



The flickering connectivity system of the north Andean páramos

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Abstract

Aim: To quantify the effect of Pleistocene climate fluctuations on habitat connectivity across páramos in the Northern Andes.

Location: Northern Andes.

Methods: The unique páramos habitat underwent dynamic shifts in elevation in response to changing climate conditions during the Pleistocene. The lower boundary of the páramos is defined by the upper forest line, which is known to be highly responsive to temperature. Here, we reconstruct the extent and connectivity of páramos over the last 1 million years (Myr) by reconstructing the upper forest line from the long fossil pollen record of Funza09, Colombia, and applying it to spatial mapping on modern topographies across the Northern Andes for 752 time slices. Data provide an estimate of how often and for how long different elevations were occupied by páramos and estimate their connectivity to provide insights into the role of topography in biogeographical patterns of páramos.

Results: Our findings show that connectivity amongst páramos of the Northern Andes was highly dynamic, both within and across mountain ranges. Connectivity amongst páramos peaked during extreme glacial periods but intermediate cool stadials and mild interstadials dominated the climate system. These variable degrees of connectivity through time result in what we term the 'flickering connectivity system'. We provide a visualization (video) to showcase this phenomenon. Patterns of connectivity in the Northern Andes contradict patterns observed in other mountain ranges of differing topographies.

Main conclusions: Pleistocene climate change was the driver of significant elevational and spatial shifts in páramos causing dynamic changes in habitat connectivity across and within all mountain ranges. Some generalities emerge, including the fact that connectivity was greatest during the most ephemeral of times. However, the timing, duration and degree of connectivity varied substantially among mountain ranges depending on their topographical configuration. The flickering connectivity

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system of the páramos uncovers the dynamic settings in which evolutionary radiations shaped the most diverse alpine biome on Earth.

KEY WORDS

alpine biome, evolutionary arenas, evolutionary radiations, flickering connectivity system, fossil pollen, mountain fingerprint, neotropical biodiversity, Páramos, past habitat connectivity, species pump

1 | INTRODUCTION

Mountains are regarded as powerhouses of biodiversity in the world (Antonelli et al., 2018; Barthlott, Rafiqpoor, Kier, & Kreft, 2005; Kreft & Jetz, 2007) and harbour numerous examples of very rapid and recent species diversifications ('radiations'; Hughes & Atchison, 2015). It is thought that a large part of this diversity arose geologically recently, during the Plio-Pleistocene (last 5.3 million years [Myr]), but there is no consensus on the drivers of these radiations. One favoured hypothesis is that the combination of high topographical relief and Plio-Pleistocene climatic oscillations led to rapidly changing distributions of montane species, which generated new lineages (e.g. Graham et al., 2014; Mutke, Jacobs, Meyers, Henning, & Weigend, 2014; Qian & Ricklefs, 2000). However, the relative contributions of isolation (e.g. Schönswetter, Stehlík, Holderegger, & Tribsch, 2005; Wallis, Waters, Upton, & Craw, 2016; Weir, Haddrath, Robertson, Colbourne, & Baker, 2016) versus gene flow and dispersal (e.g. Cadena, Pedraza, & Brumfield, 2016; Knowles & Massatti, 2017; Kolář, Dušková, & Sklenář, 2016; Smith et al., 2014) in driving fast diversification rates (i.e. the 'species-pump' effect, Rull, 2005; Rull & Nogué, 2007; Winkworth, Wagstaff, Glenny, & Lockhart, 2005; Ramírez-Barahona & Eguiarte, 2013; Steinbauer et al., 2016; Flantua & Hooghiemstra, 2018) are still debated. It is likely that these radiations have been the results of the interchange between phases of isolation, causing allopatric, *in situ* speciation, and connectivity, triggering diversification through dispersal and settlement in new areas and hybridization of differentiated taxa from previously isolated populations (Flantua & Hooghiemstra, 2018). The fastest and most spectacular radiations may therefore occur in mountain regions with variable degrees of past connectivity and isolation during climate fluctuations, which, complex in space and time, are inherently related to the mountain topography (Flantua & Hooghiemstra, 2018). It is therefore critical to quantify connectivity of montane habitats using our understanding of topography and past climate fluctuations (Figure 1).

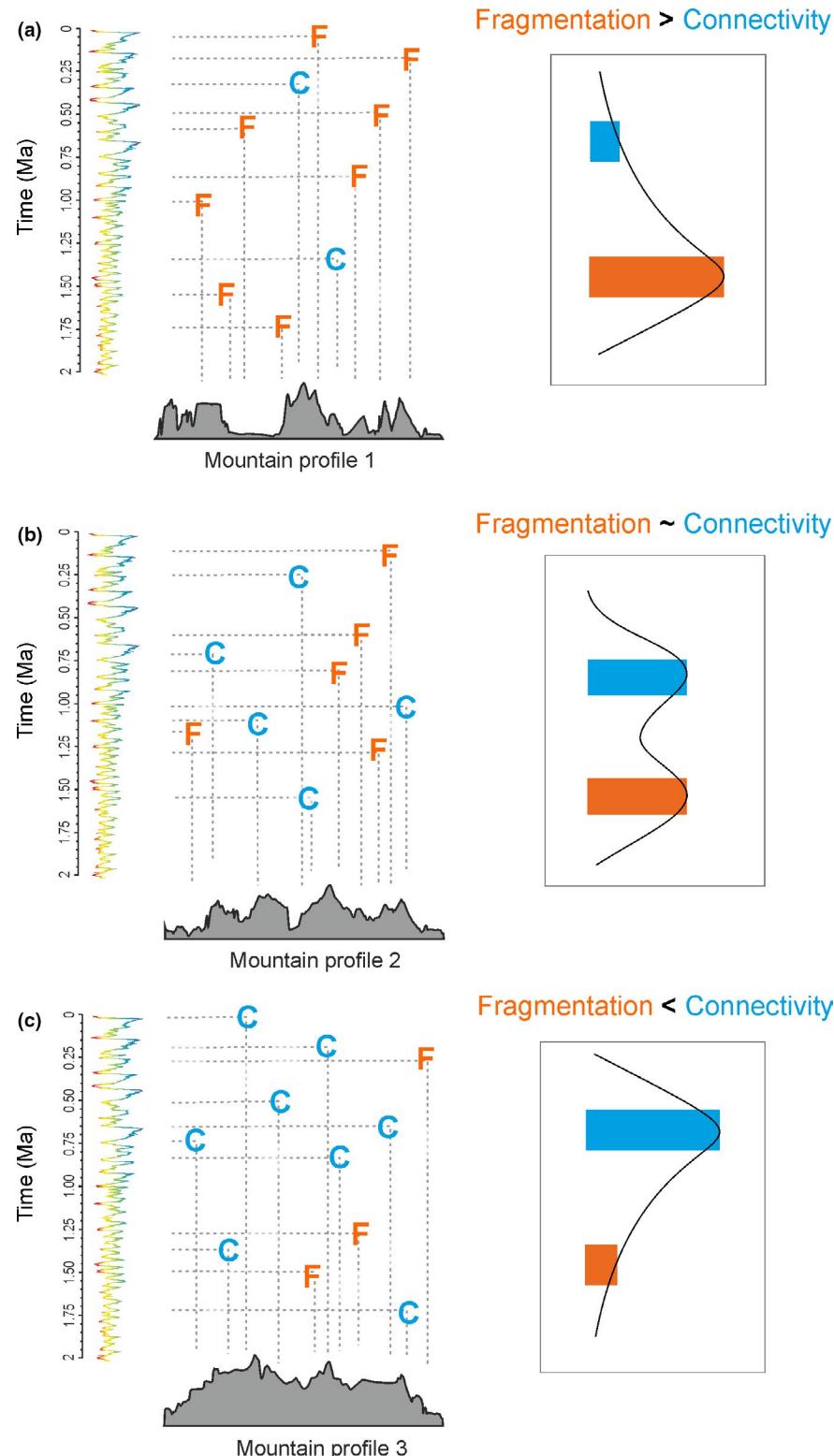
The Northern Andes is an ideal model system to quantify connectivity, due to the large variation in topography and the advanced palaeoecological knowledge on Plio-Pleistocene climate fluctuations derived during the last five decades (Hooghiemstra & Flantua, 2019). The Northern Andes is topographically rich with high elevations, steep ridges and valleys (see illustrations by Von Humboldt during his trips in Latin America, 1773–1858), composed of several mountain ranges, some of which are parallel running from North to South. The area hosts the treeless tundra-like alpine biome, the páramos, regarded as

the richest alpine flora in the world in terms of endemism and species richness (Sklenář, Hedberg, & Cleef, 2014) and is known for its bursts of Plio-Pleistocene species diversification amongst plants (Hughes & Atchison, 2015; Madriñán, Cortés, & Richardson, 2013). In terms of quantifying Plio-Pleistocene temperature fluctuations, the palaeoecological history of the páramos has been studied extensively (e.g. Cleef, 1979; Hooghiemstra, 1984; Hooghiemstra & Van der Hammen, 2004; Van der Hammen, 1974; Van der Hammen & Cleef, 1986) because of the unique high elevation fossil pollen records that cover most of the Pleistocene (Bogotá-A, Hooghiemstra, & Berrio, 2016; Bogotá-Angel et al., 2011; Groot, Hooghiemstra, Berrio, & Giraldo, 2013; Groot et al., 2011; Torres, Hooghiemstra, Lourens, & Tzedakis, 2013). Under current conditions, the páramos form isolated archipelagos of 'alpine (sky) islands' (McCormack, Huang, & Knowles, 2009; Sklenář et al., 2014) but the rich collection of fossil pollen sequences throughout this region (Flantua et al., 2015) show that the páramos underwent substantial elevational shifts during the Pleistocene, resulting in extensive changes in surface area and connectivity (Flantua et al., 2014; Hooghiemstra & Van der Hammen, 2004; Sklenář et al., 2014; Van der Hammen, 1974). Thus, the topographical diversity and the robust catalogue of palaeoecological reconstructions make the Northern Andes a highly suitable model region to explore patterns of connectivity in mountain biomes in response to Pleistocene climate fluctuations.

In this study, we aim to quantify the biogeographic changes of the páramos in terms of spatial scale and connectivity based on modern topography and pollen-based records of past climate change. Specifically, we developed a novel tool to explore the complex temporal and spatial patterns of páramo connectivity. We constrain our model by using the last 1 Myr of the high-resolution fossil pollen record of Funza09, a composite 586 m deep core taken from the Bogotá basin of Colombia (Torres et al., 2013). Available surface area (Elsen & Tingley, 2015) and connectivity (Bertuzzo et al., 2016; Flantua & Hooghiemstra, 2017; Flantua et al., 2014) is variable along elevational gradients of mountains. We therefore hypothesize that the different mountain ranges that compose the Northern Andes display variable patterns of past páramo connectivity dependent upon their topography (Figure 1). We discuss the implications of our outcomes for evolutionary processes and how defining and quantifying past connectivity in mountain systems is essential to help reveal mechanisms of ecological, biogeographical and evolutionary change. Ultimately, our quantification of páramo connectivity through space and time provides a unique opportunity to disentangle some of the mechanistic drivers ('modulators') of radiations in this biome (Bouchenak-Khelladi, Onstein, Xing, Schwery, & Linder, 2015).



FIGURE 1 Connectivity and fragmentation in a mountain landscape. Connectivity (blue) and fragmentation (orange) events occurred in a spatially and temporally variable manner. This complex pattern in space (latitude, longitude, elevation) and time resemble a multi-dimensional ‘mountain fingerprint’ which is unique for each mountain range (Flantua & Hooghiemstra, 2018). Three hypothetical mountain profiles are shown where elevational shifts in vegetation distribution driven by climate change (pollen-based record at the left indicating temperature) cause events of increased fragmentation (F) and connectivity (C) of mountain ecosystems. We recognize mountains where (a) only few events of connectivity occurred during the Pleistocene compared to fragmentation events (‘fragmentation-prone mountain fingerprint’), (b) connectivity events interchanged with isolation events in an evenly manner (‘mixed connectivity-fragmentation mountain fingerprint’), (c) connectivity is facilitated and occurred more often than fragmentation events (‘connectivity-prone mountain fingerprint’). The right panel is only based on frequency, not the duration of each event



2 | MATERIAL AND METHODS

2.1 | Geographical features

The Northern Andes (ca. 448,000 km²) covers parts of Venezuela, Colombia and Ecuador (Figure 2a), and can be partitioned into six

principal mountain ranges or ‘cordilleras’ (Figure 2c), namely the Sierra Nevada de Santa Marta (SNSM), Cordillera de Mérida, Eastern, Central and Western Cordillera and the Ecuadorian Cordilleras. Most of the Northern Andes is considered a highly to extremely high rugged landscape (Figure 2b; See mountain illustrations by Von

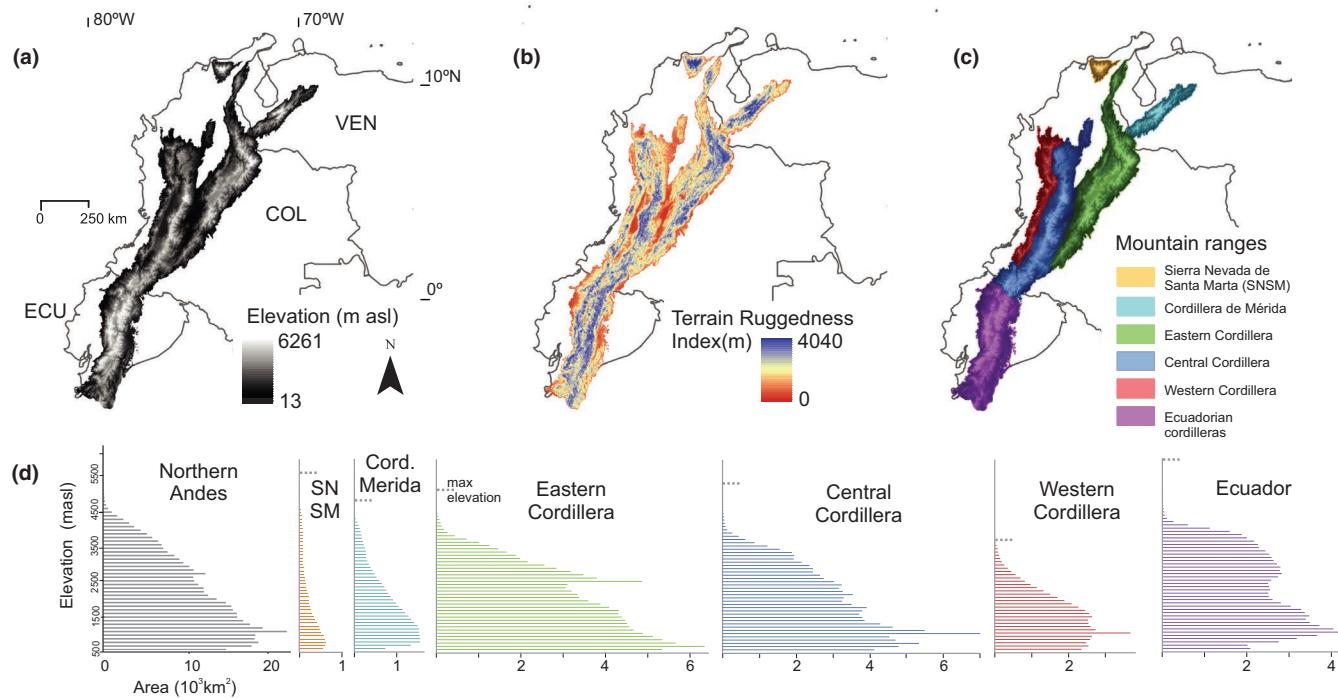


FIGURE 2 Hypsographical curves of the Northern Andes. (a) Elevation (m a.s.l.). (b) Terrain ruggedness index calculates the sum change in elevation between a grid cell and its eight neighbour grid cells (Riley, DeGlria, & Elliot, 1999) using a ca. 30 m DEM (NASA STRM Global 1arc second V003). (c) Delimitation of mountain ranges. (d) Elevational availability of surface area for the Northern Andes and each mountain range separately shown for 100 m bins. Hypsographical curves based on the Shuttle Radar Topography Mission 1-arc second Digital Terrain Elevation Data (~30 m resolution; USGS), taking an elevational threshold of 500 m a.s.l. as the horizontal reference plane. Maximum elevation per cordillera is indicated. VEN: Venezuela; COL: Colombia; ECU: Ecuador

Humboldt, 1845) where the high peaks and deep inter-Andean valleys cause strong contrasts in climate throughout the region (Flantua et al., 2016). Surface area in mountains does not decrease monotonically with elevation as has been shown previously in southern Colombia by Flantua et al. (2014) and on a global scale by Elsen and Tingley (2015). The Northern Andes shows a decrease of surface area going upslope where there is a slight peak around 900–1,200 m above sea level (a.s.l.) but then continues to decrease up to 6,260 m a.s.l. (Figure 2d), following a typical 'pyramid shape'. However, the different cordilleras show different patterns of elevational surface area (Figure 2d) where the Eastern Cordillera shows a sharp peak around 2,600 m a.s.l. and the Ecuadorean Cordillera shows high values of surface area at much higher elevations than the other cordilleras (for more details see Table S1.1, Appendix S1 in Supporting Information). The páramos today are spread out over the Northern Andes as a 'mountain archipelago' of small and highly fragmented páramo complexes (See Figs S2.1, S2.2 for more details and photos of different páramo complexes) but their full range also cover isolated páramo islands in Costa Rica and northern Peru (Luteyn, 1999). Of all tropical alpine floras, such as in East Africa and New Guinea, the páramos are home to the highest species richness and endemism (Luteyn, 1999; Sklenář et al., 2014), with low between-mountain similarity in species (Sklenář et al., 2014). They also provide numerous ecosystem services on a local and regional scale (Herzog, Martínez, Jørgensen, Tiesse, 2011) and references therein), and especially in

terms of hydrological services, they are vital for the provision of fresh water to several large cities in South America, such as Bogotá, Medellín, Quito, Cuenca, Piura and Cajamarca.

