PERSPECTIVE

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Volcanoes, evolving landscapes, and biodiversity in Neotropical mountains

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Abstract

The longstanding view of Neotropical mountain uplift as a promoter of species diversification has become commonplace in the last decades and could benefit from more specific Earth-Life evolution associations. We now know that mountain formation has contributed to the outstanding levels of richness and endemism of Neotropical mountains. Nonetheless, we are lacking conceptual and empirical frameworks where geological and biological processes are causally linked through testable hypotheses. In this perspective, we present volcanic activity in the Neotropics, not as phenomena occurring "on top of" mountain uplift, the latter being the phenomena of biogeographical interest, but rather as geological processes that directly impact biodiversity and are themselves the phenomenon of biogeographical interest. Volcanoes deserve biogeographical attention because their effects on landscape evolution generate predictable biodiversity process counterparts that can be integrated into biogeographical models enabling hypothesis testing. We review examples in the literature emphasizing the spatio-temporal scale of volcanism's predicted and recorded effects on biodiversity. We illustrate our perspective by two recent study cases, focusing on wax palms and passerine birds. In the first one, wax palm genomic sampling was used to test 2 hypotheses: that the northern Andes have been disconnected in the past and connected by rapid but repeated eruptions of caldera-forming eruptions in the Colombian Massif fostering episodic dispersal, or alternatively, that they have always been continuous and have gradually uplifted hosting continuous diversification and dispersal through time. In broadly this same area, genetic and phenotypic data revealed the existence of a hybrid zone between species in the warbler genus *Myioborus*. Because hybridization is likely younger than volcanic activity, topographic connection spurred by volcanism could have also enabled secondary contact between previously isolated species, a hypothesis that merits formal testing. Altogether, we emphasize the pertinence of the volcanic record in offering opportunities for the evaluation of biogeographical hypotheses in the context of Neotropical mountains and their singularly outsized biodiversity.

Highlights

- Biogeography requires geological and biodiversity patterns to be linked through hypothesis testing and temporally and spatially constrained predictions
- The effects of continental volcanoes on mountain biodiversity have been disregarded possibly due to persistent attention to mountain uplift alone as the phenomenon of interest to biogeographers
- Volcanic activity has many direct effects on biodiversity particularly in the context of mountain formation, and is a spatially and temporally constrained process
- We explain why continental volcanoes in the context of Neotropical mountains deserve special attention and illustrate this perspective with two research cases in the Colombian Andes

Keywords: Andes, biogeography, magmatism, naturalism, palm, relief, topography, warbler.

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On the morning of February 20, 1835, a British naturalist travelling in South America witnessed a remarkable geological event: a devastating earthquake near the cities of Concepción and Yalcahuano in the coast of Chile. The naturalist observed the consequences of the earthquake and other ensuing events:

> "…To the northward a volcano bursts out at the bottom of the sea adjoining the island of Juan Fernandez, and several of the great chimneys in the Cordillera of central Chile commenced a fresh period of activity. We thus see a permanent elevation of the land, renewed activity through habitual vents, and a submarine outburst, forming parts of one great phenomenon" (…) "The most remarkable effect (or perhaps speaking more correctly, cause of this earthquake was the permanent elevation of the land (…) the elevation of the land to the amount of some feet during these earthquakes, appears to be a paroxysmal movement, in a series of lesser and even insensible steps, by which the whole west coast of South America has been raised above the level of the sea"

The naturalist was no other than a young Charles Darwin, who, by coincidence, had been reading Sir Charles Lyell's Principles of Geology while aboard the Beagle. Darwin's thinking was influenced by his reading of Lyell and by his first-hand experience with the earthquake and its impact on the landscape he carefully observed. Such experience motivated Darwin (1840) to review hypotheses about the formation of mountains, relating earthquakes and volcanoes to the mountain building process in which fractures, rock tilting and volcanism help form continuous mountain chains like the Andes.

> "…volcanic action, even on a very grand scale, as in the Andes, is only one effect of the power which elevates continents, at the slow rate at which the South American coast is now rising. (…) It may, therefore, be questioned, whether we are justified in admitting the hypothesis of a paroxysmal elevation of any mountain-chain, without distinct proofs in each particular case, that a series of impulses, like those, which now acting frequently on the same lines, rend the earth's crust, and elevate unequally portions of it, could not have affected the observed effects. It is, however, a subordinate question, whether there exist proofs of paroxysmal violence in some mountain-chains; the important fact which appears to me proved, is, that there is a power now in action, and which has been in action with the same average intensity (volcanic eruptions being the index) since the remotest periods, not only sufficient to produce, but which almost inevitably must have produced, unequal elevation on the lines of fracture. "

As noted by various scholars and summarized aptly by paleontologist Richard Fortey, "Lyell made time available to Darwin". In line with the Lyellian uniformitarian school of thought in the geosciences, Darwin's gradualistic view of evolution poses that small changes acting over long periods of time may have profound cumulative effects not only in geophysical properties of the Earth (e.g., as in the uplift of mountains), but also on the species inhabiting the planet. While the explanatory power of such theory is vast, Darwin did not explicitly link geological mechanisms like those generating topography with identifiable events in the evolution of life.

