Climate change and topography as drivers of Latin American biome dynamics

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Unravelling the mountain fingerprint: topography, paleoclimate and connectivity as drivers of contemporary biodiversity patterns in the Northern Andes

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PREFACE

This chapter should be cited as follows:


The conceptual frameworks introduced in Chapter 7 are the baseline for the methodology developed in this current chapter, but while Chapter 7 focused on describing the importance of each process of the flickering connectivity system (fragmentation, intermixing, colonization, hybridization), this current chapter focuses on how to quantify connectivity through time. Having argued in Chapter 7 that historical connectivity played an important role in shaping contemporary biodiversity and facilitated the conditions for evolutionary radiations to occur, in this current chapter I address this postulate by a) proposing a quantitative methodology to estimate historical connectivity, b) showcasing this methodology in a mountain region, c) making the link to current patterns of species richness and endemism.

The Northern Andes stands out in several ways: High topographic ruggedness of the landscape, relatively young mountain formation, high species richness, and it’s a region famous for its recent and rapid diversification during the Plio-Pleistocene. Furthermore, unique long fossil pollen records provide unprecedented insights into the dynamic history of the high Andean biome, the páramos. As shown in Chapter 7, paleotopographic reconstructions are strong tools to visualize processes and patterns through time. In this chapter these reconstructions are further detailed and different connectivity metrics are implemented to provide spatially explicit models on the Pleistocene history of the páramos.

I will begin to recapitulate the conceptual frameworks presented in Chapter 7 with some adjustments that aim to support the methodology introduced in this chapter. Then I explain the approach used to quantify the flickering connectivity system of the alpine biomes of the Northern Andes. In the discussion I argue that the degree of historical connectivity is a strong explanatory in understanding current patterns of species richness, having a high potential to be explored in other mountain regions as well.
Unravelling the mountain fingerprint: topography, paleoclimate and connectivity as drivers of contemporary biodiversity patterns in the Northern Andes

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Abstract

The Pleistocene climate cycles caused dramatic elevational shifts of montane species. A topographically rich landscape had species resided in a spatially complex matrix of isolated and connected populations which were constantly reshuffled during climate fluctuations. To understand the spatial and temporal complexity of Pleistocene mountain dynamics we present a new conceptual framework called the ‘mountain fingerprint’. We emphasize the overlooked role of historical connectivity in shaping contemporary biodiversity and phylogenetic signatures. The consecutive processes of connecting and disconnecting populations, the ‘flickering connectivity system’, is considered key in driving evolutionary processes and explaining current patterns of species richness and endemism in mountains. This framework is implemented in the Northern Andes, an area characterized by rapid diversification during the Pleistocene and extraordinary species richness. Our innovative spatially explicit models quantify the degree of historical connectivity that the Andean alpine species, the páramos, endured throughout the Northern Andes during the last million years of the Pleistocene. This new framework and index are suitable to be implemented in mountains around the world and other temporally dynamic systems, such as archipelagos of oceanic islands.

Keywords: Pleistocene, flickering connectivity system, mountain fingerprint, historical connectivity metrics, spatially explicit models, Northern Andes.
1. Introduction

The complexity of the geological and biological diversity of mountains has fascinated many researchers for centuries. Mountains come in a wide range of different shapes and sizes (Elsen & Tingley, 2015) and are the combined result of deep-time geological processes (Antonelli et al., in review and references therein). They make a major manifestation on all continents (Körner et al., 2011), and importantly, are among the highest biodiversity hotspots in the world (Barthlott et al., 2005; Kret & Jetz, 2007). Their uplift and interaction with the surrounding environments affects not only abiotic factors, such as precipitation patterns, oceanic currents, and sediment deposits, but also offers a novel landscape where biotic speciation intensifies and results in a diverse pattern of species richness (Antonelli et al., in review). How and when current mountain biodiversity came about is still largely unresolved as each mountain region seems to tell its own story, and these are difficult to unravel and capture in one overarching explanation (Antonelli et al., in review).

What is certain is that the Pleistocene, the last 2.6 million years (2.6 Ma) has been a dynamic period to live in. Cold episodes caused extensive glaciers on mountains across the globe (Ehlers et al., 2011), mountain erosion rates increased (Herman et al., 2013), and species’ ranges shifted latitudinally and altitudinally in an effort to keep living within their individual ecological range (Donoghue, 2008; Feeley et al., 2011; Lenoir & Svenning, 2015). It is therefore not surprising that numerous studies have detected Pleistocene imprints on genetic variations of montane species (Hewitt, 2000, 2004; Kadereit et al., 2004; Dynesius & Jansson, 2000).

Interestingly, mountain speciation seemed to have intensified during the relatively short period of the Plio-Pleistocene (since 5.3 Ma). Different mountains around the world harbour examples of very rapid and recent species diversification (radiations) making an important contribution to contemporary species richness. Birds, plants, and insects all seemed to have endured a common denominator or set of triggers (Bouchenak-Khelladi et al., 2015) that stimulated diversification in different mountains around the world (e.g. Comes & Kadereit, 2003; Byrne, 2008; Smith et al., 2014; Gu et al., 2013; Lei et al., 2014; Ye et al., 2016; Winkworth et al., 2005).

The main causes of diversification are widely discussed in the literature, but there is a general consensus that the combination of high topographic relief with climatic oscillations had a profound effect in shaping montane species distributions and, as a result, the generation of new lineages (e.g. Qian & Ricklefs, 2000; Graham et al., 2014; Mutke et al., 2014). For instance populations in the Alps were isolated into glacial refugia (e.g. Schönswetter et al., 2005) causing geographic vicariance and allopatric speciation, considered to be the most common mode for speciation (e.g. Barraclough & Vogler, 2000; Turelli et al., 2001). Repeated glacial fragmentation occurred due to extensive glaciers causing phylogeographic breaks and consequently driving speciation (Wallis et al., 2016; Weir et al., 2016). Areas with climate ‘stability’ or long-term habitat persistence have been suggested to harbour high diversity due to in situ population divergence (e.g. Carnaval et al., 2014; Qu et al., 2014). Many of these concepts accentuate isolation as the main driver of species diversification leading to high species richness.

A growing body of phylogenetic studies is now providing evidence for a driver of diversification and species richness that, while rarely discussed and quantified, has been widely overlooked: historical connectivity. Recent studies suggested that not isolation but gene flow was a key driver of montane species divergence (e.g. birds: Smith et al., 2014; Cadena et al., 2016; plants: Kolář et al., 2016; Knowles & Massatti, 2017). The role of historical connectivity in
explaining contemporary species richness also emerged in other fields of research such as island biogeography (Rijsdijk et al., 2014; Weigelt & Krefl, 2013; Weigelt et al., 2016; Wepfer et al., 2016), fresh water biodiversity (e.g. Dias et al., 2014), spatial reconstructions of habitat history (e.g. Graham et al., 2006; Kissling et al., 2016), and modern landscape ecology (e.g. Lindborg & Eriksson, 2004; Münzbergová et al., 2013).

