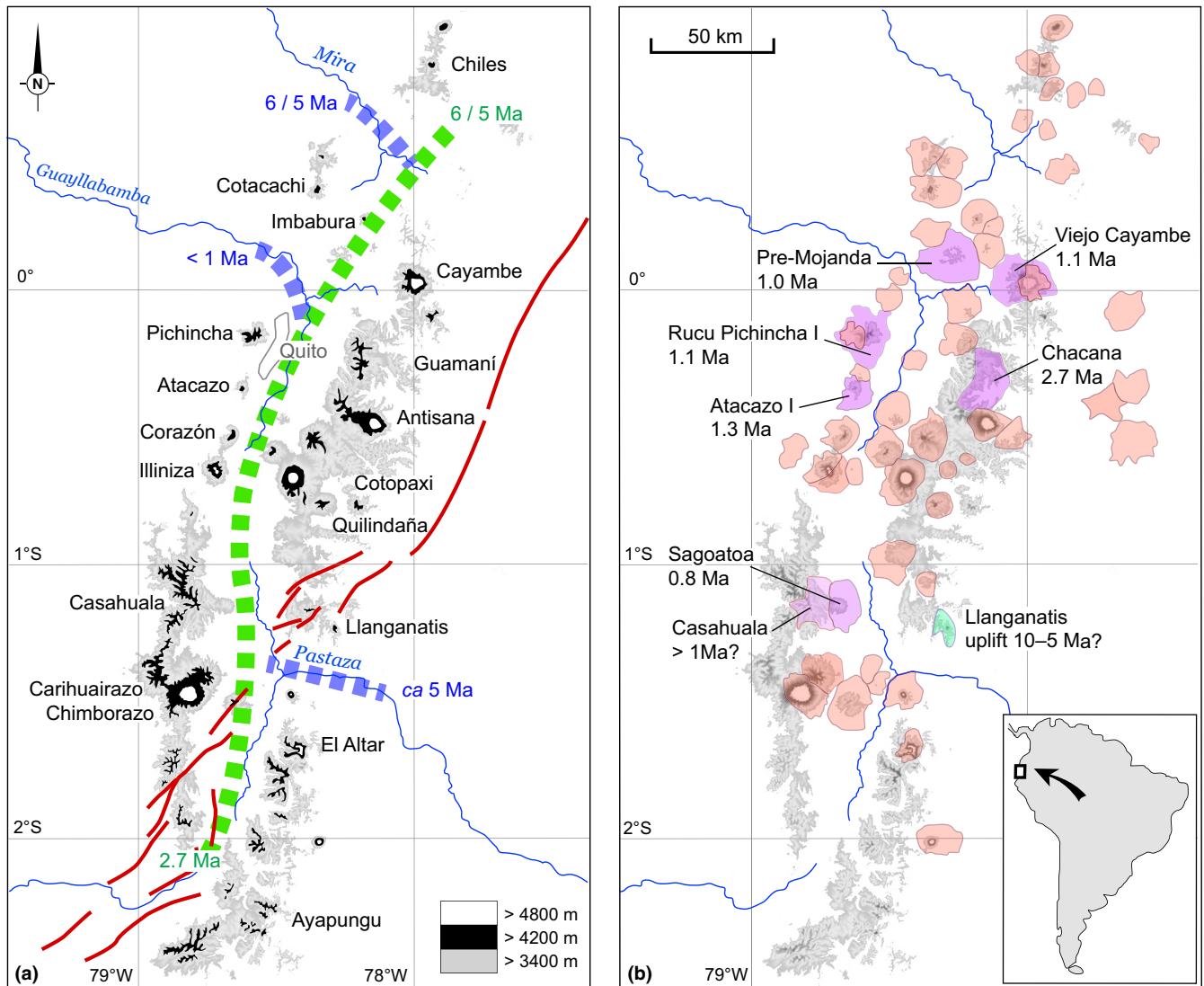


FIGURE 2 Map of northern Ecuadorian Andes, featuring orography and some major elements of the tectonic (panel a) and volcanic setting (panel b) and their respective maximum ages (see main text for references). (a): Blue dashed lines indicate transverse basins; green dashed line, the Interandean Valley; red lines, the Chingual-Cosanga-Pallatanga-Puna fault system. (b): In red, Pleistocene stratovolcanoes <0.5 Ma; in violet, rhyolitic centres dated around 1 Ma or earlier; in green, uplifted Jurassic/cretaceous limestone.

line to the permanent snow line (Gobbi et al., 2018; Moret, 2005). Ground beetles were systematically sampled above 4200 m on 17 of the 21 superpáramo patches currently existing between 1° N and 2°30' S, which led to the recognition of 45 *Dyscolus* species as exclusive superpáramo specialists (Table S1). Identification at species level is supported by a recent taxonomic revision coupling morphology with DNA barcoding (Moret & Murienne, 2020). Based on this first set of species, the number of species shared by 120 pairs of currently isolated superpáramo units was calculated (Table S2).

To analyse the timing of diversification of the species under study, we selected four core species which present a relatively similar distribution over several mountains (Figure 3), namely *D. orthomus*, *D. oopterooides*, *D. rotundiceps* and *D. diopsis*. For each species, we selected specimens from five to seven different localities. We included additional species either based on their taxonomic relationship to the core species (Moret & Murienne, 2020) or because of their particular

ecology. We included all the members of the diopsis group (*D. diopsis*, *D. rotundiceps*, *D. oreas*, *D. fuspilpis*, *D. montivagus*) which represent a monophyletic group of closely related species, all endemic to the superpáramo. We also included *D. irriguus* which is located at the southern margin of the study area. Finally, we added to this set one fully winged species, *D. purpuratus*, widespread in the montane forest from Mesoamerica to Bolivia. Our dataset thus includes representatives of 34 currently isolated populations belonging to 12 species, for which shallow shotgun sequencing was performed (Figure 3).