Since Darwin's time, however, there has been broad interest in connecting Earth processes with the origins of biological diversity. For example, the uplift of the Andes, the formation of the Isthmus of Panama, or the origin of drainages in the Amazon River system figure prominently in seminal theories of Neotropical biogeography seeking to explain the distribution and evolutionary diversification of plants and animals (e.g., various chapters in Rull & Carnaval 2021). Nonetheless, there are outstanding challenges for those interested in the interplay between Earth history and biological evolution in physically complex and species-rich regions like the Neotropics because narratives linking geological and evolutionary processes can fall short in providing exclusive predictions that would enable researchers to falsify hypotheses or gauge support for alternative historical scenarios. For example, given that the Andean uplift has extended over tens of millions of years, and is the result of different mechanisms operating at different temporal (millions to tens of millions of years) and spatial scales (tens to thousands of km), that the diversification of many clades coincides with uplift is not unexpected. Limitations of previous works (Antonelli & Sanmartín 2011, Sanín et al. 2016,) rely on the fact that uplift, just as diversification, can be continuous or episodic. This lack of scale specificity can give rise to problems of biogeographical pseudo-congruence (Donoghue & Moore 2003).

A potential way to move forward in testing spatially and temporally explicit hypotheses involving Earth processes and the distribution and diversification of species is to carefully consider (1) the mechanisms potentially underlying such associations and (2) other sources of information which may be informative about the explanatory power of alternative scenarios (Dolby 2021). For example, did the "uplift of the Andes" spur diversification because it created topographic relief isolating populations, because it generated novel habitats for lineages to colonize, or because it altered local climates promoting evolutionary adaptation? Can one evaluate scenarios in which Andean uplift is dissected into separate underlying mechanisms with specific putative effects on biodiversity? What sort of data on the physical environmental and organismal traits may one use alongside genetic or genomic data to evaluate predictions of alternative hypotheses?

We are convinced that productive dialogues between the Earth and life sciences in biogeography can best be established when one seeks to address questions like those posed above to understand how biodiversity responds to Earth processes. Indeed, the Neotropics has been the regional context in which many of these dialogues have been proposed (e.g Baker et al. 2014) and reviewing such dialogues is not our purpose.

Rather, we want to underline that the Earth processes studied and their purported effects on biodiversity should be temporally and spatially circumscribed as a first step in testing causal Earth-Life associations. Our main purpose is to show that volcanic centres are suitable areas where one can test links between Earth history and biodiversity because of their spatially and temporally explicit genesis, and their multiple and predictable effects on biodiversity. We illustrate this idea with examples of the influence of volcanoes on biodiversity in montane regions. We focus on the Neogene in the Tropical Andes and surrounding areas, a highly diverse region with complex topography and dynamic history where biogeographers have long sought links between Earth history and the evolution and distribution of life (e.g. Hoorn et al. 2010; Antonelli and Sanmartín 2011; Antonelli et al. 2018, Rahbek et al. 2019; Muellner-Riehl et al. 2019), but where the role of volcanism as a driver of biotic evolution has been insufficiently explored.

Volcanoes and biodiversity

Volcanoes may trigger effects on biotas from local to regional scales, are aggregated in space, and have a traceable duration determined by their unique deposits. Thus, the study of the influence of volcanism on biodiversity appears especially promising, given the possibility of spatially and temporally explicit hypothesis-testing. However, in our view, volcanism has not received sufficient attention as a driver of biotic evolution in montane regions for two reasons. First, presumably because intermediate to large-scale volcanic eruptions have a substantial effect on the landscape over short, contemporary (i.e. ecological) time frames (i.e. plant early succession after volcanism: Tsuyuzaki 2009; diversity response to volcanism in animals: Elizalde 2014, in birds: Daalsgard et al. 2007), interest about their deeper-time effects has been limited (but see Beheregaray et al. 2003 & Bemmels et al. 2022), and research has focused on understanding whether and how ecosystems and communities recover after them (Major et al. 2009). Second, researchers have focused on island volcanoes (i.e. Ali and Meiri 2019) and often considered continental volcanism only as a biogeographical epiphenomenon (*sensu* Dolby 2021) associated with tectonic mountain building or uplift, the purported main phenomenon of interest affecting biodiversity (e.g., Chaves et al. 2011, Antonelli and Sanmartín 2011). This view often disregards other geological processes associated with volcanic eruptions (e.g., faulting and bulging, climate forcing), which on their own may affect dispersal, speciation and extinction, and should thus be incorporated in biogeographical hypotheses.

Examining causal relationships between Earth and life evolution in montane regions requires attention to scale: how fast, for how long, and where might Earth processes have affected biodiversity? Scale largely determines what one may expect of the relationship between volcanoes and biodiversity. For instance, tectonic mountain uplift spans over tens of millions of years, whereas continental arc volcanic construction spans over hundreds of thousands of years to a few million years (Fig. 1, Table 1). Over relatively short periods (weeks, months, years, decades), volcanoes often have destructive effects on ecosystems.