The cyclical effect of shifting distributions on the potential surface for mountain biota with varying degrees of isolation and connectivity is not a new concept, and various insightful schematic representations of this ‘species pump’ have been developed (Rull, 2005; Rull & Nogué, 2007; Winkworth et al., 2005; Ramírez-Barahona & Eguiarte, 2013; Steinbauer et al., 2016). Additionally, comparative studies between mountains already suggested that the degree of historical connectivity possibly explains differences in species richness and composition (Sklenář et al., 2014). However, it remains elusive how to explain the differences observed between and within mountains in timing and degree of diversification resulting in a spatially diverse pattern of montane species richness.

We propose a new conceptual framework that captures the spatial and temporal complexity of Pleistocene mountain environments, namely the ‘mountain fingerprint’. This framework combines in an innovative manner the intrinsic characteristics of the mountain topography (Elsen & Tingley, 2015) with our understanding of Pleistocene climate change in mountains (Torres et al., 2013). The mountain fingerprint deepens our understanding on how species could have proliferated under such dramatically changing conditions. By emphasizing the integration of past phases of fragmentation and connectivity highly enriched insights into patterns of species diversification and species richness are gained. Different from previous studies, we quantify the degree of historical connectivity through time in a spatially explicit model, called the ‘flickering connectivity system’ (FCS).

We showcase the framework and spatially explicit models in the Northern Andes and specifically for the Andean tropical alpine ecosystem called páramo. It is a topographically rich mountainous area where the individual páramos areas are currently isolated in an archipelago of ‘sky islands’ (Warschall, 1994; McCormack et al., 2009; Figure 1). Their biogeographical history has been studied for decades (e.g. Van der Hammen, 1974; Cleef, 1979; Hooghiemstra & Van der Hammen, 2004) and supported by long high-resolution fossil pollen records (Groot et al., 2011; 2013; Bogotá-Angel et al., 2011; 2016; Torres et al., 2013). During the Pleistocene páramos underwent drastic shifts in elevation, maximally 1500 m, causing substantial changes in area and connectivity (Van der Hammen, 1974; Hooghiemstra & Van der Hammen, 2004; Flantua et al., 2014; Sklenář et al., 2010; 2014). Furthermore, the páramo biome has become known for its bursts of Plio-Pleistocene species diversification among plants (e.g. Espeletiinae: Madriñán et al., 2013; Diazgranados & Barber, 2017; Pouchon et al., in review; Halenia: Gentianaceae (Von Hagen & Kadereit, 2001, 2003; Hypericum: Nürk et al., 2013; Lupinus: (Hughes & Eastwood, 2006; Contreras-Ortiz et al., in review; Valerianaceae: Bell & Donoghue, 2005; see overview in Hughes & Atchison, 2015). These characteristics make the Northern Andes highly suitable to showcase the proposed framework and models on historical connectivity. We continue to describe the mountain fingerprint and the FCS in more detail, after which the methodology section will focus on the methodological steps to quantitatively express these new concepts.
**Historical connectivity through space and time**

The FCS embodies a temporally and spatially dynamic system, where the temporal domain is set by the Pleistocene climate and the spatial terrain is the mountain topography (Figure 2a). The ‘flickering’ refers to a system that moves back and forth between states by rapid or gradual change. In our case, the temporal flickering refers to the climate oscillations driven by variations in the Earth’s orbit (Torres et al., 2013). This spatial flickering refers to the mountain topography that undoubtedly is highly influential for mountain ecosystems (e.g. Mutke et al., 2014; Stein et al., 2014; Verboom et al., 2015, among many others).

There are four processes inherent to the FCS related to the degree of connectivity: fragmentation, colonization (dispersal), intermixing, and hybridization, where all, except the first, are facilitated when periods of increased connectivity arise. Each individual process has been identified as important for species diversification (Petit et al., 2003; Moore & Donoghue, 2007; Linder, 2008; Uribe-Convers & Tank, 2015; Weigelt et al., 2016) and the combined effect is postulated to cause radiations. The mountain fingerprint (Figure 2b) is the interaction between climate and topography, defining where and when each process of the FCS potentially occurs. Contemporary species richness and phylogenetic signatures carry the legacy of the mountain fingerprint that defined the frequency and duration of the four mentioned processes.

Surface availability, degree of elevational connectivity and duration of historical connectivity (Figure 2c) are proxies along the elevational gradient that relate the mountain topography characteristics with connectivity, and provide insights on where and for how long connectivity occurred in the past. The degree of connectivity between the alpine ‘core areas’ (areas of highest suitability) can be quantified at the level of patches and landscape corridors (Figure 2d). We first provide background information on the drivers of the FCS, the temporal and the topographic flickering, and how they are estimated for the Northern Andes. Then, we calculate historical connectivity of the páramos during the last 1 Ma of the Pleistocene using pollen-based records of Pleistocene climate change.

**2. Methods**

**2.1 Temporal flickering**

**2.1.1 Pleistocene paleoclimate and mountains**

During the Pleistocene there has been a temperature asymmetry: cool-to-cold and relatively dry climatic conditions (the ‘glacials’) prevailed, while warm and relatively moist interglacial conditions were relatively infrequent, covering only an estimated ~15% of the time (based on the δ18O global stack record; Lisiecky & Raymo 2005). Extremely cold conditions, such as during the Last Glacial Maximum (LGM), prevailed probably no more than ~10% of Pleistocene time. The remaining 75% mainly showed a slowly cooling trend to almost full glacial conditions with ‘stadial’ (cold) and ‘interstadial’ (cool to mild) periods superimposed on the long-term trend (Lisiecki & Raymo, 2005; Bogotá-Angel et al., 2011; Groot et al., 2011; Torres et al., 2013). This means that species spent most of the Pleistocene time in a glacial regime characterized by lower temperatures and lower atmospheric CO2 concentrations as today (Weib III & Bartlein, 1992). Warm interglacials, like the Holocene, the last 11,500 calendar years before present (cal yr BP), can be regarded on the Pleistocene time scale as short-term anomalies embedded in much longer, cooler and drier glacial periods.
Paleoclimate records in the tropical parts of the continents have shown that the temperature decreases during Pleistocene glacial periods were substantial (Flenley, 1979). In the Northern Andes mean annual temperatures (MAT) could have been 7.5-8.8°C even up to 10°C lower as today (Van der Hammen, 1974; Hooghiemstra, 1984; Helmens, 2004; Stansell et al., 2007; Groot et al., 2011). Temperature decrease during cooler episodes such as the LGM, caused considerable elevational lowering of tropical alpine ecosystems around the world, e.g. Andes (c. 1500 m: Van der Hammen, 1974; Hooghiemstra, 1984; Groot et al., 2011), Pantepui (c. 1100 m: Rull & Nogué, 2007), East African Rift (c. 1000 m: Gehrke & Linder, 2014), New Guinea (c. 900 m: Flenley, 1979, and references therein) and New Zealand (c. 800 m: McGlone et al., 2010).

