

1 **TITLS: The flickering connectivity system of the north Andean páramos**

2 **SHORT RUNNING TITLE: Andean flickering connectivity since 1 Ma**

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26 the Northern Andes and Francisco Cuesta for facilitating the map by Josse et al. (2009).

27 **ABSTRACT AND KEYWORDS**

28 **Aim** To quantify the effect of Pleistocene climate fluctuations on habitat connectivity across páramos in
29 the Neotropics.

30 **Location** The Northern Andes

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

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

45 **Main conclusions** Pleistocene climate change was the driver of significant elevational and spatial shifts in
46 páramos causing dynamic changes in habitat connectivity across and within all mountain ranges. Some
47 generalities emerge, including the fact that connectivity was greatest during the most ephemeral of times.
48 However, the timing, duration and degree of connectivity varied substantially among mountain ranges
49 depending on their topographic configuration. The flickering connectivity system of the páramos uncovers
50 the dynamic settings in which evolutionary radiations shaped the most diverse alpine biome on Earth.

51 **Keywords (6-10):** alpine biome, evolutionary radiations, flickering connectivity system, fossil pollen,
52 mountain fingerprint, Neotropical biodiversity, páramos, paleotemperature, past habitat connectivity,
53 species pump

54

55 MAIN TEXT

56 1. INTRODUCTION

57 Mountains are regarded as powerhouses of biodiversity in the world (Barthlott, Rafiqpoor, Kier, & Kreft,
58 2005; Kreft & Jetz, 2007; Antonelli et al., 2018) and harbour numerous examples of very rapid and recent
59 species diversifications ('radiations'; Hughes & Atchison, 2015). It is thought that a large part of this
60 diversity arose geologically recently, during the Plio-Pleistocene (last 5.3 million years, [Ma]), but there is
61 no consensus on the drivers of these radiations. One favoured hypothesis is that the combination of high
62 topographic relief and Plio-Pleistocene climatic oscillations led to rapidly changing distributions of
63 montane species, which generated new lineages (e.g. Qian & Ricklefs, 2000; Graham et al., 2014; Mutke,
64 Jacobs, Meyers, Henning, & Weigend, 2014). However, the relative contributions of isolation (e.g.
65 Schönswetter, Stehlik, Holderegger, & Tribsch, 2005; Wallis, Waters, Upton, & Craw, 2016; Weir,
66 Haddrath, Robertson, Colbourne, & Baker, 2016) vs. gene flow and dispersal (e.g. Smith et al., 2014;
67 Cadena, Pedraza, & Brumfield, 2016; Kolář, Dušková, & Sklenář, 2016; Knowles & Massatti, 2017) in
68 driving fast diversification rates (i.e. the 'species-pump' effect, Rull, 2005; Rull & Nogué, 2007;
69 Winkworth, Wagstaff, Glenney, & Lockhart, 2005; Ramírez-Barahona & Eguiarte, 2013; Steinbauer et al.,
70 2016; Flantua & Hooghiemstra, 2018) are still debated. It is likely that these radiations have been the
71 results of the interchange between phases of isolation, causing allopatric, *in situ* speciation, and
72 connectivity, triggering diversification through dispersal and settlement in new areas and hybridization of
73 differentiated taxa from previously isolated populations (Flantua & Hooghiemstra, 2018). The fastest and
74 most spectacular radiations may therefore occur in mountain regions with variable degrees of past
75 connectivity and isolation during climate fluctuations, which, complex in space and time, are inherently
76 related to the mountain topography (Flantua & Hooghiemstra, 2018). It is therefore critical to quantify
77 connectivity of montane habitats using our understanding of topography and past climate fluctuations
78 **(Fig. 1)**.

79 The Northern Andes is an ideal model system to quantify connectivity, due to the large variation in
80 topography and the advanced paleoecological knowledge on Plio-Pleistocene climate fluctuations derived
81 during the last five decades (Hooghiemstra & Flantua, 2019). The Northern Andes is topographically-rich
82 with high elevations, steep ridges and valleys (see illustrations by Von Humboldt during his trips in Latin
83 America, 1773-1858), composed of several mountain ranges, some of which are parallel running from
84 North to South. The area hosts the treeless tundra-like alpine biome, the páramos, regarded the richest
85 alpine flora in the world in terms of endemism and species richness (Sklenář, Hedberg, & Cleef, 2014)
86 and is known for its bursts of Plio-Pleistocene species diversification amongst plants (see overview in

87 Hughes & Atchison, 2015). In terms of quantifying Plio-Pleistocene temperature fluctuations, the
88 palaeoecological history of the páramos has been studied extensively (e.g. Van der Hammen, 1974; Cleef,
89 1979; Hooghiemstra, 1984; Hooghiemstra & Van der Hammen, 2004) because of the unique high
90 elevation fossil pollen records that cover most of the Pleistocene (Groot et al., 2011; Groot, Hooghiemstra,
91 Berrio, & Giraldo, 2013; Bogotá-Angel et al., 2011; Bogotá-A., Hooghiemstra, & Berrio, 2016; Torres,
92 Hooghiemstra, Lourens, & Tzedakis, 2013). Under current conditions, the páramos form isolated
93 archipelagos of alpine (sky) islands (McCormack, Huang, & Knowles, 2009) but the rich collection of
94 fossil pollen sequences throughout this region (Flantua et al., 2015) show that the páramos underwent
95 substantial elevational shifts during the Pleistocene, resulting in extensive changes in surface area and
96 connectivity (Van der Hammen, 1974; Hooghiemstra & Van der Hammen, 2004; Flantua et al., 2014;
97 Sklenář et al., 2014). Thus, the topographic diversity and the robust catalogue of palaeoecological
98 reconstructions make the Northern Andes a highly suitable model region to explore patterns of
99 connectivity in mountain biomes in response to Pleistocene climate fluctuations.