2.2 | Quantifying temperature and upper forest line based on fossil pollen data

To quantify temperature fluctuations during the Pleistocene (and consequently estimate páramo connectivity), we used fossil pollen data from the Northern Andes. The composite pollen record Funza09 (4.83°N, 75.2°W; 2,550 m a.s.l., Fig. S2.1. Red star) reveals vegetation and climate dynamics over the past 2.25 Myr (Torres et al., 2013). We reconstructed the páramos' elevational fluctuations, and consequently páramo connectivity, by estimating the upper forest line (UFL; the transition from the upper montane forest to the páramos) from the Funza09 record. Though this record covers the last 2.25 Myr, we only used the last 1 Myr as this interval reflects continuous lake conditions in comparison with variable hydrological conditions between 2.2 and 1 million years ago (Ma) which makes a quantification of changes to the UFL less precise. We follow the methodology described and implemented by Hooghiemstra (1984), Groot et al. (2011) and Hooghiemstra et al. (2012) to derive the Andean UFL and palaeotemperature curve (for detailed methodology on the UFL reconstruction see Appendix S3).

2.3 | Calculations of connectivity per páramo 'island'

To calculate the degree of connectivity between páramos, we used a graph-based habitat availability index called probability of connectivity (PC) metric. This metric takes into account the area of the páramo 'island' itself and the distances to other islands where a user-defined distance threshold defines the 'reachability' of other islands (Saura, Estreguil, Mouton, & Rodríguez-Freire, 2011; Saura & Pascual-Hortal, 2007), even if they are not physically connected (i.e. 'structural connectivity', Tischendorf & Fahrig, 2000). The metric assigns a value to each páramo island representing its contribution in maintaining the overall connectivity of the páramo biome (Saura & Pascual-Hortal, 2007; Saura et al., 2011). The total PC is built up in three 'fractions', namely the 'intrapatch', the 'flux' and the 'connector' fractions (Saura & Rubio, 2010). The first fraction focuses on the available surface area and habitat quality (if applicable) within the individual island. The second fraction assesses how well the individual island is connected to other islands given additional importance to the other islands' attributes (surface and quality) and its strategic position to other páramo islands. The third fraction quantifies the contribution of the island to maintain connectivity between the rest of the islands, in other words its role as an intermediate stepping stone between non-adjacent islands. Additionally, we calculated the equivalent connected area (ECA), which is derived directly from the PC, as a measure of the overall connectivity of a region (Saura et al., 2011). Here, CONEFOR SENINODE (V2.2; Saura & Pascual-Hortal, 2007; Saura & Torné, 2009) and ESRI ArcGIS 10.3 (ESRI, 2014) were used to calculate the straight-line distances between islands, the PC and ECA. We calculated connectivity for the entire Northern Andes and for each mountain range separately.

2.4 | Calculations of corridors between páramo islands

We identified corridors between páramo islands within and between cordilleras under different climatic conditions. We used the GLEANLY LANDSCAPE UTILITIES (V0.1.3; McRae, Shirk, & Platt, 2013) with ESRI ArcGIS 10.3 to create a raster grid of 'landscape resistance' based on ruggedness (Figure 2b) and habitat suitability. We assumed an increased landscape resistance with increased ruggedness, assigning values between 0 (no resistance) to 100 (maximum resistance) using an equal interval classification. For the habitat suitability map, we started by assigning a 'perfectly suitable' score of 100 to each páramo island, while outside the island the score of 0 reflects maximum unsuitability. To soften this boundary, an exponential decay function was then used by increasing resistance in five elevational steps of 100 m where we assigned a suitability score of 40 to the boundary of the páramo. As a result of the decay function the highest suitability of páramo – its core area – was restrained 200 m above the UFL and 200 m below the snowline.

We used LINKAGE MAPPER to calculate the least-cost pathways, or corridors, based on the produced raster grid of landscape resistance

(McRae & Kavanagh, 2011). These corridors are expressed as 'conductance maps' that represent gradients of cumulative corridors. Where the densities of corridors is highest, it is assumed that there is a high probability of dispersal and migration possible between islands (McRae, Dickson, Keitt, & Shah, 2008). The full landscape of the Northern Andes is considered an area where corridors could exist, with exception of the region between SNSM and the Sierra de Perijá (Fig. S2.1).

We resampled the 30 m Digital Elevation Model (DEM, Figure 2) to a 1 km resolution to reduce computing time for each LINKAGE MAPPER down to on average 2 hr. We allowed LINKAGE MAPPER to create corridors through (instead of only between) core areas to represent the full arsenal of connectivity through the landscape. Only corridors between páramo islands larger than 1 km² were considered at any given moment in time. From the final output maps, only values lower than 200k conductance (default threshold) are selected to highlight the strongest corridors. The outputs were weighted according to the percentage of time they occurred during the last 1 Myr.

3 | RESULTS

3.1 | A million years of temperature fluctuations

Temperatures at Funza (2,550 m a.s.l.) are estimated to have fluctuated between ca. 15 and 6°C causing an estimated maximum 1,600 m elevational shift of the UFL between ca. 3,500 and ca. 1,900 m a.s.l. (Figure 3). The Pleistocene glacial-interglacial dynamics were not replicated cycles of temperature change showing repeated patterns of high and lows, but display a high temporal variability between each glacial-interglacial cycle. Conditions similar to the current warm, interglacial conditions occurred several times during the last 1 Myr and accounted for around a quarter of the time. Extreme cool glacial conditions, ~6–8°C cooler than today, were relatively rare, occurring less than 10 percent of the time. On the whole, intermediate cool stadials and mild interstadials dominated the last 1 Myr, occurring over two-thirds of the time.

3.2 | Calculations of páramo connectivity

Our estimations on the spatial and elevational extent of ancient páramos and their connectedness at different times in the past reveals that páramos underwent frequent spatial alterations between fragmented and connected spatial configurations, but the exact patterns were highly dependent on mountain chain topography (Figure 4a,b. See Appendices S4 and S5). The páramos in the Ecuadorian Cordillera generally maintained a high degree of connectivity over the last 1 Myr, rarely enduring severe fragmentation. Fragmentation did however occur when the snowline plunged significantly during colder and wetter glacial periods, causing a break up of páramo areas on lateral flanks of the mountains. Likewise, the level of connectivity between páramos on the Central Cordillera fragmented substantially through a descending snowline, breaking the upper elevation limit of páramo connectivity. In contrast, the Eastern

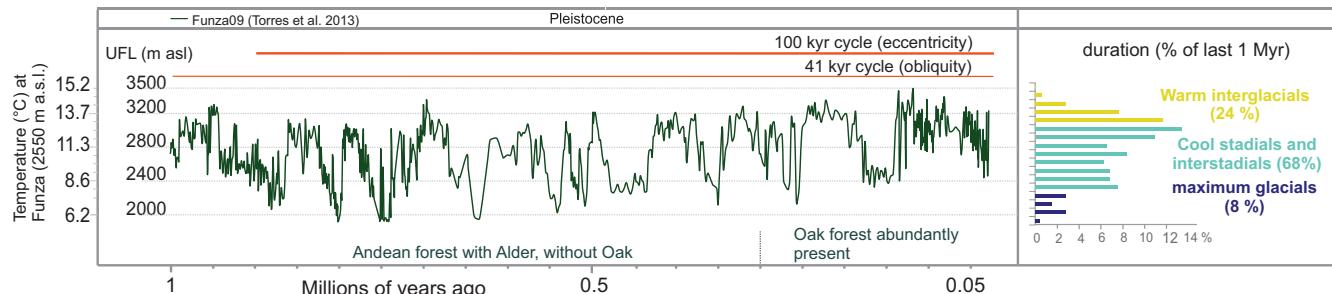


FIGURE 3 Upper forest line (UFL) curve of Funza09 (Torres et al., 2013) and reconstructed temperature record covering the last 1 Myr (last ca. 30 kyr BP not included)

Cordillera shifted substantially between periods of connectivity and fragmentation, always, however, maintaining two large páramo islands surrounded by smaller 'satellite islands'. Páramos in the Cordillera de Mérida seem to have been restricted during interglacials to one core area only, while during colder periods a relatively high fragmentation is observed possibly due to glaciers pushing páramos to lateral distributions. Here, connectivity increased mainly towards the southwest and during colder periods ($\text{UFL} \leq 2,300 \text{ m a.s.l.}$). The páramos of the SNSM and the Western Cordillera endured the highest degree of rates of change in fragmentation of all ranges. In the latter, páramo habitats are estimated to have often completely disappeared. In contrast, páramos of the Central Cordillera maintained a long latitudinal distribution, forming a chain of isolated populations in small patches that on the whole remained connected. Even in very cold conditions, no continuous connectivity of core areas seems to have been possible between the Eastern Cordillera and Cordillera de Mérida, or the region of Sierra de Perijá. Towards the south of the Eastern Cordillera a low-elevation barrier was possibly crossed at 1,900 m a.s.l. forming a brief bridge suitable for páramo habitat into the Macizo Colombiano of the Central Cordillera.

The reconstruction of putative corridors shows a complex spatial pattern through the mountainous landscapes of the Northern Andes (Figure 5a,b). The long ridge of the Central Cordillera forms the starting point of numerous corridors to the páramos in the Western Cordillera. The Eastern Cordillera shows a complex internal pattern of corridors, where there are neither strong corridors towards Sierra de Perijá in the North, nor towards the Cordillera de Mérida, while a high concentration of corridors is found between the large páramos complexes in the Eastern Cordillera (Páramos of Boyacá and Cundinamarca, Fig. S2.1). In the Ecuadorian Cordillera a more lateral pattern of high/low potential corridors is observed following the intra-Andean valleys and peaks within this mountain range. Corridors to the southernmost páramos of Ecuador as also the northernmost páramos of the Western Cordillera are weak and occurred infrequent during the last million years, shown by the thin lines.

3.3 | Flickering connectivity systems

Páramo connectivity through time shows a highly variable pattern (Figure 6a) introduced by Flantua and Hooghiemstra (2018) as a

flickering connectivity system (see visualization video in Appendix S6). We find support for the hypothesis that this system with fluctuating, highly variable connectivity in spatial and temporal dimension is unique for each mountain range of the Northern Andes (Figure 1). For example, changes in connectivity within the Ecuadorian Cordillera are substantial but the system 'flickers' around a high average when compared to other mountain ranges. The flickering connectivity systems within the Eastern and Central Cordillera are surprisingly similar, though the peaks of connectivity during glacial periods and the dips of connectivity during interglacials are more extreme in the former (Figure 6a). The Western Cordillera is a larger mountain range than the Cordillera of Mérida and the SNSM (Table S1.1), and its variation of connectivity has been correspondingly larger (Figure 6b) but with the lowest occurrence of connectivity compared to the other mountain ranges (Figure 6a). Considering only the frequency in the distribution of data (Figure 6b), the Ecuadorian Cordillera and the SNSM stand out for their relatively small within-mountain range variation in connectivity, compared to the Eastern and Central Cordillera (similar patterns) and the Western Cordillera.

When frequencies of connectivity are weighted by the amount of time that connectivity lasted two main patterns emerge (Figure 6c). The first is shared by the Western, Central and Eastern Cordilleras, which all display an elongated pattern where the highest values are around a centroid, resembling a 'humming top' or, as Elsen and Tingley (2015) recognized in mountain hypsographies, a 'diamond' shape. Ecuadorian Cordilleras, Cordillera de Mérida and SNSM instead reveal a different pattern with a narrower centroid that widens towards the upper and lower section, resembling an 'hourglass' shape. Here, the Ecuadorian Cordillera and SNSM show a surprising similarity though at different connectivity ranges. The Central and Eastern Cordilleras are strikingly similar overall.

4 | DISCUSSION

4.1 | Variable degrees of past connectivity of different mountain ranges

Although currently isolated, evolutionary radiations and the assembly of the páramo ecosystem formed during times when the páramos were flickering in and out of different degrees of connectivity (Figure 6). The concept of 'mountain fingerprints' (Flantua &

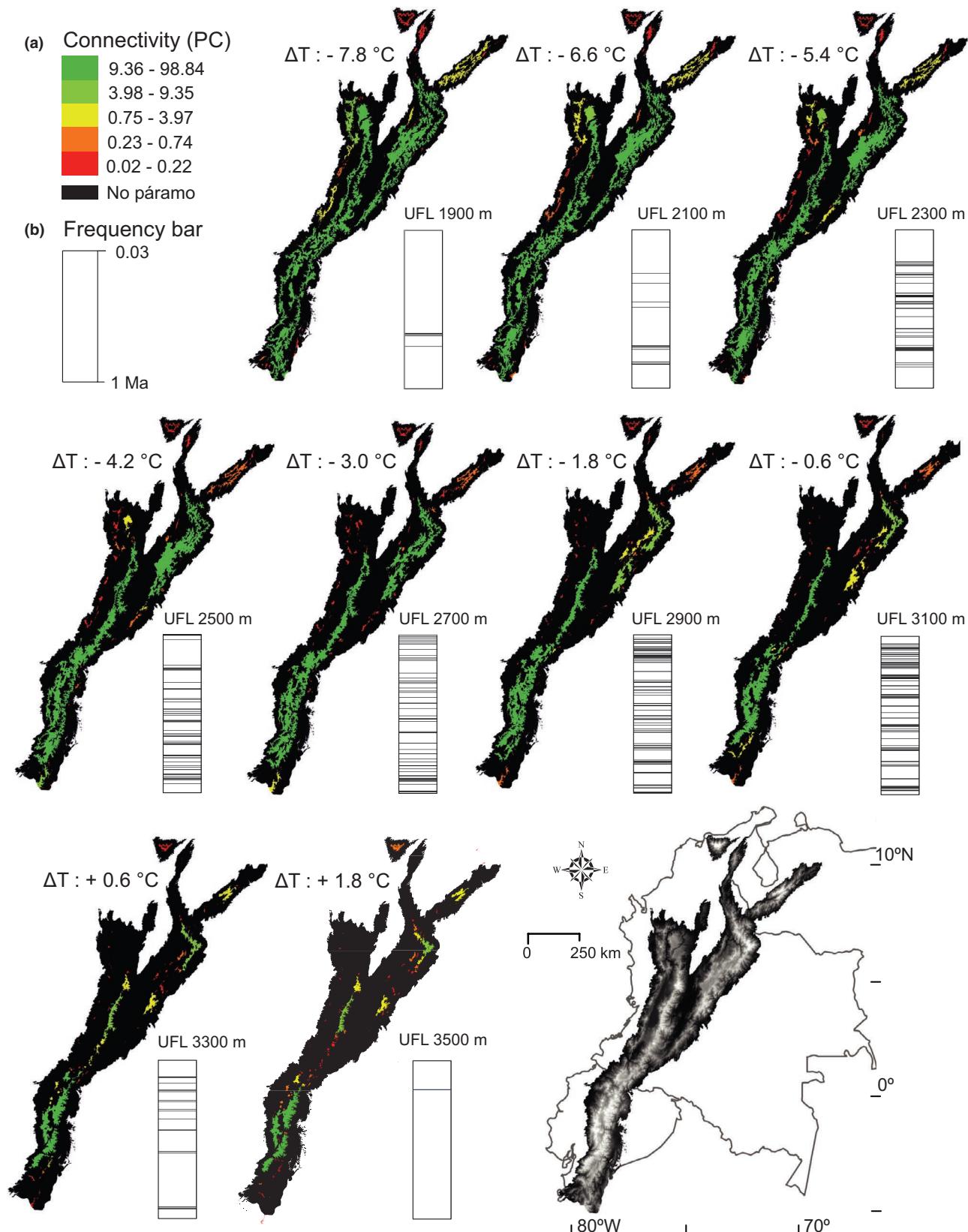


FIGURE 4 Páramo connectivity at different upper forest line (UFL) elevations. (a) Probability of connectivity metric (PC; distance = 10 km, $p = 0.5$; Saura & Rubio, 2010) calculated for all páramos larger than 1 km^2 . Maps are plotted with natural-breaks classification. Temperature at 2,550 m elevation are relative to the present. (b) Frequency bar indicates when the corresponding UFL elevation occurred during the last 1 Myr. See Appendices S4 and S5 for all maps and frequencies

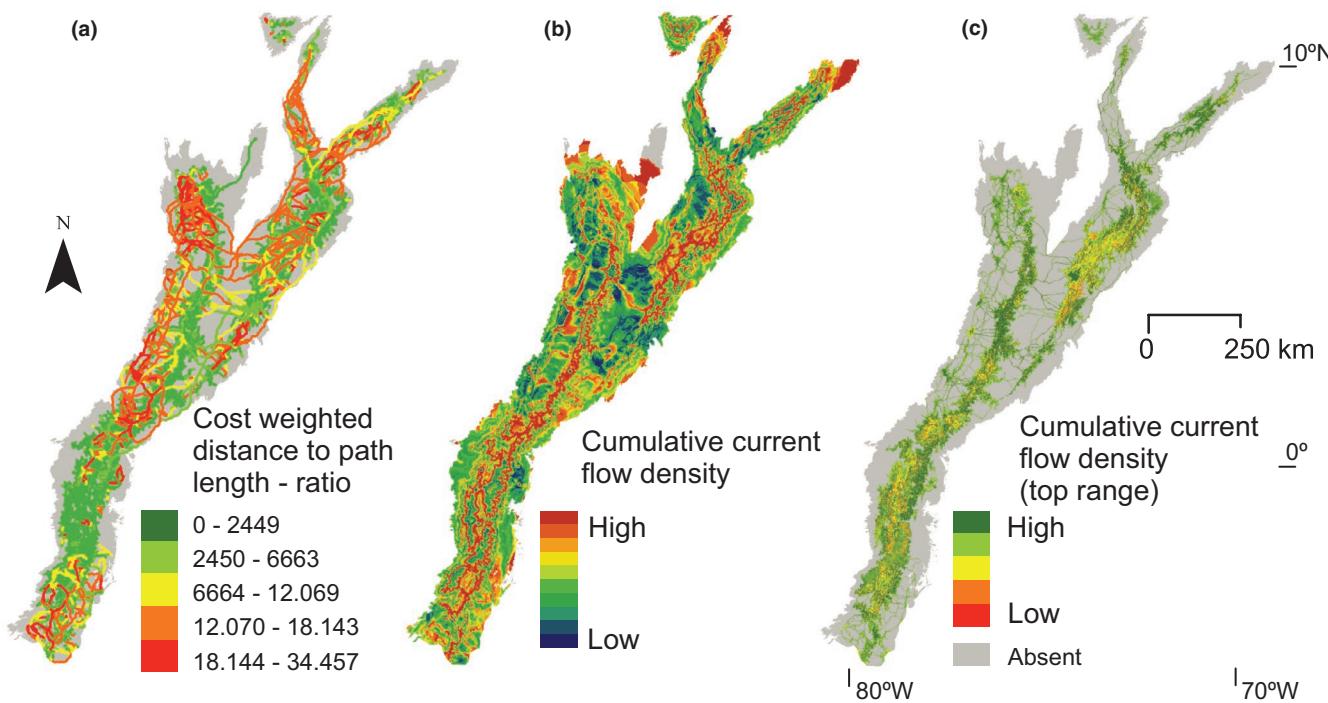


FIGURE 5 Dispersal pathways among páramos during the last 1 Myr weighted by frequency and duration. (a) Least cost pathways calculated by the cost weighted distance to path length – ratio. Circuit model (McRae et al., 2008) expressed in cumulative current flow density using the full range of values (b) and only the strongest corridors (threshold of 200k used) before calculating the weighted sum (c). Areas with low least cost pathways (a) and high current flows (b and c) indicate frequent and highly possible corridors during the last 1 Myr