2.1.2 Temporal flickering of the Northern Andes
Long and continuous paleoclimate records of the Pleistocene in mountains are rare. Due to a unique combination of subsidence and sediment infill, the intramontane basin of Bogotá, Colombia (4°N, 2550 meters above sea level, m asl; Figure 1) accumulated sediments during most of the Pleistocene (Torres et al., 2013). The composite pollen record Funza09 (Torres et al., 2013) represents the vegetation and climate dynamics of the past 2.25 Ma. 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 overprints the 41 kyr cycle, leading to the well-known glacial-interglacial cycles of the middle and late Pleistocene (Lisiecki & Raymo, 2007). The 100 kyr cycles show a higher temperature amplitude and in particular the glacial intervals reached colder temperatures than before.

Here, we use the last 1 Myr of this record as this interval reflects continuous lake conditions that allows a quantitative interpretation of the pollen spectra in upper forest line (UFL) positions (Torres et al., 2013) and pollen spectra allow a rather uniform interpretation into UFL positions. The UFL is the transition from upper montane forest to páramo, i.e. the uppermost contour of closed forest (Bakker et al., 2008), and coincides with the 9.5 °C MAT isotherm (Hooghiemstra, 1984; Hooghiemstra et al., 2012). We follow the method in Groot et al. (2011) based on Hooghiemstra (1984) to calculate the record of UFL positions and past temperature change in the Northern Andes (Figure 3).

Here we discuss how we got insights into the relative duration of warm (interglacial), transitional (cool) and cold (full glacial) conditions of the Pleistocene. There is a broad correspondence between long pollen sequences (reflecting regional land temperature) and the deep-sea oxygen isotope record (a global ice-volume record corresponding to mean global temperature). Pollen records contain a higher degree of climate sensitivity and better reflect regional conditions (Tzedakis et al., 1997). Therefore, the long record from the Bogotá basin provides the best template to calculate for the Northern Andes the altitudinal position and surface area of the páramo biome, and the duration of its residence within 100-m increments. Apart from immigration events, variance in taxonomic composition of montane forest assemblages is low (Groot et al., 2013; Bogotá-A. et al., 2016; Felde et al., 2016) supporting the vision that climate change-driven altitudinally shifting biomes show a high assemblage stability. Therefore, biome-specific assemblage variance is low. However, site-specific assemblage variance may change rapidly when an ecotone (e.g. the UFL) is shifting over the elevation of the record.

In order to make a link with the terminology in the biogeographical literature we consider conditions as ‘interglacial’ (warm) in the uppermost 400 m of UFL variance (UFL is above 3000
change-driven altitudinally shifting biomes show a high assemblage stably (Groot et al., 2013; Bogotá-Angel et al., 2016; Felde et al., 2016) supporting the vision that climate immigration events, variance in taxonomic composition of montane forest assemblages is low area of the páramo biome, and the duration of its residence within 100-m increments. Apart from regional conditions (Tzedakis et al., 1997). Therefore, the long record from the Bogotá basin temperature). Pollen records contain a higher degree of climate sensitivity and better reflect 100 kyr) driven frequency overprints the 41 kyr cycle, leading to the well-known 2.2.1 Surface availability and ruggedness

Mountains around the world differ substantially in their elevation and ‘roughness’ or ‘ruggedness’ (the “mountainess” of a landscape, variability of the topographical surface; (Grohmann et al., 2011; Spehn & Körner, 2010; Körner et al., 2011). Here we exemplify a selected set of mountains around the world showing their topographic ‘flickering’ as a simplified cross-section (Figure 4). The Northern Andes in Colombia consists of three parallel north-south and northeast-southwest positioned mountain chains, called ‘cordilleras’. Deep inter-Andean valleys separate these cordilleras from each other, but they join in Ecuador to form a high elevation mountain block with numerous volcanos throughout the region. The Altiplano in Bolivia-Peru-Chile and the Tibetan plateau are relatively flat areas at high elevations, characterized by steep decrease to their forelands. High roughness of relatively low elevation mountain peaks is found in the Alps. Most mountains of the East African Rift system are of volcanic origin giving a rise to sharp features in the landscape. In Venezuela, so called table-top mountains or ‘tepuis’, form isolated plateaus with stunning escarpments where numerous waterfalls originate. In conclusion, each mountain region has a different degree of topographic flickering, in which species resided and endured the effects of climate change differently.

2.2.2 Topographic flickering of the Northern Andes

To characterize the topographic flickering of the Northern Andes, we calculate three different elevational metrics (Figure 1), namely 1) surface availability, 2) degree of connectivity, and 3) duration of connectivity.

1) Surface availability: Species responding to climate fluctuations by elevational change face a topographically complex landscape. Their capacity to survive depends on habitat availability in terms of surface as their ranges shifted altitudinally along the mountain slopes.
Surface availability does not change monotonically; this has been shown previously in a smaller mountainous area by Flantua et al. (2014) and on a global scale by Elsen and Tingley (2015). Hypsometric curves are created based on the Shuttle Radar Topography Mission 1-arc second Digital Terrain Elevation Data (~30 m resolution; USGS, 2006), taking an elevational threshold of 500 m asl as the horizontal reference plane. Changing sea level positions during the Pleistocene have not been taken into account as this is merely 140 m maximally (Spratt & Lisiecki, 2016).

2) Degree of connectivity along the elevational gradient: The degree of connectivity along the elevational gradients is calculated following the method proposed by Flantua et al. (2014). This elevation driven connectivity corresponds to a 100 m elevational bin in which the probability is estimated that a species encounters a suitable patch of at least 1km² in surface and within a distance of 10 km from its current patch. The connectivity probability metrics (PC) and related equivalent connected area (EC) take into account the size of the patch itself and the distances between all patches within a defined threshold (Saura & Pascual-Hortal, 2007; Saura et al., 2011a, 2011b). We calculate connectivity for the entire Northern Andes and for each of the cordilleras, from 1000 m asl upwards to focus mainly on the highlands. The computations of the ECA are performed by Conefor Sensinode 2.2 software (Saura & Torné, 2009).

3) Duration of connectivity along the elevational gradient: The lower limit of páramo, the UFL, resided at different elevations at different moments in the past. Based on the Funza09 AP% record and the derived temperature curve we calculate the total duration and the frequency of each UFL elevation during the last 1 Ma, and derive the historical connectivity of páramos as a result of the shifting elevations.