100 In this study, we aim to quantify the biogeographic changes of the páramos in terms of spatial scale and
101 connectivity based on modern topography and pollen-based records of past climate change. Specifically,
102 we developed a novel tool to explore the complex temporal and spatial patterns of páramo connectivity.
103 We constrain our model by using the last 1 Myr of the high-resolution fossil pollen record of Funza09, a
104 586 m deep core taken from the Bogotá basin of Colombia (Torres et al., 2013). Available surface area
105 (Elsen & Tingley, 2015) and connectivity (Flantua et al., 2014; Bertuzzo et al., 2016) is variable along
106 elevational gradients of mountains. We therefore hypothesize that the different mountain ranges that
107 compose the Northern Andes display variable patterns of past páramo connectivity dependent upon their
108 topography (**Fig. 1**). We discuss the implications of our outcomes for evolutionary processes and how
109 defining and quantifying past connectivity in mountain systems is essential to help reveal mechanisms of
110 ecological, biogeographical and evolutionary change. Ultimately, our quantification of páramo
111 connectivity through space and time provides a unique opportunity to disentangle some of the mechanistic
112 drivers ('modulators') of radiations in this biome (Bouchenak-Khelladi, Onstein, Xing, Schwery, &
113 Linder, 2015).

114

115 **2. METHODS**

116 **2.1 Geographical features**

117 The Northern Andes (ca. 448.000 km²) covers parts of Venezuela, Colombia and Ecuador (**Fig. 2a**), and

118 can be partitioned into six principal mountain ranges or 'cordilleras' (**Fig. 2c**), namely the Sierra Nevada
119 de Santa Marta (SNSM), Cordillera de Mérida, Eastern, Central and Western Cordillera and the
120 Ecuadorian Cordilleras. Most of the Northern Andes is considered a highly to extremely high rugged
121 landscape (**Fig. 2b**; See mountain illustrations by Von Humboldt (1845) where the high peaks and deep
122 inter-Andean valleys cause strong contrasts in climate throughout the region (Flantua et al., 2016). Surface
123 area in mountains does not decrease monotonically with elevation as has been shown previously in
124 southern Colombia by Flantua et al. (2014) and on a global scale by Elsen & Tingley (2015). The
125 Northern Andes shows a decrease of surface area going upslope where there is a slight peak around 900-
126 1200 m asl but then continues to decrease up to 6260 m asl (**Fig. 2d**), following a typical 'pyramid shape'.
127 However, the different cordilleras show different patterns of elevational surface area (**Fig. 2d**) where the
128 Eastern Cordillera shows a sharp peak around 2600 m asl and the Ecuadorian Cordillera shows high
129 values of surface area at much higher elevations than the other cordilleras (**for more details see Table**
130 **S1.1, Appendix S1 in Supporting Information**). Of all tropical alpine floras, such as in East Africa and
131 New Guinea, the páramos are home to the highest species richness and endemism (Luteyn, 1999; Sklenář,
132 Dušková, & Balslev, 2011), with low between-mountain similarity in species; (Sklenář et al., 2014). The
133 páramos today are spread out over the Northern Andes as an archipelago of small and highly fragmented
134 páramo complexes (**Figure S2.1, Appendix S2**).

135

136 **2.2 Quantifying temperature and upper forest line based on fossil pollen data**

137 To quantify temperature fluctuations during the Pleistocene (and consequently estimate páramo
138 connectivity), we used fossil pollen data from the Northern Andes. The composite pollen record Funza09
139 (4.83°N, 75.2°W; 2550 m asl, **Fig. S2.1. Red star**) reveals vegetation and climate dynamics over the past
140 2.25 Myr (Torres et al., 2013). We reconstructed the páramos' elevational fluctuations, and consequently
141 páramo connectivity, by estimating the upper forest line (the transition from the upper montane forest to
142 the páramos; UFL) from the Funza09 record. Though this record covers the last 2.2 Myr, we only used the
143 last 1 Myr as this interval reflects continuous lake conditions in comparison with variable hydrological
144 conditions between 2.2-1 Ma which obscure the quantification of changes to the UFL. We follow the
145 methodology described and implemented by Hooghiemstra (1984), Groot et al. (2011), and Hooghiemstra
146 et al. (2012) to derive the Andean UFL and paleotemperature curve (for detailed methodology on the UFL
147 reconstruction see **Appendix S3**)

148

149 **2.3 Calculations of connectivity per páramo “island”**

150 To calculate the degree of connectivity between páramos, we used a graph-based habitat availability index
151 called probability of connectivity (PC) metric. This metric takes into account the area of the páramo
152 "island" itself and the distances to other islands where a user-defined distance threshold defines the
153 ‘reachability’ of other islands (Saura & Pascual-Hortal, 2007; Saura, Estreguil, Mouton, & Rodríguez-
154 Freire, 2011), even if they are not physically connected (i.e. ‘structural connectivity’, Tischendorf &
155 Fahrig, 2000). The metric assigns a value to each páramo island representing its contribution in
156 maintaining the overall connectivity of the páramo biome (Saura & Pascual-Hortal, 2007; Saura et al.,
157 2011). The total PC is built up in three ‘fractions’, namely the ‘intrapatch’, the ‘flux’, and the ‘connector’
158 fractions (Saura & Rubio, 2010). The first fraction focusses on the available surface area and habitat
159 quality (if applicable) within the individual island. The second fraction assesses how well the individual
160 island is connected to other islands given additional importance to the other islands’ attributes (surface and
161 quality) and its strategic position to other páramo islands. The third fraction quantifies the contribution of
162 the island to maintain connectivity between the rest of the islands, in other words its role as an
163 intermediate stepping stone between non-adjacent islands. Additionally, we calculated the equivalent
164 connected area (ECA), which is derived directly from the PC, as a measure of the overall connectivity of a
165 region (Saura et al., 2011). Conefor Sensinode 2.2 software and ESRI ArcGIS 10.3 were used to calculate
166 the straight-line distances between islands, the PC and ECA (Saura & Pascual-Hortal, 2007; Saura &
167 Torné, 2009). We calculated connectivity for the entire Northern Andes and for each mountain range
168 separately.

169

170 **2.4 Calculations of corridors between páramo islands**

171 We identified corridors between páramo islands within and between cordilleras under different climatic
172 conditions. We used the Gnarly Landscape Utilities (V0.1.3; McRae, Shirk, & Platt, 2013) with ESRI
173 ArcGIS 10.3 to create a raster grid of 'landscape resistance' based on ruggedness (**Fig. 2b**) and habitat
174 suitability. We assumed an increased landscape resistance with increased ruggedness, assigning values
175 between 0 (no resistance) to 100 (maximum resistance) using an equal interval classification. For the
176 habitat suitability map, we started by assigning a “perfectly suitable” score of 100 to each páramo island,
177 while outside the island the score of 0 reflects maximum unsuitability. To soften this boundary, an
178 exponential decay function was then used by increasing resistance in 5 elevational steps of 100 m where
179 we assigned a suitability score of 40 to the boundary of the páramo. As a result of the decay function the
180 highest suitability of páramo - its core area - was restrained 200 m above the UFL and 200 m below the

181 snowline.