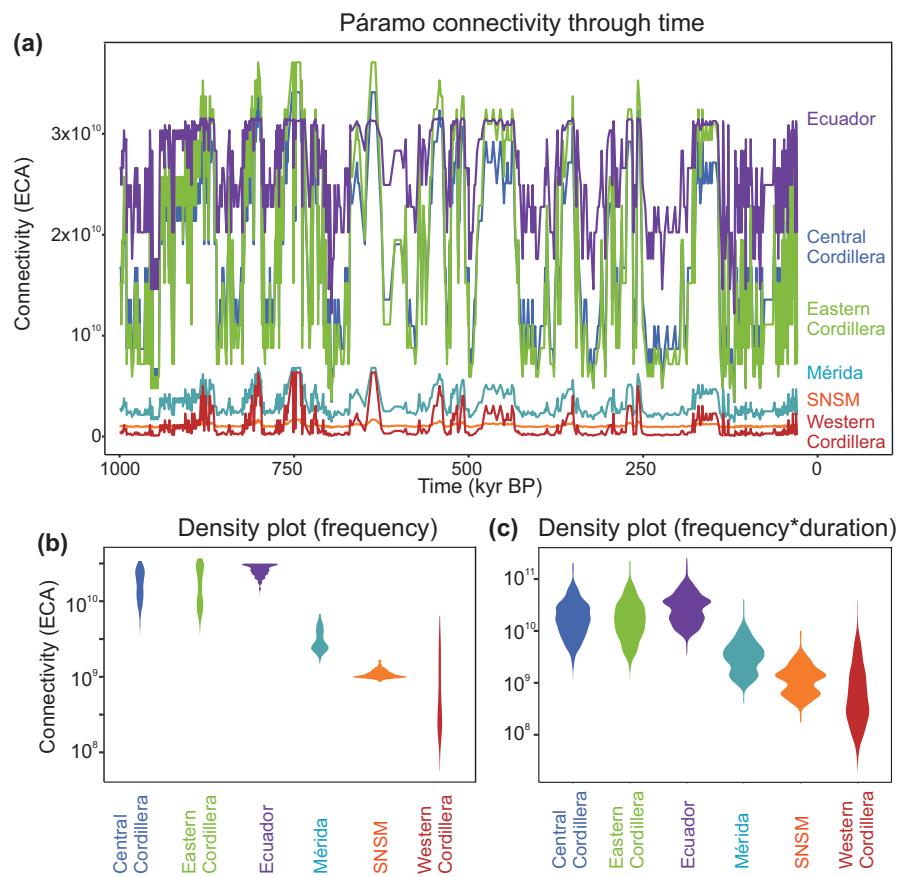


FIGURE 6 The ‘Flickering Connectivity System’ of the Northern Andes. (a) Páramo connectivity (here expressed as equivalent connected area, ECA) through time (1,000–30 kyr BP) for each cordillera. ECA has area units (m^2) representing the amount of ‘reachable or available habitat area’ (Saura et al., 2011). (b) ‘Beanplots’ (Kampstra, 2008) or ‘violin plot’ showing kernel densities summarizing the data distribution of past connectivity of each cordillera, only considering how often certain degree of connectivity occurred, not how long it lasted. (c) Beanplot showing kernel densities summarizing the data distribution of past connectivity of each cordillera multiplied by how long connectivity persisted to represent both how often an event occurred and how long it lasted

TABLE 1 Overview of studies with phylogeographic/phylogenetic/biogeographical support for the flickering connectivity system in the Northern Andes. Note that this is not a comprehensive list and is only aimed at providing an overview of available studies

Level of analysis/ Mountain range	Group	Taxon	Family	Dataset/markers	Approach	Result/finding	Reference
Ecuadorian Cordillera	Birds	<i>Spinus</i>	Fringillidae	cyt b, ND2, ND3, MUSK, MYC2	Phylogenetic	Recent radiation	Beckman and Witt (2015)
Andes	Plants	<i>Valeriana</i>	Valerianaceae	psbA-trnH intron, trnK-matK intron, trnL-F, ITS	Phylogenetic	Recent radiation	Bell and Donoghue (2005)
Eastern and Central Cordillera	Birds	<i>Buarremom</i>	Emberizidae	ND2, cyt b, ATPase 6, ATPase 8, ACO1, MUSK	Phylogeographic	High genetic divergence	Cadena, Klicka, and Ricklefs (2007)
Western and Central Cordillera	Birds	<i>Buarremom</i>	Emberizidae	ND2, cyt b, ATPase 6, ATPase 8, ACO1, MUSK	Phylogeographic	High genetic resemblance and likely high migration	Cadena et al. (2007)
Andes	Plants	<i>Oreobolus</i>	Cyperacea	ITS, trnL intron and trnL-F intergenic spacer	Phylogenetic	Recent radiation; South to north migration	Chacón, Madriñán, Chase, and Bruhl (2006)
Andes	Birds	<i>Muscisaxicola</i>	Tyrannidae	COII and ND3	Phylogenetic	Recent radiation	Chessier (2000)
Central and Eastern Cordillera, Ecuadorian Cordillera	Plants	<i>Lupinus</i>	Leguminosae	Genome-scale nextRADseq	Phylogeographic/Phylogenomic	High genetic divergence	Contreras-Ortíz, Atchison, Hughes, and Madriñán (2018)
Central and Eastern Cordillera	Plants	<i>Espeletia</i>	Asteraceae	Genotyping by sequencing	Phylogeographic	Rapid morphological radiations	Cortés, Garzón, Valencia, and Madriñán (2018)
Northern Andes	Plants	<i>Calceolaria</i>	Calceolariaceae	ITS, matK and morphology	Phylogenetic	Recent radiation	Cosacov et al. (2009)
Northern Andes	Plants	<i>Espeletiinae</i>	Asteraceae	n.a.	Biogeographic	Step-wise but irregular migration of species	Cuatrecasas (1979, 2013)
Eastern Cordillera	Plants	<i>Espeletiinae</i>	Asteraceae	ITS, ETS, rpl16, AFLP data	Phylogenetic	High genetic diversity in the larger páramo complexes with multiple distinct clades somewhat related to each other	Diazgranados and Barber (2017)
Eastern Cordillera	Plants	<i>Espeletiinae</i>	Asteraceae	ITS, ETS, rpl16, AFLP data	Phylogenetic	Hybridization	Diazgranados and Barber (2017)
Ecuadorian Cordillera	Plants	<i>Senecio</i>	Asteraceae	ITS, AFLP data	Phylogenetic/Phylogeographic	Genetic differences between northern and southern populations within Ecuador	Dušková et al. (2017)
Northern Andes	Plants	<i>Oxalis</i>	Oxaliaceae	ITS and ncpGS	Phylogenetic	Recent radiation	Emshwiller (2002)
Northern Andes	Plants	<i>Oreobolus</i>	Cyperacea	ITS, trnL-F, trnH-psbA and rpl32-trnL	Phylogeographic	Incomplete lineage sorting, cryptic speciation, genetic divergence, suggests evidence of repeated vicariance and secondary contact	Gómez-Gutiérrez et al. (2017)
Andes	Birds	Many	n.a.	n.a.	Phylogenetic	Bioregion formations correlates with Andean uplift and mountain dispersal	Hazzi et al. (2018)

(Continues)

TABLE 1 (Continued)

Level of analysis/ Mountain range	Group	Taxon	Family	Dataset/markers	Approach	Result/finding	Reference
Central and Eastern Cordillera	Plants	<i>Lupinus</i>	Leguminosae	ITS/LEGACYCIA genes	Phylogenetic	Recent radiation, higher diversification at higher elevations	Hughes and Eastwood (2006); Drummond, Eastwood, Miotto, and Hughes (2012); Hughes and Atchison (2015)
Eastern and Central Cordillera	Plants	<i>Puya</i>	Bromeliaceae	AFLP data	Phylogenetic	Genetic divergence, suggest multiple migration events from the Eastern Cordillera to the Western Cordillera	Jabaily and Sytsma (2013)
Northern Andes	Plants	<i>Puya</i>	Bromeliaceae	AFLP data	Phylogenetic	Step-wise but irregular migration of páramo plant species, recent rapid radiation	Jabaily and Sytsma (2013)
Western and Central Cordillera	Plants	<i>Puya</i>	Bromeliaceae	AFLP data	Phylogenetic	Frequent gene flow events	Jabaily and Sytsma (2013)
Ecuadorian Cordillera	Plants	<i>Loricaria</i>	Asteraceae	AFLP and plastid DNA	Phylogeographic	Step-wise but irregular migration of páramo plant species	Kolář et al. (2016)
Ecuadorian Cordillera	Plants	<i>Loricaria</i>	Asteraceae	AFLP and plastid DNA	Phylogeographic	Lack of genetic divergence. Suggests extensive gene flow.	Kolář et al. (2016)
Andes	Plants	Many	n.a.	n.a.	Phylogenetic	Environmental change, adaptation and biotic interactions as drivers of Andean radiations	Luebert and Weigend (2014)
Andes	Plants	<i>Polystichum</i>	Dryopteridaceae	Cytosolic phosphoglucose isomerase gene	Phylogenetic	Gene evolution during radiation	Lyons, McHenry, and Barrington (2017)
Northern Andes	Plants	Many	Asteraceae	n.a.	Phylogenetic	Recent radiation	Madrinán et al. (2013)
Andes	Plants	<i>Polystichum</i>	Dryopteridaceae	trnS-rps4, rbcL	Phylogenetic	Recent radiation, multiple secondary dispersal events from central Andes to Northern Andes	McHenry and Barrington (2014)
Northern Andes	Plants	<i>Lachemilla</i>	Rosaceae	ITS, trnL-F	Phylogenetic	Recent radiation	Morales-Briones, Romoleroux, Kolář, and Tank (2018)
Central and Eastern Cordillera	Plants	<i>Lupinus</i>	Leguminosae	Genomic and transcriptomic data	Phylogenomic/ Phylogeographic	High genetic divergence but events of gene flow detected	Nevado et al. (2018)
Eastern Cordillera	Plants	<i>Lupinus</i>	Leguminosae	Genomic and transcriptomic data	Phylogenomic/ Phylogeographic	High genetic diversity in the larger páramo complexes with multiple distinct clades somewhat related to each other	Nevado et al. (2018)
Eastern Cordillera	Plants	<i>Lupinus</i>	Leguminosae	Genomic and transcriptomic data	Phylogenomic/ Phylogeographic	Hybridization	Nevado et al. (2018)

(Continues)



TABLE 1 (Continued)

Level of analysis/ Mountain range	Group	Taxon	Family	Dataset/markers	Approach	Result/finding	Reference
Andes	Plants	<i>Hypericum</i>	Hypericaceae	n.a.	n.a.	Suggests niche expansion/evolution and shifts in temperature optima that may have facilitated páramo radiations	Nürk, Michling, and Linder (2017)
Andes	Plants	<i>Hypericum</i>	Hypericaceae	ITS	Phylogenetic	Recent radiation	Nürk, Scheriau, and Madriñán (2013)
Eastern Cordillera and Merida Cordillera	Plants	<i>Espeletia</i>	Asteraceae	Metabolomics	n.a.	Metabolic fingerprints linked to high genetic divergence but with events of gene flow	Padilla-González, Díazgranados, and Da Costa (2017)
Western and Central Cordillera	Plants	<i>Espeletia</i>	Asteraceae	Metabolomics	n.a.	Apparent clustering	Padilla-González et al. (2017)
Merida Cordillera, northern tip of Eastern Cordillera	Plants	<i>Espeletiinae</i>	Asteraceae	Whole plastomes, <i>de novo</i> assembly	Phylogenomic	Hybridization, suggests two independent centers of radiations and no dispersal between cordilleras. Increase of diversification during last 1 Myr	Pouchon et al. (2018)
Andes	Birds	Many	n.a.	n.a.	Phylogenetic	Higher diversification rates at higher elevations	Quintero and Jetz (2018)
Northern Andes	Plants	Espeletia complex	Asteraceae	ITS	Phylogenetic	Recent radiation	Rauscher (2002)
Andes	Birds	<i>Pionus</i>	Psittacidae	cpta and ND2	Phylogenetic	Recent radiation	Ribas, Moyle, Miyaki, and Cracraft (2007)
Northern Andes	Plants	Jamesonia- Eriosorus Complex	Pteridaceae	ETS, 18S-26S rDNA, rps4, intergenic spacer rps4-trnS	Phylogenetic	Fast speciation of páramo species, possibly linked to morphological adaptation	Sánchez-Baracaldo and Thomas (2014)
Northern Andes	Plants	<i>Jamesonia</i> , <i>Eriosorus</i>	Pteridaceae	ETS, 18S-26S rDNA, rps4, intergenic spacer rps4-trnS	Phylogenetic	Recent radiation	Sánchez-Baracaldo (2004)
Andes	Plants	<i>Astragalus</i>	Leguminosae	ITS and chloroplast spacers trnD-trnT and trnM-trnS1	Phylogenetic	Recent radiation	Schertson, Vidal, and Sanderson (2008)
Andes	Plants	<i>Bartsia</i>	Orobanchaceae	trnT-trnF region and the rps16 intron	Phylogenetic	Recent radiation, suggests to be related to dispersification	Uribe-Convers and Tank (2015)
Andes	Plants	<i>Diplostiphium</i>	Asteraceae	ITS, rpoB, rpoC1, and psbA-trnH	Phylogenetic	Radiation originated in páramo, with diversification slowdowns associated with colonization of Andean forests. Phylogeny shows large uncertainty.	Vargas and Madriñán (2012)

(Continues)

TABLE 1 (Continued)

Level of analysis/ Mountain range	Group	Taxon	Family	Dataset/markers	Approach	Result/finding	Reference
Northern Andes	Plants	Diplostephium	Asteraceae	Complete nuclear ribosomal cistron, the complete chloroplast genome, a partial mitochondrial genome and nuclear-ddRAD	Phylogenomic	Hybridization, recent radiation	Vargas, Ortiz, and Simpson (2017)
Eastern Cordillera, Cordilleras of Colombia	Plants	Lupinus alopecuroides	Leguminosae	11 microsatellite markers	Phylogeographic	High genetic diversity in the larger páramo complexes with multiple distinct clades somewhat related to each other	Vásquez, Balslev, Hansen, Sklenář, and Ronoléroux (2016)
Andes	Plants	Gentianella, Habenaria	Gentianaceae	ITS, matK, rpl16 intron	Phylogenetic	Recent radiation	von Hagen and Kadereit (2001, 2003)
Andes	Birds	Many	n.a.	n.a.	Phylogenetic	Recent radiation, increase in diversification in last 1 Myr	Weir (2006)
Northern Andes	Plants	Escallonia	Escalloniaceae	trnH-psbA, MYC, NIA	Phylogenetic	Recent radiation	Zapata (2013)

Hooghiemstra, 2018) proposes that the region's complex topography would have meant that páramos in different mountain regions would have fragmented and connected at different periods of time, at different elevations, and with different rates and frequencies (as summarized in Figure 1). This means that in some mountain ranges the páramos are a mix of somewhat even occurrence of connectivity and fragmentation events through time (Figure 1b, exemplified by the Eastern Cordillera), or could have been dominantly fragmented (Figure 1a, e.g. Western Cordillera), or more connected (Figure 1c, e.g. Ecuadorian Cordilleras). These regional differences in the temporal and spatial variation in past páramo connectivity (Figures 4–6) are likely to have resulted not only in regional differences in biogeographical patterns through time, but also varying ecological and evolutionary processes. We therefore propose that our data and models can be used to test hypotheses of the drivers of species richness, endemism and degrees of Pleistocene diversification in the Northern Andes, and the approach applicable to other mountain regions around the world.

4.2 | Evolutionary implications of the flickering connectivity system

Several insightful schematic representations of Pleistocene diversification models in the Neotropics have been developed in recent years (Flantua & Hooghiemstra, 2018; Hazzi, Moreno, Ortiz-Movilav, & Palacio, 2018; Ramírez-Barahona & Eguiarte, 2013; Rull, 2005). Phylogeographical and phylogenetic synthesis work within and among páramo taxa is currently still largely lacking (see for instance Yu et al., 2019 for the Qinghai-Tibet Plateau), inhibiting the direct testing of these models. However, here we highlight several recent studies that are considered valuable in the light of the flickering connectivity system reconstruction (see Table 1), emphasizing the expectation that the rapidly growing body of phylogeographical/phylogenetic literature in the region will support future comparative analyses.

