# Editorial Preface to Special Issue

*Exploring the impact of Andean uplift and climate on life evolution and landscape modification: From Amazonia to Patagonia*

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# Editorial Preface to Special Issue: Exploring the impact of Andean uplift and climate on life evolution and landscape modification: From Amazonia to Patagonia

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## 1. Introduction

The aim of this Special Issue is to improve the general understanding of the uplift of the Andes and its far-reaching impact on climate and biodiversity in South America from the late Mesozoic onwards. The Andes form the backbone of the South American continent and are the world's most biodiverse mountain system (Pérez-Escobar et al., 2022). This biodiversity is directly related to the spatial heterogeneity and altitudinal gradients that formed during mountain building that initiated in the Cretaceous, but was not uniform across the Andes (Boschman, 2021). Geologically, the uplift of the Andes is directly linked to subduction at the western margin of the South American plate, with deformation phases due to changes in plate motion, direction, and subduction style (Ramos, 2009). All this implies that the Andes were not uplifted uniformly through time. Piecing this history together requires research along the almost 9000 km long stretch from the Caribbean to Patagonia. This uplift process generated new habitats and promoted biotic isolation and diversification (Pérez-Escobar et al., 2022; Hoorn et al., 2018; Perrigo et al., 2020; Hagen et al., 2021), but also formed a dramatic topographic barrier to atmospheric circulation and caused one of the most important orographic rain shadows on Earth (Poulsen et al., 2010). Hence, the developments of massive steppes in South America (Patagonia), and even extreme hyperaridity (Atacama), are also linked to the formation of the Andes (Rech et al., 2006).

This special volume was inspired by the interdisciplinary meetings that were held in 2019, in celebration of the 250th birth anniversary of Alexander von Humboldt (Becker and Faccenna, 2019; Hoorn et al., 2019, 2022; Linder et al., 2019). Alexander von Humboldt (1769–1859) is best known for his contributions in geology and botany and was one of the founding fathers of the field of biogeography (Linder et al., 2019). He pioneered an integrative scientific vision in combination with a great thirst for exploration and systematic data collection (Wulf, 2016). At the turn of the 19th century, Humboldt and his French colleague Aimee Bonpland ventured into the Andes and Amazon lowlands. Following from this voyage, Humboldt formulated his famous model of plant distribution across the Andean slopes in the context of geology, climate, landscape, and elevational gradient (Humboldt, 1805).

In this volume we took example from Humboldt's interdisciplinary approach and solicited papers from different authors who with their research covered the Andes north to south, and from Amazonia to Patagonia. The resulting compilation consists of twenty papers that cover different aspects of the geological formation of the Andes, the effects of this on landscape and drainages, but also the biotic response this generated. We also looked at the Cenozoic history and the effects of climate change across the Andes, and from Amazonia to Patagonia. Furthermore, we devoted a section of the special issue to the history of Amazonia and the extensive Pebas wetland system that once covered large parts of western Amazonia. We conclude with a paper that models past climate and evaluates the effects of climate change on rainforest growth with implications for future scenarios of global warming.

Below we present a summary of the content of the papers and how they each contribute to the field.

## 2. The uplift of the Andes and effects on landscape and drainage

Vallejo et al. (2021, this VSI; Fig. 1.8) provide us with an overview of the sedimentary history from the Mesozoic and early Cenozoic and reconstruct the paleogeography of northwestern South America. They provide detailed data on stratigraphy, sedimentology, provenance, and geochronology from sedimentary records in the Oriente Basin (Ecuador), which is bound by the Putumayo Basin (Colombia) in the north, and the Marañon Basin (Peru) in the south. In the Early Jurassic (~160 to 175 Ma) most of northwestern South America was formed by deep marine environments. In the Oriente Basin this phase is represented by a carbonate platform and deltaic deposits. At the transition from Middle Jurassic to Early Cretaceous (~160 to 130 Ma) volcaniclastic and alluvial fan deposition prevail; this episode is coeval with regional extension and the emergence of the Andes westwards of the basin. A mixed sediment source, however, also points at sediment contribution from the Amazon Craton. From ~110 to 115 Ma (Early Cretaceous), coastal deposition takes place, with the Amazon Craton remaining the principal source for sediment deposition by westward-