182 We used Linkage mapper to calculate the least-cost pathways, or corridors, based on the produced raster
183 grid of landscape resistance (McRae & Kavanagh, 2011). These corridors are expressed as ‘conductance
184 maps’ that represent gradients of cumulative corridors. Where the densities of corridors is highest, it is
185 assumed that there is a high probability of dispersal and migration possible between islands (McRae,
186 Dickson, Keitt, & Shah, 2008). The full landscape of the Northern Andes is considered an area where
187 corridors could exist, with exception of the region between SNSM and the Sierra de Perijá (**Fig. S2.1**).

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

195

196 **3. RESULTS**

197 **3.1 A million years of temperature fluctuations**

198 Temperatures at Funza (2550 masl) are estimated to have fluctuated between ca. 15 and 6°C causing an
199 estimated maximum 1600 m elevational shift of the UFL between ca. 3500 and ca. 1900 m asl (**Fig. 3**).
200 The Pleistocene glacial-interglacial dynamics were not replicated cycles of temperature change showing
201 repeated patterns of high and lows, but display a high temporal variability between each glacial-
202 interglacial cycle. Conditions similar to the current warm, interglacial conditions occurred several times
203 during the last 1 Myr and accounted for around a quarter of the time. Extreme cool glacial conditions, ~ 6
204 - 8°C cooler than today, were relatively rare, occurring less than 10 percent of the time. On the whole,
205 intermediate cool stadials and mild interstadials dominated the last 1 Myr, occurring over two thirds of the
206 time.

207

208

209

210 **3.2 Calculations of páramo connectivity**

211 Our estimations on the spatial and elevational extent of ancient páramos and their connectedness at
212 different times in the past reveals that páramos underwent frequent spatial alterations between fragmented
213 and connected spatial configurations, but the exact patterns were highly dependent on mountain chain
214 topography (**Fig. 4a,b. See Appendices 4 and 5**). The páramos in the Ecuadorian Cordillera generally
215 maintained a high degree of connectivity over the last 1 Myr, rarely enduring severe fragmentation.
216 Fragmentation did however occur when the snowline plunged significantly during colder and wetter
217 glacial periods, causing a break up of páramo areas on lateral flanks of the mountains. Likewise, the level
218 of connectivity between páramos on the Central Cordillera fragmented substantially through a descending
219 snowline, breaking the upper elevation limit of páramo connectivity. In contrast, the Eastern Cordillera
220 shifted substantially between periods of connectivity and fragmentation, always, however, maintaining
221 two large páramo islands surrounded by smaller ‘satellite islands’. Páramos in the Cordillera de Mérida
222 seem to have been restricted during interglacials to one core area only, while during colder periods a
223 relatively high fragmentation is observed possibly due to glaciers pushing páramos to lateral distributions.
224 Here connectivity increased mainly towards the southwest and during colder periods ($UFL \leq 2300$ m asl).
225 The páramos of the SNSM and the Western Cordillera endured the highest degree of rates of change in
226 fragmentation of all ranges. In the latter, páramo habitats are estimated to have often completely
227 disappeared. In contrast, páramos of the Central Cordillera maintained a long latitudinal distribution,
228 forming a chain of isolated populations in small patches that on the whole remained connected. Even in
229 very cold conditions, no continuous connectivity of core areas seems to have been possible between the
230 Eastern Cordillera and Cordillera de Mérida, or the region of Sierra de Perijá. Towards the south of the
231 Eastern Cordillera a low-elevation barrier was possibly crossed at 1900 m asl forming a brief bridge
232 suitable for páramo habitat into the Macizo Colombiano of the Central Cordillera.

233 The reconstruction of putative corridors shows a complex spatial pattern through the mountainous
234 landscapes of the Northern Andes (**Fig. 4c,d**). The long ridge of the Central Cordillera forms the starting
235 point of numerous corridors to the páramos in the Western Cordillera. The Eastern Cordillera shows a
236 complex internal pattern of corridors, where there are neither strong corridors towards Sierra de Perijá in
237 the North, nor towards the Cordillera de Mérida, while a high concentration of corridors is found between
238 the large páramos complexes in the Eastern Cordillera (Páramos of Boyacá and Cundinamarca, **Fig. 1**). In
239 the Ecuadorian Cordillera a more lateral pattern of high/low potential corridors is observed following the
240 intra-Andean valleys and peaks within this mountain range. Corridors to the southernmost páramos of
241 Ecuador as also the northernmost páramos of the Western Cordillera are weak and occurred infrequent
242 during the last million years, shown by the thin lines.

243 **3.3 Flickering connectivity systems**

244 Páramo connectivity through time shows a highly variable pattern (**Fig. 5.a**) introduced by Flantua &
245 Hooghiemstra (2018) as a flickering connectivity system (see **visualization in Appendix S6**). We find
246 support for the hypothesis that this system with fluctuating, highly variable connectivity in spatial and
247 temporal dimension is unique for each mountain range of the Northern Andes (**Fig. 1**). For example,
248 changes in connectivity within the Ecuador Cordillera are substantial but the system ‘flickers’ around a
249 high average when compared to other mountain ranges. The flickering connectivity systems within the
250 Eastern and Central Cordillera are surprisingly similar, though the peaks of connectivity during glacial
251 periods and the dips of connectivity during interglacials are more extreme in the former (**Fig. 5a**). The
252 Western Cordillera is a larger mountain range than the Cordillera of Mérida and the SNSM (**Table S.1**),
253 and its variation of connectivity has been correspondingly larger (**Fig. 5b**) but with the lowest occurrence
254 of connectivity compared to the other mountain ranges (**Fig. 5a**). Considering only the frequency in the
255 distribution of data (**Fig. 5b**), the Ecuadorian Cordillera and the SNSM stand out for their relatively small
256 within-mountain range variation in connectivity, compared to the Eastern and Central Cordillera (similar
257 patterns) and the Western Cordillera.