2.3 | DNA extraction, sequencing, genome assembly and annotations

The páramo region underwent a recent explosive phase of diversification (Madriñán et al., 2013). This situation leads to short



	<i>D. arauzae</i>	<i>D. diopsis</i>	<i>D. funereus</i>	<i>D. fusiipalpis</i>	<i>D. irriguus</i>	<i>D. lucifuga</i>	<i>D. montivagus</i>	<i>D. oopteroideus</i>	<i>D. oreas</i>	<i>D. orthomus</i>	<i>D. pollens</i>	<i>D. rotundiceps</i>
Chiles												
Cotacachi												
Pichincha												
Atacazo												
Corazón												
Illiniza												
Casahuala												
Chimborazo												
Carihuairazo												
Cayambe												
Guamaní												
Antisana												
Cotopaxi												
Quilindaña												
Llanganatis												
Ayapungu												

FIGURE 3 Distribution of the 12 high-altitude species under study in 16 superpáramo sky islands. Dark grey: Populations from which specimens were selected for the present genome-skimming analysis. Light grey: Populations from which only DNA barcodes were retrieved (Moret & Murienne, 2020 and unpublished data)

internodes with very few informative characters, rendering the estimation of a robust phylogeny from classical Sanger sequencing almost impossible. Several studies investigating lineage diversification in the páramo thus failed to provide well-resolved phylogenetic trees with good statistical support (Bell et al., 2015; Diazgranados & Barber, 2017; Drummond et al., 2012; Nürk et al., 2013; Uribe-Convers & Tank, 2015; Zapata, 2013). Alternatively, some studies have taken advantage of the most recent high-throughput sequencing technologies to provide fully resolved phylogenetic trees for local diversification as for *Lupinus* (Nevado et al., 2016), *Diplostephium* (Vargas et al., 2017) and *Espeletia* (Pouchon et al., 2018). We here used a 'genome-skimming' approach (Straub et al., 2012) which allows us to retrieve the high-copy fraction of the genome (complete mitochondrial genome and nuclear ribosomal clusters) using shallow shotgun sequencing (see Supporting Information for a detailed methodology).

2.4 | Phylogenetic analyses and molecular dating

Phylogenetic inference combined with fossil calibration is classically used for divergence dating. However, reliable fossil evidence is often lacking for invertebrate groups and alternative approaches can be used such as tectonic calibration, secondary calibration or by applying rates of molecular evolution. In the case of the tribe Platynini, the two nearest fossils, both from the Baltic amber (Gamboa & Ortuño, 2018;

Schmidt, 2015), are related to the current genus *Platynus* which is too distant from the tropical lineage of *Dyscolus* (Moret & Murienne, 2020) to constitute a reliable landmark. Indeed, the Baltic amber (37.2–33.9 Ma) is at least three times older than the onset of the last phase of Andean orogeny (since 10Ma), and much older than the Plio-Pleistocene when we believe that most of the diversification occurred in the genus *Dyscolus*. As an alternative to fossil calibration, we used an approach based on rates of molecular evolution. Based on the use of multiple fossil and biogeographical calibration points, the seminal study of the Carabid genus *Carabus* (Andújar et al., 2012) investigated the impact of analytical conditions (treatment of ambiguous characters, partitioning scheme, clock model, etc.) on the inference of rates of evolution for various mitochondrial and nuclear genes. For example, they found that the optimal analytical conditions for cob were two codon partitions (where first and second positions are considered together) and a strict clock model, inferring a rate of 0.0251 (0.0151–0.0369). Andújar et al.'s, 2012 study thus not only provided rate estimates for specific genes used in our study, but also provided specific guidelines about the optimal analytical conditions. As the phylogenetic analyses and time estimates are intimately linked, we used the optimal analytical conditions (treatment of ambiguous characters, partitioning scheme, clock model) of Andújar et al. (2012).

Ribosomal genes were aligned using clustalW2 (Larkin et al., 2007) while protein coding genes were aligned using TranslatorX (Abascal et al., 2010). Possible misaligned regions were trimmed with Gblock (Castresana, 2000) using the 'all-gaps' option as in Andújar et al. (2012) (see Table S3 for details). Preliminary analyses were performed by rooting the tree using the genus *Calathus* (Carabidae, Sphodrini) for which partial sequences of the mitochondrial genome and the nuclear rRNA cluster are available (mitogenome: *Calathus melanocephalus* KT876884; 18S: *Calathus mollis* FJ173117; 28S: *Calathus ruficollis* AF438033). The results confirm that the non-páramo *Dyscolus purpuratus* (PM085-01) is sister to all the other páramo-endemic *Dyscolus* species, so it was used as an outgroup in the remaining analyses.

A maximum likelihood (ML) phylogenetic analysis was performed on all the 13 protein coding genes and mitochondrial rRNA as well as the nuclear rRNAs (18S, 5.8S and 28S) and the Internal Transcribed Spacer 2. The ITS1 was too variable and was discarded from the analysis. Following Andújar et al. (2012), for the mitochondrial genes, we applied a partition by gene and each protein coding gene with two codon partitions where the first and second positions are considered together. For the nuclear genes, the different loci were considered as a single partition. Tree search was performed using RAxML-ng (Kozlov et al., 2019) with nodal support estimated using Transfer Bootstrap Expectation (Lemoine et al., 2018).