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**Fig. 1.** Topographic map of South America (© MSchmeling - Can Stock Photo Inc.) showing the studied areas covered in our Special Issue. 1) Serrano et al. (2021, this VSI); 2) Lörch et al. (2021, this VSI); 3) Antoine et al. (2021, this VSI); 4) Kukla et al. (2021, this VSI); 5) García-Delgado et al. (2021, this VSI); 6) Zapata et al. (2021, this VSI); 7) Albert et al. (2021, this VSI); 8) Vallejo et al. (2021, this VSI); 9) Barreda and Palazzesi (2021, this VSI); 10) Jimenez et al. (2021, this VSI); 11) Espinosa et al. (2021, this VSI); 12) Martínez et al. (2021, this VSI); 13) Pérez-Consuegra et al. (2021, this VSI); 14) Villalba Ulberich et al. (2021, this VSI); 15) Renny et al. (2021, this VSI); 16) Boschman and Condamine (2021, this VSI) 17) Salazar-Jaramillo et al. (2021, this VSI); 18) Hoorn et al. (2021, this VSI); 19) Pino et al. (2021, this VSI); and 20) Sanín et al. (2022, this VSI).

flowing rivers. Towards the Late Cretaceous (~100 to 80 Ma), shortening in the Northern Andes coincides with the collision of the Caribbean Plateau, while in the Oriente Basin renewed deepening and marine (carbonate) deposition takes place. Finally, during the Late Cretaceous-Paleocene transition (~72–60 Ma), the Andes became the prime sediment source for fluvial deposition in the Oriente Basin, with basin inversion and continental-scale drainage reorganization marking this transition. Similar observations were made in the Peruvian Madre de Dios (Louterbach et al., 2018) and Huallaga basins (Hurtado et al., 2018), reaffirming the regional extent of this event.

Zapata et al. (2021, this VSI; Fig. 1.6) investigate the uplift history of the Antioquia Plateau (Central Cordillera, Northern Andes) and present their stratigraphic, structural, and thermal data in a 3D thermo-kinematic model that shows three stages of development. The first stage is from Late Cretaceous to Paleocene (72 and 60 Ma) and comprises mountain building that coincides with the collision of the continental margin with the Caribbean Plateau. The remainder of the Paleogene is characterized by tectonic and climatic quiescence. In the Neogene, a final stage of tectonic uplift and low erosion leads to a topography of higher elevation than at present. This paper illustrates well how mountain building should be reconstructed based on an array of data, and that this process progresses through alternating stages of low and high topography due to feedback mechanisms between tectonism and climate.

Pérez-Consuegra et al. (2021, this VSI; Fig. 1.13) also focus on the Central Cordillera (Northern Andes), and investigate whether tearing and flattening of a subducting tectonic plate (slab) could have driven changes in topography and drainage systems in both the Western and Central Cordillera (Northern Andes, Colombia). To test their hypothesis, the team applied geomorphologic and topographic analysis, combined with estimated erosion rates. Notably, the northern part of the Central Cordillera presents a low relief with indications for a recent increase in uplift, whereas the southern part has a high relief and indications of long-term uplift. The intersection of these areas coincides with slab flattening in the subsurface. This suggests that slab flattening led to uplift in the Northern Andes (c. ~2 km of surface uplift) and drainage reorganization from 8 to 4 Ma, which subsequently influenced biodiversity evolution on the Antioquia Plateau and the Cauca and Porce river systems.