258 When frequencies of connectivity are weighted by the amount of time that connectivity lasted two main
259 patterns emerge (**Fig. 5c**). The first is shared by the Western, Central, and Eastern Cordilleras, which all
260 display an elongated pattern where the highest values are around a centroid, resembling a ‘humming top’
261 or, as Elsen & Tingley (2015) recognized in mountain hypsographies, a ‘diamond’ shape. Ecuadorian
262 Cordilleras, Cordillera de Mérida and SNSM instead reveal a different pattern with a narrower centroid
263 that widens towards the upper and lower section, resembling an ‘hourglass’ shape. Here, the Ecuadorian
264 Cordillera and SNSM show a surprising similarity though at different connectivity ranges. The Central
265 and Eastern Cordilleras are strikingly similar overall.

266

267 **4. DISCUSSION**

268 **4.1 Variable degrees of past connectivity of different mountain ranges**

269 Although currently isolated, evolutionary radiations and the assembly of the páramo ecosystem formed
270 during times when the páramos were flickering in and out of connectivity (**Fig. 5b**.) The concept of
271 ‘mountain fingerprints’ (Flantua & Hooghiemstra 2018) proposes that the region’s complex topography
272 would have meant that páramos in different mountain regions would have fragmented and connected at

273 different periods of time and with different rates and frequencies (as summarized in **Fig. 1**). This means
274 that in some mountain ranges the páramos are a mix of somewhat even occurrence of connectivity and
275 fragmentation events through time (**Fig.1b**, here representative of the Eastern Cordillera), or could have
276 been dominantly fragmented (**Fig.1a**, e.g. Western Cordillera), or more connected (**Fig. 1c**, e.g.
277 Ecuadorian Cordilleras). These regional differences in the temporal and spatial variation in past páramo
278 connectivity (**Figs 4 and 6**) are likely to have resulted not only in regional differences in biogeographical
279 patterns through time, but also varying ecological and evolutionary processes. We therefore propose that
280 the data we present can be used to test hypotheses of the drivers of species richness, endemism and
281 degrees of Pleistocene diversification in the Northern Andes, and likewise are applicable to other
282 mountain regions around the world.

283

284 **4.2 Evolutionary implications of the flickering connectivity system**

285 The dynamic history of the páramos elucidated by the flickering connectivity system can provide three
286 important insights in terms of evolutionary processes. First of all, the regional differences in past páramo
287 connectivity - the mountain fingerprint – support temporally and spatially discordant phylogeographic
288 patterns (Pennington et al., 2010; Massatti & Knowles, 2014; Papadopoulou & Knowles, 2015; 2016).
289 This means that the timing of diversification in the different mountain regions would not be expected to
290 have occurred synchronously, even if all phylogenetic studies on páramo species could overcome current
291 issues in techniques, spatial resolution and time-calibration points (Rull, 2011). Secondly, diversification
292 rates might differ along the elevational gradient and this might be the rule rather than the exception.
293 Elevational differences in surface availability and connectivity are likely to influence at what elevation the
294 strongest phylogeographic processes will occur, and these processes are thus expected to differ between
295 mountain systems resulting in elevational differences of diversification (see for instance Kropf, Kadereit,
296 & Comes, 2003; Lagomarsino, Condamine, Antonelli, Mulch, & Davis, 2016). And thirdly, the flickering
297 connectivity system, which is expected to cause isolation followed by connectivity of populations, is
298 expected to cause pulses of diversification (Knowles, 2000), possibly resulting in series of sub-radiations
299 in the páramos. Where isolation resulted in allopatric, *in situ* speciation, connectivity triggered
300 diversification through dispersal and settlement in new areas (“dispersification”, Moore & Donoghue,
301 2007), and hybridization of differentiated taxa from previously isolated populations (Petit et al., 2003;
302 Grant, 2014). Phylogenetic studies are increasingly supportive of the important role of gene flow,
303 dispersification and hybridization, alongside periods of isolation, in driving (explosive) diversification in
304 mountains (e.g. Knowles & Massatti, 2017; Hazzi, Moreno, Ortiz-Movliav, & Palacio, 2018), as well as in

305 other systems such as tropical rainforests (e.g. Onstein et al., 2017) and islands (e.g. Ali & Aitchison
306 (2014). In the páramos, examples originate from studies on birds (Quintero & Jetz, 2018; Cadena et al.,
307 2016) and plants, such as *Neobartsia* (Uribe-Convers & Tank, 2015), *Lupinus* (Hughes & Eastwood,
308 2006; Nevado, Contreras-Ortiz, Hughes, & Filatov, 2018; Contreras-Ortiz, Aitchison, Hughes, &
309 Madriñán, 2018), *Loricaria* (Kolář et al., 2016), *Espeletia* (Diazgranados, 2012; Diazgranados & Barber,
310 2017; Pouchon et al., 2018) and *Hypericum* (Nürk, Scheriau, & Madriñán, 2013), supporting the strong
311 relationship between changing degrees of connectivity and radiations (Flantua & Hooghiemstra, 2018).
312 Interestingly, the Funza09 pollen record shows a clear shift in the rhythm of climate change around the
313 mid-Pleistocene transition (ca. 0.9 Ma) after which 100 kyr cycles with high amplitudes started to
314 dominate the climate, overruling the lower-amplitude 41-kyr cycles that continued in the background.
315 Strikingly, changes in speciation rates of high elevation birds (Weir, 2006) and the Espeletiinae in the
316 Cordillera de Mérida (Pouchon et al., 2018), echo the mid-Pleistocene transition by an acceleration of
317 diversification during the last 1 Myr suggesting a close link between the intensity of the flickering
318 connectivity system and radiations.

319

320 **4.3 Limitations and model assumptions**

321 Inherent to any model in mountains and concerning connectivity are simplifications of the temporal and
322 spatial complexity of the real world. For instance, the UFL is asymmetric on wet and dry mountain slopes
323 (e.g. Cleef, 1981), the current elevation of the UFL shows a range of variation of ca. 200 m (incidentally
324 to 300 m), surface processes have changed topography on a million years time scale (Herman et al., 2013;
325 Antonelli et al., 2018), the elevational temperature gradient (lapse rate) seems higher during glacial
326 conditions than at present (Wille, Hooghiemstra, Behling, van der Borg, & Negret, 2001; Loomis et al.,
327 2017), and the current subdivision of páramo vegetation into a 300 m : 600 m : 200 m interval for
328 shrubpáramo, grasspáramo, and superpáramo, respectively, is subject to change (Van der Hammen, 1981;
329 Hooghiemstra, 1984), potentially related to changing atmospheric pCO₂ levels (Boom, Mora, Cleef, &
330 Hooghiemstra, 2001; Boom, Marchant, Hooghiemstra, & Sinninghe Damsté, 2002). We estimate the
331 potential impact of these factors on the estimated connectivity of little significance in determining the
332 overall patterns observed in the flickering connectivity systems.