The dynamic history of the páramos elucidated by the flickering connectivity system can provide three important insights in terms of evolutionary processes. First of all, the regional differences in past páramo connectivity – the mountain fingerprint – support temporally and spatially discordant phylogeographical patterns (Massatti & Knowles, 2014; Papadopoulou & Knowles, 2015, 2016; Pennington et al., 2010). This means that the timing of diversification in the different mountain regions would not be expected to have occurred synchronously, even if all phylogenetic studies on páramo species could overcome current issues in model inference, taxonomy and distribution, spatial resolution and time-calibration points (Rull, 2011). Secondly, diversification rates might differ along the elevational gradient and this might be the rule rather than the exception. Elevational differences in surface availability and connectivity (Bertuzzo et al., 2016; Flantua & Hooghiemstra, 2017; Flantua et al., 2014) are likely to influence at what elevation the strongest geographical processes will occur, and these processes are thus expected to differ between mountain systems resulting in elevational



differences of diversification (see e.g. Hughes & Eastwood, 2006; Kropf, Kadereit, & Comes, 2003; Lagomarsino, Condamine, Antonelli, Mulch, & Davis, 2016; Quintero & Jetz, 2018). Furthermore, the climate fluctuations of the Pleistocene caused connectivity to occur at different moments through time (Figure 1), a process facilitating the step-wise but irregular migration of páramo plant species throughout the landscape, such as *Puya*, *Loricaria* and *Espeletiinae* (Table 1). Thirdly, the flickering connectivity system, which is expected to cause phases of increased isolation followed by increased connectivity of populations, is expected to result in pulses of diversification (Knowles, 2000), possibly resulting in series of sub-radiations in the páramos. Where isolation resulted in allopatric, *in situ* speciation, connectivity triggered diversification through dispersal and settlement in new areas ('dispersification', Moore & Donoghue, 2007), and hybridization of previously isolated populations (Grant, 2014; Petit et al., 2003). Much evidence suggests that hybridization is not the processes of species becoming 'reabsorbed' into their parental forms but contributes by bringing evolutionary novelty and gene flow operating at different introgression rates (Dušková et al., 2017; Nevado, Contreras-Ortiz, Hughes, & Filatov, 2018; Pouchon et al., 2018), and thus a likely trigger of speciation and morphological diversity. Interestingly, population-level processes such as gene flow, dispersification and hybridization, alongside periods of isolation, have been increasingly recognized to play out at the phylogenetic scale, leading to (rapid) lineage diversification, for example in mountains (e.g. Hazzi et al., 2018; Knowles & Massatti, 2017), tropical rain forests (e.g. Onstein et al., 2017) and islands (e.g. Ali & Aitchison, 2014). Interestingly, the Funza09 pollen record shows a clear increase in the amplitude of climate change around the mid-Pleistocene transition (ca. 0.9 Ma) coinciding with accelerated diversification of high elevation birds (Weir, 2006) and the *Espeletiinae* in the Cordillera de Mérida (Pouchon et al., 2018; Table 1). Indeed, these studies signal a potential link between the intensity of the flickering connectivity system and biological radiations (Flantua & Hooghiemstra, 2018). Thus, the flickering connectivity system is expected to have left an imprint on geographical patterning of genetic divergence (between populations) and within-populations genetic diversity with obvious inter-cordillera differences. Furthermore, extinction events may further complicate the observed patterns of divergence between cordilleras.

4.3 | Future research

Our spatio-temporal estimates of past connectivity lay a foundation for further research on elucidating the causal mechanisms of mountain diversifications (see also Appendix S7). Models of past connectivity (Figures 4–6), when combined with phylogeographic data, could help reveal the role of interspecific gene flow and allopatric speciation in driving radiations in the high Andes and contribute to a better understanding of the relative importance of geography versus adaptive radiation that underpin Andean diversifications. In such a complex system it may also be useful to pay attention to commonalities. For example, when considering

both frequency and duration, our data show that two connectivity patterns emerge (i.e. hourglass versus non-hourglass; Figure 6c). Research could explore if cordilleras with shared connectivity patterns also share phylogenetic histories and contemporary (endemic) species' biogeographies to test for universal mechanisms that have shaped present day alpine biomes. This would be especially useful if used in conjunction with information on the reproductive life histories, growth and dispersal capacities of specific taxa.

Finally, past patterns of connectivity are critical to interpret biogeographical patterns of currently isolated or fragmented systems in a wide variety of terrestrial ecosystems including mountains (Flantua & Hooghiemstra, 2018), islands (e.g. Simpson, 1974; Weigelt, Steinbauer, Cabral, & Kreft, 2016; Norder et al., 2018), fresh water systems (e.g. Dias et al., 2014), rain forests (e.g. Graham, Moritz, & Williams, 2006), grasslands (e.g. Lindborg & Eriksson, 2004; Münzbergová et al., 2013) and marine coastal ecosystems (Hoeksema, 2007) that similarly experienced major spatial changes during rapid sea-level fluctuations over the Pleistocene. The approach developed here, to quantify historical connectivity, can therefore provide a platform for interpreting contemporary biogeographies and past drivers of diversification in a wide array of both marine and terrestrial ecosystems where available space has been altered by climatic fluctuations. We postulate that quantifying flickering connectivity systems will facilitate a much more detailed and much needed quantitative basis to compare phylogeographic/phylogenetic patterns, e.g. the Tibeto-Himalayan region (Muellner-Riehl, 2019), and species (endemic) richness (e.g., Sklenář et al., 2014), from different mountain regions of the world.

5 | CONCLUSIONS

We present a pollen record-based biogeographical model for the páramo biome spanning the northern Andes (Venezuela, Colombia and Ecuador) over the last 1 Myr. Our models suggest substantial temperature oscillations where extreme temperature lows were ca. 8°C cooler than today, causing a total amplitude of the UFL of up to 1,600 vertical meters. These extreme cold events were, however, rare (See frequency bars in Figure 4) and during glacial periods most of the time cool stadial and interstadial climate conditions prevailed (Figure 3). Our analysis shows that páramos on all mountain ranges underwent frequent alterations between fragmented and connected configurations (Figures 4 and 5), but the estimated degrees and amount of connectivity varied among mountain ranges (Figure 6). Most páramos expanded during glacial periods even though extensive glaciers were present. To a large extent the current páramo distribution (located near their highest Pleistocene elevational position) was replaced by the lowermost ice extensions during the cool stadials, and during the coldest events replaced by the thick ice masses of mountain glaciers, implicating a substantial range size change of populations and a highly dynamic system during Pleistocene times. Depending on the location of initial dispersal – originating from ancestral areas – species would have experienced



the flickering connectivity system differently and thus a mosaic of contrasting patterns of genetic divergence and diversity is expected among cordilleras mirroring the mountain fingerprint signatures.

In light of Von Humboldt's work of relevance of different topographies for mountain biota, we show that topography and climate change together dictated páramo connectivity through time with high spatial variability. The interplay of the topographical and palaeoclimatic conditions created a unique pattern of connecting and fragmenting páramo patches through time, here described as the flickering connectivity system. Our spatially explicit model quantifies the complexity of mountain biome dynamics during climate oscillations, in terms of the degree, frequency and duration of past connectivity of high mountain biome (Figures 4–6) and can be applied to other mountain regions. Our connectivity estimates can contribute to answering long-standing questions on the drivers of evolutionary diversification in phylogenetic and phylogeographical studies, and enrich our understanding of the biogeographical history of mountain ecosystems more generally.

There the different climates are ranged the one above the other, stage by stage, like the vegetable zones, whose succession they limit; and there the observer may readily trace the laws that regulate the diminution of heat, as they stand indelibly inscribed on the rocky walls and abrupt declivities of the Cordilleras.

(Von Humboldt, 1877 (1845), I, p 46)

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REFERENCES

- Ali, J. R., & Aitchison, J. C. (2014). Exploring the combined role of eustasy and oceanic island thermal subsidence in shaping biodiversity on the Galápagos. *Journal of Biogeography*, 41(7), 1227–1241. <https://doi.org/10.1111/jbi.12313>
- Antonelli, A., Kissling, W. D., Flantua, S. G. A., Bermúdez, M. A., Mulch, A., Muellner-Riehl, A. N., ... Hoorn, C. (2018). Geological and climatic influences on mountain biodiversity. *Nature Geoscience*, 11(10), 718–725. <https://doi.org/10.1038/s41561-018-0236-z>
- Barthlott, W., Rafiqpoor, D., Kier, G., & Kreft, H. (2005). Global centers of vascular plant diversity. *Nova Acta Leopoldina NF*, 92(342), 61–83.
- Beckman, E. J., & Witt, C. C. (2015). Phylogeny and biogeography of the New World siskins and goldfinches: Rapid, recent diversification in the Central Andes. *Molecular Phylogenetics and Evolution*, 87, 28–45. <https://doi.org/10.1016/j.ympev.2015.03.005>
- Bell, C. D., & Donoghue, M. J. (2005). Phylogeny and biogeography of Valerianaceae (Dipsacales) with special reference to the South American valerians. *Organisms Diversity & Evolution*, 5(2), 147–159. <https://doi.org/10.1016/j.ode.2004.10.014>
- Bertuzzo, E., Carrara, F., Mari, L., Altermatt, F., Rodriguez-Iturbe, I., & Rinaldo, A. (2016). Geomorphic controls on elevational gradients of species richness. *Proceedings of the National Academy of Sciences*, 113(7), 1737–1742.
- Bogotá-A, R. G., Hooghiemstra, H., & Berrio, J. C. (2016). North Andean environmental and climatic change at orbital to submillennial time-scales: Vegetation, water-levels and sedimentary regimes from Lake Fúquene between 284 and 130 ka. *Review of Palaeobotany and Palynology*, 226, 91–107. <https://doi.org/10.1016/j.revpalbo.2015.09.007>
- Bogotá-Angel, R. G., Groot, M. H. M., Hooghiemstra, H., Lourens, L. J., Van der Linden, M., & Berrio, J. C. (2011). Rapid climate change from north Andean Lake Fúquene pollen records driven by obliquity: Implications for a basin-wide biostratigraphic zonation for the last 284 ka. *Quaternary Science Reviews*, 30(23–24), 3321–3337. <https://doi.org/10.1016/j.quascirev.2011.08.003>
- Bouchenak-Khelladi, Y., Onstein, R. E., Xing, Y., Schwery, O., & Linder, H. P. (2015). On the complexity of triggering evolutionary radiations. *New Phytologist*, 207(2), 313–326. <https://doi.org/10.1111/nph.13331>
- Cadena, C. D., Klicka, J., & Ricklefs, R. E. (2007). Evolutionary differentiation in the Neotropical montane region: Molecular phylogenetics and phylogeography of Buarremón brush-finches (Aves, Emberizidae). *Molecular Phylogenetics and Evolution*, 44(3), 993–1016. <https://doi.org/10.1016/j.ympev.2006.12.012>
- Cadena, C. D., Pedraza, C. A., & Brumfield, R. T. (2016). Climate, habitat associations and the potential distributions of Neotropical birds: Implications for diversification across the Andes. *Revista de La Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 40(155), 275–287.
- Chacón, J., Madriñán, S., Chase, M. W., & Bruhl, J. J. (2006). Molecular phylogenetics of Oreobolus (Cyperaceae) and the origin and diversification of the American species. *Taxon*, 55(2), 359–366. <https://doi.org/10.2307/25065583>
- Chesser, R. T. (2000). Evolution in the High Andes: The phylogenetics of Muscisaxicola ground-tyrants. *Molecular Phylogenetics and Evolution*, 15(3), 369–380. <https://doi.org/10.1006/mpev.1999.0774>
- Cleef, A. M. (1979). The phytogeographical position in the Neotropical vascular páramo flora with special reference to the Colombian Cordillera Oriental. In K. Larsen, & L. B. Holm-Nielsen (Eds.), *Tropical botany* (pp. 175–184). London, UK: Academic Press.
- Contreras-Ortiz, N., Aitchison, G. W., Hughes, C. E., & Madriñán, S. (2018). Convergent evolution of high elevation plant growth forms and geographically structured variation in Andean Lupinus (Fabaceae). *Botanical Journal of the Linnean Society*, 187(1), 118–136. <https://doi.org/10.1093/botlinnean/box095>



- Cortés, A. J., Garzón, L. N., Valencia, J. B., & Madriñán, S. (2018). On the causes of rapid diversification in the Páramos: Isolation by ecology and genomic divergence in Espeletia. *Frontiers in Plant Science*, 9, https://doi.org/10.3389/fpls.2018.01700
- Cosacov, A., Sérsic, A. N., Sosa, V., De-Nova, J. A., Nylander, S., & Cocucci, A. A. (2009). New insights into the phylogenetic relationships, character evolution, and phytogeographic patterns of Calceolaria (Calceolariaceae). *American Journal of Botany*, 96(12), 2240–2255.
- Cuatrecasas, J. (1979). Comparación fitogeográfica de páramos entre varias Cordilleras. In M. L. Salgado-Labouriau (Ed.), *El medio ambiente paramo. Actas del seminario de Mérida, Venezuela* (pp. 89–99). Caracas, Venezuela: Instituto Venezolano de Investigaciones Científicas, Ediciones Centro de Estudios Avanzados.
- Cuatrecasas, J. (2013). *A systematic study of the subtribe Espeletiinae*. New York, NY: The New York Botanical Garden.
- Dias, M. S., Oberdorff, T., Hugueny, B., Leprieur, F., Jézéquel, C., Cornu, J.-F., ... Tedesco, P. A. (2014). Global imprint of historical connectivity on freshwater fish biodiversity. *Ecology Letters*, 17(9), 1130–1140. https://doi.org/10.1111/ele.12319
- Díazgranados, M., & Barber, J. C. (2017). Geography shapes the phylogeny of frailejones (Espeletiinae Cuatrec., Asteraceae): A remarkable example of recent rapid radiation in sky islands. *PeerJ*, 5, e2968 https://doi.org/10.7717/peerj.2968
- Drummond, C. S., Eastwood, R. J., Miotto, S. T. S., & Hughes, C. E. (2012). Multiple continental radiations and correlates of diversification in Lupinus (Leguminosae): Testing for key innovation with incomplete taxon sampling. *Systematic Biology*, 61(3), 443–460. https://doi.org/10.1093/sysbio/syr126
- Dušková, E., Sklenář, P., Kolář, F., Vásquez, D. L. A., Romoleroux, K., Féret, T., & Marhold, K. (2017). Growth form evolution and hybridization in Senecio (Asteraceae) from the high equatorial Andes. *Ecology and Evolution*, 7, 6455–6468 https://doi.org/10.1002/ece3.3206
- Elsen, P. R., & Tingley, M. W. (2015). Global mountain topography and the fate of montane species under climate change. *Nature Climate Change*, 5(8), 772–776. https://doi.org/10.1038/nclimate2656
- Emshwiller, E. (2002). Biogeography of the oxalis tuberosa alliance. *The Botanical Review*, 68(1), 128–152. https://doi.org/10.1663/0006-8101(2002)068[0128:botota]2.0.co;2
- ESRI (2014). *ArcGIS Desktop (Version 10.3)*. Redlands, CA: Environmental Systems Research Institute.
- Flantua, S.G.A., & Hooghiemstra, H. (2017). Unravelling the mountain fingerprint: topography, paleoclimate and connectivity as drivers of contemporary biodiversity patterns. In S.G.A. Flantua, Climate change and topography as drivers of Latin American biome dynamics (PhD Dissertation, pp. 266–308). Amsterdam: University of Amsterdam. ISBN: 978-94-91407-48-2
- Flantua, S.G.A., & Hooghiemstra, H. (2018). Historical connectivity and mountain biodiversity. In C. Hoorn, A. Perrigo & A. Antonelli (Eds.), *Mountains, climate and biodiversity* (1st ed., pp. 171–185). Oxford, UK: Wiley-Blackwell.
- Flantua, S. G. A., Hooghiemstra, H., Grimm, E. C., Behling, H., Bush, M. B., González-Arango, C., ... Van Boxel, J. H. (2015). Updated site compilation of the Latin American Pollen Database. *Review of Palaeobotany and Palynology*, 223, 104–115. https://doi.org/10.1016/j.revpalbo.2015.09.008
- Flantua, S. G. A., Hooghiemstra, H., Van Boxel, J. H., Cabrera, M., González-Carranza, Z., & González-Arango, C. (2014). Connectivity dynamics since the Last Glacial Maximum in the northern Andes: a pollen-driven framework to assess potential migration. In W. D. Stevens, O. M. Montiel, & P. H. Raven (Eds.), *Paleobotany and biogeography: A festschrift for Alan graham in his 80th year*, Vol. 2014, 1st ed. (pp. 98–123). St. Louis, MO: Missouri Botanical Garden.
- Flantua, S. G. A., Hooghiemstra, H., Vuille, M., Behling, H., Carson, J. F., Gosling, W. D., ... González-Arango, C. (2016). Climate variability and human impact in South America during the last 2000 years: Synthesis and perspectives from pollen records. *Climate of the Past*, 12(2), 483–523. https://doi.org/10.5194/cp-12-483-2016
- Gómez-Gutiérrez, M. C., Pennington, R. T., Neaves, L. E., Milne, R. I., Madriñán, S., & Richardson, J. E. (2017). Genetic diversity in the Andes: Variation within and between the South American species of Oreobolus R. Br. (Cyperaceae). *Alpine Botany*, 127(2), 155–170. https://doi.org/10.1007/s00035-017-0192-z
- Graham, C. H., Carnaval, A. C., Cadena, C. D., Zamudio, K. R., Roberts, T. E., Parra, J. L., ... Sanders, N. J. (2014). The origin and maintenance of montane diversity: Integrating evolutionary and ecological processes. *Ecography*, 37(8), 711–719. https://doi.org/10.1111/ecog.00578
- Graham, C. H., Moritz, C., & Williams, S. E. (2006). Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences of the United States of America*, 103(3), 632–636. https://doi.org/10.1073/pnas.0505754103
- Grant, P. R. (2014). Adaptive radiation. In J. B. Losos, D. A. Baum, D. J. Futuyma, H. E. Hoekstra, R. E. Lenski & A. J. Moore, ... M. C. Whitlock (Eds.), *The Princeton guide to evolution*. Princeton, NJ: Princeton University Press.
- Groot, M. H. M., Bogotá, R. G., Lourens, L. J., Hooghiemstra, H., Vriend, M., Berrio, J. C., ... Westerhoff, W. (2011). Ultra-high resolution pollen record from the northern Andes reveals rapid shifts in montane climates within the last two glacial cycles. *Climate of the Past*, 7(1), 299–316. https://doi.org/10.5194/cp-7-299-2011
- Groot, M. H. M., Hooghiemstra, H., Berrio, J. C., & Giraldo, C. (2013). North Andean environmental and climatic change at orbital to submillennial time-scales: Vegetation, water levels and sedimentary regimes from Lake Fúquene 130–27 ka. *Review of Palaeobotany and Palynology*, 197, 186–204. https://doi.org/10.1016/j.revpalbo.2013.04.005
- von Hagen, K. B., & Kadereit, J. W. (2001). The phylogeny of Gentianella (Gentianaceae) and its colonization of the southern hemisphere as revealed by nuclear and chloroplast DNA sequence variation. *Organisms Diversity & Evolution*, 1(1), 61–79. https://doi.org/10.1078/1439-6092-00005
- von Hagen, K. B., & Kadereit, J. W. (2003). The diversification of Halenia (gentianaceae): Ecological opportunity versus key innovation. *Evolution*, 57(11), 2507–2518. https://doi.org/10.1111/j.0014-3820.2003.tb01495.x
- Hazzí, N. A., Moreno, J. S., Ortiz-Movilav, C., & Palacio, R. D. (2018). Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences*, 115(31), 7985–7990. https://doi.org/10.1073/pnas.1803908115
- Herzog, S. K., Martínez, R., Jørgensen, P. M., & Tiesse, H. (2011). Climate change and biodiversity in the tropical Andes. Inter-American Institute for Global Change Research, International Council of Scientific Unions, Scientific Committee on Problems of the Environment (SCOPE), p. 348.
- Hoeksema, B. W. (2007). Delineation of the Indo-Malayan centre of maximum marine biodiversity: The coral triangle. In W. Renema (Ed.), *Biogeography, time, and place: Distributions, barriers, and Islands* (pp. 117–178). Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-1-4020-6374-9_5
- Hooghiemstra, H. (1984). Vegetational and climatic history of the high plain of Bogotá, Colombia. (*Dissertationes Botanicae*, Vol. 79).
- Hooghiemstra, H., Berrio, J. C., Groot, M. H. M., Bogotá-A, R. G., Olivera, M. M., & González-Carranza, Z. (2012). The dynamic history of the upper forest line ecotone in the Northern Andes. In R. W. Myster (Ed.), *Ecotones between forest and Grassland* (pp. 229–246). New York, NY: Springer.
- Hooghiemstra, H., & Flantua, S. G. A. (2019). Colombia in the Quaternary: An overview of environmental and climatic change. In J. Gómez-Tapias (Ed.), *The Geology of Colombia Book*. Servicio Geológico Colombiano, Quaternary, Bogotá, Vol. 4, Chapter 2, pp. 33–57.