The general contours of the area of interest are delimited using the Northern Andes boundary defined by Josse et al. (2009) and including the Sierra Nevada de Santa Marta (SNSM) by a 500 m asl isoline. To define the boundaries of the different cordilleras, the geological faults are identified using Bermúdez et al. (2013), Baldock (1982) and Aleman & Ramos (2000). Then, the deepest sections of the main canyons are identified using ESRI ArcHydro tool (Environmental Systems Research Institute (ESRI), 2014) and consequently used to define boundaries between the three different cordilleras of Colombia, and to define a boundary between the Central Cordillera in Colombia and Ecuador. These boundaries are preferred over using geological faults as canyons are considered more relevant as a natural boundary for montane species. Furthermore, the terrain ruggedness index (TRI) is calculated following Riley et al. (1999). ESRI ArcGIS 10.3 is used for all calculations (ESRI, 2014).

2.3 Historical connectivity of the páramos

2.3.1 Páramo patch analysis

Previous studies in Colombia estimated that the UFL migrated between c. 2000 m asl (coldest glacial conditions) and c. 3400 m asl (warmest parts of interglacials) (e.g. Van der Hammen, 1974; Hooghiemstra, 1984; Van ‘t Veer et al., 2000; Wille et al., 2001). We reconstructed the elevational range of páramos, including the subpáramo (dominated by shrub), grasspáramo (dominated by herbaceous vegetation), and superpáramo (incomplete vegetation cover due to harsh climatic conditions; Van der Hammen, 1973; Van der Hammen & Cleef,
probability is estimated that a species encounters a suitable patch of at least 1km² in surface and
(2014). This elevation driven connectivity corresponds to a 100 m elevational bin in which the
Surface availability does not change monotonically, this has been shown previously in a smaller
mountainous area by Flantua et al. (2014) and on a global scale by Elsen and Tingley (2015).

2.3 Historical connectivity of the páramos

2.3.1 Páramo patch analysis

Previous studies in Colombia estimated that the UFL migrated between c. 2000 m asl
and c. 200 m in the lowermost part of the superpáramo. The upper part of the superpáramo is
almost devoid of vascular plants. The elevational range above the páramo is assigned to snow as
extensive ice sheets were present in the Northern Andes during colder and humid periods
(Helmens, 1990; IDEAM, 2012; Schubert & Vivas, 1993). We disregard any asymmetrical
zonation between the dry and wet side of the mountains (e.g. Colombia: Cleef, 1981; Van der
Hammen & Cleef, 1986; Venezuela: Acosta-Solis, 1984). Based on the derived UFL elevations,
we make palaeotopographical reconstructions of the páramo distribution using Geographical
Information System (GIS) software (see examples from southern Colombia in Flantua et al.
(2014) and for the Guyana highlands in Rull and Nogué (2007)).

To calculate the degree of connectivity, we use the same PC metric as implemented for
the elevational connectivity, but specify the importance individual páramo patches play in
maintaining the overall connectivity. There are three ways in which a patch can contribute to PC,
namely the ‘intrapatch’ fraction, the ‘flux’ fraction and the ‘connector’ fraction (Saura & Rubio,
2010). The first focuses on the available surface area and also habitat quality - if applicable -
within the individual patch. The second fraction assesses how well the individual patch is
connected to other patches taking into account the patch’s attributes (surface and quality) and its
strategical position within the configuration or network of páramo patches. The third fraction
quantifies the contribution of the individual patch to maintain connectivity between the rest of
the patches, thus its role as an intermediate stepping stone between non-adjacent patches (Saura
and Rubio, 2010). Conefor Sensinode 2.2 software (Saura and Torné, 2009) is used to calculate
the straight line distances between all existing patches and the fractions composing the PC metric
for each individual patch. For each 100 m bin from 1000 m asl up to the maximum elevation the
probability of connectivity is calculated among patches that are within a range of 10 km, 5 km, 1
km, 500 m and 100 m, and compared between the different cordilleras.

2.3.2 Dispersal corridor analysis

The topographically rich landscape of mountains poses barriers and creates corridors that
impede or facilitate movement of species (Taylor et al., 1993; Taylor et al., 2006; Correa Ayram
et al., 2016). The network of possible corridors is structured around and between core areas of
habitat. The landscape poses a certain level of “resistance” in a sense that it poses a degree of
difficulty for species to disperse, where in higher resistance areas it is assumed that species will
be more likely to disperse through routes of less resistance. With this we aim to display past gene
flow between páramo core areas by identifying putative corridors between patches and
cordilleras.

The ‘circuit theory’ predicts movement and dispersal patterns through the landscape by a
graph model that resembles electrical currents that run between core areas or ‘nodes’ (McRae &
Beier, 2007; McRae et al., 2008). ‘Circuits’ are created by connecting nodes through conducting
multiple pathways (‘current flows’) and as a result, the conductance grid defines where possible
pathways are located. This dispersal route analysis used habitat heterogeneity (e.g. steepness of
the landscape) to predict geographical connectivity here defined by the isolated-by-resistance
imposed by the landscape.
The appeal of this approach lies in: a) the output integrates all possible pathways between patches, b) it takes into account the irregular habitat shapes commonly observed for alpine ecosystems, c) it can incorporate the spatial heterogeneity of the landscape, such as topographic roughness in mountainous regions (e.g. Hagerty et al., 2011; Noguerales et al., 2016), d) although more often applied for animal movement (e.g. Bell et al., 2010) also plants can be assessed (e.g. Andrew et al., 2012), e) landscapes can be assessed in space and time, e.g. different climatic conditions in the past (e.g. Gehara et al., 2014).

For the Northern Andes, three different models are developed to identify putative corridors. In the first model, the boundaries of the páramo core areas are set exactly at their 1200 m range as previously used in the patch connectivity analysis. Here within the core area the habitat was “perfectly suitable” with score of 100 (or minimal resistance of 0), while outside de core area the score of 0 to reflect total unsuitability, represented by a total resistance of a 100. In the second model, a different resistance scenario was used: an exponential decay function softens the boundary by increasing resistance in 5 elevational steps of 100 m where the UFL represents a suitability score of 40. As a result of the decay function the highest suitability of páramo - its core area - is restrained 200 m above the UFL and 200 m below the snowline. For these models the resistance imposed by the landscape is only defined by climatic restrictions of the species’ envelope, thus restricted by elevation. In other words, further down the elevational gradients, climate conditions become too unsuitable for páramo species and thus impose a gradually higher resistance for dispersal or successful settlement. In the third model terrain ruggedness is an additional factor of resistance where high ruggedness is assumed to impose restrictions to dispersal.

We used the Gnarly Landscape Utilities (V0.1.3; McRae et al., 2013) with ESRI ArcGIS 10.3 (ESRI, 2014) to create a raster grid representation of landscape resistance. The software tool Linkage mapper was used to calculate the corridors based on the identified core areas and created resistance rasters (McRae & Kavanagh, 2011). It calculates the least-cost corridors based on minimum resistance values, where the final output is expressed in ‘conductance maps’ that represent gradients of cumulative least-cost paths. Where the densities of pathways is highest, it is assumed that flows represent a high probability of moving between habitat patches (McRae et al., 2008). Landscape resistance values were assigned to inter-Andean valleys between cordilleras, except for the region between SNSM and the Sierra de Perijá. Here the first represents a vicariance scenario (possible gene flow through occasional corridors) and the latter a long distance dispersal scenario (mostly gene flow through sporadic long distance dispersal events).