333 Any study concerning connectivity also uses a number of assumptions on the probability of dispersal
334 through the landscape. Here, we used a generalized PC value of 0.5 at 10 km to estimate the degree of
335 connectivity. However, species traits, life histories and dispersal capacities may strongly influence
336 dispersal distances (Onstein et al., 2017), and thus influence the probability of connectivity between

337 populations. Implementing taxon-specific traits when calculating the landscape resistance grid (see
338 Methodology) may thus improve the accuracy of the connectivity estimates. Also, family or taxa specific
339 connectivity maps could uncover why certain plant genera do not show any evolutionary diversification
340 during the Pleistocene, e.g. *Distichia* (Juncaceae; Colin Hughes, personal comm.) and *Arcytophyllum*
341 (Rubiaceae; Madriñán, Cortés, & Richardson, 2013). Additionally, *a priori* "hard" barriers can be imposed
342 to emphasize areas where habitat connectivity is unlikely to have occurred (see for instance how we
343 maintained SNSM isolated from the other mountain ranges). Defining these barriers *a priori* is not
344 indispensable, though, as the connectivity analysis hints at strong dispersal restrictions when resistance
345 values of corridors are high and indicative of highly constrained dispersal. In the Northern Andes, this is
346 shown by the multiple single line corridors between the Central and Eastern Cordillera, confirmed by the
347 lack of gene flow between plant populations of these regions (Jabaily & Sytsma, 2013; Diazgranados &
348 Barber, 2017; Contreras-Ortiz et al., 2018). This example illustrates the added value of integrating
349 different lines of evidence (e.g. genetic, fossil, paleoclimate) in a spatial and temporal context to
350 understand the biogeographical patterns observed in phylogeographic studies.

351

352 **4.4 Future research**

353 Our spatio-temporal estimates of past connectivity lay a foundation for further research on elucidating the
354 causal mechanisms of mountain diversifications. Models of past connectivity (**Figs. 4 and 5**), when
355 combined with phylogeographic data, could help reveal the role of interspecific gene flow and allopatric
356 speciation in driving radiations in the high Andes (Nevado et al., 2018) and contribute to a better
357 understanding of the relative importance of geography vs adaptive radiation that underpin Andean
358 diversifications (Contreras-Ortiz et al., 2018). In such a complex system it may also be useful to pay
359 attention to commonalities. For example, when considering both frequency and duration, our data show
360 that two connectivity patterns emerge (i.e. hourglass vs. non hourglass; **Fig.5.c**). Research could explore if
361 cordilleras with shared connectivity patterns also share phylogenetic histories and contemporary
362 (endemic) species' biogeographies to test for universal mechanisms that have shaped present day alpine
363 biomes. This would be especially useful if used in conjunction with information on the reproductive life
364 histories, growth and dispersal capacities of specific taxa.

365 Finally, past patterns of connectivity are critical to interpret biogeographical patterns of currently isolated
366 or fragmented systems in a wide variety of terrestrial ecosystems including mountains (Flantua &
367 Hooghiemstra, 2018), islands (e.g. Simpson, 1974; Weigelt, Steinbauer, Cabral, & Kreft, 2016; Norder et
368 al., 2018), fresh water systems (e.g. Dias et al., 2014), rainforests (e.g. Graham, Moritz, & Williams,

369 2006), and grasslands (e.g. Lindborg & Eriksson, 2004; Münzbergová et al., 2013), and marine coastal
370 ecosystems (Hoeksema, 2007) that similarly experienced major spatial changes during rapid sea-level
371 fluctuations over the Pleistocene. The approach developed here, to quantify historical connectivity, can
372 therefore provide a platform for interpreting contemporary biogeographies and past drivers of
373 diversification in a wide array of both marine and terrestrial ecosystems where available space has been
374 altered by climatic fluctuations. We postulate that quantifying flickering connectivity systems will
375 facilitate a much more detailed and much needed quantitative basis to compare diversity patterns across
376 the mountain regions of the world.

377

378 **5. CONCLUSIONS**

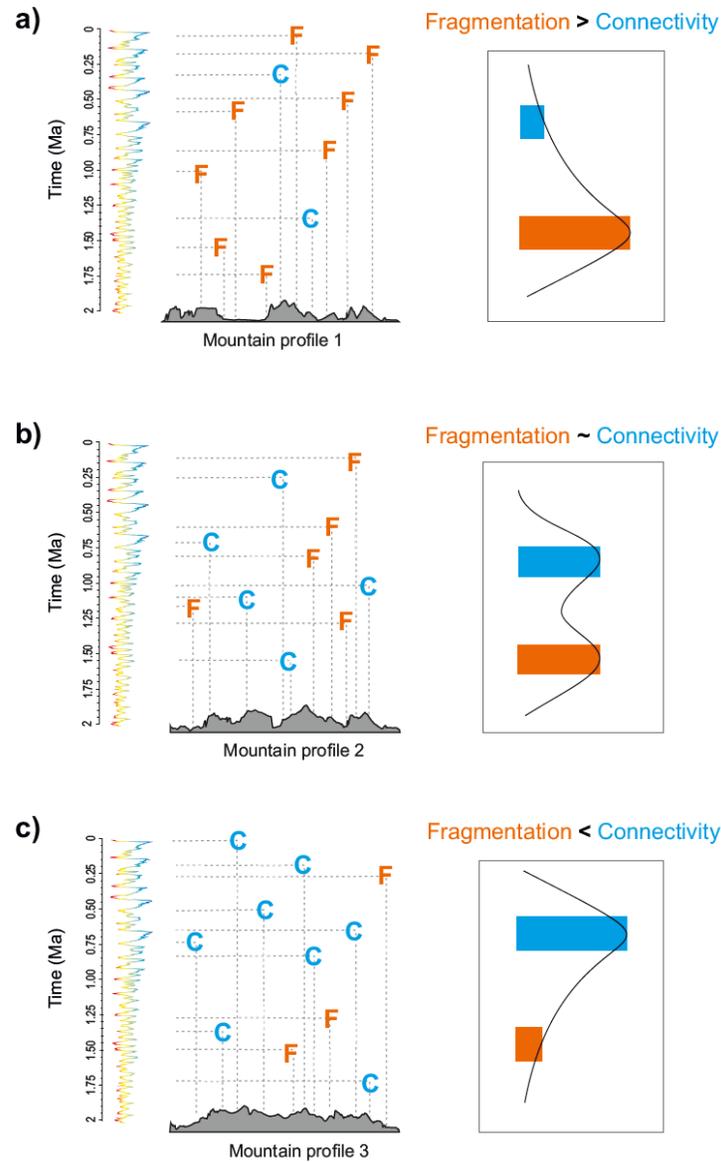
379 We present a pollen-based biogeographical model for the páramos biome spanning the northern Andes
380 (Venezuela, Colombia and Ecuador) over the last 1 Myr. Our models suggest substantial temperature
381 oscillations where extreme temperature lows were ca. 8°C cooler than today, causing a lowering of the
382 UFL of ca. 1600 vertical meters. These extreme cool events were however rare and during glacial periods
383 most of the time cool stadials and interstadials prevailed. Our analysis shows that páramos on all mountain
384 ranges underwent frequent alterations between fragmented and connected configurations, but the
385 estimated degrees and amount of connectivity varied among mountain ranges. Most páramos expanded
386 during glacial periods even though extensive glaciers were present. To a large extent the current páramo
387 distribution was replaced by glaciers, implicating a substantial range size change of populations and a
388 highly dynamic system during Pleistocene times.