Divergence times were estimated using BEAST 2.5 (Bouckaert et al., 2019). Analyses were conducted using the same partitioning scheme as for the ML analysis. To reduce computational burden, the rate parameters of the GTR model as well as the shape of the Gamma distribution were fixed to the ones optimized under ML. Rates of molecular evolution for a large panel of mitochondrial and nuclear genes

have already been estimated for the related genus *Carabus* in the same family Carabidae (Andújar et al., 2012). Because this study presents rates for only a subset of the genes used in the present study, we decided to apply a mean rate of 0.0134 (0.0108–0.0162) to the mitochondrial clock partition and a mean rate of 0.0029 (0.002–0.0039) for the nuclear clock partition. Following Andújar et al. (2012), we applied a Strict Clock model to the mitochondrial partition and an Uncorrelated relaxed clock model to the nuclear partition. Because our sampling includes a mix of likely recent species and populations, we used as *tree prior* a coalescent. Analyses were run for 50 million generations, sampling trees every 2000 generations. The Maximum Clade Credibility tree was estimated with TreeAnnotator by discarding 20% of the burn-in fraction.

3 | RESULTS

3.1 | Distribution patterns

Based on the distribution of the 45 species of our extended dataset (Table S1), three areas of endemism, exclusive to each other, can be traced. The largest one extends from 0°30' N to

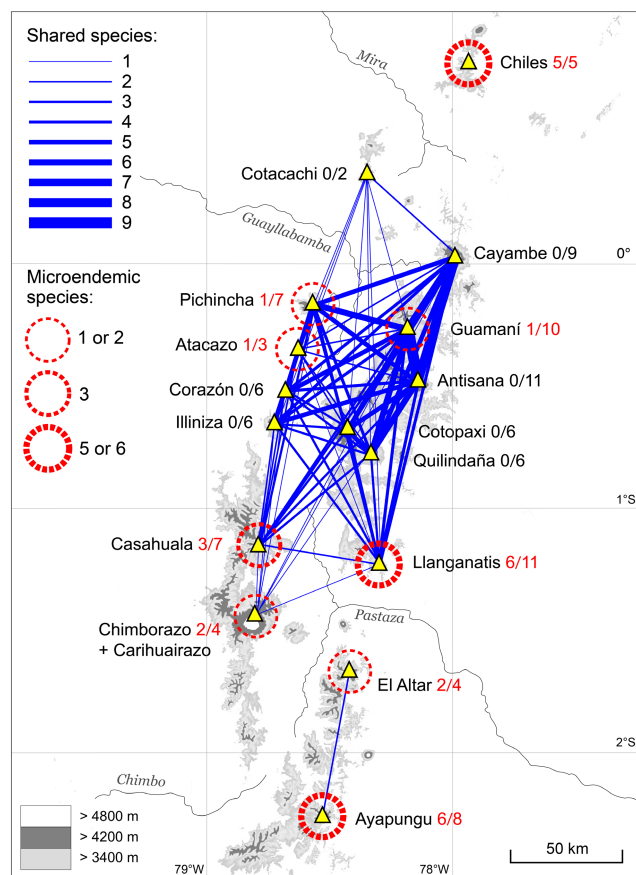


FIGURE 4 Areas of endemism in northern Ecuadorian Andes, based on the distribution of 45 superpáramo species of the ground beetle genus *Dyscolus*. First number after the mountain name: Microendemic species; second number: Total number of recorded species.

1°30' S, a zone previously defined as the Pichincha–Chimborazo area of endemism (hereafter PCAE) (Moret, 2009), encompassing both cordilleras and limited by three transverse valleys: north the Mira/Chota, southeast the Pastaza and southwest the Chimbo (Figure 4). These limits are the same as those of a biogeographical clade including three districts, 'Northern Cordillera Oriental', 'Northern Cordillera Occidental' and 'Central Cordillera Occidental', in the endemism area cladogram of Jiménez-Rivillas et al. (2018), which is based on plants and vertebrates. The Chiles area to the north, and the Ayapungu area to the south, do not have a single superpáramo species in common with the PCAE (Table S2 and Figure 4). Within the PCAE, microendemic species, that is, species that are only known from a single mountain summit or from a single superpáramo sky island, are more frequent in mountains situated at the margin of the area. As a whole, 27 of the 45 sampled species –a very high 60%– are microendemic.

The 12 species subject of a phylogenetic analysis exhibit the same broad distribution pattern (Figure S1). They all belong to the PCAE except *D. montivagus* at the northern end of the study area and *D. irriguus* at its southeastern end. Within the PCAE, eight species are distributed over several isolated island-like superpáramos (*D. arauzae* in two, *D. oreas* in three, *D. fusipalpis* in four, *D. lucifuga* in five, *D. orthomus* in eight, *D. diopsis* in ten, *D. oopteroideis* and *D. rotundiceps* in eleven sky islands), while *D. funereus* and *D. pollens* are microendemics restricted to a single mountain area. The *Dyscolus* communities are significantly more diverse in the Cordillera Oriental, especially in its broadest section between Cayambe and Cotopaxi. Seven of the ten PCAE species are sympatric in the Guamaní plateau superpáramo (which is part of the Chacana volcanic complex), while only four in the Pichincha superpáramo, which is the most diverse of the Cordillera Occidental.