Gene flow was allowed among all core areas where core areas needed to be at least 1 km². We resampled the 30 m Digital Elevation Model (DEM) to a 1 km resolution to have computing time for each Linkage mapper run $\bar{t} \approx 2$ hours. We allowed Linkage mapper to create corridors through (instead of only between) core areas to represent the full arsenal of connectivity through the landscape. Optionally, by selecting only values lower than 200,000 from the produced conductance maps the strongest corridors can be highlighted. We ran the three models for 100 m elevation bins of the UFL as identified by Funza09 (Figure 3). The outputs were weighted and summed according to the percentage of time they occurred during the last 1 Myr.
3. Results

3.1 Surface availability and ruggedness
The Northern Andes covers a total surface of 448,000 km² (following the delimitation by Josse et al., 2009) divided over 6 subregions, hereafter referred to as cordilleras (Table 1). Its highest peaks are located in Ecuador (c. 6300 m asl) and SNSM (c. 5800 m asl). The largest cordillera in terms of surface area is the Eastern Cordillera, followed by the Central Cordillera and the Ecuadorian Andes (Figure 5a). The SNSM is the smallest, forming an extraordinary high peak in the north of Colombia. Most of the Northern Andes is considered a highly rugged or extremely high rugged landscape (Riley et al., 1999) where the high peaks and deep inter-Andean valleys cause strong contrasts throughout the region (Figure 5b).

According to elevational availability of surface areas in mountains, Elsen and Tingley (2015) identified four hypsographic patterns, namely a pyramid, inverse pyramid, diamond and hourglass. Here the Northern Andes shows a decreasing trend of surface availability having a slight peak around 900-1200 m asl and then decreasing up to 6260 m asl (Figure 5c), thus following a pyramid shape. The different cordilleras separately show very different patterns (Figure 5d), with pyramids (SNSM and Central Cordillera), diamonds (Cordillera de Mérida and Western Cordillera) and hourglass shapes (Ecuadorian Cordillera and the Eastern Cordillera) (Elsen and Tingley, 2005). The SNSM and the Ecuadorian Cordillera have the longest stretch to higher elevation, where the large bulk of surface availability between 3000 and 4200 m asl in Ecuador contrasts heavily against the other regions.

3.2 Degree of connectivity along the elevational gradient
Similarly to surface availability, the degree of connectivity varies significantly along the elevational gradient in the Northern Andes (Figure 6a) and among different cordilleras (Figure 6b-f). All cordilleras start with a relatively high connectivity along lower elevations (< 1300 m asl) gradually decreasing towards 2000 m asl. The Ecuadorian Cordillera, Eastern Cordillera and Central Cordillera show distinct patterns. The first has a hump-shaped increase of connectivity along a wide elevational range (2400-4000 m asl) showing the highest degree of connectivity, its ‘connective zone’, at high elevations. The Eastern Cordillera has a sharp increase of connectivity at mid elevations between 2400-3000 m asl achieving the highest values compared to lower elevations and compared to other cordilleras. The Central Cordillera shows a fluctuating trend at mid-elevations before decreasing after 3000 m asl. Thus, the connective zone of each mountain region lays along different elevations, with the highest positioned connective zone in the Ecuadorian Cordillera and the strongest at mid-high elevations in the Eastern Cordillera.

Similar patterns are observed at different dispersal distances (Figure 6b-f) although cordilleras tend to fall within similar ranges towards lower distances. For example, when dispersal distances decreases the hump shape of the Ecuadorian Cordillera is less pronounced, but is nevertheless still the highest among all cordilleras. The remarkable high peak for the Eastern Cordillera remains strong at different dispersal distances suggesting that the distances between patches are small and remain within connectivity distances.

3.3 Páramo patch analysis
During the last 1Ma the UFL moved between c. 1900 and 3500 m asl showing a positive (right) skew around 3000 m asl (Figure 7a). There is no hard threshold between a glacial and
interglacial condition, but here we consider an UFL lower than 2300 m asl as maximum glacial conditions and an UFL at 3100 m asl and higher as exemplary for interglacial conditions.

The degree of historical connectivity has been substantially different between the cordilleras (Figure 7b). The páramos in the Ecuadorian Cordillera maintained a high degree of connectivity throughout the Pleistocene, rarely achieving severe fragmentation. Their fragmentation was probably mostly caused by a lower positioned snowline during colder and wet periods (e.g. UFL 2100) causing a break up of páramo areas on lateral flanks of the mountain. To a lesser extent – but still substantial – is the connectivity of the páramos on the Central Andes where a higher degree of patchiness occurred compared to Ecuador, possibly equally influenced by extensive glaciers during glacial periods. The Eastern Cordillera underwent considerable periods of both connectivity (e.g. UFL 2300) and fragmentation (e.g. UFL 2900), always, however, maintaining two large core areas surrounded by smaller ‘satellite’ patches, nowadays composed of páramos of Boyacá and Cundinamarca (Figure 1). Likewise in Ecuador, high connectivity could occur at relatively high elevations.

Páramos in the Cordillera de Mérida seem to have been restricted to one core area only during interglacials, while during colder periods a relatively high fragmentation is observed possibly due to glaciers pushing páramos to lateral distributions. Increased connectivity was mainly directed towards the southwest and achieved during colder periods (≤ UFL 2300). The páramos of the Western Cordillera and SNSM endured the highest degree of fragmentation during most of the Pleistocene. Possibly frequent extirpation occurred in the Western Cordillera as shifting UFL caused suitable páramo habitat to disappear along most of the cordillera. On the contrary, the páramos of the Central Cordillera maintained a long latitudinal distribution, forming a chain of isolated populations in small patches but somehow 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 cross-passed at UFL1900 forming a brief bridge towards the Central Cordillera.

The frequency bars alongside each scenario reflects the interchanging stages between glacials, stadials-interstadials and interglacials during the last 1 Myr (Figure 7c and frequency bars with each scenario; Supplementary Figures 1 and 2). Cool stadials and interstadials prevailed while some cooler and warmer extremes occurred more often during respectively the first or second half. Páramos on different cordilleras underwent frequent shifts between connectivity and fragmentation at different periods in time. For instance, the Eastern Cordillera possibly represents the highest degree of reshuffling of populations as relatively small temperature changes affected connectivity substantially and recurrently during the last 1 Myr (e.g. between UFL 2700 and UFL 3100). Similarly, the southernmost páramos of Ecuador was connected to the central part of Ecuador during colder periods while fragmentation was substantial during warmer conditions (e.g. between UFL 2300 and UFL 2700). Frequent breaks between the Central Cordillera and Ecuadorian Cordillera occurred during warmer periods interrupting gene flow and species intermixing. Importantly to note is that the current UFL is estimated to be between 3500-3600 m asl in Colombia, a stage which only occurred once during the last 1 Myr.