389 In light of Von Humboldt's work of relevance of different topographies for mountain biota, we show that
390 topography and climate change together dictated páramo connectivity through time with high spatial
391 variability. The interplay of the topographic and paleoclimatic conditions created a unique pattern of
392 connecting and fragmenting páramo patches through time, here described as the flickering connectivity
393 system. Our spatially explicit model quantifies the complexity of mountain biome dynamics during
394 climate oscillations, in terms of the degree, frequency and duration of past connectivity of alpine biome
395 mountains (**Figs 4 and 5**) and can be applied to other mountain regions. Our connectivity estimates can
396 contribute to answering long-standing questions on the drivers of evolutionary diversification in
397 phylogenetic and phylogeographic studies, and enrich our understanding of the biogeographic history of
398 mountain ecosystems more generally.

399

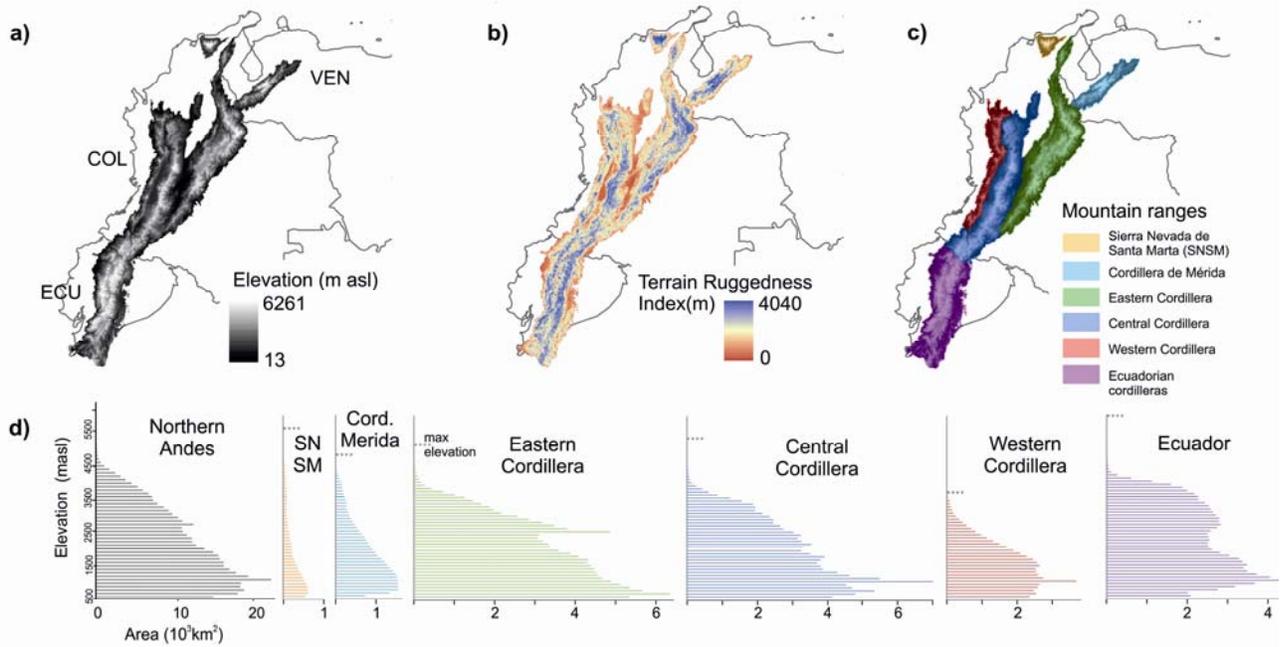
400 *“There the different climates are ranged the one above the other, stage by stage, like the vegetable zones,*
401 *whose succession they limit; and there the observer may readily trace the laws that regulate the*
402 *diminution of heat, as they stand indelibly inscribed on the rocky walls and abrupt declivities of the*
403 *Cordilleras”* (Von Humboldt, 1877 (1845), I, p 46).