3.2 | Phylogeny and divergence time estimation

The ML (Figure S2) and the Bayesian topologies (Figure 5) are almost identical. Two deep lineages are retrieved (node 1), one composed of *D. orthomus* and *D. arauzae* (clade A), and the second one with all the remaining species (clade B + C). The difference between the two topologies lies in the placement of *D. irriguus* which groups with clade A in the ML analysis (though with low bootstrap support, 52%) and is sister to clade B + C in the Bayesian analysis. The main lineage is split into two groups (node 4), with clade B comprising *D. pollens*, *D. funereus*, *D. lucifuga* and *D. oopteroideis* while clade C is composed of *D. montivagus*, *D. fusipalpis*, *D. rotundiceps*, *D. oreas* and *D. diopsis*. As expected, the topology is rather different from the one inferred from a single marker (Moret & Murienne, 2020), except for the monophyly of the *diopsis* group which was already retrieved by the COI alone. When the nuclear and mitochondrial datasets are analysed separately under ML (see Figures S3 and S4), the results are very stable with only minor changes in the topology.



For each of the following species (*D. diopsis*, *D. rotundiceps*, *D. oreas*, *D. fusipalpis*, *D. oopteroides*, *D. lucifuga* and *D. orthomus*), we recorded the molecular ages of currently isolated populations and compared them to geochronological data (Figure 8). Taking into account the error margins as inferred from the Bayesian dating, we found that for most volcanoes, the ages are not congruent between the different species. Colonization of Guamani happened during three different time periods while colonization of Cayambe, Antisana, Llanganatis, Pinchincha, Illiniza and Carihuairazo happened during two different time periods.

4 | DISCUSSION

4.1 | Speciation caused by tectonic events and valley incision processes

4.1.1 | What was the impact of the incision of deep trans-andean valleys?

Based on distributional data, the PCAE is limited north and south by deep transverse valleys, respectively, the Chota-Mira valley

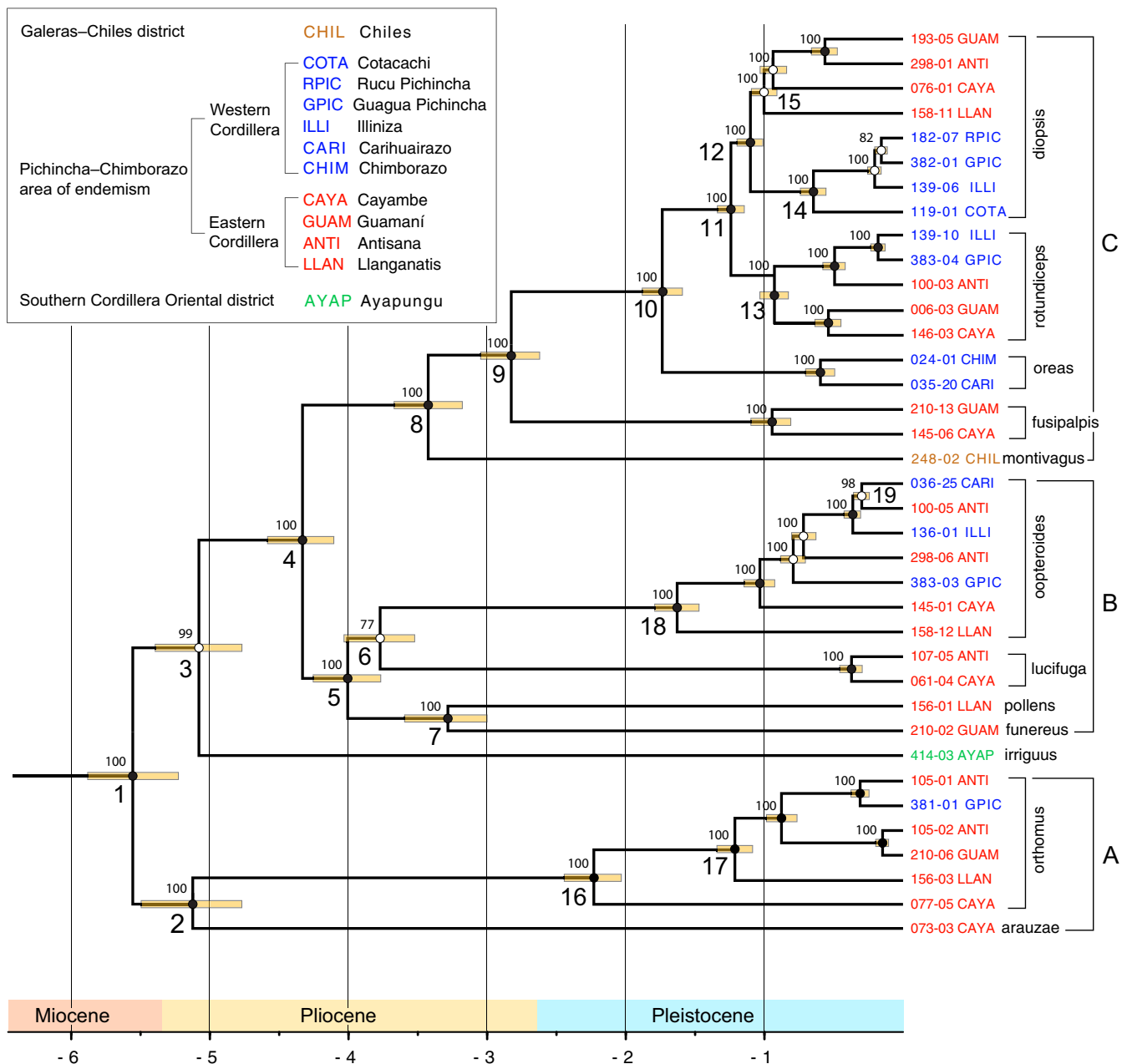


FIGURE 5 Diversification of the genus *Dyscolus* inferred with BEAST2. Node bars represent the node ages 95% confidence intervals. Node posterior probabilities are indicated on nodes. Black dots represent nodes that are supported by high bootstrap frequencies (above 85%) in the maximum likelihood analysis.