Uplift of the Northern Andes is further investigated by García-Delgado et al. (2021, this VSI; Fig. 1.5), who explore the drivers of denudation rates for the Eastern Cordillera (Colombia), and assess the relevance of tectonism versus climate through statistical analysis. Climate forcing has been previously hypothesized as the primary driver of rapid Pliocene exhumation rates (Mora et al., 2008), but in a later publication this view was corrected to a combined tectonic-climatic driven orogenetic model (Ramirez-Arias et al., 2012). The research team integrated geomorphic, seismic, geological and published low-temperature thermochronological, and cosmogenic nuclide data. Overall, they found no statistical support for a climate-driven exhumation event in the Eastern Cordillera and climate only seemed to have played a role in local, short-term erosion rates. Instead, long to short-term erosion rates are controlled by tectonic history. Notably, they estimated a post-Miocene surface uplift of at least 1.4 km by using paleo-profiles of four rivers.

Villalba Ulberich et al. (2021, this VSI; Fig. 1.14) provide new insights into landscape and environmental evolution in the southern Central Andes. Their data include new age determinations from volcanic tuff and a re-evaluation of the stratigraphy, paleoenvironments and provenance in Jujuy, northwestern Argentina, an area situated in the Subandean Ranges. They found that late Miocene tectonics in the eastern margin of the Puna Plateau resulted in the deformation of the foreland and uplift of the Eastern Cordillera and Subandean Ranges. Subsequently, the orographic barrier formation generated a southward deflection in drainage direction while sedimentary environments transitioned from braided river to alluvial fan conditions. This study showed how uplift of the Puna Plateau and Eastern Cordillera is linked with eastward migration of deformation, changes in sedimentary environment and climate aridification.

## 3. Biotic response to Andes mountain uplift

Boschman and Condamine (2021, this VSI; Fig. 1.16) analyze the evolutionary diversification of several frog and lizard clades within the context of the Andean orogeny and climate change. Their paleogeographic reconstructions provide a detailed account of our current understanding of the Andean uplift from the Late Cretaceous to the Recent and its spatial heterogeneity. The authors show that the Andes and their long and complex history do not only owe their unique species richness to recent species migrations and radiations but also to the presence of ancient clades. While the identification of the mechanisms that might have facilitated species diversification processes in deep time remains difficult, the interplay between tectonic activity and climate change is likely to have had an important role in the origination and persistence of clades across mountain ranges.

Pino et al. (2021, this VSI; Fig. 1.19) provide several biotic and abiotic hypotheses to explain the cause of the enigmatic extinction of the Sparassodonta, a group of carnivorous non-placental mammals that dominated South American landscapes during most of the Cenozoic. Among contrasting hypotheses, they explore those related to competitive displacement, and body size evolution, as well as those related to major habitat changes triggered by environmental change, such as Andean uplift and global cooling after the middle Miocene. They show that biotic interactions (competition and predation) and body size evolution may not have been the primary drivers of extinction in sparassodonts. Instead, they find that their decline can be linked to the continent's geological, landscape, and ecosystem history during the Miocene associated with Andean uplift.

Sanín et al. (2022, this VSI; Fig. 1.20) investigate the geological processes that formed the Central Cordillera (Colombia) in the Northern Andes and question the effects on plant dispersal. In their study they focus on the iconic *Ceroxylon* wax palm, which —contrary to most other palms— grows at elevations ranging from 1400 to 3500 m. A phylogenetic analysis of 12 species enabled a reconstruction of the diversification history of these palms. Furthermore, they analyzed ignimbrites in a key area that connects different segments of Andes. The combined results show that volcanic processes during the late Miocene connected the Northern Andes and facilitated dispersal pathways for the *Ceroxylon* palm.

Lörch et al. (2021, this VSI; Fig. 1.2) explore the historical biogeography and climatic niches in an Andean group of the sunflower subfamily Barnadesioideae. They focused on the clade comprising *Fulcaldea*, *Archidasyphyllum* and *Arnaldoa*, with disjunct species between the southern (*Archidasyphyllum*) and the tropical (*Fulcaldea-Arnaldoa*) Andes, and one non-Andean species (*Fulcaldea stuessyi*). Lörch et al. find that this group originated during the Miocene from a Central Andean ancestor and split into two disjunct clades (*Archidasyphyllum* vs *Fulcaldea-Arnaldoa*). They conclude that the development of aridity in the Central Andes might be responsible for the origin of this disjunct pattern and that the colonization of non-Andean regions (such as northeast Brazil) by *Fulcaldea* may have occurred later, during the Pliocene.