404



405

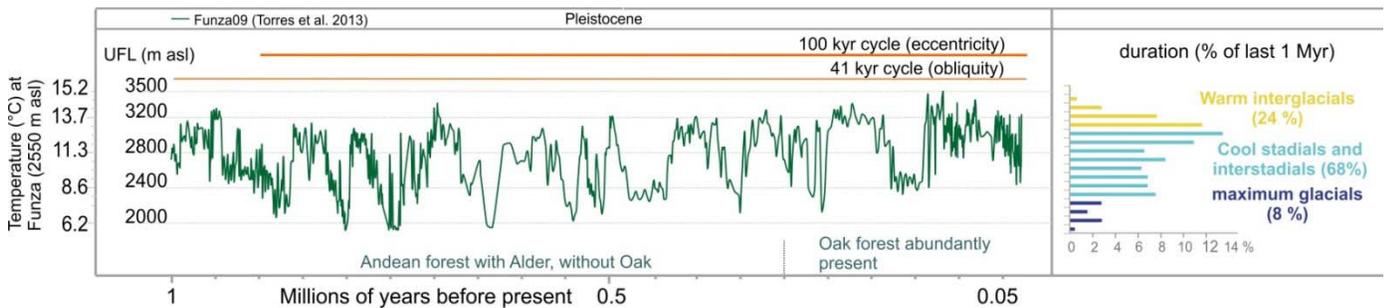
406 **Figure 1 | Connectivity and fragmentation in a mountain landscape.** Connectivity (blue) and fragmentation
407 (orange) events occurred in a spatially and temporally variable manner. This complex pattern in space (latitude,
408 longitude, elevation) and time resembles a multi-dimensional “mountain fingerprint” which is unique for each
409 mountain range (Flantua & Hooghiemstra, 2018). Three hypothetical mountain profiles are shown with elevational
410 shifts in vegetation distribution driven by climate change (pollen-based record at the left indicating temperature). We
411 recognise mountains with where a) only few events of connectivity occurred during the Pleistocene compared to
412 fragmentation events (‘fragmentation-prone mountain fingerprint’), connectivity events interchanged with isolation
413 events in an evenly manner (‘mixed connectivity-fragmentation mountain fingerprint’), c) connectivity is facilitated
414 and occurred more often than fragmentation events (‘connectivity-prone mountain fingerprint’). The right panel is
415 only based on frequency, not the duration of each event.



416

417 **Figure 2 | Hypsographic curves of the Northern Andes.** a) Elevation (m asl). b) Terrain ruggedness index
 418 calculates the sum change in elevation between a grid cell and its eight neighbor grid cells (Riley et al. (1999) using
 419 a ca. 30m DEM (NASA STRM Global 1arc second V003). c) Delimitation of mountain ranges. d) Elevational
 420 availability of surface area for the Northern Andes and each mountain range separately shown for 100 m bins.
 421 Hypsographic curves based on the Shuttle Radar Topography Mission 1-arc second Digital Terrain Elevation Data (~
 422 30 m resolution; USGS), taking an elevational threshold of 500 m asl as the horizontal reference plane. Maximum
 423 elevation per cordillera is indicated. VEN: Venezuela; COL: Colombia; ECU: Ecuador.