3.4 Dispersal corridor analysis
Model-1 (hard páramo boundary) and model-2 (soft páramo boundary) show very similar results in terms of the distribution and potentiality of the corridors, here emphasizing the corridors
selected by a conductance threshold of 200k (see methods; Figure 8a). Potential corridors run through the region with generally mid-range values and no clear difference between the different cordilleras. The wide cross-over corridors between the different cordilleras of Colombia are striking, as also between Sierra de Perijá and the páramos of Boyacá, and the latter with Cordillera de Mérida. These single flow corridors seem to have a high conductance value suggesting a concentration of corridors following the same pathway. The choice for a hard barrier created between SNSM and the Sierra de Perijá caused a lack of corridors as the model was given no option to find a least cost corridor between core areas.

The third model is substantially different in terms of location and intensity of corridors (Figure 8a). Corridors are clearly restricted by topographic characteristics delimitating potential pathway more than in model 1 and 2. Differences among and within cordilleras are now clearly visible, showing a diverse pattern of pathways of different widths and intensities. As in models 1 and 2, a cross-over pattern is observed between the cordilleras in Colombia. This is the result of the model finding less resistance crossing over than alternatively finding its way southwards to where the Central Cordillera touches the Eastern Cordillera. In the real world these cross overs may reflect seed dispersal routes by birds.

The feasibility of these corridors or ‘corridor quality’ can be indicated by calculating the average resistance encountered along the least cost pathway (Figure 8b, here shown for model 3). The long ridge of the Central Cordillera forms the starting point of numerous possible corridors to the isolated core areas in the Western Cordillera. The Eastern Cordillera shows a complex internal pattern of corridors, where there is no high quality corridor towards Sierra de Perijá in the north, nor towards the Cordillera de Mérida, while a high concentration of potential corridors is found between the páramos in Boyacá and Cundinamarca. In the Ecuadorian Cordillera a more lateral pattern of high/low potential corridors is observed following the intra-Andean valleys and peaks within this region. Corridors to the southernmost páramos of Ecuador as also the northernmost páramos of the Western Cordillera are mostly of high resistance. The composite conductance map of all corridors according to model 3 (Figure 8c) shows the complexity of corridors throughout the region as a result of their frequency and duration during the last 1 Myr.

4. Discussion

The Pleistocene reshuffling and re-arrangement of the spatial configurations of montane species played an important role in evolutionary and ecological histories. We propose that the degree of historical connectivity is a powerful explanatory factor as a driver of species diversification and thus in understanding contemporary patterns of species richness. We have 1) developed an innovative conceptual framework to comprehend the spatial and temporal complexity of Pleistocene climate oscillations in mountains, 2) postulated that processes facilitated by historical connectivity drove species richness to a larger extent than those caused by isolation, 3) applied this framework to tropical alpine ecosystems in the Northern Andes, and 4) provide a new methodology to quantitatively estimate the degree of connectivity in mountains through space and time.
FCS in the Northern Andes

At the start of the Pleistocene there was still a species-poor version of páramo (‘protopáramo’; Van der Hammen et al., 1973; Hooghiemstra, 1984) that gradually became enriched during the Pleistocene (Hooghiemstra, 1984; Van der Hammen and Cleef, 1986; Torres et al., 2013). The mountain fingerprint of the Northern Andes facilitated dispersal at different moments during the Pleistocene, helping the step-wise migration of páramo plant species throughout the landscape, e.g. *Puya* (Jabaily & Sytsma, 2013), *Loricaria* (Kolář et al., 2016) and *Espeletiinae* (Cuatrecasas, 1979; 2013). Frequent phases of fragmentation probably prevented homogenizing effects of species interchange and gene flow, and as a consequence, differences in species composition between cordilleras are observed. Depending on the location of initial dispersal - originating from ancestral areas - species experienced the FCS differently as each cordillera provided opportunities and restrictions at different elevations (Figures 4 and 5) and at different moments in time (Figure 7).

The legacy of historical connectivity in the Northern Andes is seen at three levels of analysis, namely species richness and/or composition, number of endemic species and evolutionary processes. Here we provide examples of these levels for different groups of species.

A. Species richness and/or composition

During the Pleistocene, páramos frequently reached low elevations causing an overall dispersal-prone landscape. Consequently, trans-Andean species distribution (shared species in adjacent mountain regions) is commonly seen in plants (e.g. Sklenář & Balslev, 2005), butterflies (e.g. Hall, 2005), mammals (e.g. Patterson et al., 2012) and birds (e.g. Arctander & Fjeldså, 1994; Fjeldså et al., 2012). Connectivity between the Western and Central Cordillera was likely through multiple pathways, and there was a general high connectivity between Ecuadorian Cordillera and the Central Cordillera (Figures 6 and 7), causing high similarity in species composition (Moscol Olivera & Cleef, 2009; Sklenář & Balslev, 2005; Jabaily & Sytsma, 2013).

The SNSM is the smallest and the most isolated mountain range of the Northern Andes, with lower number of species compared to the other cordilleras (e.g. butterflies: Adams, 1984; 1985; páramo plants species: Londoño et al., 2014). The lower number of species cannot be attributed to available surface area alone (MacArthur & Wilson, 1967). The Sierra de Perijá is significantly smaller but has similar species richness as the Cordillera de Mérida (Adams, 1983; 1984), possibly as a result of lowland corridors (c. 1200 m) with the Eastern Cordillera and occasional exchange with SNSM (e.g. *Libanothamnus*, *Espeletiinae*: Diazgranados, 2012; Hooghiemstra et al., 2006; Cuatrecasas, 2016). Similar patterns of discrepancy between area and richness around found in other Colombian Cordilleras (Alzate-Guarin & Murillo-Serna, 2016). This confirms that species richness is only partly driven by isolation (Benham & Witt, 2016) and that there is a strong legacy of historical connectivity in contemporary biodiversity patterns of páramos (Simpson, 1975; Sklenář & Balslev, 2005).

Páramo complexes of the Eastern Cordillera have the highest diversity in terms of total species richness (Londoño et al., 2014) and for several species groups such as the *Espeletia* (Diazgranados, 2012) and *Loricaria* (Kolář et al., 2016). Here, this is postulated to be the result of the high frequency of interchange between connected and fragmented states (Figure 7) driving the build-up of biodiversity through the different processes of the FCS (Van der Hammen & Cleef, 1986).
B. Number of endemics

Historical connectivity influences the number of endemics in comparable cordilleras. For instance, the Ecuadorian Cordillera shows a high degree of surface availability (Figure 4) and connectivity (Figure 5) at high elevations, and páramos endured fragmentation during less than 2% of the Pleistocene (Figure 7). The low number of single-mountain top endemics compared to the Eastern Cordillera (Skenář & Balslev, 2005) and the lack of genetic differentiation among páramo populations from separate cordilleras (e.g. Loricaria: Kolář et al., 2016) could be related to this predominantly migration-prone area at high elevations. Interestingly, this might explain the striking decrease of endemism from low to high elevations (Sklenář & Jørgensen, 1999). Contrastingly, high relative endemism in plants and butterflies (c. 50%) in the SNSM is due to the high degree of isolation and the lack of lowland corridors with other cordilleras (Adams 1983; 1984), a similar pattern is observed for isolated patches of Andean dry forests (Särkinen et al., 2012).