Serrano et al. (2021, this VSI; Fig. 1.1) estimate the diversification of lowland neotropical rainforest trees, using the angiosperm family Sapotaceae (subfamily Chrysophylloideae) as a case of study. This clade is a good model to test diversification hypotheses largely because of its wide distribution and high number of species and specimens in neotropical rainforests. Using a large dataset and a calibrated phylogeny, these authors explore how Andean uplift, the formation of the Panama land bridge, and Pleistocene climatic fluctuations all influenced the dispersal and diversification of this angiosperm clade. They suggest that dispersal has played an important role in the evolutionary history of neotropical Chrysophylloideae at various scales, yet they did not find evidence supporting the hypotheses of increasing diversification rates caused by the Andean uplift or the Pleistocene climatic shifts.

Renny et al. (2021, this VSI; Fig. 1.15) analyze the evolutionary history of the plant species *Arachnitis uniflora* (Corsiaceae), which obtain nutrients through symbiotic fungi rather than from photosynthesis. Plant and fungus grow in the tropical semi-humid forests of Peru and Bolivia, in the temperate Andean-Patagonian forests of Argentina and Chile, and in the moorlands of Malvinas/Falkland Islands. The authors perform phylogeographic, dating analyses, spatio-temporal diffusion models, and species paleo-distribution projections to study when the major genetic divergences within populations of this species occurred. Modern genetic groups within *Arachnitis uniflora* appear to have diverged since the late Miocene, giving origin to the northern and Patagonian groups. Climatic shifts promoted by Andean uplift during the Miocene may have driven the main ancient genetic divergence. Interestingly, all subsequent colonizations occurred from the early Pliocene to the beginning of the Pleistocene, before the Great Patagonian Glaciation, thus revealing a low influence of the Last Glacial Maximum glaciation on the evolutionary history of this species.

Jimenez et al. (2021, this VSI; Fig. 1.10) analyze evolutionary processes in ant-plant mutualism along the Andean range in South America. They use a comparative phylogeographic approach to assess the consequences of the Andean uplift on the mutualism between Azteca ants and *Tococa guianensis* (Melastomataceae), and whether plant and ant diversification were promoted by geography or by this mutualism. They find that phylogeographic structure in ant-plant mutualism coincides spatially and temporally with peaks of activity during the Andean uplift. The authors hypothesize that Andean uplift had a greater impact on lineage diversification than mutualism.

Albert et al. (2021, this VSI; Fig. 1.7) present historical biogeographic analyses based on novel (two clades of freshwater fishes) and published (riverine and upland clades of plants, insects, and vertebrate classes) studies of Amazonian taxa. Using time-calibrated molecular phylogenies, they demonstrate that tectonically driven megariver capture events promoted biotic interchange between the western and eastern part of the Amazon drainage basin. These megariver captures represented rare but large landscape changes and played a significant role in shaping biodiversity in Amazonia across many taxonomic groups. The authors named this process of biotic exchange between western and eastern Amazonia the Great Amazonian Biotic Interchange (or GAzBI).

## 4. The effects of Cenozoic climate change: examples from the Andes, Amazonia, and Patagonia

In general, landscape and biotic changes related to the Cenozoic global thermal extremes are very poorly documented for terrestrial environments, and this is even more the case for South America. This gap is addressed in the following studies.

Martínez et al. (2021, this VSI; Fig. 1.12) date and describe the fossil plant flora from the middle to late Eocene (~47.3 to ~33.9 Ma) Esmeraldas Formation in northern Colombia. In their study, fossil plants are used to reconstruct the Eocene climate, which point at warm temperatures and seasonal precipitation that fall within the range of modern tropical dry forests. These forests inhabited the floodplains of a meandering river system and were dominated by typical dry forest taxa from the *Pterocarpus* clade, Bombacoideae (Malvaceae) and Euphorbiaceae. The authors also hypothesize that towards the end of the Early Eocene Climatic Optimum (EECO), mean annual precipitation declined and seasonality increased in the Neotropics.