across the northern Western Cordillera, the Chimbo-Pangor valley across the southern Western Cordillera, and the Pastaza valley across the Eastern Cordillera (Figure 4). Our dataset sheds light on the timing of the emergence of the northern topographic barrier. The split between *D. montivagus* and the rest of the *diopsis* group [*fusipalpis* + *oreas* + *diopsis* + *rotundiceps*] is dated c. 3.5 Ma (Node 8). This diversification event is likely related to the formation of the Chota-Mira deep and arid depression. Our molecular dating is broadly congruent with the tectonic and geomorphological history of the region. By analogy with the Peruvian cordillera, fluvial erosion likely began to create deeply incised transverse valleys during the late Miocene or the early Pliocene (Montario et al., 2005 with dates for the north of Peru; Thouret et al., 2007 with ages from southern Peru). In northern Ecuador, the Chota basin began to form c. 6–5 Ma (Spikings & Crowhurst, 2004; Winkler et al., 2005). Its tectonic history triggered strong erosion processes and put time constraints on the formation of the deep Chota-Mira valley across the Cordillera Occidental. The effect of this topographic gap is currently enhanced by a sharp contrast between the aridity that reigns at the bottom of the depression (Quintana et al., 2016) and the humidity of the adjacent páramos. Our molecular data suggest that the deepening of the Chota-Mira valley took place at a relatively early date after the formation of the Chota basin.

More recently, a fourth transverse valley had a similar impact. A little north of Quito, a deep gap in the Cordillera Occidental appeared during the Middle Pleistocene, as a consequence of the formation of the Quito-San Antonio-Guayllabamba basin (Figure 2),

which is much more recent than the more northern Mira-Chota basin (Winkler et al., 2005). According to the dating of two volcanic deposits located beneath and inside its first sedimentary succession, the Quito-San Antonio-Guayllabamba basin began to form between 1.15 and 1 Ma (Alvarado et al., 2014; Bablon et al., 2020a). The subsequent incision of its outlet towards the western lowlands, through the deep gorge of the Guayllabamba river, was likely fostered by the high activity of the Quito fault over the Middle Pleistocene, although no precise timing is available (Alvarado et al., 2014). However, the erosion of the southern slopes of old volcanic edifices at the northern edge of the Quito-Guayllabamba basin suggests that the drainage network was already in place at c. 0.4 Ma (Bablon et al., 2020a). In our dataset, the only allopatric event that can be related to the formation of this biogeographical barrier is dated around 0.65 Ma (node 14), when two infraspecific clades separated within the Western lineage of *D. diopsis*: north of the Guayllabamba valley an isolated population on the Cotacachi volcano, and south of the valley a clade formed by several populations scattered on the Illiniza, Pichincha and Corazón volcanoes (Figure 6). Our molecular data are thus congruent with the scenario of a gradual deepening of the Guayllabamba valley after 1 Ma, leading to a complete transverse biogeographical break around 0.65 Ma.

4.1.2 | What was the impact of the Interandean Valley?

The opening of the Interandean Valley during the Pliocene does not seem to have played a major role in the diversification of the Andean *Dyscolus* lineages. It began to open c. 6–5 Ma in northern Ecuador and propagated southward, reaching its complete opening probably by the Late Pliocene c. 2.7 Ma (Spikings & Crowhurst, 2004; Winkler et al., 2005). During this period, our dataset does not reveal any evidence of an east-west divergence pattern. On the contrary, speciation events prior to 2.5 Ma appear to occur on a north-south axis within the Cordillera Oriental (node 7).

According to our results, the Interandean Valley appears to have been more involved in diversification events during the Pleistocene than during the Pliocene. The infraspecific clade structure of *D. diopsis* and *D. rotundiceps*, the two most recent species of our dataset, shows a clear east-west partition (nodes 12 and 13). In *D. diopsis*, a group of Western populations separated from a group of Eastern populations slightly before 1 Ma, that is, long after the Interandean Valley started to form. In *D. rotundiceps*, a similar pattern is dated to c. 0.9 Ma, but in a less systematic way, as the Antisana population groups with the western clade of this species. On the other hand, no such east-west partition at infraspecific level is observed in two other widespread species, *D. oopteroides* and *D. orthomus*. These results suggest that the Interandean Valley could be significantly younger than commonly accepted based on K-Ar dating performed in the 1980s (Barberi et al., 1988), which calls for the need of a new dating program focused on the older volcanic rocks of the Interandean Valley.