- Hooghiemstra, H., & Van der Hammen, T. (2004). Quaternary ice-age dynamics in the Colombian Andes: Developing an understanding of our legacy. *Philosophical Transactions: Biological Sciences*, 359(1442), 173–181.
- Hughes, C. E., & Atchison, G. W. (2015). The ubiquity of alpine plant radiations: From the Andes to the Hengduan Mountains. *New Phytologist*, 207(2), 275–282. <https://doi.org/10.1111/nph.13230>
- Hughes, C., & Eastwood, R. (2006). Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences*, 103(27), 10334–10339. <https://doi.org/10.1073/pnas.0601928103>
- Jabaily, R. S., & Sytsma, K. J. (2013). Historical biogeography and life-history evolution of Andean Puya (Bromeliaceae). *Botanical Journal of the Linnean Society*, 171(1), 201–224. <https://doi.org/10.1111/j.1095-8339.2012.01307.x>
- Josse, C., Cuesta, F., Navarro, G., Barrena, V., Chacón-Moreno, E., Ferreira, W., ... Tovar, A. (2009). Mapa de ecosistemas de los Andes del Norte y Centro, Bolivia, Colombia, Ecuador, Perú, Venezuela. Secretaría General de la Comunidad Andina, Programa Regional ECOBONA, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, LTA-UNALM, IAvH, ICAE-ULA, CDC-UNALM, RUMBOL SRL, Lima.
- Kampstra, P. (2008). Beanplot: A boxplot alternative for visual comparison of distributions. *Journal of Statistical Software*, 28. <https://doi.org/10.18637/jss.v028.c01>
- Knowles, L. L. (2000). Tests of Pleistocene speciation in montane grasshoppers (genus *Melanoplus*) from the sky islands of Western North America. *Evolution*, 54(4), 1337–1348. <https://doi.org/10.1111/j.0014-3820.2000.tb00566.x>
- Knowles, L. L., & Massatti, R. (2017). Distributional shifts – not geographic isolation – as a probable driver of montane species divergence. *Ecography*, 40(12), 1475–1485. <https://doi.org/10.1111/ecog.02893>
- Kolář, F., Dušková, E., & Sklenář, P. (2016). Niche shifts and range expansions along cordilleras drove diversification in a high-elevation endemic plant genus in the tropical Andes. *Molecular Ecology*, 25(18), 4593–4610. <https://doi.org/10.1111/mec.13788>
- Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences*, 104(14), 5925–5930. <https://doi.org/10.1073/pnas.0608361104>
- Kropf, M., Kadereit, J. W., & Comes, H. P. (2003). Differential cycles of range contraction and expansion in European high mountain plants during the Late Quaternary: Insights from *Pritzelago alpina* (L.) O. Kuntze (Brassicaceae). *Molecular Ecology*, 12(4), 931–949. <https://doi.org/10.1046/j.1365-294X.2003.01781.x>
- Lagomarsino, L. P., Condamine, F. L., Antonelli, A., Mulch, A., & Davis, C. C. (2016). The abiotic and biotic drivers of rapid diversification in Andean bellflowers (Campanulaceae). *New Phytologist*, 210(4), 1430–1442. <https://doi.org/10.1111/nph.13920>
- Lindborg, R., & Eriksson, O. (2004). Historical landscape connectivity affects present plant species diversity. *Ecology*, 85(7), 1840–1845.
- Luebert, F., & Weigend, M. (2014). Phylogenetic insights into Andean plant diversification. *Frontiers in Ecology and Evolution*, 2, 1–17. <https://doi.org/10.3389/fevo.2014.00027>
- Luteyn, J. L. (1999). *Paramos: A checklist of plant diversity, geographical distribution and botanical literature*, Vol. 84. New York, NY: The New York Botanical Garden.
- Lyons, B. M., McHenry, M. A., & Barrington, D. S. (2017). Insights into evolution in Andean *Polystichum* (Dryopteridaceae) from expanded understanding of the cytosolic phosphoglucose isomerase gene. *Molecular Phylogenetics and Evolution*, 112, 36–46. <https://doi.org/10.1016/j.ympev.2017.04.010>
- Madriñán, S., Cortés, A. J., & Richardson, J. E. (2013). Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Frontiers in Genetics*, 4, 1–7. <https://doi.org/10.3389/fgene.2013.00192>
- Massatti, R., & Knowles, L. L. (2014). Microhabitat differences impact phylogeographic concordance of codistributed species: Genomic evidence in montane sedges (*Carex* L.) from the Rocky Mountains. *Evolution*, 68(10), 2833–2846. <https://doi.org/10.1111/evo.12491>
- McCormack, J. E., Huang, H., & Knowles, L. L. (2009). Sky islands. In R. G. Gillespie, & D. Clague (Eds.), *Encyclopedia of Islands* (pp. 839–843). Berkeley, CA: University of Chicago Press.
- McHenry, M. A., & Barrington, D. S. (2014). Phylogeny and biogeography of exindusiate Andean *Polystichum* (Dryopteridaceae). *American Journal of Botany*, 101(2), 365–375. <https://doi.org/10.3732/ajb.1300191>
- McRae, Brad H., Dickson, B. G., Keitt, T. H., & Shah, V. B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, 89(10), 2712–2724. <https://doi.org/10.1890/07-1861.1>
- McRae, B. H., & Kavanagh, D. M. (2011). *Linkage mapper connectivity analysis software*. Seattle, WA: The Nature Conservancy. Retrieved from <http://www.circuitscape.org/linkagemapper>.
- McRae, B. H., Shirk, A. J., & Platt, J. T. (2013). *Gnarly landscape utilities: Resistance and habitat calculator user guide*. Fort Collins, CO: The Nature Conservancy. Retrieved from <http://www.circuitscape.org/gnarly-landscape-utilities>.
- Moore, B. R., & Donoghue, M. J. (2007). Correlates of diversification in the plant clade dipsacales: Geographic movement and evolutionary innovations. *The American Naturalist*, 170(S2), S28–S55. <https://doi.org/10.1086/519460>
- Morales-Briones, D. F., Romoleroux, K., Kolář, F., & Tank, D. C. (2018). Phylogeny and evolution of the Neotropical radiation of *Lachemilla* (Rosaceae): Uncovering a history of reticulate evolution and implications for infrageneric classification. *Systematic Botany*, 43(1), 17–34. <https://doi.org/10.1600/036364418X696897>
- Muellner-Riehl, A. N. (2019). Mountains as evolutionary arenas: Patterns, emerging approaches, paradigm shifts, and their implications for plant phylogeographic research in the Tibeto-Himalayan region. *Frontiers in Plant Science*, 10(195). <https://doi.org/10.3389/fpls.2019.00195>
- Münzbergová, Z., Cousins, S. A. O., Herben, T., Plačková, I., Mildén, M., & Ehrlén, J. (2013). Historical habitat connectivity affects current genetic structure in a grassland species. *Plant Biology*, 15(1), 195–202. <https://doi.org/10.1111/j.1438-8677.2012.00601.x>
- Mutke, J., Jacobs, R., Meyers, K., Henning, T., & Weigend, M. (2014). Diversity patterns of selected Andean plant groups correspond to topography and habitat dynamics, not orogeny. *Frontiers in Genetics*, 5. <https://doi.org/10.3389/fgene.2014.00351>
- Nevado, B., Contreras-Ortiz, N., Hughes, C., & Filatov, D. A. (2018). Pleistocene glacial cycles drive isolation, gene flow and speciation in the high elevation Andes. *New Phytologist*, 219(2), 779–793.
- Norder, S. J., Proios, K., Whittaker, R. J., Alonso, M. R., Borges, P. A. V., Borregaard, M. K., ... Rijsdijk, K. F. (2018). Beyond the Last Glacial Maximum: Island endemism is best explained by long-lasting archipelago configurations. *Global Ecology and Biogeography*, 28, 184–197. <https://doi.org/10.1111/geb.12835>
- Nürk, N. M., Michling, F., & Linder, H. P. (2017). Are the radiations of temperate lineages in tropical alpine ecosystems pre-adapted? *Global Ecology and Biogeography*, 27(3), 334–345. <https://doi.org/10.1111/geb.12699>
- Nürk, N. M., Scheriau, C., & Madriñán, S. (2013). Explosive radiation in high Andean Hypericum—rates of diversification among New World lineages. *Evolutionary and Population Genetics*, 4, 175. <https://doi.org/10.3389/fgene.2013.00175>
- Onstein, R. E., Baker, W. J., Couvreur, T. L. P., Faubert, S., Svennning, J.-C., & Kissling, W. D. (2017). Frugivory-related traits promote speciation of tropical palms. *Nature Ecology & Evolution*, 1(12), 1903. <https://doi.org/10.1038/s41559-017-0348-7>
- Padilla-González, G. F., Diazgranados, M., & Da Costa, F. B. (2017). Biogeography shaped the metabolome of the genus *Espeletia*: a phytochemical perspective on an Andean adaptive radiation. *Scientific Reports*, 7, 8835.



- Papadopoulou, A., & Knowles, L. L. (2015). Species-specific responses to island connectivity cycles: Refined models for testing phylogeographic concordance across a Mediterranean Pleistocene Aggregate Island Complex. *Molecular Ecology*, 24(16), 4252–4268. <https://doi.org/10.1111/mec.13305>
- Papadopoulou, A., & Knowles, L. L. (2016). Toward a paradigm shift in comparative phylogeography driven by trait-based hypotheses. *Proceedings of the National Academy of Sciences*, 113(29), 8018–8024. <https://doi.org/10.1073/pnas.1601069113>
- Pennington, R. T., Lavin, M., Särkinen, T., Lewis, G. P., Klitgaard, B. B., & Hughes, C. E. (2010). Contrasting plant diversification histories within the Andean biodiversity hotspot. *Proceedings of the National Academy of Sciences*, 107(31), 13783–13787. <https://doi.org/10.1073/pnas.1001317107>
- Petit, R. J., Aguinagalde, I., de Beaulieu, J.-L., Bittkau, C., Brewer, S., Cheddadi, R., ... Vendramin, G. G. (2003). Glacial Refugia: Hotspots but not melting pots of genetic diversity. *Science*, 300(5625), 1563–1565. <https://doi.org/10.1126/science.1083264>
- Pouchon, C., Fernández, A., Nassar, J. M., Boyer, F., Aubert, S., Lavergne, S., ... Antonelli, A. (2018). Phylogenomic analysis of the explosive adaptive radiation of the Espeletia complex (Asteraceae) in the Tropical Andes. *Systematic Biology*, 67(6), 1041–1060. <https://doi.org/10.1093/sysbio/syy022>
- Qian, H., & Ricklefs, R. E. (2000). Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, 407(6801), 180–182. <https://doi.org/10.1038/35025052>
- Quintero, I., & Jetz, W. (2018). Global elevational diversity and diversification of birds. *Nature*, 555(7695), 246–250. <https://doi.org/10.1038/nature25794>
- Ramírez-Barahona, S., & Eguiarte, L. E. (2013). The role of glacial cycles in promoting genetic diversity in the Neotropics: The case of cloud forests during the Last Glacial Maximum. *Ecology and Evolution*, 3(3), 725–738. <https://doi.org/10.1002/eee.3.483>
- Rauscher, J. T. (2002). Molecular phylogenetics of the Espeletia complex (Asteraceae): Evidence from nrDNA ITS sequences on the closest relatives of an Andean adaptive radiation. *American Journal of Botany*, 89(7), 1074–1084. <https://doi.org/10.3732/ajb.89.7.1074>
- Ribas, C. C., Moyle, R. G., Miyaki, C. Y., & Cracraft, J. (2007). The assembly of montane biotas: Linking Andean tectonics and climatic oscillations to independent regimes of diversification in Pionus parrots. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1624), 2399–2408. <https://doi.org/10.1098/rspb.2007.0613>
- Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, 5, 23–27.
- Rull, V. (2005). Biotic diversification in the Guayana Highlands: A proposal. *Journal of Biogeography*, 32(6), 921–927. <https://doi.org/10.1111/j.1365-2699.2005.01252.x>
- Rull, V. (2011). Neotropical biodiversity: Timing and potential drivers. *Trends in Ecology & Evolution*, 26(10), 508–513. <https://doi.org/10.1016/j.tree.2011.05.011>
- Rull, V., & Nogué, S. (2007). Potential migration routes and barriers for vascular plants of the Neotropical Guyana highlands during the Quaternary. *Journal of Biogeography*, 34(8), 1327–1341.
- Sánchez-Baracaldo, P. (2004). Phylogenetics and biogeography of the neotropical fern genera Jamesonia and Eriosorus (Pteridaceae). *American Journal of Botany*, 91(2), 274–284. <https://doi.org/10.3732/ajb.91.2.274>
- Sánchez-Baracaldo, P., & Thomas, G. H. (2014). Adaptation and convergent evolution within the Jamesonia-Eriosorus complex in high-elevation biodiverse Andean hotspots. *PLoS ONE*, 9(10), e110618. <https://doi.org/10.1371/journal.pone.0110618>
- Saura, S., Estreguil, C., Mouton, C., & Rodríguez-Freire, M. (2011). Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). *Ecological Indicators*, 11(2), 407–416. <https://doi.org/10.1016/j.ecolind.2010.06.011>
- Saura, S., & Pascual-Hortal, L. (2007). A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *Landscape and Urban Planning*, 83(2–3), 91–103. <https://doi.org/10.1016/j.landurbplan.2007.03.005>
- Saura, S., & Rubio, L. (2010). A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography*, 33, 523–537. <https://doi.org/10.1111/j.1600-0587.2009.05760.x>
- Saura, S., & Torné, J. (2009). Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. *Environmental Modelling & Software*, 24(1), 135–139. <https://doi.org/10.1016/j.envsoft.2008.05.005>
- Scherson, R. A., Vidal, R., & Sanderson, M. J. (2008). Phylogeny, biogeography, and rates of diversification of New World Astragalus (Leguminosae) with an emphasis on South American radiations. *American Journal of Botany*, 95(8), 1030–1039. <https://doi.org/10.3732/ajb.0800017>
- Schönwetter, P., Stehlík, I., Holderegger, R., & Tribsch, A. (2005). Molecular evidence for glacial refugia of mountain plants in the European Alps. *Molecular Ecology*, 14(11), 3547–3555. <https://doi.org/10.1111/j.1365-294X.2005.02683.x>
- Simpson, B. B. (1974). Glacial migrations of plants: Island biogeographical evidence. *Science*, 185(4152), 698–700. <https://doi.org/10.1126/science.185.4152.698>
- Sklenář, P., Hedberg, I., & Cleef, A. M. (2014). Island biogeography of tropical alpine floras. *Journal of Biogeography*, 41(2), 287–297. <https://doi.org/10.1111/jbi.12212>
- Smith, B. T., McCormack, J. E., Cuervo, A. M., Hickerson, M. J., Aleixo, A., Cadena, C. D., ... Brumfield, R. T. (2014). The drivers of tropical speciation. *Nature*, 515(7527), 406–409. <https://doi.org/10.1038/nature13687>
- Steinbauer, M. J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., ... Beierkuhnlein, C. (2016). Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography*, 25(9), 1097–1107. <https://doi.org/10.1111/geb.12469>
- Tischendorf, L., & Fahrig, L. (2000). On the usage and measurement of landscape connectivity. *Oikos*, 90(1), 7–19. <https://doi.org/10.1034/j.1600-0706.2000.900102.x>
- Torres, V., Hooghiemstra, H., Lourens, L., & Tzedakis, P. C. (2013). Astronomical tuning of long pollen records reveals the dynamic history of montane biomes and lake levels in the tropical high Andes during the Quaternary. *Quaternary Science Reviews*, 63, 59–72. <https://doi.org/10.1016/j.quascirev.2012.11.004>
- Uribe-Convers, S., & Tank, D. C. (2015). Shifts in diversification rates linked to biogeographic movement into new areas: An example of a recent radiation in the Andes. *American Journal of Botany*, 102(11), 1854–1869. <https://doi.org/10.3732/ajb.1500229>
- Van der Hammen, T. (1974). The Pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography*, 1, 3–26. <https://doi.org/10.2307/3038066>
- Van der Hammen, T., & Cleef, A. M. (1986). Development of the high Andean páramo flora and vegetation. In F. Vuilleumier, & M. Monasterio (Eds.), *High altitude tropical biogeography* (pp. 153–201). New York, NY: Oxford University Press.
- Vargas, O. M., & Madriñán, S. (2012). Preliminary phylogeny of Diplostephium (Asteraceae): Speciation rate and character evolution. *Lundellia*, 2012(15), 1–15. <https://doi.org/10.25224/1097-993x-15.1.1>
- Vargas, O. M., Ortiz, E. M., & Simpson, B. B. (2017). Conflicting phylogenetic signals reveal a pattern of reticulate evolution in a recent high-Andean diversification (Asteraceae: Astereae: Diplostephium). *New Phytologist*, 214(4), 1736–1750. <https://doi.org/10.1111/nph.14530>
- Vásquez, D. L. A., Balslev, H., Hansen, M. M., Sklenář, P., & Romoleroux, K. (2016). Low genetic variation and high differentiation across sky island populations of Lupinus alopecuroides (Fabaceae) in the northern Andes. *Alpine Botany*, 27(3), 334–345. <https://doi.org/10.1007/s00035-016-0165-7>