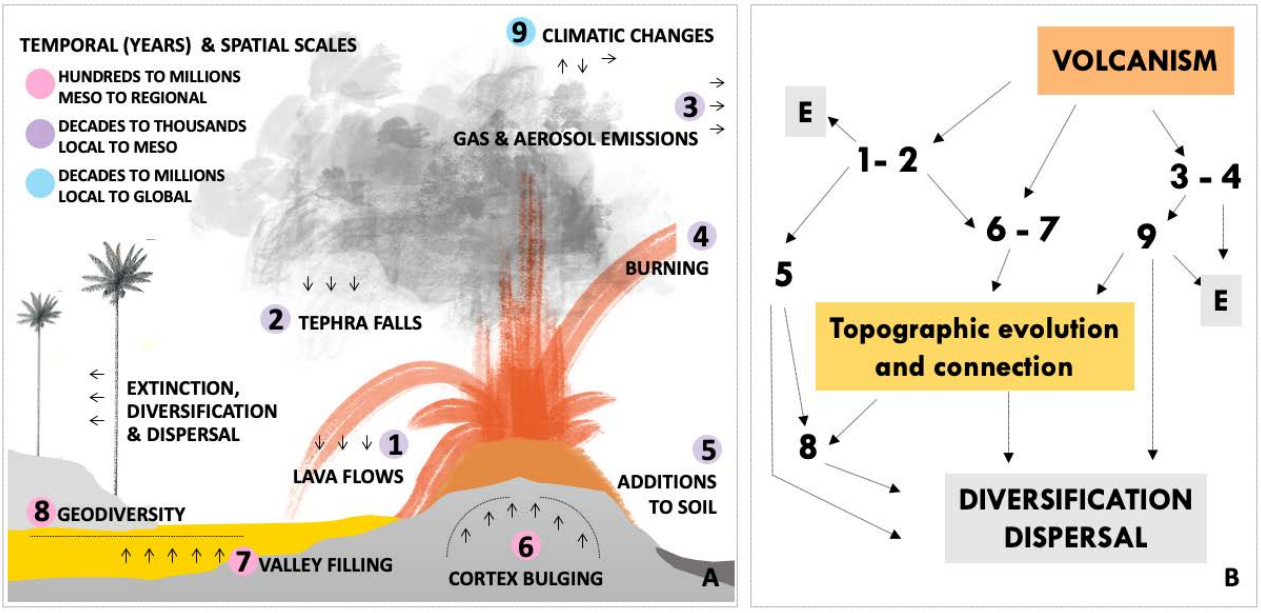

Figure 1. Many-fold effects of volcanism on relief, landscape, soil, climate and biodiversity, to which species can respond by adapting and diversifying, dispersing or becoming extinct (E); for a revision of published works on these processes, see Table 1; A) Graphic representation of the effects of volcanism, and B) the relationship between these effects and biological processes.

Table 1. Different scale effects of volcanism on terrestrial biodiversity.