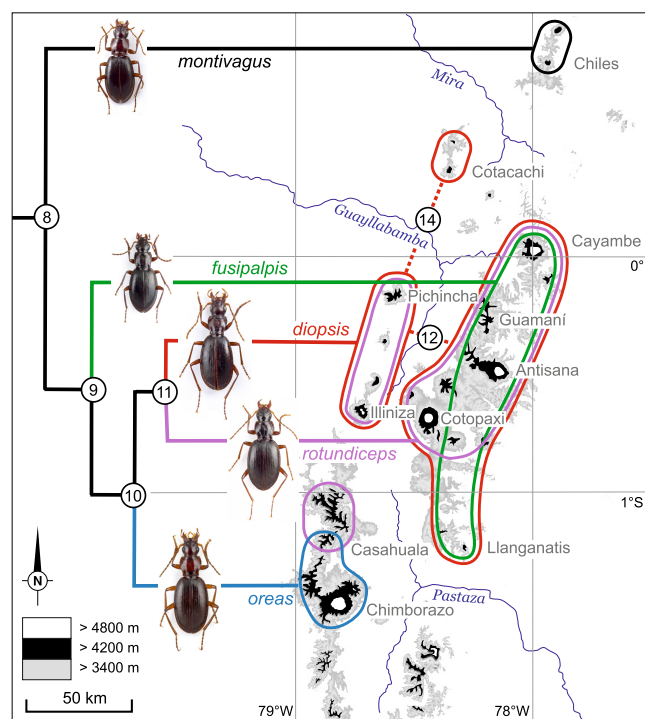


FIGURE 6 Geographical distribution in northern Ecuador and phylogeny of the *Dyscolus diopsis* species group (clade C in Figure 5). Node numbers refer to Figure 5. Branch lengths are arbitrary.



Even though the Interandean Valley may have acted as an impassable gap for cold-adapted species under the relatively warm climate of the early Pleistocene, later cool periods allowed for secondary contacts through two east–west passes, or *Nudos* (west–east structures formed by volcanic and tectonic processes) at elevations above 3000 m. The first one, named Nudo de Mojanda, is located between Cotacachi, Imbabura and Cayambe at the northern end of the Interandean Depression, the other one, named Nudo de Tiopullo, between Illiniza, Santa Cruz and Cotopaxi at its middle. These *Nudos* were, during the cooler phases, easy pathways from one Cordillera to the other, especially between Illiniza, Cotopaxi and Antisana which form an almost continuous páramo area (Figure 7). This is probably the reason why, at infraspecific level in *D. rotundiceps* and *D. oopteroideis*, the Antisana population (in the Cordillera Oriental) is nested within a clade composed of western populations.

4.2 | Volcanic growth and climatic oscillations shaped the current patterns of diversity

The uplift of the Andes accelerated after 4 Ma at the Pliocene–Pleistocene transition, attaining current or near current elevations (Gregory-Wodzicki, 2000), while the Interandean Valley reached its complete opening by the Late Pliocene c. 2–3 Ma (Spikings & Crowhurst, 2004; Villagomez et al., 2005). Throughout this period, alternating warmer and cooler phases led to isolation

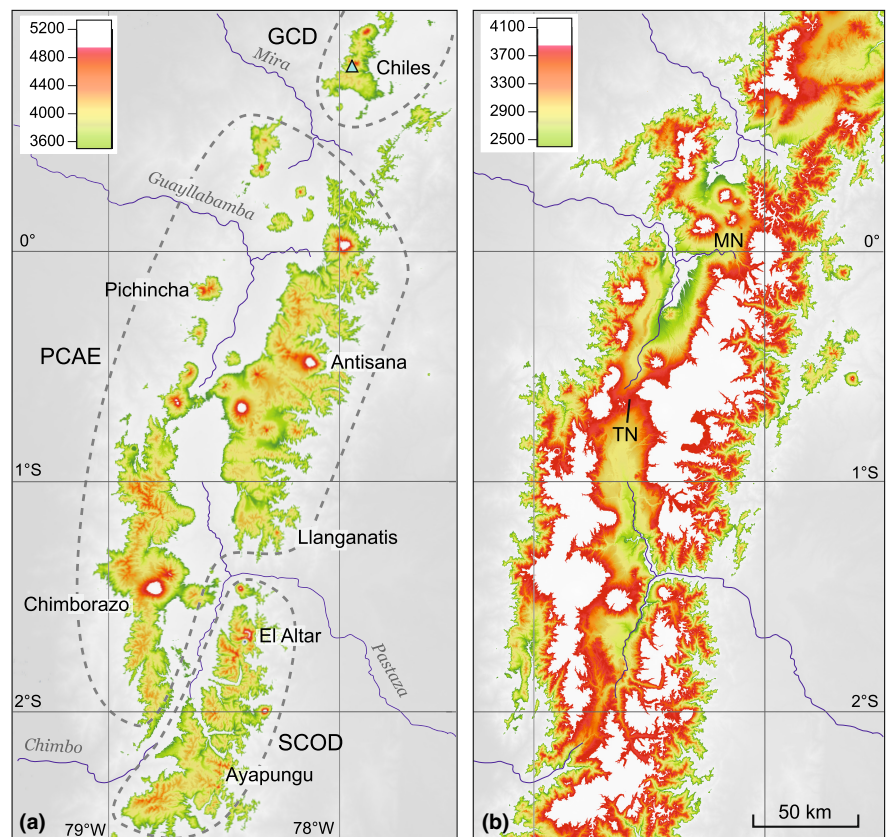
followed by re-contact (Figure 7) (Flantua et al., 2019; Flantua & Hooghiemstra, 2018).