- Von Humboldt, A. (1845). *Kosmos: Entwurf einer physischen Weltbeschreibung* (Vol. 1). Berlin, Germany: Eichborn Verlag.
- Wallis, G. P., Waters, J. M., Upton, P., & Craw, D. (2016). Transverse alpine speciation driven by glaciation. *Trends in Ecology & Evolution*, 31(12), 916–926. <https://doi.org/10.1016/j.tree.2016.08.009>
- Weigelt, P., Steinbauer, M. J., Cabral, J. S., & Kreft, H. (2016). Late Quaternary climate change shapes island biodiversity. *Nature*, 532(7597), 99–102. <https://doi.org/10.1038/nature17443>
- Weir, J. T. (2006). Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution*, 60(4), 842–855. <https://doi.org/10.1554/05-272.1>
- Weir, J. T., Haddrath, O., Robertson, H. A., Colbourne, R. M., & Baker, A. J. (2016). Explosive ice age diversification of kiwi. *Proceedings of the National Academy of Sciences*, 113, E5580–7. <https://doi.org/10.1073/pnas.1603795113>
- Winkworth, R. C., Wagstaff, S. J., Glenny, D., & Lockhart, P. J. (2005). Evolution of the New Zealand mountain flora: Origins, diversification and dispersal. *Organisms Diversity & Evolution*, 5(3), 237–247. <https://doi.org/10.1016/jоде.2004.12.001>
- Yu, H., Favre, A., Sui, X., Chen, Z., Qi, W., & Xie, G. (2019). Mapping the genetic patterns of plants in the region of the Qinghai-Tibet Plateau: Implications for conservation strategies. *Diversity and Distributions*, 25(2), 310–324. <https://doi.org/10.1111/ddi.12847>
- Zapata, F. (2013). A multilocus phylogenetic analysis of Escallonia (Escalloniaceae): Diversification in montane South America. *American Journal of Botany*, 100, 526–545. <https://doi.org/10.3732/ajb.1200297>

BIOSKETCHES

Suzette Flantua has a background in palaeoecology, biogeography, landscape ecology and spatial analyses, and enjoys integrating them all. She is interested in a wide range of topics from the Miocene to the present, from islands to mountains, to understand contemporary patterns of species richness and endemism.

Henry Hooghiemstra is a terrestrial and marine tropical palynologist with interest in climate change, evolution of ecosystems, and how civilizations coped with environmental change. He is working on time-scales from the full Quaternary to the Anthropocene. His research focuses on a wide variety of biomes in Latin America, Saharan and East Africa, and in Mauritius.

Aaron O'Dea is a marine palaeobiologist who uses the marine fossil record of Tropical America to explore drivers of macroevolution in the seas, and takes cores on coral reefs from French Polynesia to the Dominican Republic to reconstruct how reefs changed over millennia with the aim of improving their future resilience.

Renske E. Onstein is an evolutionary ecologist who enjoys collecting (and eating) tropical megafaunal fruits, e.g. on Borneo and Madagascar, while studying how fruit functional traits interact with frugivores to affect diversification dynamics. She is generally interested in the broad-scale distribution and diversification of functional and taxonomic diversity of flowering plants.

Catalina Giraldo is an environmental artist (www.catalhinagiraldo.com/) who combines her scientific background with visual media to raise awareness of environmental issues. She co-founded Fundación Biodiversa Colombia (www.fundacionbiodiversa.org), a biodiversity foundation that carries out research and educational projects in Colombia to protect the environment and help local communities develop a sustainable way of living.

Author contributions: S.G.A.F. and H.H. conceived the ideas. H.H. provided the AP% of the Funza09 dataset. S.G.A.F. performed the spatial analyses. S.G.A.F and H.H. led the writing and figure design with critical contributions by all authors. C.G. developed the visualization with S.G.A.F. and H.H.

SUPPORTING INFORMATION

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

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SUPPORTING INFORMATION

Appendix S1. Surface areas, elevational ranges and hypsographies of the Northern Andes

The highest peaks of the Northern Andes are located in Ecuador (ca. 6300 m a.s.l.) and Sierra Nevada de Santa Marta (SNSM; ca. 5800 m a.s.l.). In Colombia, three parallel positioned cordilleras cross in north-south and northeast-southwest direction the region, separated by deep inter-Andean valleys, of which the highest is the Central Cordillera. They join in Ecuador to form a high elevation mountain block with numerous volcanos throughout the region as often displayed in the work by Von Humboldt & Bonpland (1805; 1807). The largest cordillera is the Eastern Cordillera, followed by the Central Cordillera and the Ecuadorian Andes (**Table S1.1**). The SNSM is the smallest but highest in Colombia, forming an isolated mountain range just of the Caribbean coastline.

Mountain range	Total surface area (km ²)	Elevational range (m a.s.l.)	Hypsographic shape (Elsen & Tingley, 2015)	Hypsographic shape (this study)
Northern Andes	448.000	13-6300	Hourglass (total Andes)	Pyramid
Sierra Nevada de Santa Marta (SNSM)	9190	430-5700	Pyramid (included in Eastern Cordillera)	Pyramid
Cordillera de Mérida	30.340	80-5000	Pyramid	Diamond
Eastern Cordillera	130.630	106-5400	Pyramid	Hourglass/Pyramid (with high elevation plateau)
Central Cordillera	122.000	81-5300	Diamond (joined with Ecuador)	Pyramid
Western Cordillera	48.100	13-4100	Pyramid	Diamond
Ecuadorian Cordilleras	107.800	25-6300	Diamond	Hourglass/Diamond

Table S1.1 | Surface availability and hypsographic shape for each mountain range of the Northern Andes.

To understand elevational availability of surface areas in mountains, hypsographic curves provide estimates of elevational differences (See for a global analysis of mountains Elsen & Tingley, 2015). To calculate these curves for each cordillera, we first delimitated the Northern Andes by using the boundary defined by Josse et al. (2009). Then we added the SNSM by a 500 m asl isoline as the previous study included all but this mountain range. To define the boundaries between the three different cordilleras of Colombia, and between the Central Cordillera in Colombia and the Ecuadorian Cordillera, we identified the main geological faults following Bermúdez, Van der Beek & Bernet (2013), Baldock (1982) and Ramos & Alemán (2000), and then provided additional detail to the cordillera boundaries by defining the deepest sections of the main canyons using ESRI ArcHydro tool (ESRI, 2014).

REFERENCES

- Baldock, M. W. (1982). *Geology of Ecuador (Explanation of National Map)*. Quito, Ecuador: Dirección general de Geología y Minas.
- Bermúdez, M., Van der Beek, P., & Bernet, M. (2013). Strong tectonic and weak climatic control on exhumation rates in the Venezuelan Andes. *Lithosphere*, 5(1), 3–16.
- Elsen, P. R., & Tingley, M. W. (2015). Global mountain topography and the fate of montane species under climate change. *Nature Climate Change*, 5(8), 772–776. <https://doi.org/10.1038/nclimate2656>
- ESRI. (2014). ArcGIS Desktop (Version 10.3). Redlands, CA: Environmental Systems Research Institute.
- Josse, C., Cuesta, F., Navarro, G., Barrena, V., Chacón-Moreno, E., Ferreira, W., ... Tovar, A. (2009). *Mapa de ecosistemas de los Andes del Norte y Centro, Bolivia, Colombia, Ecuador, Perú, Venezuela*. Lima: Secretaría General de la Comunidad Andina, Programa Regional ECOBONA, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, LTA-UNALM, IAyH, ICAE-ULA, CDC-UNALM, RUMBOL SRL. Retrieved from www.infoandina.org/ecosistemasandinos
- Ramos, V., & Alemán, A. (2000). Tectonic evolution of the Andes. In U. G. Cordani, E. J. Milani, A. Thomaz Filo, & D. A. Campos (Eds.), *Tectonic evolution of South America* (pp. 635–685). Rio de Janeiro.
- Von Humboldt, A., & Bonpland, A. (1805). *Essai sur la Géographie des Plantes; Accompagné d'un Tableau Physique des Régions Équinoxiales*. Paris: Chez Levrault, Schoell.
- Von Humboldt, A., & Bonpland, A. (1807). *Geographie der Pflanzen in den Tropenlandern*. Paris.

SUPPORTING INFORMATION

Appendix S2. The páramo alpine biome

The páramos of the Eastern Cordillera of Colombia (Fig. S2.1) currently cover the largest surface area (ca. 15,800 km²) compared to those of the Central Cordillera (ca. 8200 km²) and the Western Cordillera of Colombia (ca. 690 km²). Plant species richness in the páramos estimates range from ca. 3500 (Sklenář, Dušková, & Balslev, 2011) to ca. 3700, much of which are in the families Asteraceae, Orchidaceae and Poaceae (Rangel, 2015). Páramos along the east side of the Northern Andes (facing the Amazon basin) are generally more humid than those along the west side (facing the Pacific) (see Figure S2.2).

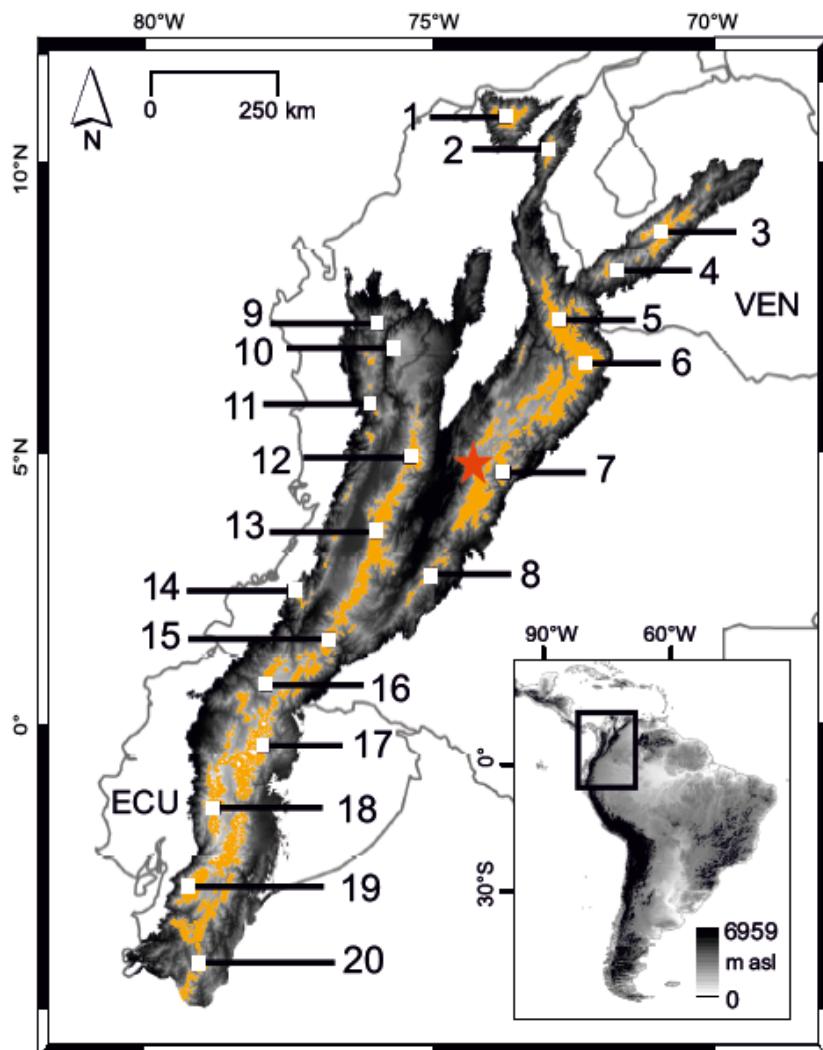


Figure S2.1 | The Northern Andes showing the current distribution of páramos. Main (but not all) páramos complexes are: 1. Sierra Nevada de Santa Marta, 2. Sierra de Perijá, 3. Sierra Nevada de Mérida and Santa Domingo, 4. Páramo del Batallón, 5. Páramos de los Santanderes, 6. Páramos de Boyacá, 7. Páramos de Cundinamarca, 8. Páramos Los Picachos and Miraflores, 9. Páramo Paramillo, 10. Páramo Belmira, 11. Páramos Frontino-Tatamá, 12. Páramos Viejo Caldas-Tolima, 13. Páramos Valle-Tolima, 14. Páramos del Duende-Cerro Plateado, 15. Páramos Macizo Colombiano, 16. Páramos de Galeras-Chiles, 17. Páramos del Norte de la Cordillera Real Oriental, 18. Páramos centrales de las Cordillera Occidental Ecuatorianos. 19. Páramos Macizo de Cajas, 20. Páramos de Lagunillas-Piura-Podocarpus. Red star indicates location of fossil pollen record of Funza09 (Torres, Hooghiemstra, Lourens, & Tzedakis, 2013). VEN: Venezuela; COL: Colombia; ECU: Ecuador. Northern Andes limits adapted from Josse et al. (2009) and páramos (orange) as defined by Beltrán et al. (2009), Sarmiento Pinzón, Cadena Vargas, Sarmiento Giraldo, & Zapata Jiménez (2013) and IAvH (2012),

Figure S2.2 | Photographs of páramo areas in the Northern Andes from Venezuela to Ecuador highlighting the treeless vegetation. With increasing elevation páramo is characterised by dwarf trees and shrub (subpáramo); herbaceous vegetation, bunch grasses, dwarf shrub, and cushion vegetation (grasspáramo); and an incomplete vegetation cover including few angiosperm pioneers, mosses and blue algae (superpáramo). The iconic woody stem rosettes of Espeletiinae (Asteraceae) occur from the uppermost montane forest into the lowermost superpáramo.



Piedras Blancas Páramo, Mérida Cordilleras (Fig. S2.1.#3).
4250 m a.s.l.. Photo courtesy of Luis Daniel Llambi.

The Piedras Blancas Páramo is located in the Sierra de La Culata National Park. The area is in the driest region of the Mérida Andes, with less than 900 mm yr⁻¹. It is one of the best studied páramos in Northern Andes, with a long tradition of research on *Espeletia* population ecology, ecophysiology (particularly of adaptations to low temperatures and drought), studies of plant-insect relationships, and climate change monitoring (including three summits of the GLORIA-Andes monitoring network). Seen on the foreground are *Coespeletia moritziana* and *Hypericum laricifolium* in flower.



Páramo del Almorzadero, Eastern Cordillera (Fig. S2.1.#5). Photo by Henry Hooghiemstra

Grasspáramo in a wet valley where stagnating water gives rise to a mosaic of *Swallenochloa* sp. (Poaceae), *Espeletia conglomerata* (Asteraceae), and wet cushion bogs of *Plantago* sp. and *Distichia muscoides*.



Sierra Nevada del Cocuy- Güicán, Eastern Cordillera (Fig. S2.1.#6).
3900 m a.s.l.. Photo by Suzette G.A. Flantua

Traces of extensive glaciers during glacial times are found throughout the landscape of the Sierra Nevada de Cocuy-Güicán as in many other parts of the Northern Andes (Helmens, 1990; Schubert & Clapperton, 1990; Clapperton, 1993; Braun & Bezada, 2013), having shaped and carved the high elevation landscape of the páramos during a significant part of the last million years. In current times, Sierra Nevada El Cocuy-Güicán still has among the largest ice covers in Colombia, exposed to the moisture supply from the Amazon basin. Here, *Hypericum* and *Espeletia* spp. (seen on the foreground) have their niche on eroded and rocky underground.