Antoine et al. (2021, this VSI; Fig. 1.3) report on the sedimentary environments and the fossil record of the Pozo Formation that is exposed in western Amazonia (Peru). The sediments range in age from c. 36 to 32.5 Ma, covering the Eocene Oligocene Transition (EOT), and are formed by fluvial to coastal plain deposits (Eocene). As sea level dropped, environments transitioned into strictly fluvial conditions (Oligocene). This shallowing upwards in the large ‘Pozo’ wetland system is accompanied by the disappearance of coastal taxa and a decrease in mammal species richness. The authors question if these changes are due to regional or global change, and they conclude that Eocene depositional environments are driven by basin subsidence due to tectonic loading. However, Oligocene aridification and sea level drop are primarily driven by global climatic cooling.

Barreda and Palazzesi (2021, this VSI; Fig. 1.9) present palynological evidence from 9 sections that are situated in Patagonia and range in age from Oligocene to Miocene (~34–10 Ma). In this record, five phases of taxonomic diversity were recognized. The early Oligocene ‘icehouse’ (c. 34 Ma) stands out for an impoverished pollen flora with relatively few species. During the Miocene Climate Optimum (MCO) the palynoflora includes arid taxa, but is overall enriched with tropical elements. Towards the late Miocene (10 Ma), the rise of arid plant taxa mark the completion of the orographic barrier. This Patagonian record further suggests that the ancestral Gondwanan flora in this region was tolerant to global cooling and aridification in the Oligocene, as well as to the warm and wetter climate of the Miocene. However, the Gondwanan flora was not resilient to the aridification imposed by rain shadow from the Andes, which permanently changed the character of the floral composition and favoured arid species.

In northern South America, the relation between Neogene climatic cooling and accelerated uplift of the Northern Andes are still poorly understood. Salazar-Jaramillo et al. (2021, this VSI; Fig. 1.17) address this issue in a paleosol study in La Tatacoa, a desert situated in the southwest of Colombia. This desert is famous for the La Venta mammal fossil record that forms part of the Miocene Honda Group (e.g. Cadena et al., 2020). The sedimentary sequence is characterized by a sharp contrast at ~13.1 Ma (late middle Miocene) between gray and red–bed paleosols. This change is consistent with a shift in soil redox conditions in response to a change in soil moisture regime. The authors propose that annual patterns of rainfall in the Neotropics change from a unimodal to a bimodal precipitation pattern, which points towards aridification following northward migration of the Intertropical Convergence Zone due to the establishment of a fully glaciated Antarctica.

## 5. Marine incursions and forest resilience in Amazonia

For centuries, scientists have been puzzled about the origins of Amazonian biodiversity (Humboldt, 1805). An intriguing aspect of the Amazonian history are the Miocene marine incursions that are thought to have affected both aquatic and terrestrial diversity (Lovejoy et al., 1998; Fontenelle et al., 2021; Bernal et al., 2019). Traces of these marine incursions can be found in the modern landscape in the form of nutrient-enriched soils linked with higher plant diversity (Higgins et al., 2011; Tuomisto et al., 2019).

Espinosa et al. (2021, this VSI; Fig. 1.11) present new palynological data from a borehole (1-AS-9-AM) that was drilled in western Amazonia, which suggest that the marine incursions may have lasted until the late Miocene, longer than previously thought. Besides dating this cored section, the authors also show that the marine assemblage comprises c. ~17% of the palynological count and is formed by coastal indicators such as foraminiferal linings, dinoflagellate cysts and acritarchs. In an informative subsurface cross section across the principal sedimentary basins in western Amazonia, the authors provide an overview of the three Miocene marine events and relate these to reference sections in the Llanos Basin (northern Colombia).