The formation of the páramo ecosystem gradually took place between 2.2 and 1.6 Ma (Hooghiemstra et al., 2019). The oldest known volcanic edifice of the Quaternary arc is the large rhyolitic Chacana volcanic complex, in the Eastern Cordillera, with ages as old as c. 2.7 Ma (Opdyke et al., 2006), followed by mostly andesitic edifices such as ‘Viejo Cayambe’ at c. 1.1 Ma (Samaniego et al., 2005). In the Western Cordillera, Atacazo started to form at c. 1.3 Ma (Hidalgo, 2007), Rucu Pichincha at c. 1.1 Ma (Robin et al., 2010) and old Mojanda edifice at 1 Ma (Bablon et al., 2020a).

However, most of the Pleistocene andesitic volcanic centres developed during the last 0.5–0.6 Ma: later eruptive stages of Cayambe started from 0.4 Ma, of Rucu Pichincha from 0.45 Ma; Illiniza–Santa Cruz from 0.7 Ma (Santamaría et al., 2022), Cotopaxi from c. 0.5 Ma (Hall & Mothes, 2008), Antisana at 0.4 Ma (Hall et al., 2017), Quilindaña and Chalupas at 0.2 Ma (Bablon et al., 2020b), Cotacachi at 0.2 Ma (Bablon et al., 2020b), Carihuairazo successively at 0.5 and 0.2 Ma (Bablon et al., 2019), and Chimborazo at 0.1–0.15 Ma (Samaniego et al., 2012) [see Figure 2b for a graphical summary].

Our results (Figure 8) indicate that the volcanic construction alone cannot fully explain the current patterns of diversity. Indeed, it seems that only a combination of volcano growth followed by various cycles of connection–disconnection related to climatic cycles could explain them. Throughout the Quaternary, alternating warmer and cooler phases have been well documented (Flantua

FIGURE 7 Location of the páramo ecosystem in northern Ecuadorian Andes at two time periods. Green: subpáramo and lower grassland páramo; yellow: Grassland páramo; red: superpáramo; white: Ice cap. (a): Current situation. GCD, Galeras–Chiles district; PCAE, Pichincha–Chimborazo area of endemism; SCOD, Southern cordillera oriental district. (b): Hypothetical glacial scenario with the bottom limit of the ice cap at ca. 3800 m and the bottom limit of the superpáramo at ca. 3100 m, which might roughly correspond to the final last glacial maximum and the oldest dryas, ca. 18–15 ka (Angel et al., 2017). MN: Mojanda Nudo; TN: Tiopullo Nudo.



et al., 2019; Flantua & Hooghiemstra, 2018), leading to isolation of the superpáramo followed by re-contact (Figure 7). While the early divergence at the infra-specific level is broadly congruent with the history of volcanic construction (especially for Pichincha, Illiniza and Carihuairazo), the ages of populations on each volcano are not congruent between the different species (see Hypothesis 2). This suggests that each species had a different colonization history, with its populations reaching the different volcanoes at different glacial-interglacial cycles. Even taking into account the uncertainty of our age estimates, our results suggest that during the last million year, each volcano was colonized during multiple periods (Cayambe at least twice, Guamaní three times, Antisana, Pichincha, Illiniza and Carihuairazo twice). In addition, extinctions could also have an impact on the resulting topologies, but the fact that for several species we found populations younger than the age of volcanoes also supports Hypothesis 2.

It is interesting to note that for *D. orthomus* and *D. oopterooides*, the two earliest emerging populations were those located on the Cayambe and on the Llanganatis mountains. The Llanganatis, situated at the Southern end of the Cordillera Oriental, is a non-volcanic mountain with an uplift history estimated between 10 and 5 Ma (Aspden & Litherland, 1992). The Cayambe, situated at the Northern part of the Cordillera Oriental, is a volcanic mountain dated to 1.1 Ma and is thus one of the oldest Pleistocene volcanoes of the cordillera. The intraspecific patterns of diversity are thus congruent with geological history, with the earliest emerging populations situated on the oldest mountains.

The molecular ages of other divergence events that occurred on Cayambe c. 2.2 Ma, on Antisana from 0.7 to 0.5 Ma, and on Cotacachi c. 0.65 Ma, far precede the oldest radiochronological ages from these three volcanoes. We could assume that these events took place in situ on a still undetected volcanic edifice, but this would imply that Cayambe is twice as old as currently documented by geological research, and Cotacachi three times, which is a costly

assumption. The divergence event may rather have occurred not on Cayambe, but in the neighbouring area of the old rhyolitic Chacana complex (Figure 2b), dated to 2.7 Ma. This proximity can also explain the oldest dates documented at Guamaní, close to the core area of the Chacana complex, and farther south at Antisana.

A similar scenario can be drawn at the southwestern end of the PCAE. *D. oreas*, which is endemic to the Chimborazo, Carihuairazo and Casahuala volcanoes, diverged from (*D. diopsis* + *D. rotundiceps*) at c. 1.7 Ma (node 10). As the ages of Chimborazo (0.1 Ma) and Carihuairazo (0.2 Ma) are much younger (Samaniego et al. 2012), it can be assumed that *D. oreas* originated on Casahuala (also named Pilisurco in Bablon et al., 2019), a strongly eroded volcano 34 km north of the Chimborazo (Figure 2b). There has been no direct dating of the eruptive products of this volcano, but according to its advanced degree of erosion, Casahuala is certainly older than its immediate neighbour, the Sagoatoa volcano where K-Ar dating indicates an initial stage prior to 0.83 Ma (Bablon et al., 2019). The molecular age of *D. oreas* is therefore fully consistent with a geological reconstruction in which Casahuala would be the oldest Pleistocene volcanic edifice of the southern Cordillera Occidental. *D. oreas* would then have spread to the Carihuairazo and the Chimborazo when these volcanoes were constructed at younger ages (<0.8 Ma).