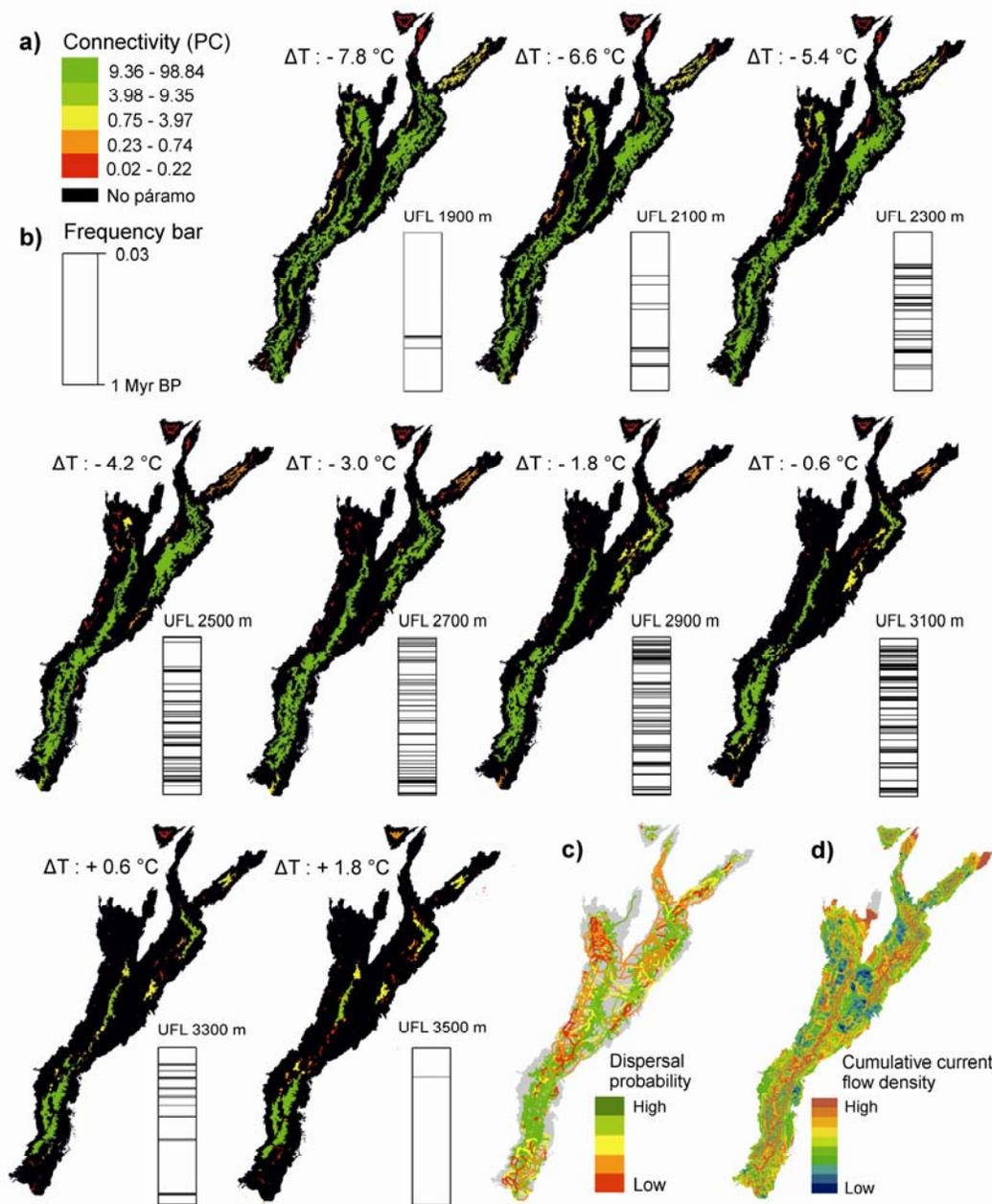
424



425

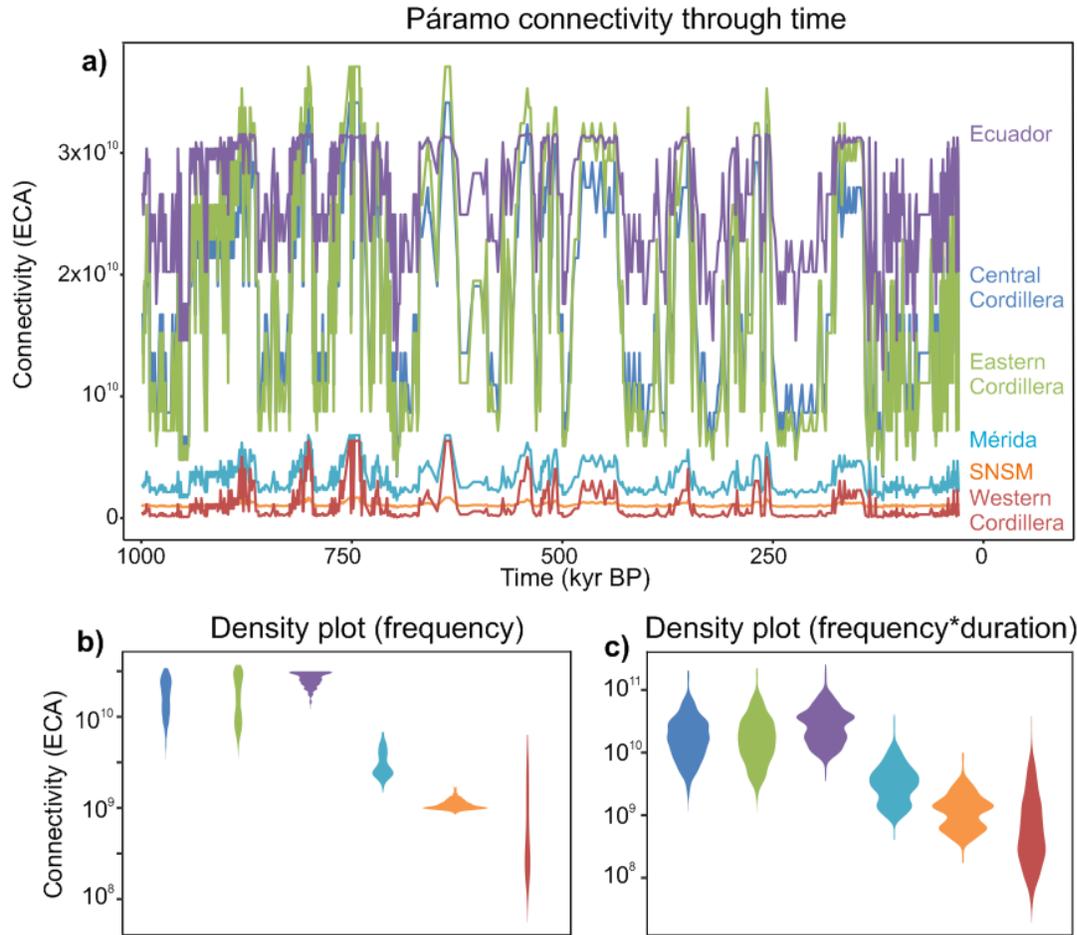
426 **Figure 3 | Upper forest line (UFL) curve of Funza09 (Torres et al. 2013) and reconstructed temperature record**
 427 covering the last 1 Myr (last ca. 30 kyr BP not included).

428



429

430 **Figure 4 | Páramo connectivity at different upper forest line (UFL) elevations.** a) Probability of connectivity
431 metric (PC; distance = 10 km, $p = 0.5$) (Saura & Rubio, 2010) calculated for all páramos larger than 1 km². Maps are
432 plotted with natural-breaks classification. Temperature at 2550 m elevation are relative to the present. b) Frequency
433 bar indicates when the corresponding UFL elevation occurred during the last 1 Myr. Dispersal pathway analysis
434 among páramos using c) Least cost pathways and d) Circuit model expressed in cumulative current flow density
435 (McRae et al., 2008). Areas with high dispersal probability (c) and high current flow (d) indicate frequent and highly
436 probable corridors during the last 1 Myr (weighted by frequency and duration). See Appendices 4 and 5 for all maps
437 and frequencies.



438
439 **Figure 5 | The 'Flickering Connectivity System' of the Northern Andes.** a) Páramo connectivity (ECA) through
440 time (3000-30 kyr BP) for each cordillera. b) Violin plot showing the distribution of the data and its probability
441 density. Plot only considers how often certain connectivity occurred, not how long it lasted. c) Violin plot showing
442 the distribution of the data and its probability density multiplied by how long connectivity persisted.

443

444

445

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712

713 BIOSKETCHES

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

718 **Henry Hooghiemstra** is a terrestrial and marine tropical palynologist working on time-scales from the
719 full Quaternary to the Anthropocene. His research focuses on a wide variety of biomes in Central and
720 South America, Saharan and East Africa and in Mauritius.

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

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

729

730 **APPENDICES**

731 Additional Supporting Information may be found in the online version of this article:

732 **Appendix 1** | Surface areas, elevational ranges and hypsographies of the Northern Andes

733 **Appendix 2** | Background on the páramo alpine biome

734 **Appendix 3** | Methodology underlying the use of fossil pollen data to reconstruct the upper forest line
735 changes

736 **Appendix 4** | Degree of connectivity of páramos at all UFL elevations during the last 1 Myr.

737 **Appendix 5** | Frequency analysis of all UFL elevations during the last 1 Myr.

738 **Appendix 6** | **Visualization of the flickering connectivity system in the Northern Andes.** Artwork by
739 Catalina Giraldo Pastrana in collaboration with Suzette G.A. Flantua and Henry Hooghiemstra.

740 **Appendix 7** | Further suggestions for future work.

741

742 **AUTHOR CONTRIBUTIONS**

743 S.G.A.F. and H.H. conceived the ideas. H.H. provided the AP% of the Funza09 dataset. S.G.A.F.
744 performed the spatial analyses. S.G.A.F and H.H. led the writing and figure design with critical
745 contributions by A.O. and R.E.O. All authors contributed to versions of the manuscript and revisions.

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