Factor related to the process of Volcanism	Effect on landscape and climate	Geographical Scale; Temporal Scales (yrs)	Effect on Biodiversity	References
Large-scale lava flows and pyroclastic density-currents, lahars and debris avalanches	Valley and low land infills, burning, hydrogeomorphology disturbance/ responses (deviation and blockage of water ways) and of microhabitats (i.e. nests, caves), destruction of vegetation, flooding, new soil development, topographic inversion, new soil development	Local to Meso; 10-10^6	**Macroevolutionary**: extinction, speciation. **Microevolutionary**: population decline or local extirpation due to reduction of habitat, loss of genetic diversity, population subdivision and isolation. **Ecological:** biased taxonomical representation, depression of the treeline (expansion of open highland vegetation); promotes habitat heterogeneity and patchiness, primary (and secondary) succession. Regional species pool.	Moral & Grishin 1999; Beheregaray et al. 2003; Dale et al. 2005; Tsuyuzaki 2009; Major et al. 2009; Arnalds et al. 2013; Elizalde 2014; Del Crisafulli et al. 2015; Hsu et al. 2017; Payne and Egan, 2019; Nogales et al. 2022; Bemmels et al. 2022; Thacker et al. 2023
Tephra fall deposits	Mantling topography, burial, aerosol scavenging, biogeochemical disturbance, volcanic winters, nutrient deposition	Meso to regional; 10-10^3	**Macroevolutionary**: species turnover, local adaptation **Microevolutionary**: population enhancement through increased resource offer or population declines due to soil turnover Ecological: changes in primary productivity due to fertilization or limited light availability, trophic changes, changes in community structure and composition. Promotes secondary succession.	Moral & Grishin 1999; Dalsgaard et al. 2007; Tsuyuzaki 2009; Bagnato et al. 2012; Arnalds et al. 2013, Cárdenas et al. 2014; Langmann 2014; Crisafulli et al. 2015; Gunnarsson et al. 2015; López de Heredia et al. 2015; Williams-Linera & Vizcaíno_ Bravo 2016; Loughlin et al. 2018; Beierkuhnlein et al. 2023
Mountain building on top of already existing mountain chain	Generation of steeper slopes and / or higher peaks, valley filling, bulging, isostatic rebound (vertical uplift), habitat heterogeneity increases, connectivity/isolation	Local to regional; 10^3-10^6	**Macroevolutionary**: local adaptation and anagenesis, dispersal **Microevolutionary**: gene flow dynamics, dispersal across corridors, population isolation.	Parra-Olea et al. 2012, Osuna et al. 2020; Sanín et al. 2022; Murienne et al. 2022
Mountain building on flat areas	Generation of elevated areas, slopes, valley filling, bulging, isostatic rebound (vertical uplift), habitat heterogeneity increases	Local to regional; 10^3-10^6	**Macroevolutionary**: local adaptation and anagenesis, dispersal. **Microevolutionary**: gene flow dynamics. **Ecological:** biogeochemical cycling due to increased erosion and weathering, changes in structure and composition due to elevation gradients.	Mastretta-Yanes et al. 2015; Murienne et al. 2022
Warm refugia during cold periods, cold refuge during warm periods	Increase climatic heterogeneity, warm refuges	Local to meso; 10-10^3	**Macroevolutionary**: extinction decreases, immigration increases. **Microevolutionary**: population refugia during glacials .	Fraser et al. 2014
Gas and aerosol emissions	Aerosol dispersal, volcanic winters, acid rain, soil and water pollution, affect carbon flux and plant gas interchange (physiology), enhanced UV-B radiation	Local to global; 10-10^2	**Macroevolutionary**: local adaptation. **Microevolutionary**: local adaptation, mutagenesis. **Ecological:** stress and mortality due impediment to gas exchange and toxicity exposure.	Benca et al. 2018; Chen et al. 2019; Nogales et al. 2022
Progressive climate change		Regional to global; 10-10^6	**Macroevolutionary**: accelerate or decelerate diversification **Microevolutionary**: migration (range size contraction or expansion). **Ecological:** changes in composition and structure	Guex et al. 2016; Chen et al. 2019; Wang et al. 2023
Volcanic winters	Decrease temperatures	Regional to global; 10-10^6	**Macroevolutionary**: massive extinction of plant lineages. **Microevolutionary**: population bottlenecks. **Ecological:** primary productivity declines, trophic cascades, acclimation, changes in migration patterns, pathogens and disease.	Oppenheimer et al. 2003; Sobolev et al. 2011; Sigl et al. 2015; Guex et al. 2016; Alexander et al. 2017
Fumarolic and lightning activity	Increase humidity in high elevation areas, air, modify water and soil composition, diverse impact on microbial communities	Local; 10-10^2	**Macroevolutionary:** increase biodiversity. **Microevolutionary:** local adaptation to extreme environments, frequent lightning and nitrogen rich habitats. **Ecological:** composition and structure change due to lightning-related fires, increased humidity, and nitrogen fixation.	Costello et al. 2009; Medrano-Santillana et al. 2017; Solon et al. 2018
Geodiversity	Increase soil chemistry and nutrient content from diverse weathered bedrocks and volcaniclastic sediments, increase sulphur concentrations	Local to regional; 10^3-10^6	**Macroevolutionary:** increase biodiversity by promoting diversification and local adaptation. **Ecological:** increased diversity as increased heterogeneity of habitats, distance-from-source environmental gradients, metabolic changes in biota, phenotypic adaptation to darker, richer soils	Moretti et al. 2021; Kienle et al. 2022; Romano et al. 2023

However, in the long-term (thousands to millions of years), their addition of voluminous lava and volcaniclastic materials, emission of gases, the establishment of hydrothermal settings, or the modification of isostatic equilibrium due to thermal perturbations can have positive influences on biodiversity. Indeed, surface processes such as the formation of relief, drainages and soil, can have a variety of effects on colonization and speciation dynamics (Fig. 1, Table 1).

One of two main effects of volcanoes promoting biodiversity in the time frame of centuries to millennia relates to the soils that form after volcaniclastic deposition and subsequent weathering, which favour the accumulation of organic matter, water and nutrients (Tonneijck et al. 2010), and thus promote biodiversity by various mechanisms related to changes in resource availability and in the physical environment (Pardo et al. 2021). Volcanic ash soils harbor persistent carbon stocks and assimilable phosphorus that can be gradually absorbed by plants and are more fertile than soils that have evolved by exhumed rock weathering alone. Soil organic carbon stocks in andosols of high-elevation Andean forest and paramo almost double global averages for other volcanic ash soils due to chemical and physical stabilization mechanisms (Tonneijck et al. 2010). Also, andosols have higher water retention potential and a strong resistance to water sediment erosion (Shoji et al. 1993) related to their high soil porosity (Poulenard et al. 2011). A net positive effect of volcanoes on organic matter accumulation and resistance to erosion in areas of significant relief and weathering can promote plant colonization and succession dynamics, leading to higher and more sustained plant diversity (Kienle et al. 2022, Moretti et al. 2021). The spatial distribution of andosols may also foster patterns in phenotypic variation across space via adaptation or phenotypic plasticity. For example, plumage coloration in populations of Barn Owls (*Tyto alba*) is darker in areas where andosols are present or recent volcanic activity has occurred, a pattern attributable to greater production of phaeomelanin due to adaptation to darker soil surfaces (background matching) or to the influence of sulfur on metabolic pathways involved in pigment synthesis (Romano et al. 2023).