Páramo of Chingaza, Eastern Cordillera (Fig. S2.1.#7).
3460 m a.s.l.. Photo by Suzette G.A. Flantua

The páramos of Chingaza are located within the Chingaza National Park and is the main source of water to the Colombian capital of Bogotá at only a few hours distance. These páramos are considered to be among the wettest in the Northern Andes, with several areas within the National Park receiving over 4000 mm yr-1 (compare to the c. 1000 mm yr-1 in the páramos of the Western Cordillera) (Cárdenas & Tobón, 2017). Photo shows the Laguna Chingaza at c. 3200 m a.s.l. and flowering *Espeletia spp.*



Páramo de Belmira, Central Cordillera (Fig. S2.1.#10).
3200 m a.s.l.. Photo by Suzette G.A. Flantua

The Páramo of Belmira is an isolated island of páramo vegetation to the north of the Central Cordillera where annual precipitation fluctuates around c. 2000 mm yr-1. Highest elevations of this páramo only reach c. 3350 m a.s.l.. Here, the elevational organization of uppermost Andean forest and páramo vegetation at the highest elevations is replaced by a mosaic of pockets of grasspáramo vegetation interchanged with high Andean dwarf forest.



National Park of Los Nevados, Central Cordillera (Fig. S2.1.#12).
4100 m a.s.l.. Photo by Henry Hooghiemstra

Most Andean glaciers are small remnants of what were once massive glaciers covering most, if not all, mountain ridges, but are now either rapidly decreasing or have disappeared in the last decades (IDEAM, 2012; Braun & Bezada, 2013). The Nevado del Ruiz (seen in the background) is among the few glaciers left in Colombia (IDEAM, 2012). Shown are Laguna del Otún and *Espeletia* sp. interchanged with *Hypericum* sp. on the foreground.



Paramo de Guandera, Ecuadorian Cordillera (Fig. S2.1.#16).
3800 m a.s.l.. Photo by Henry Hooghiemstra

The most striking taxonomic difference among the páramos of the Venezuela, Colombia, and northernmost Ecuador is the presence of the emblematic stem rosette of the Espeletiinae, which are absent in the páramos with a more southern location and in the Costa Rican paramos (Luteyn, 1999). El Angel National Park on the Ecuadorian-Colombian border is the most southern distribution of Espeletia. Highest peaks reach over 3800 m a.s.l. and are extensively covered by *Calamagrostis* sp., *Espeletia pycnophylla* and *Puya hamata*.



Llanganates National Park, Ecuadorian Cordillera (Fig. S2.1.#17).
3900 m a.s.l.. Photo by Suzette G.A. Flantua

Grasspáramo in the Llanganates National Park, centrally located in Ecuador. Two thousand years of human activities in these páramos have reduced the proportion of shrubs significantly. Increasingly pressure on páramos comes from agriculture, intensive cattle grazing, pine plantations, among others (Buytaert et al., 2006).



Chimborazo, (Fig. S2.1.#17).
4800 m a.s.l.. Photo by Suzette G.A. Flantua

The superpáramo (highest part of the páramo, also called the ‘desert páramo’) often borders the snowline as can be found around the Chimborazo Volcano. It often has less than 20% vegetation cover with e.g. tussocks of *Calamagrostis* sp. and shrub of *Chuquiraga* sp. Seen here on the foreground is *Senecio nivalis* and the Chimborazo Volcano is seen on the background.



Podocarpus National Park, Ecuadorian Cordillera (Fig. S2.1.#17).
3300 m a.s.l.. Photo by Suzette G.A. Flantua

This wet subpáramo is rich in Asteraceous (central in photograph) and Ericaceous (foreground)
shrub and rosettes of *Puya* sp. (Bromeliaceae) with spined leaves

REFERENCES

- Beltrán, K., Salgado, S., Cuesta, F., León-Yáñez, S., Romoleroux, K., Ortiz, E., ... Velástegui, A. (2009). *Distribución Espacial, Sistemas Ecológicos y Caracterización Florística de los Páramos en el Ecuador.* Quito: EcoCiencia, Proyecto Páramo Andino y Herbario QCA.
- Braun, C., & Bezada, M. (2013). The history and disappearance of glaciers in Venezuela. *Journal of Latin American Geography*, 12(2), 85–124.
- Buytaert, W., Céller, R., De Bièvre, B., Cisneros, F., Wyseure, G., Deckers, J., & Hofstede, R. (2006). Human impact on the hydrology of the Andean páramos. *Earth-Science Reviews*, 79(1–2), 53–72.
<https://doi.org/10.1016/j.earscirev.2006.06.002>
- Cárdenas, M. F., & Tobón, C. (2017). Recuperación del funcionamiento hidrológico de ecosistemas de páramo en Colombia. *Revista U.D.C.A Actualidad & Divulgación Científica*, 20(2), 403–412.
<https://doi.org/10.31910/rudca.v20.n2.2017.381>
- Clapperton, C. M. (1993). Nature of environmental changes in South America at the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 101(3), 189–208.
- Helmens, K. F. (1990). *Neogene-Quaternary geology of the High plain of Bogota, Eastern Cordillera, Colombia (stratigraphy, paleoenvironments and landscape evolution)*. Berlin: J Cramer.
- IAvH. (2012). Actualización del Atlas de páramos de Colombia Esc. 1:100.000. Bogotá, Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt y Ministerio de Ambiente y Desarrollo Sostenible.
- IDEAM. (2012). *Glaciares de Colombia, más que montañas con hielo*. Bogotá, Colombia: Comité de Comunicaciones y Publicaciones del IDEAM.
- Josse, C., Cuesta, F., Navarro, G., Barrena, V., Chacón-Moreno, E., Ferreira, W., ... Tovar, A. (2009). *Mapa de ecosistemas de los Andes del Norte y Centro, Bolivia, Colombia, Ecuador, Perú, Venezuela*. Lima: Secretaría General de la Comunidad Andina, Programa Regional ECOBONA, CONDESAN-Proyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, LTA-UNALM, IAvH, ICAE-ULA, CDC-UNALM, RUMBOL SRL.
- Luteyn, J. L. (1999). *Paramos: A checklist of plant diversity, geographical distribution and botanical literature* (Vol. 84). New York: The New York Botanical Garden.

Rangel, J. O. (2015). La biodiversidad de Colombia: significado y distribución regional. *Revista de la Academia*

Colombiana de Ciencias Exactas, Físicas y Naturales, 39(151), 176–200.

Sarmiento Pinzón, C. E., Cadena Vargas, C. E., Sarmiento Giraldo, M. V., & Zapata Jiménez, J. A. (2013). *Aportes a la conservación estratégica de los páramos de Colombia: actualización de la cartografía de los complejos de páramo a escala 1:100.000* (Primera edición). Bogotá, D.C., Colombia: Ministerio de Medio Ambiente y Desarrollo Sostenible.

Schubert, C., & Clapperton, C. M. (1990). Quaternary glaciations in the northern Andes (Venezuela, Colombia and Ecuador). *Quaternary Science Reviews*, 9(2–3), 123–135.

Sklenář, P., Dušková, E., & Balslev, H. (2011). Tropical and temperate: Evolutionary history of Páramo flora. *The Botanical Review*, 77(2), 71–108. <https://doi.org/10.1007/s12229-010-9061-9>

Torres, V., Hooghiemstra, H., Lourens, L., & Tzedakis, P. C. (2013). Astronomical tuning of long pollen records reveals the dynamic history of montane biomes and lake levels in the tropical high Andes during the Quaternary. *Quaternary Science Reviews*, 63, 59–72. <https://doi.org/10.1016/j.quascirev.2012.11.004>

SUPPORTING INFORMATION

Appendix S3 | Methodology underlying the use of fossil pollen data to reconstruct the upper forest line changes

Long and continuous records of past climate change of the Pleistocene, in mountains in particular, are rare. Due to a unique combination of subsidence and sediment infill, the intramontane basin of Bogotá, Colombia (4.83°N, 75.2°W; 2550 m a.s.l.) accumulated sediments during most of the Pleistocene (Torres, Hooghiemstra, Lourens, & Tzedakis, 2013). This interval starts with climate change driven by obliquity (41 kyr rhythm) and from ca. 0.9 Ma onwards the eccentricity (100 kyr) driven frequency overrules the obliquity signal, showing the change in glacial-interglacial dynamics after the mid-Pleistocene transition (1-0.9 Ma; Imbrie et al., 1984; Lisiecki & Raymo, 2005).

The upper forest line (UFL) is the transition from the upper montane forest to the páramo, i.e., the uppermost contour of closed forest (Bakker, Moscol Olivera, & Hooghiemstra, 2008), which coincides with the ca. 9.5 °C mean annual temperature (MAT) isotherm (Hooghiemstra, 1984; Groot et al., 2011; Hooghiemstra et al., 2012). Following the reconstructions by Hooghiemstra (1984) and Groot et al. (2011), we assumed that during the last 0.4 Myr, when Oak (*Quercus*) was present, the empirical level of 40% arboreal pollen (AP) concurs with having the UFL at the level of the Bogotá basin (2550 m a.s.l.). For the period after the arrival of Alder (*Alnus*; 1.01 Ma) and before the arrival of Oak (0.43 Ma) a 35% AP level is used. We applied the empirical relationship of 5% increments in AP% as reflecting steps of 100 m UFL displacement following Hooghiemstra (1984). We used a lapse rate of 0.6°C/100 m and an offset of -5.8°C to calculate fluctuations in temperature through time.

In our model, the páramos occupied an elevational range of 1200 m during the Pleistocene (Hooghiemstra, 1984; Groot et al., 2011; Bogotá-Angel et al., 2011; Bogotá-A., Hooghiemstra, & Berrio, 2016; Torres et al. 2013), consisting of subpáramo (ca. 300 m; dominated by shrub), grasspáramo (ca. 700 m; dominated by herbs), and súperparamo where vegetation is limited to the lowermost c. 200 m of the 600 m wide belt (Cleef, 1981). The elevational range above the páramos was assigned to being glaciers representing the extensive ice sheets present in the Northern Andes during colder and humid periods (Helmens, 1990; Schubert & Vivas, 1993; IDEAM, 2012). Páramos and glaciers show an asymmetrical zonation of the vegetation belts between the dry and wet side of the mountain (Cleef, 1981; Schubert & Clapperton, 1990), and also regional differences among cordilleras are observed (Moreno, Andrade, & Ruíz-Contreras, 2017). For instance, the UFL is often located at higher elevations when the mountain range is larger or higher, or along the atmospherically humid side of the mountain (but see the Eastern Cordillera; Van der Hammen & Cleef, 1986). We simplified these regional differences in our models by using the same

elevational gradients for all mountain ranges, as these regional differences are unknown for the past and humans have modified the natural limit of the UFL through high elevation agriculture, afforestation, and reforestation (Bakker et al., 2008).

We assume that during the studied time period the most substantial uplift of the Andes had already occurred (Hughes & Eastwood, 2006; Hoorn et al., 2010; Hazzi, Moreno, Ortiz-Movliav, & Palacio, 2018) meaning that we consider the elevations of the current digital elevation model representative for the last 1 Myr. Additionally, we do not take into account Quaternary sea level changes which would affect the meters above sea level calculation.

REFERENCES

- Bakker, J., Moscol Olivera, M., & Hooghiemstra, H. (2008). Holocene environmental change at the upper forest line in northern Ecuador. *The Holocene*, 18(6), 877–893.
<https://doi.org/10.1177/0959683608093525>
- Bogotá-A., R. G., Hooghiemstra, H., & Berrio, J. C. (2016). North Andean environmental and climatic change at orbital to submillennial time-scales: Vegetation, water-levels and sedimentary regimes from Lake Fúquene between 284 and 130ka. *Review of Palaeobotany and Palynology*, 226, 91–107. <https://doi.org/10.1016/j.revpalbo.2015.09.007>
- Bogotá-Angel, R. G., Groot, M. H. M., Hooghiemstra, H., Lourens, L. J., Van der Linden, M., & Berrio, J. C. (2011). Rapid climate change from north Andean Lake Fúquene pollen records driven by obliquity: implications for a basin-wide biostratigraphic zonation for the last 284 ka. *Quaternary Science Reviews*, 30(23–24), 3321–3337. <https://doi.org/10.1016/j.quascirev.2011.08.003>
- Cleef, A. M. (1981). *The vegetation of the páramos of the Colombian Cordillera Oriental*. J Cramer, Vaduz. Retrieved from <http://repository.naturalis.nl/record/534752>
- Groot, M. H. M., Bogotá, R. G., Lourens, L. J., Hooghiemstra, H., Vriend, M., Berrio, J. C., ... Westerhoff, W. (2011). Ultra-high resolution pollen record from the northern Andes reveals rapid

shifts in montane climates within the last two glacial cycles. *Clim. Past*, 7(1), 299–316.

<https://doi.org/10.5194/cp-7-299-2011>

Hazzi, N. A., Moreno, J. S., Ortiz-Movliav, C., & Palacio, R. D. (2018). Biogeographic regions and events

of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the*

National Academy of Sciences, 115(31), 7985–7990. <https://doi.org/10.1073/pnas.1803908115>

Helmens, K. F. (1990). *Neogene-Quaternary geology of the High plain of Bogotá, Eastern Cordillera, Colombia (stratigraphy, paleoenvironments and landscape evolution)*. Berlin: J Cramer.

Hooghiemstra, H. (1984). *Vegetational and climatic history of the high plain of Bogotá, Colombia*.

(Dissertationes Botanicae, Vol. 79). J. Cramer, Vaduz.

Hooghiemstra, H., Berrio, J. C., Groot, M. H. M., Bogotá-A, R. G., Olivera, M. M., & González-Carranza,

Z. (2012). The dynamic history of the upper forest line ecotone in the Northern Andes. In R. W.

Myster (Ed.), *Ecotones Between Forest and Grassland* (pp. 229–246). Springer New York.

Hoorn, C., Wesselingh, F. P., Steege, H. ter, Bermudez, M. A., Mora, A., Sevink, J., ... Antonelli, A.

(2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and

biodiversity. *Science*, 330(6006), 927–931. <https://doi.org/10.1126/science.1194585>

Hughes, C., & Eastwood, R. (2006). Island radiation on a continental scale: Exceptional rates of plant

diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences*,

103(27), 10334–10339. <https://doi.org/10.1073/pnas.0601928103>

IDEAM. (2012). *Glacieres de Colombia, más que montañas con hielo*. Bogotá, Colombia: Comité de

Comunicaciones y Publicaciones del IDEAM.

Imbrie, J., Hays, J. D., Martinson, D. G., McIntyre, A., Mix, A. C., Morley, J. J., ... Shackleton, N. J.

(1984). The orbital theory of Pleistocene climate: support from a revised chronology of the marine

$\delta^{18}\text{O}$ record. In A. L. Berger, J. Imbrie, J. Hays, G. Kukla, B. Saltzman, & D. Reidel (Eds.),

Milankovitch and climate (pp. 269–305).

Lisiecki, L. E., & Raymo, M. E. (2005). A Pliocene-Pleistocene stack of 57 globally distributed benthic

$\delta^{18}\text{O}$ records. *Paleoceanography*, 20(1), PA1003. <https://doi.org/10.1029/2004PA001071>

Moreno, L. A., Andrade, G. I., & Ruíz-Contreras, L. F. (2017). *BIODIVERSITY 2016. Status and trends of Colombian continental biodiversity*. Bogotá, Colombia: Research Institute of Biological Resources Alexander von Humboldt.

Schubert, C., & Clapperton, C. M. (1990). Quaternary glaciations in the northern Andes (Venezuela, Colombia and Ecuador). *Quaternary Science Reviews*, 9(2–3), 123–135.

Schubert, C., & Vivas, L. (1993). *El Cuaternario de la Cordillera de Mérida - Andes Venezolanos*. Mérida, Venezuela: Universidad de Los Andes / Fundación Polar.

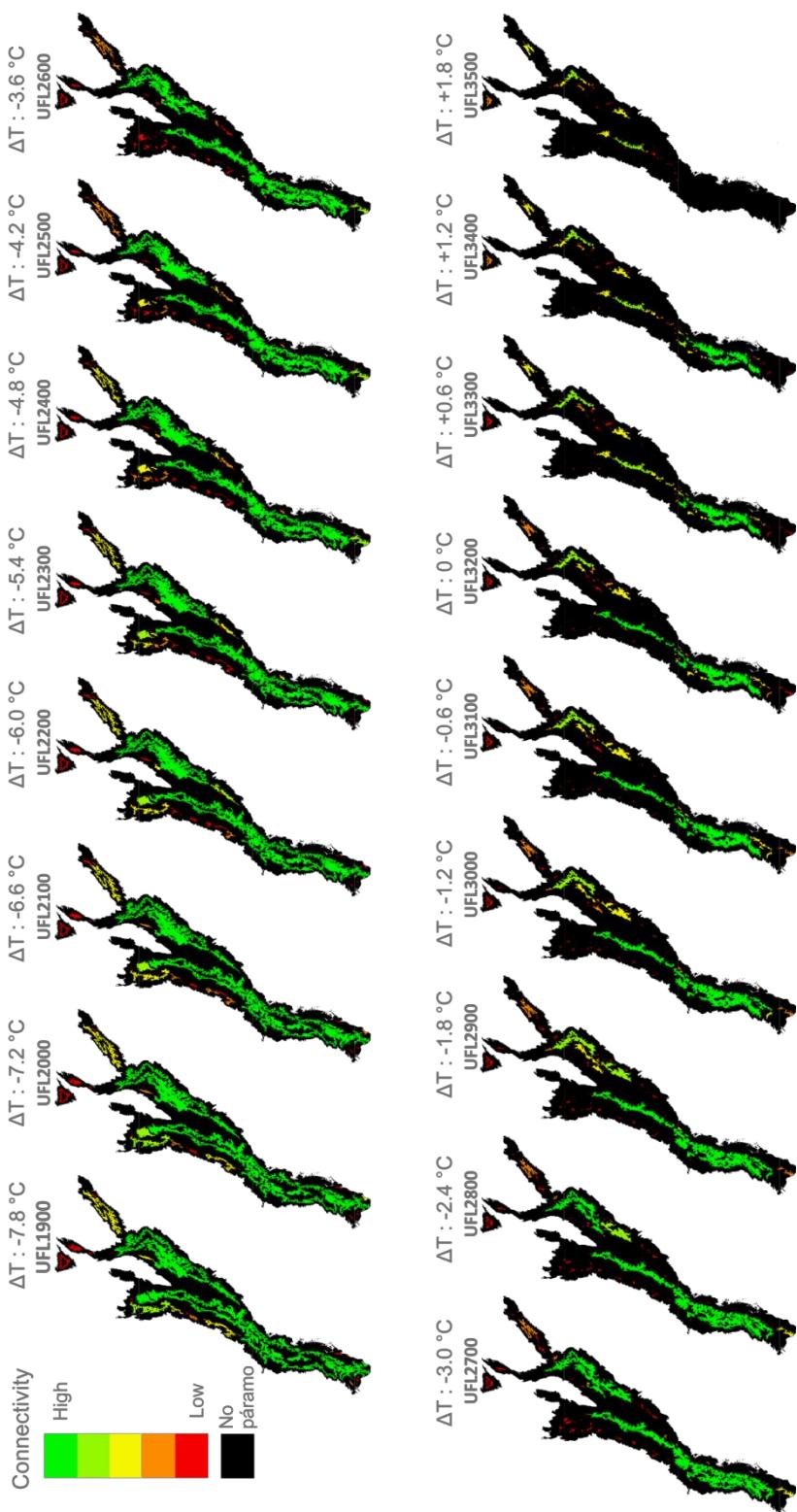
Torres, V., Hooghiemstra, H., Lourens, L., & Tzedakis, P. C. (2013). Astronomical tuning of long pollen records reveals the dynamic history of montane biomes and lake levels in the tropical high Andes during the Quaternary. *Quaternary Science Reviews*, 63, 59–72.