C. Evolutionary processes

The alpine zones of the Andes are home to a large number of recent (Plio-Pleistocene) and rapid (high species diversification rates) plant diversifications (see overviews by Sklenář et al., 2010; Turchetto-Zolet et al., 2013; Luebert & Weigend, 2014; Hughes & Atchison, 2015; Contreras-Ortiz et al., in review). The connectivity-prone landscape facilitated increases in diversification through dispersal and settlement in new geographical areas (“dispersification”, Moore & Donoghue, 2007), e.g. Neobartsia (Uribe-Convers & Tank, 2015) and Lupinus (Bell & Donoghue, 2005; Hughes & Eastwood, 2006; Drummond et al., 2012). Historical connectivity not only increases plant species richness through intermixing (Weigelt et al., 2016), but also through pulses of hybridization after recurrent reconnection (Ali & Aitchison, 2014; Gillespie & Roderick, 2014). Interestingly, there is evidence of extensive gene flow and hybridization in páramos plant species (e.g. Loricaria: Kolář et al., 2016; Espeletia: Diazgranados, 2012; Diazgranados & Barber, 2017; Hypericum: Nürk et al., 2013), suggesting a relationship between connectivity, hybridization and radiation (Petit et al., 2003; Grant, 2014).

On the other hand, for plants that occupy the superpáramo the elevational shifts in the past were insufficient to enter the ‘connective zone’ that facilitates gene flow. As a result a high genetic differentiation can be found among populations even within the same cordillera (e.g. Lupinus alopecuroides: Vásquez et al., 2016).

The Funza09 record shows a clear shift in the rhythm of climate change around 1 Ma, also known as the mid-Pleistocene transition (MPT, 0.9 Ma) after which high-amplitude c. 100 kyr cycles start dominating the climate fluctuations and overruling the lower-amplitude 41-kyr cycles that, however, do continue. Strikingly, changes in speciation rates of the Espeletinaceae in the Cordillera de Mérida (Pouchon et al., in review) echo the MPT by an acceleration of diversification during the last 1 Myr, suggesting a close link between the degree of connectivity flickering and rapid radiations.

Spatial reconstructions of historical connectivity

With the release of paleoclimate models, an increasing number of studies engage in paleoecological niche modelling (see overview in Svenning et al., 2011). Consequently, more studies are expected to employ landscape connectivity tools to map putative corridors and enrich phylogeographic research (Chan et al., 2011). Only few studies have intended to quantify historical connectivity but findings are promising (e.g. Cadena et al., 2016; Kissling et al., 2016; Knowles & Massatti, 2017). However, paleoclimatic scenarios are restricted to three periods in
time (mid Holocene climatic optimum at c. 6 ka, LGM at c. 21 ka, and the last interglacial maximum at c. 125 ka) and are particularly problematic in tropical mountains showing consistent overestimation of Pleistocene temperatures (Loomis et al., 2017). Our spatially explicit models circumvent paleoclimate data and rely on an unprecedented continuous temperature record derived from a 2.25 Ma long fossil pollen record. Our proposed methodology is unprecedented as we quantify historical connectivity in a spatially and temporally unified manner, using metrics not previously integrated in historical perspective.

Inherent to any study concerning connectivity are assumptions on the probability of dispersal through the landscape. Depending on species traits and dispersal capacities, different distances can be compared (Figure 6), topographic complexity included (Figure 8), and a priori hard barriers can be imposed (see example of SNSM). Furthermore, connectivity analysis can hint at strong dispersal restrictions when resistance values of corridors are high and indicative of highly constrained dispersal (Figure 8b). 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 these regions (Jabaily & Sytsma, 2013; Contreras-Ortiz et al., in review; Diazgranados and Barber, 2017). These examples illustrate the importance of engaging in multidisciplinary studies that integrate different lines of evidence in a spatial and temporal context.

**Implications for studying temporal and spatial dynamics of mountain systems**

The introduced concepts of the FCS and the mountain fingerprint provide three important elucidations in terms of evolutionary processes. First of all, the inherent heterogeneity of the mountain fingerprint supports temporally and spatially discordant phylogeographic patterns as a null hypothesis (Rull, 2011; Pennington et al., 2010; Massatti & Knowles, 2014; Papadopoulou & Knowles, 2015; 2016) This means that even if all phylogenetic studies on páramo species could overcome current issues in techniques, resolution and time-calibration points (Rull, 2011), timing of diversification would not be expected to have occurred synchronously. Secondly, elevational differences in diversification are expected to be the rule rather than the exception (see Kropf et al., 2003; Lagomarsino et al., 2016). Elevational differences in surface availability and connectivity will influence at what elevation the strongest phylogeographic signals will occur and thus these are expected to differ between mountain systems. And thirdly, the flickering character is expected to cause pulses of diversification possibly resulting in a series of sub-radiations (e.g. Knowles, 2000; Contreras-Ortiz et al., in review).

Importantly to highlight is that tropical mountains do no endure similar degrees of temporal flickering. Apart from the dominant eccentricity rhythm during the last 0.9 Myr, the tropical high mountains of Colombia show a strong obliquity (41 kyr) rhythm (Bogotá-Angel et al., 2011; Groot et al., 2011; Torres et al., 2013; Figure 3) whereas the Andean lakes in the highlands of Bolivia and Peru show during the last 150 ka precession (21 kyr) forcing as co-dominant (Gosling et al., 2008). This means that during the last glacial cycles the alpine ecosystems of the Northern Andes endured a slower flickering (100 kyr and 41 kyr) than the Central Andes (100 kyr and 21 kyr). Differences in signals of orbital forcing are not surprising given the complex nature of climate modes influencing the moisture balance and temperature over the Neotropics (Flantua et al., 2016). These differences in oscillations are expected to influence the duration and frequency of connectivity and, as a result the timing and the intensity of alpine species diversification.
The diverse signature of mountain topography has implications for the degree of potential connectivity and thus gene flow that species encounter at different elevations. We show that montane species are dispersal-prone at dissimilar elevations and that the elevation of the ‘connective zone’ of a cordillera determines whether species endured continuous isolation or whether species were facilitated gene flow during shifting climate oscillations. Depending on the location of initial dispersal - originating from ancestral areas - species experienced the FCS differently as each cordillera provided opportunities and restrictions at different elevations (Figures 4 and 5) and at different moments in time (Figure 7). Hence, the mountain fingerprint can be more fragmentation driven (e.g. SNSM, Figure 9a), or more connectivity driven (e.g. the Ecuadorian Cordillera; Figure 9b), or display a complex mix of interchanging fragmentation and connectivity (e.g. the Eastern Cordillera, Figure 9c), each resulting in a different set of species richness, endemism and Pleistocene diversification pattern.