Secondly, volcanoes affect topographic evolution and may therefore influence evolutionary processes in various ways (Hoorn et al. 2013, Murienne et al. 2022). These processes tend to occur at the 1 y-1 My time scales. First, large-scale volcanic eruptions alter local geomorphology by filling low valleys with volcanic material and inducing drastic changes in drainage basins (Pierson & Major 2014; Cárdenas et al. 2014; Galve et al. 2022). Second, volcanic areas have steep geothermal gradients that promote kilometer-scale crustal doming and deformation, a process ultimately resulting in surface uplift. We here offer two examples of likely links between such processes and biotic evolution: in Ecuador, volcanoes shaped the topographic landscape where endemic ground beetles diversified by repeated connection-isolation dynamics in volcanic areas amidst Pleistocene climatic cycling (Murienne et al. 2022), and in Mexico, the volcano rabbit evolved after volcanic uprising of the Sierras Chichinautzin and Nevada (Osuna et al. 2020). Finally, volcanic deposits may be easier to erode than surrounding bedrocks (Moosdorf et al. 2018) and can, in conjunction with climate, contribute to higher topographic destruction and accelerated drainage evolution, a process that may have substantial effects on biodiversity. For example, drainage evolution of the Cauca River valley in the Northern Andes of Colombia, related to volcanism in the Central Cordillera (i.e. the transition from several short river segments and lakes to a continuous river basin; Pérez-Consuegra et al. 2022) not only affected aquatic life but also contributed to the isolation of seasonally dry orographic rain-shadowed enclaves and their unique biota (González et al. 2018; Idárraga-Piedrahíta et al. 2021). In the Eastern Cordillera flanks of Ecuador, 8 m-thick tephra deposits blocked valley river incision, favoring Andean forest species turnover (Cárdenas et al. 2014). In sum, volcanism interacts in conjunction with climate and tectonics to generate particular environments where species evolve over time.

One may also consider the compounding effects of volcanoes via substrate enrichment and their influence on topography on the evolution and distribution of mountain biodiversity. Low-elevation valleys are often inhabitable areas for highland tropical species because of their higher temperatures and distinct precipitation regimes. On the other hand, areas that were recently exhumed through orogeny usually have parental material that will end in limited soil formation or nutrient-poor soils in which species with particular requirements cannot occur. Filling valleys with volcanic lava flows that will elevate surfaces (topographic inversion; Cas et al. 2011) and then also enrich soil composition by releasing biodiversity-limiting elements may therefore favour the establishment and accumulation of montane species, facilitate dispersal by range expansion, and foster local adaptation. Below, we provide a context of biogeography related to volcanic activity in the Northern Andes, then bring attention on the area of the Colombian Massif, and finalize by illustrating cases in which volcanic activity in the broader context of Andean uplift could be potentially related to biogeographic patterns (Fig. 3 [[Q1: Q1]]).

Volcanoes in the Northern Andes and biogeography

The North-Andean volcanic province

Neogene volcanic activity in the Northern Andes results from the subduction of the Nazca oceanic plate beneath South America and has been relatively persistent since the Neogene (van Houten, 1976; Pennington, 1981; Marín-Cerón et al. 2019). In northern Colombia, the volcanic front in which most of the edifices concentrate has experienced major spatial changes between the Miocene and the Recent (Wagner et al. 2017), with shifts in the distribution of volcanic-influenced landscapes and deposits between the Western and Central Cordillera (Jaramillo et al. 2019; Fig. 2).

This long-term history causes both superficial volcanic piling over hundreds of thousands of years and deep magmatic addition to the lower crust over tens of millions of years (Fig. 2), which contribute to changes in crustal thickness, hydrogeomorphic changes in the inter-Andean valleys and to topographic elevation or connection due to valley filling (Fig. 2; Thouret et al. 1990, 1995; Suter et al. 2008; Poveda et al. 2015; Monsalve et al. 2019; Espinosa-Vaquero 2020). Calc-alkaline volcanic products have also determined soil composition and evolution, ultimately contributing to geodiversity (Kienle et al. 2022), a factor positively associated with species richness (Muellner-Riehl et al. 2019, Rahbek et al. 2019).