Hoorn et al. (2021, this VSI; Fig. 1.18) use a multidisciplinary approach to evaluate cyclic deposition in the Miocene wetland of western Amazonia, to better understand the deep time history and evolution of the modern Amazonian rainforest. They analyze a fossil-bearing sedimentary section (Los Chorros succession) that includes repeated flood-fill packages accumulated during the MCO. Using a multi-proxy record (i.e. molluscs, sporomorphs, algae, sediments, and terrestrial biomarkers), they find shifts in local vegetation, salinity, nutrient levels and water depths. This suggests the Andes were the most important sediment source, with the Amazon Craton as an additional supplier. Also, they find that the surface elevation of the Andes was up to ~3500 m and hosted a proto-paramo vegetation at the time of the Los Chorros deposition. The reconstructed landscape for the Miocene contrasts to that reported today in the region (western Amazonia), leading them to assume that geological and astronomical forcing may have driven the floral and faunal distribution and controlled sediment deposition.

Finally, Kukla et al. (2021, this VSI; Fig. 1.4) reconstruct how the rainforest in central and western Amazonia responded to aridity and fire during the mid-Holocene, and in this way determine the strength of vegetation-climate feedbacks and the resilience of tree cover to drying. To achieve this, they use pollen, charcoal, and speleothem oxygen isotope analyses. Notably, they attribute the persistence of high central and western Amazonian tree cover in the mid-Holocene to resilience to drying rather than to nominal aridification. By applying a dynamic global vegetation model (LPJ-GUESS), they also show that by reducing fire and limiting human interference, modern tree cover might be as resilient as the mid-Holocene forest. The authors conclude that human-driven fire and deforestation are likely to be a greater threat to the future of Amazonian ecosystems than drying alone.

## 6. Concluding remarks

- Uplift of the Northern Andes (from Peru to Colombia) took place from Late Cretaceous to Paleocene (72 and 60 Ma), and was driven by collision of the South American plate with the Caribbean Arch. This process affected drainage directions and paleogeography shaping the present Andes configuration.
- Studies in the Northern Andes concur with Late Cretaceous tectonism and suggest that uplift took place in three-stages. During the final Neogene uplift stage, the Antioquia Plateau (Central Cordillera, Northern Andes) would have achieved elevations higher than present.
- Subsurface processes, such as slab-flattening drove uplift in Central Cordillera (Northern Andes), causing an asymmetric topography that affected drainages and biodiversity development.
- Throughout the Cenozoic, Andean uplift has determined changes in regional climate, landscape and drainages.
- Multiple studies found that Andean uplift played a key role in shaping the evolutionary history and biodiversity patterns in both plants and animals, even in mutualistic species relationships. The effect of uplift on biogeographic history is not limited to the Andes mountains, but also extends into the Amazon drainage basin with soils in the western Amazonia being most species rich. During the Neogene, eastern Amazonia gradually became species-enriched through biotic interchange.
- The effects of Andean uplift on biota add to other fundamental factors, such as climate, environment, and dispersal, all of which contribute to the modern biodiversity patterns in South America and their evolutionary history.
- The Neotropics were hot and humid during Eocene global warming. Paleobotanical studies in the Northern Andes suggest that towards the end of the Eocene a shift towards arid and seasonal climatic conditions occurred. In western Amazonia the EOT is further marked by a sea level drop, and a shift from deltaic to fluvial conditions that is accompanied by a decline in species richness.
- In Patagonia the Oligocene ‘icehouse’ is characterized by species poor assemblages. Towards the MCO there is an increase in species diversity with a subsequent decline in the Middle Miocene Climatic Transition (MMCT). The biggest paleobotanical change occurs in the late Miocene and is marked by the rise in arid taxa. This coincides with the uplift of the easternmost flank of the Andes and formation of a rain shadow. In the Northern Andes this transition is recognized by a dramatic change in paleosol profiles.
- Marine incursions and fluctuating sea level played an important part in Amazonia’s history, evidence of this can be found in middle and late Miocene deposits in western Amazonia. Sediment records in the large Pebas wetland system (western Amazonia) indicate that orbital forcing controlled sedimentation while the towering Central and Northern Andes provided the bulk of the sediment supply.
- Holocene records of Amazonia suggest rainforest trees are resilient to natural drying but not to fire and deforestation. A stark warning that human influence is more devastating than climate change.

## Declaration of Competing Interest

None.

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