5. Conclusions

The ‘mountain fingerprint’ describes the inherent complexity of the interaction between mountains and the Pleistocene climate changes that caused substantial changes to species’ distributions through time. We have presented here an innovative framework, the ‘flickering connectivity system’, that captures the history of fragmentation and connectivity of alpine populations as a result of the mountain fingerprint. We focus on the consequences of the reshuffling of species distributions in mountain landscapes, emphasizing how historical connectivity plays an overlooked but vital role in shaping patterns of contemporary species richness, endemism, and evolutionary radiations. We have developed new methodologies and spatially explicit models to quantify the degree of historical connectivity through time.

We showcase these new concepts and methods in the Northern Andes, a topographically rich region with high biodiversity and with numerous recent and rapid species diversification. The Pleistocene evolution of the Andean alpine biome, the páramos, took place in a predominantly migration-prone, glacial-conditioned landscape, in which connectivity was possible within most cordilleras, thanks to the downward bioclimatic shift caused by climatic cooling. The ‘topographic flickering’ of the landscape is expressed by surface availability, degree of elevational connectivity, and terrain ruggedness, and important differences are observed between the different cordilleras. The spatial configuration of páramos is unevenly distributed in time due to the flickering climate character of the Pleistocene. As a result, fragmentation and connectivity occurred in different cordilleras during different periods in time and with different frequencies. Importantly, identified differences are reflected by current patterns of number of endemic species and total species richness, and provide enriched insights in explaining exceptionally recent evolutionary radiations. Insights derived from palaeotopographic reconstructions, as exemplified here, provide the necessary platform for new hypothesis development to improve our understanding of biological evolution in island systems that were dynamic in the past such as archipelagos of oceanic islands and other ‘sky island’ systems.
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<tr>
<th>Mountain region</th>
<th>Total surface area (km²)</th>
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Table 1. Surface availability and shape category for each Cordillera.
Figures

Figure 2. Conceptual framework of the ‘flickering connectivity system’ (FCS). a) The background drivers of speciation are Pleistocene climate fluctuations and montane topography. The $\delta^{18}O$ curve is an indicator of global ice volume and temperature (Lisiecki and Raymo, 2005) and is based on composite stable oxygen isotope ratios from benthic foraminifera. b) The ‘mountain fingerprint’ is defined by the interaction between climate and topography. It is a unique mountain identifier as connectivity and fragmentation events occur in a spatially and temporally complex way, and therefore causes different timing and patterns of species diversification in different mountains. c) The degree and duration of connectivity differs along the elevational gradient in a topographic rich area (Flantua et al., 2014). This is quantified by surface availability, degree of connectivity and duration of connectivity in historical perspective, e.g. the period of time a species or ecosystem resided at certain elevation. d) Historical connectivity is estimated at a patch level taking into account surface area and the contribution the patch has within the network. Corridors are created as conductance pathways using isolation-by-resistance criteria.
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**Figure 3.** Upper forest line (UFL) curve of Funza09 (Torres et al., 2013) as estimated by the method summarized in Groot et al. (2011) and temperature record covering the last 1 Myr. There is a strong obliquity signal before 0.9 Ma and a eccentricity-obliquity signal in the last 0.9.
Figure 4. Topographic profiles of different mountains showing that the characteristic topography of a mountain is decisive for the potential impact and frequency of connectivity breaks caused by Pleistocene glacial cycles. The brown area emphasizes the topography where alpine ecosystems endured climate changes. Different sky islands types (Warschall, 1994; McCormack et al., 2009) are displayed: Andes and Himalaya: cordilleras of high altitude archipelagos. Alps: massif with outliers. Pantepuy: chains of relictual mountain plateaus. East African Rift: circular complex of mountains with isolated peaks.
Figure 5. Degree of topographic flickering of the Northern Andes as defined by (a) elevation (m asl), (b) terrain ruggedness index, (c) surface availability for the entire Northern Andes and (d) each mountain range separately. Surface availability is shown by a hypsographic curve (histograms of area versus elevation) for 100 m bins. The colours of the areas indicated in a) concur with the colon of the hypsographic curves in d). Maximum elevation per cordillera is indicated. VEN: Venezuela; COL: Colombia; ECU: Ecuador; SNSM: Sierra Nevada de Santa Marta.
Figure 6. Degree of topographic flickering of the Northern Andes as defined by the degree of elevational connectivity. Equivalent connectivity (EC) was calculated for each 100 m along the elevational gradient, for each cordillera and at different distances (10 km, 5 km, 1 km, 500 m, 100 m). EC at a mountain (Northern Andes, top left) and regional scale (cordillera) was calculated between patches $\geq 10$ km$^2$ and $\geq 1$ km$^2$ respectively. Colours concur with the cordilleras in Figure 5.
Figure 7. Historical connectivity of páramo distribution during the Pleistocene in terms of duration (a), degree of connectivity (b) and frequency (c). Based on the upper forest line (UFL) curve (Figure 2c), the duration of the elevation of the UFL during the last 1 Myr is calculated (a). The UFL indicates the lowest elevation of páramos and its shift causes substantial changes in the distribution of páramos patches and their connectivity. The different páramo positions and corresponding connectivity are shown by the distribution maps. UFL elevations not only differed in duration but also in timing and frequency as indicated by frequency bars alongside each distribution map. The probability of connectivity (PC) (distance = 10 km, probability = 0.5; Saura et al., 2011) is calculated for all patches larger than 1 km².
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Figure 8. Historical connectivity of páramos by corridors. a) Páramos defined by a hard boundary (model 1), soft boundary (model 2), or including terrain ruggedness (model 3). Only conductance values lower than 200k were used and outputs were weighted according to their duration and frequency during the last 1 Ma. b) Corridor quality indicated by the average resistance encountered along the least cost pathway calculated by the ratio of cost-weighted distance to the un-weighted length of the least-cost path (McRae & Kavanagh, 2011). c) Weighted corridor conductance map for all outputs (no threshold implemented) for model 3 where warm colours indicate high potential of connectivity.
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Figure 9. Different mountain fingerprint types. a) Fragmentation-prone fingerprint, e.g. Western Cordillera; b) Connectivity-prone fingerprint, e.g. Ecuadorian Cordillera; c) Mixed connectivity-fragmentation fingerprint, e.g. Eastern Cordillera.
Supplementary Figure S1. Degree of connectivity of all UFL elevations during the last 1 Myr.
Supplementary Figure S2. Frequency analysis of all UFL elevations during the last 1 Myr.