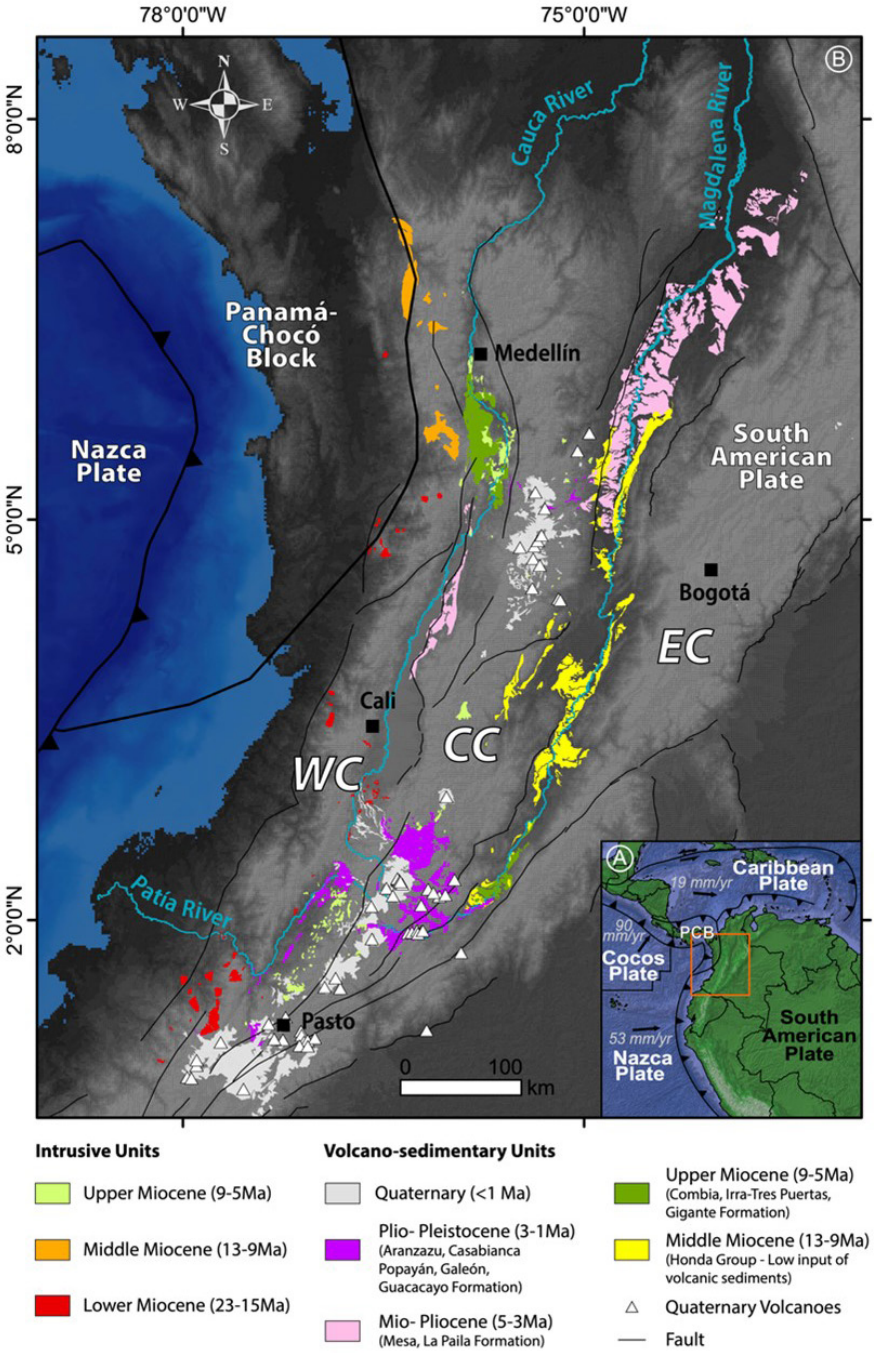

Figure 2. A. Regional map of the Colombian Andes showing the current tectonic configuration. B. Geological map showing the distribution of intrusive and volcano-sedimentary units from the Neogene. Abbreviations: PCB: Panamá-Chocó Block; WC: Western Cordillera; CC: Central Cordillera; EC: Eastern Cordillera; the volcanic cluster of the Colombian Massif is indicated north of Pasto, and the volcanic cluster of Nudo de los Pastos (southern tip of the Colombian Massif) is indicated south of Pasto (both as white triangles). Geological information taken from Gómez & Montes (2020); Digital Elevation Model (DEM) downloaded from: https://download.gebco.net/.

The Colombian Massif

The Colombian Massif is a continuous highland plateau encompassing the southern and central segments of the active volcanic arc in southern Colombia, from where major rivers flow North (i.e. Cauca, Magdalena) and West (i.e. Patía), and where the three Cordilleras of Colombia, and the Ecuadorian Andes split. Although volcanoes in the Northern Andes are compositionally related (Monstalve-Bustamante et al. 2020), the volcanic cluster of the Colombian Massif exhibits the record of widespread ignimbrites, which are large-volume deposits of high-concentration pyroclastic density currents (Branney and Kokelaard 2002) and their reworked products known as lahar deposits. They are exposed in an area of at least 2775 km^2; geochronological constraints suggest two major volcanic activity periods in the Miocene (Kroonenberg et al. 1981) and Pliocene to Pleistocene (Risnes 1995, Sanin et al. 2022, Torres-Hernández 2010, Van der Wiel 1991, Van der Wiel et al. 1992). Together with large-scale debris-avalanches and lahars, calderas contributed to topographic growth and fast landscape disturbance in the Pliocene to Pleistocene and possibly to the closure of a trans-Andean portal connecting the Amazon and magdalena-caribe basins (Montes et al. 2021).