<https://doi.org/10.1016/j.quascirev.2012.11.004>

Van der Hammen, T., & Cleef, A. M. (1986). Development of the high Andean páramo flora and vegetation. In F. Vuilleumier & M. Monasterio (Eds.), *High altitude tropical biogeography* (pp. 153–201). New York: Oxford University Press.

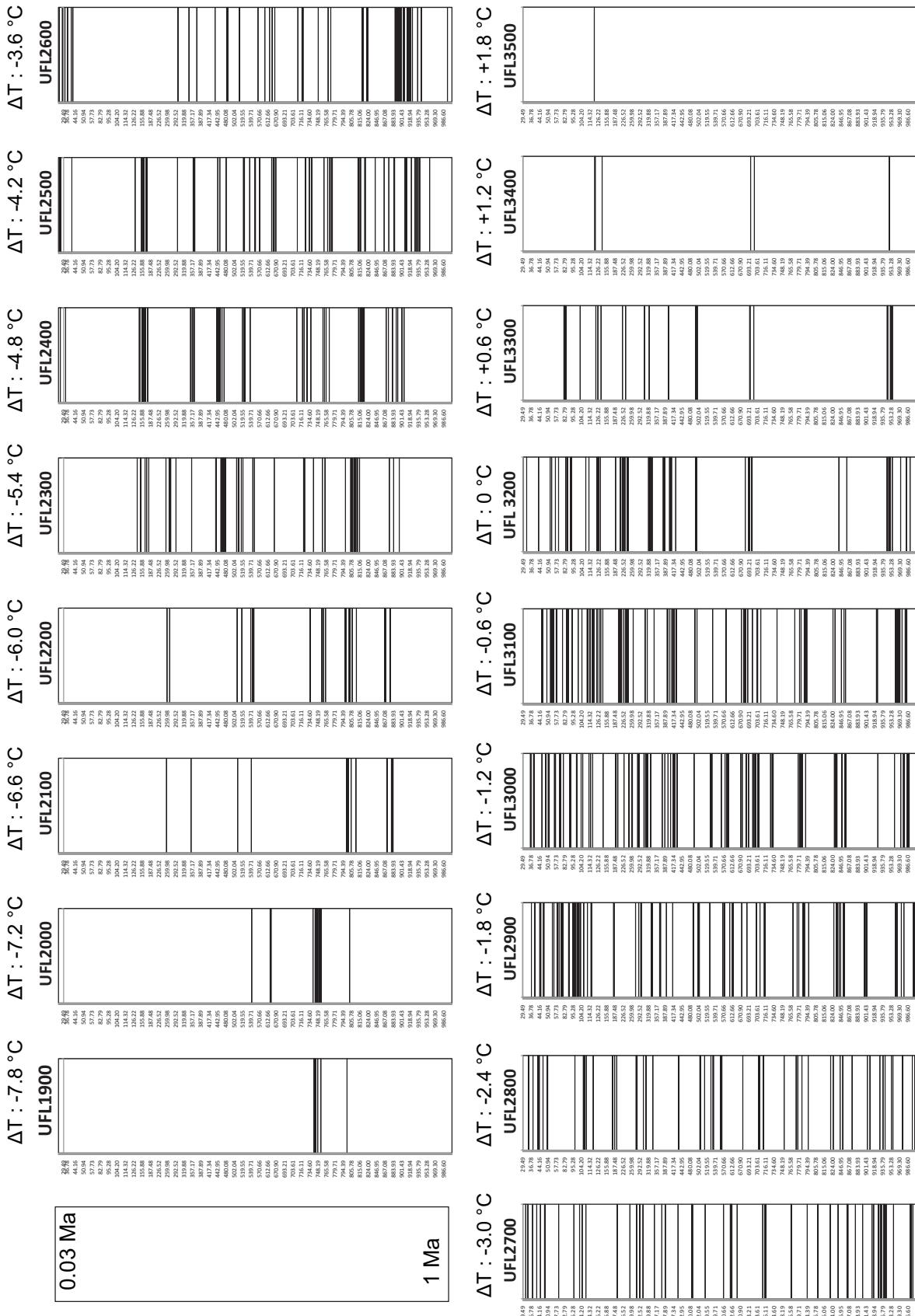
SUPPORTING INFORMATION

Appendix 4 | Degree of connectivity of páramos at all Upper Forest Line (UFL) elevations during the last 1 Myr



SUPPORTING INFORMATION

Appendix 5 | Frequency analysis of all upper forest line (UFL) elevations during the last 1 Myr



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Appendix 6 | Visualization of the flickering connectivity system in the Northern Andes.

The flickering connectivity system is visualized in the form of a 3D animation and photography film, using CINEMA 4D, ADOBE AFTER EFFECTS and ADOBE PREMIER PRO. The visualization was created by Catalina Giraldo as Master student in Arts in Media Design and Communication at the Piet Zwart Institute, Rotterdam University of Applied Sciences, and in collaboration with Suzette G.A. Flantua and Henry Hooghiemstra at the Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam.

Please follow the following link to access the video (ca. 1.1GB size):

https://figshare.com/articles/Appendix_6_Visualization_of_the_flickering_connectivity_system_in_the_Northern_Andes/7408643

SUPPORTING INFORMATION

Appendix S7 | Further suggestions for future work

Inherent to any model in mountains and concerning connectivity are simplifications of the temporal and spatial complexity of the real world. For instance, the upper forest line (UFL) is asymmetric on wet and dry mountain slopes (e.g. Cleef, 1981), the current elevation of the UFL shows a range of variation of ca. 200 m (incidentally to 300 m), surface processes have changed topography on a million years time-scale (Herman et al., 2013; Antonelli et al., 2018), the elevational temperature gradient (lapse rate) seems higher during glacial conditions than at present ((Wille, Hooghiemstra, Behling, van der Borg, & Negret, 2001; Loomis et al., 2017), and the current subdivision of páramo vegetation into a 300 m : 600 m : 200 m interval for shrubpáramo, grasspáramo, and superpáramo, respectively, is subject to change (Van der Hammen, 1981; Hooghiemstra, 1984), potentially related to changing atmospheric pCO₂ levels (Boom, Mora, Cleef, & Hooghiemstra, 2001; Boom, Marchant, Hooghiemstra, & Sinninghe Damsté, 2002). We estimate the potential impact of these factors on the estimated connectivity of little significance in determining the overall patterns observed in the flickering connectivity systems but future models should assess such regional differences.

Any study concerning connectivity requires a number of assumptions on the probability of dispersal through the landscape. Here, we used a generalized PC value of 0.5 at 10 km to estimate the degree of connectivity. However, species traits, life histories and dispersal capacities may strongly influence dispersal distances (Onstein et al., 2017), and thus influence the probability of connectivity between populations. Implementing taxon-specific traits when calculating the landscape resistance grid (see Methodology) may thus improve the accuracy of the connectivity estimates. Also, family or taxa specific connectivity maps could uncover why certain plant genera do not show any evolutionary diversification during the Pleistocene, e.g. *Distichia* (Juncaceae; Colin Hughes, personal comm.) and *Arcytophyllum* (Rubiaceae; Madriñán, Cortés, & Richardson, 2013). Additionally, *a priori* "hard" barriers can be imposed to emphasize areas where habitat connectivity is unlikely to have occurred (see for instance how we maintained SNSM isolated from the other mountain ranges). Defining these barriers *a priori* is not indispensable, though, as the connectivity analysis hints at strong dispersal restrictions when resistance values of corridors are high and indicative of highly constrained dispersal. In the Northern Andes, this is shown by the multiple single line corridors between the Central and Eastern Cordillera, confirmed by the lack of gene flow between plant populations of these regions (Jabaily & Sytsma, 2013; (Diazgranados & Barber, 2017; Contreras-Ortiz, Atchison, Hughes, & Madriñán, 2018). This example illustrates the added

value of integrating different lines of evidence (e.g. genetic, fossil, paleoclimate) in a spatial and temporal context to understand the biogeographical patterns observed in phylogeographic studies.

Future work would ideally incorporate regional differences in paleoclimate as our model was based on only one paleotemperature curve. However, though fossil pollen records in the Andes are numerous, long fossil pollen records similar to Funza09 are currently not available (Flantua et al., 2015). We recommend the acquisition of more long pollen records in different parts of the Andes, not only to improve our models, but also provide better understanding of climatic and biotic changes in this biologically-important part of the world. To implement the methodology developed in this paper to other mountainous regions, one of the key constraints consists of the scarcity of continuous fossil pollen sequences in mountain areas that cover the Quaternary. Potential locations, which could provide similar results to the Bogotá basin where Funza09 was derived from, are likely in the African Rift Valley. However, drilling costs have prevented initiatives to be realized. While paleoclimate reconstructions based on computer climate models are in rapid development, and could be of use for exploring the generality of patterns observed here, they are currently restricted to selected periods in time: the Last Glacial Maximum, last interglacial and the mid-Holocene and show substantial underestimation of glacial cooling in mountainous areas (Bush & Philander, 1999; Loomis et al., 2017). An alternative to using fossil pollen records and paleoclimate reconstructions is the recent development of paleoclimate emulators, such as by Holden et al. (2018) and Rangel et al. (2018), and a comparison with the paleotemperature curve developed in this paper could be valuable validation. When the step of the paleoclimate reconstruction can be overcome, we regard the alpine flora of the temperate mountains of the Alps and the equatorial mountains of East Africa and New Guinea to be suitable to be compared to the Northern Andes due to the ‘sky island’ arrangement, topography and known influence of the Pleistocene changes on the alpine flora (Sklenář, Hedberg, & Cleef, 2014). Assessing the smaller mountain ranges that compose a large mountain system, such as the Tibeto-Himalayan region (Muellner-Riehl, 2019), can benefit the identification of the different patterns of past connectivity within a system (see Fig. 6). Also, the flickering connectivity system is modelled based on temperature-change-driven vegetation dynamics as a vertical process and the African Rift Valley, New Guinea Mountains, and the wet parts of the Himalaya could resemble such dynamics. However, outside the tropics, and mountains located in the interior of continents where changes in climatic humidity are increasingly important (e.g. Zagros Mountains, interior parts of the Himalaya), the flickering connectivity system as presented here may function less precise.

In summary, future models of the flickering connectivity system in the Northern Andes could assess the importance of regional differences in i) the elevational gradient of páramos and glaciers as they show an asymmetrical zonation of the vegetation belts between the dry and wet side of the mountain, ii) the atmospherically humid side of mountains (see Appendix S3). Both of them are influenced by complex topography of the Northern Andes and the climatic variability through time in terms of humidity influxes (Flantua et al., 2016), but how these changed during the Pleistocene is still poorly understood. iii) model connectivity based on specific species traits and test hypotheses using different dispersal probabilities.

REFERENCES

- Antonelli, A., Kissling, W. D., Flantua, S. G. A., Bermúdez, M. A., Mulch, A., Muellner-Riehl, A. N., ...
- Hoorn, C. (2018). Geological and climatic influences on mountain biodiversity. *Nature Geoscience*, 11(10), 718–725. <https://doi.org/10.1038/s41561-018-0236-z>
- Boom, A., Marchant, R., Hooghiemstra, H., & Sinninghe Damsté, J. S. (2002). CO₂- and temperature-controlled altitudinal shifts of C4- and C3-dominated grasslands allow reconstruction of palaeoatmospheric pCO₂. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 177, 151–168.
- Boom, A., Mora, G., Cleef, A. M., & Hooghiemstra, H. (2001). High Altitude C4 grasslands in the northern Andes: Relicts from glacial conditions? *Review of Palaeobotany and Palynology*, 115, 147–160.
- Bush, A. B. G., & Philander, S. G. H. (1999). The climate of the Last Glacial Maximum: Results from a coupled atmosphere-ocean general circulation model. *Journal of Geophysical Research: Atmospheres*, 104(D20), 24509–24525. <https://doi.org/10.1029/1999JD900447>
- Cleef, A. M. (1981). *The vegetation of the páramos of the Colombian Cordillera Oriental* (J Cramer). Retrieved from <http://repository.naturalis.nl/record/534752>
- Contreras-Ortiz, N., Atchison, G. W., Hughes, C. E., & Madriñán, S. (2018). Convergent evolution of high elevation plant growth forms and geographically structured variation in Andean Lupinus (Fabaceae). *Botanical Journal of the Linnean Society*, 187(1), 118–136. <https://doi.org/10.1093/botlinnean/box095>

- Diazgranados, M., & Barber, J. C. (2017). Geography shapes the phylogeny of frailejones (Espeletiinae Cuatrec., Asteraceae): a remarkable example of recent rapid radiation in sky islands. *PeerJ*, 5, e2968. <https://doi.org/10.7717/peerj.2968>
- Flantua, S. G. A., Hooghiemstra, H., Vuille, M., Behling, H., Carson, J. F., Gosling, W. D., ... González-Arango, C. (2016). Climate variability and human impact in South America during the last 2000 years: synthesis and perspectives from pollen records. *Climate of the Past*, 12(2), 483–523. <https://doi.org/10.5194/cp-12-483-2016>
- Flantua, S. G. A., Hooghiemstra, H., Grimm, E. C., Behling, H., Bush, M. B., González-Arango, C., ... Van Boxel, J. H. (2015). Updated site compilation of the Latin American Pollen Database. *Review of Palaeobotany and Palynology*, 223, 104–115. <https://doi.org/10.1016/j.revpalbo.2015.09.008>
- Herman, F., Seward, D., Valla, P. G., Carter, A., Kohn, B., Willett, S. D., & Ehlers, T. A. (2013). Worldwide acceleration of mountain erosion under a cooling climate. *Nature*, 504(7480), 423–426. <https://doi.org/10.1038/nature12877>
- Holden, P. B., Edwards, N. R., Rangel, T. F., Pereira, E. B., Tran, G. T., & Wilkinson, R. D. (2018). PALEO-PGEM v1.0: A statistical emulator of Pliocene-Pleistocene climate. *Geoscientific Model Development Discussions*, 1–26. <https://doi.org/10.5194/gmd-2018-242>
- Hooghiemstra, H. (1984). *Vegetational and climatic history of the high plain of Bogotá, Colombia*. (Dissertationes Botanicae).
- Jabaily, R. S., & Sytsma, K. J. (2013). Historical biogeography and life-history evolution of Andean Puya (Bromeliaceae). *Botanical Journal of the Linnean Society*, 171(1), 201–224. <https://doi.org/10.1111/j.1095-8339.2012.01307.x>
- Loomis, S. E., Russell, J. M., Verschuren, D., Morrill, C., Cort, G. D., Damsté, J. S. S., ... Kelly, M. A. (2017). The tropical lapse rate steepened during the Last Glacial Maximum. *Science Advances*, 3(1), e1600815. <https://doi.org/10.1126/sciadv.1600815>
- Madriñán, S., Cortés, A. J., & Richardson, J. E. (2013). Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Frontiers in Genetics*, 4. <https://doi.org/10.3389/fgene.2013.00192>

- Muellner-Riehl, A. N. (2019). Mountains as evolutionary arenas: Patterns, emerging approaches, paradigm shifts, and their implications for plant phylogeographic research in the Tibeto-Himalayan region. *Frontiers in Plant Science*, 10(195). <https://doi.org/10.3389/fpls.2019.00195>
- Onstein, R. E., Baker, W. J., Couvreur, T. L. P., Faurby, S., Svenning, J.-C., & Kissling, W. D. (2017). Frugivory-related traits promote speciation of tropical palms. *Nature Ecology & Evolution*, 1(12), 1903. <https://doi.org/10.1038/s41559-017-0348-7>
- Rangel, T. F., Edwards, N. R., Holden, P. B., Diniz-Filho, J. A. F., Gosling, W. D., Coelho, M. T. P., ... Colwell, R. K. (2018). Modeling the ecology and evolution of biodiversity: Biogeographical cradles, museums, and graves. *Science*, 361(6399), eaar5452. <https://doi.org/10.1126/science.aar5452>
- Sklenář, P., Hedberg, I., & Cleef, A. M. (2014). Island biogeography of tropical alpine floras. *Journal of Biogeography*, 41(2), 287–297. <https://doi.org/10.1111/jbi.12212>
- Van der Hammen, T. (1981). Glaciales y glaciaciones en el cuaternario de Colombia: paleoecología y estratigrafía. *Revista CIAF*, 6(1–3), 635–638.
- Wille, M., Hooghiemstra, H., Behling, H., van der Borg, K., & Negret, A. J. (2001). Environmental change in the Colombian subandean forest belt from 8 pollen records: the last 50 kyr. *Vegetation History and Archaeobotany*, 10(2), 61–77.