5 | CONCLUSIONS

The genome-skimming approach allowed us to obtain a robust phylogeny, providing a strong base to analyse the diversification of superpáramo endemic species throughout the Plio-Pleistocene. We demonstrated that the Chota–Mira deep valley that cuts the Andean range played a crucial role as a biogeographic barrier. Conversely, the impact of the Interandean Valley formation appears to have been rather limited, possibly because of frequent connections between western and eastern mountains during the cooler phases of the Pleistocene,

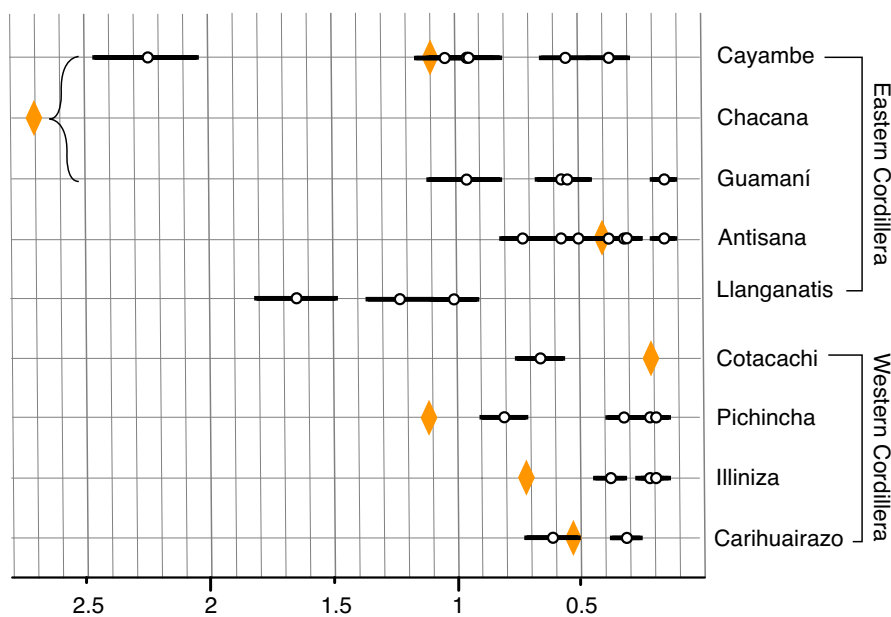


FIGURE 8 Molecular ages of currently isolated populations of *Dyscolus*, compared to geochronological data. Black and white dots: Differentiation events at infraspecific scale in *D. diopsis*, *D. rotundiceps*, *D. oreas*, *D. fusipalpis*, *D. oopterooides*, *D. lucifuga* and *D. orthomus*, involving one mountain vs. another or one mountain vs. a group of other mountains. Orange diamonds: Oldest K-Ar dates from Ecuadorian volcanoes (from Bablon et al., 2019, Bablon et al., 2020a, 2020b, Opdyke et al., 2006, Samaniego et al., 2005, 2012, Robin et al., 2010, Hidalgo et al., 2007, Hall et al., 2017). Time scale in million years.



but an age younger than commonly accepted for the formation of the Interandean Valley is a hypothesis that shall be tested in the future. Finally, the current patterns of isolation of populations on volcanic sky-islands can be explained by multiple phases of colonization linked to Quaternary climatic fluctuations. Our phylogenetic study of key endemic species proved to be a powerful tool to constraint the geological processes responsible for the topographic changes along and across the Andean Cordillera. To complete it, it would be desirable to extend its scope to other Andean peaks such as the Chachimbiro-Yanaurcu volcanoes in the northern Western Cordillera, the Casahuala-Pilisurco in the southern Western Cordillera, and the Tungurahua, Altar and Sangay volcanoes of the southern Eastern Cordillera. It is to be hoped that an integrative geogenomic approach, coupled with geochronological and thermochronological data, will help to understand the main process and the timing responsible for their formation.

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DATA AVAILABILITY STATEMENT

All the specimen metadata are available on the BOLD website (datasets DS-GLYPTO and DS-DYSGLYP). Complete mitochondrial genomes and complete nuclear ribosomal clusters generated for this study have been deposited on GenBank (accession numbers OP615216-OP615252).

ORCID

Jérôme Murienne  <https://orcid.org/0000-0003-1474-7829>

Álvaro Barragán  <https://orcid.org/0000-0001-6843-2975>

Sophie Manzi  <https://orcid.org/0000-0001-5907-6999>

Pablo Samaniego  <https://orcid.org/0000-0003-1169-3503>

Pierre Moret  <https://orcid.org/0000-0002-0141-4999>

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BIOSKETCH

Jérôme Murienne is a molecular ecologist and evolutionary biologist. He is interested in deciphering biogeographical patterns of Neotropical biodiversity.

Álvaro Barragán is the curator of the invertebrate section at QCAZ. He is interested in the effect of climatic changes on invertebrates.



Sophie Manzi is a molecular biology engineer specialized in high-throughput sequencing technologies applied to biodiversity research.

Pablo Samaniego is a geologist working on volcanism in the Andes.

Pierre Moret is an archaeologist and entomologist, interested in the biogeography and the historical ecology of the tropical Andes.

Author contributions: PM conceived the idea; JM and PM designed the research; AB and PM collected the data; JM and SM performed the molecular analyses; PS provided geological data; JM and PM led the writing with contributions from all co-authors.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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