Dispersal of wax palms to different cordilleras across a volcanic province

The genus *Ceroxylon* comprises 13 species of wax palms from montane cloud forests of the Tropical Andes. Because wax palms are endemic to this region and diversified during the Neogene, diversification and surface uplift temporally and spatially coincide. Uplift in the Tropical Andes has also extended throughout the Neogene primarily in response to plate margin convergence and deformation (Mora et al. 2010). However, biogeographical processes like dispersal, speciation and extinction occur over shorter time scales and in more restricted areas than the "Neogene" and the "Tropical Andes", respectively. Thus, this case study sought to test whether second-order processes, that are linked to mountain building, but that can usually be tied to more constrained time and spatial scales, could be causally linked to biogeographical processes in the wax palms. The regional effect of caldera-forming eruptions, and the ignimbrite deposits resulting in the filling of low valleys occur in volcanic provinces and can span from hundreds to a few million years. Intensive geographical and genomic sampling of wax palms throughout the Tropical Andes, alongside geochronological, petrographic and provenance analysis of ignimbrites and other rock outcrops surrounding the southern volcanic province of Colombia, were used to assess whether large-scale caldera-forming volcanic events could have been related to biogeographical processes in the palm genus. Dispersal would be enhanced through topographic connectivity by magmatic contribution to low passes, allowing connectivity between formerly disconnected segments of the Andes (Sanín et al. 2022). Specifically, Neogene ignimbrites occurring on the east and west slopes of the northern volcanic area of the Colombian Massif near Popayán (Cauca) and San Agustín (Huila) were studied, where extensive populations of the highland species of wax palms also exist. This area is currently topographically continuous and does not exhibit any particular relief or climatic breaks, and was shown to be a low mountain pass in the late Miocene to Pliocene (Montes et al. 2021). Through dated phylogenomic analyses, it was concluded that despite wax palms having lived in the Northern Andes since the Late Miocene, the dispersal of various highland lineages (*Ceroxylon parvifrons, C. quindiuense, C. ventricosum, C. vogelianum*) to the Western and Central Cordilleras of Colombia did not occur until the Plio-Pleistocene through the area of the Colombian Massif (Kroonenberg et al. 1981). This is congruent with the description of volcanic eruptions of great magnitude that also occurred in this area and time. The study showed that volcanic eruptions in the Colombian Massif likely contributed to filling topographic gaps and low passes, thereby connecting the Western and Central Cordilleras to the Colombian Massif during the Plio-Pleistocene. This topographic connection allowed wax palms to colonize the Western and Central Cordilleras (Fig. 3A**)** by filling the low pass or "Trans-Andean portal" in south Colombia (indicated in orange color on Fig. 3B).

Hybridization in Andean warblers across a volcanic province

Two species of high-elevation passerine birds in the warbler family Parulidae, *Myioborus ornatus* and *M. melanocephalus,* exhibit striking geographic variation in plumage coloration throughout the tropical Andes which contrasts with low levels of differentiation in mtDNA (Pérez-Emán 2005, Céspedes-Arias et al. 2021). Genetic divergence among plumage groups is particularly low among those occurring in the northern Andes, from central Ecuador to Venezuela. Near the Colombia-Ecuador boundary two of these plumage groups meet in a hybrid zone of approximately 200 km, where individuals with intermediate plumage are common and phenotypically "pure" individuals of both forms do not co-occur. Based on phenotypic patterns of variation, this hybrid zone is centered just in the south of the Colombian Massif volcanic province, in an area called Nudo de los Pastos (Fig. 3B-C), where clear topographic or climatic breaks in the cloud forest belt that these warblers inhabit do not currently exist (Graham et al. 2010). Because this hybrid zone likely formed by secondary contact of formerly isolated populations, a question that arose during this work is what prompted the period of isolation in which populations differentiated in the first place and what led to their secondary contact. Notably, the hybrid zone location corresponds to an area of important magmatic contribution to topography, which also includes widespread ignimbrites and pyroclastic deposits (Kroonemberg, 1981, Velandia et al. 2008) that connected previously isolated mountain segments at the Colombia-Ecuador border region. The changes in connectivity of *Myioborus* habitat that allowed for secondary contact between differentiated populations in the area might have been related to volcanic activity significantly modifying topographic connectivity.

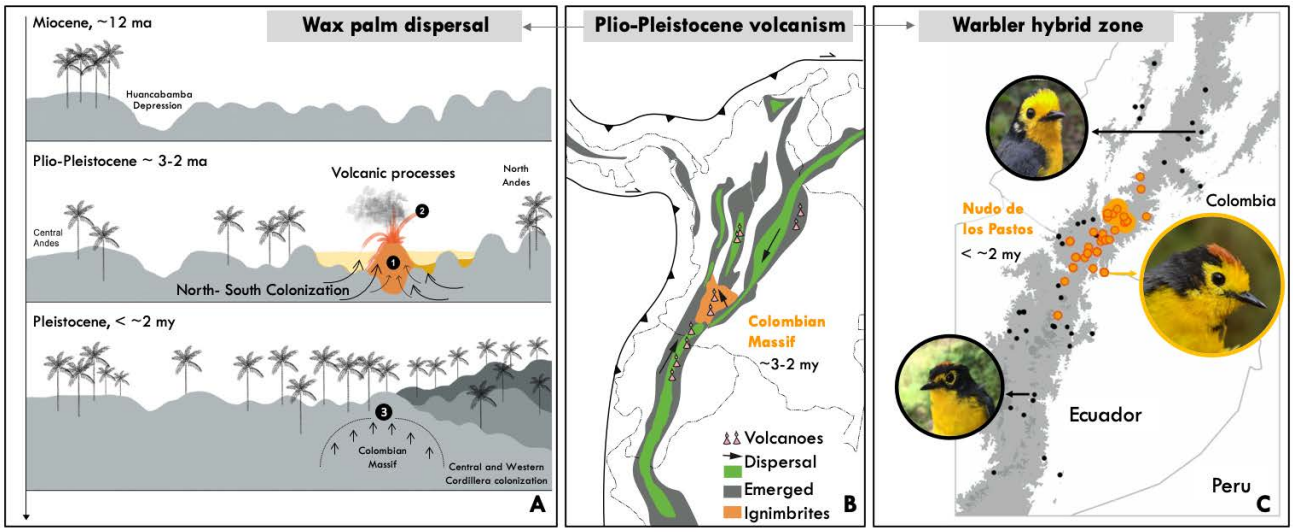

Figure 3. Plio-Pleistocene volcanism in the Colombian massif is temporally and spatially constrained and can be causally linked to two evolutionary processes in Andean endemics. **A)** wax palms, genus *Ceroxylon*, were present in the Tropical Andes since the late Miocene but absent from the elevated but previously disconnected Western and Central Cordilleras where volcanic deposition from ignimbrite-forming eruptions (1) filling of low valleys (2) and crustal bulging (3) led to topographic connectivity fostering wax palm dispersal (Illustration by Laura Ospina). **B)** The Colombian Massif and southern Nudo de los Pastos, an area where magmatic additions ignimbritic eruptions and magmatic filling of low valleys led to higher topographic connectivity. **A)** and **B)** are modified from Sanín, Cardona et al. (2022). **C)** Hybrid zone of *Myioborus* warblers located in southern Colombia. Orange dots correspond to localities where specimens with a clear intermediate plumage were collected, with the bigger orange circles denoting the ones within the estimated center of the hybrid zone (Céspedes-Arias et al 2021). Black dots correspond to localities where only parental plumage forms occur, either *M. m. ruficoronatus* in the south, or *M. ornatus chrysops* in the north. Photos around the map correspond to the two parental plumage forms, and an example of an individual with an intermediate phenotype. *Myioborus* photos top to bottom are by David Ocampo, Paulo Pulgarín and Laura Céspedes Arias.

This hypothesis predicts that the timing of secondary contact (i.e. the age of the hybrid zone) must postdate volcanic activity leading to enhanced connectivity of cloud forest in the area. Based on mtDNA data (Pérez-Emán 2005), the diversification in the complex occurred within the past 1 million years, which implies that the hybrid zone is likely younger than magmatic topographic additions and could therefore have originated following volcanic activity in the Pleistocene in the Colombian Massif and Nudo de los Pastos. These findings show another effect of second-order processes in mountain building, namely topographic contribution by caldera-forming volcanic eruptions, on biogeographic processes, in this case related to secondary contact through dispersal. By using genomic data collected from specimens of *Myioborus* across the hybrid zone, a more precise estimate of the age of the hybrid zone can be obtained (Meier et al. 2017, Pool and Nielsen 2009, Sedghifar et al. 2015), and tests of explicit demographic scenarios can be conducted, research that will deliver a better understanding of the interplay of these two Earth-Life processes.

Concluding remarks

The Andes have had disparate topographic profiles and continuity throughout their history (Anderson et al. 2016, León et al. 2018, Zapata et al. 2020, Montes et al. 2021). Second-order processes of topographic evolution, like faulting and volcanism, have played an important role in mountain building, the consolidation of cordillera and inter-Andean valley systems, and in the evolution of life in the Neotropics. Although life has evolved in the context of gradual mountain uplift, spatially and temporally constrained processes like volcanism have had a definitive role in species dispersal and diversification. As we have discussed, at deep, thousand-to-million year time scales, volcanoes can promote life via different mechanisms. Furthermore, temporally and spatially constrained volcanic events and processes allow one to draw direct causal relationships between the evolution of landscape and of life. We encourage biogeographers to further engage in establishing such causal relationships and in testing specific predictions of alternative hypotheses as a productive means to enrichen our narratives about links between Earth and life evolution in North Andean biogeography.

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Author Contributions

Writing was led by the first and last authors; all authors contributed to the writing and revision of the final versions of this manuscript (Fig. 1 by MJS, Fig. 2 by AC, Fig. 3 by MJS and LCA, Table 1 by MJS).

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