

# MOUNTAINS, CLIMATE AND BIODIVERSITY

EDITED BY  
CARINA HOORN  
ALLISON PERRIGO  
ALEXANDRE ANTONELLI



WILEY Blackwell

## 12

### Historical Connectivity and Mountain Biodiversity

Suzette G.A. Flantua and Henry Hooghiemstra

*Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, Netherlands*

#### Abstract

The distribution of species in the present is just a snapshot in time after millions of years of change. Pleistocene climatic cycles, varying from 100ky to sub-millennial scales, played an important role in shaping species' distributions. In mountains, these cycles pushed species rhythmically along the slopes, opening temporary dispersal pathways to new regions or dividing populations into isolated remnants. Here, we discuss the implications of the continuous connection and disconnection of populations in terms of their degree of historical connectivity. We introduce the "flickering connectivity system" and the "mountain fingerprint," which describe the temporal and spatial expression of habitat connectivity in tropical mountains as a biogeographical response to repetitive climate changes. We illustrate these concepts through paleotopographic reconstruction of alpine biome distributions in the northern Andes to exemplify the temporal and spatial dynamics that forced rapid evolutionary processes. Historical connectivity is shown to influence contemporary biodiversity on different spatial and temporal scales. We describe species richness and endemism as a consequence of historical connectivity, drawing parallels between oceanic islands and the sky islands in mountains. The continuously changing patterns of connectivity due to Pleistocene climate oscillations appear to have influenced diversification rates in evolutionarily recent time and are postulated to have been essential in shaping contemporary mountain diversity.

**Keywords:** *species distribution, Pleistocene, flickering connectivity system, mountain fingerprint, paleotopographic reconstruction, sky islands*

#### 12.1 Introduction

Mountains are known for their high species richness. This richness can be the result of increases in diversity during older (mature) evolutionary radiations (e.g., Neogene) or of recent and rapid radiations (e.g., during the Plio–Pleistocene). Mountainous regions in Australia and South Africa are species-rich mostly due to mature radiations, as is typical of regions that have been climatically and geologically stable throughout the Neogene (Linder 2008). The high species richness of New Zealand, on the other hand, is the result of recent and rapid radiations (McGlone et al. 2001). Recent radiations are associated with the formation of new habitats as a result of recent (Pliocene) geotectonic activity (Linder 2008).

In the Andes, both older and very recent radiations have been identified. These mountains are extremely species-rich (45 000 plant species), with a high number

of endemics (45%) (Myers et al. 2000). The geological uplift of the tropical Andes, initiated in the Oligocene, played a crucial role in the development of biodiversity in the Neotropics. As a result of this uplift, opportunities for colonization and diversification grew, leading to increased allopatric speciation owing to new high-elevation environments and greater topographic complexity. The uplift also initiated the opening of a north–south dispersal route for boreotropical lineages, and the rising orographic barrier even had an effect on the environmental conditions outside of the Andes (Chapter 8) (Luebert & Weigend 2014). Molecular phylogenies suggest that the different phases of the uplift of the Andes are echoed in the divergence times for many Andean plant groups (Luebert & Weigend 2014).

Recent diversification during the Pleistocene (the last 2.6 My) also shaped the region's species richness. For instance, most species-level variation in birds originates

after the presumed onset of the Andean uplift (Smith et al. 2014), and several prominent species groups from the páramo (the alpine ecosystem of the Andes) are among the fastest radiations in the world (Sklenář et al. 2010; Madriñán et al. 2013; Nürk et al. 2013). Currently, the páramo is found in isolated formations on the mountain tops of Venezuela, Colombia, Ecuador and northern Peru, with the vegetation mainly comprising giant rosette plants, shrubs and grasses (Luteyn 1999). Triggers for rapid diversification during the Pleistocene are still debated, although the importance of new habitats (e.g., Hughes & Eastwood 2006), topography (e.g., Verboom et al. 2015) and insular environments, including islands, lakes, valleys and mountain tops (e.g., Sklenář et al. 2014), has been highlighted frequently. How Pleistocene climate change acted to further amplify diversification and create the optimum conditions for a montane “species pump” is still poorly understood.

The Pleistocene was a period of glacial–interglacial cycles that not only influenced species’ distributions in temperate zones but also led to major environmental disruptions for Andean species. So how did these climatic conditions and the mountainous topography interact, leading to favorable conditions for evolutionary radiations and diversification? And why would the island-like settings of alpine ecosystems in sky-island formations have been important for explosive radiations? This chapter aims to review our current understanding of the past spatial dynamics of montane species and ecosystems, with a special focus on historical connectivity using the Andes as an example. We pay particular attention to the dynamic character of Pleistocene climates under which recent evolutionary diversifications occurred, while recognizing the importance of pre-Pleistocene diversification and intrinsic variables (see more in Chapter 18).

## 12.2 The Flickering Connectivity System

### 12.2.1 Introduction

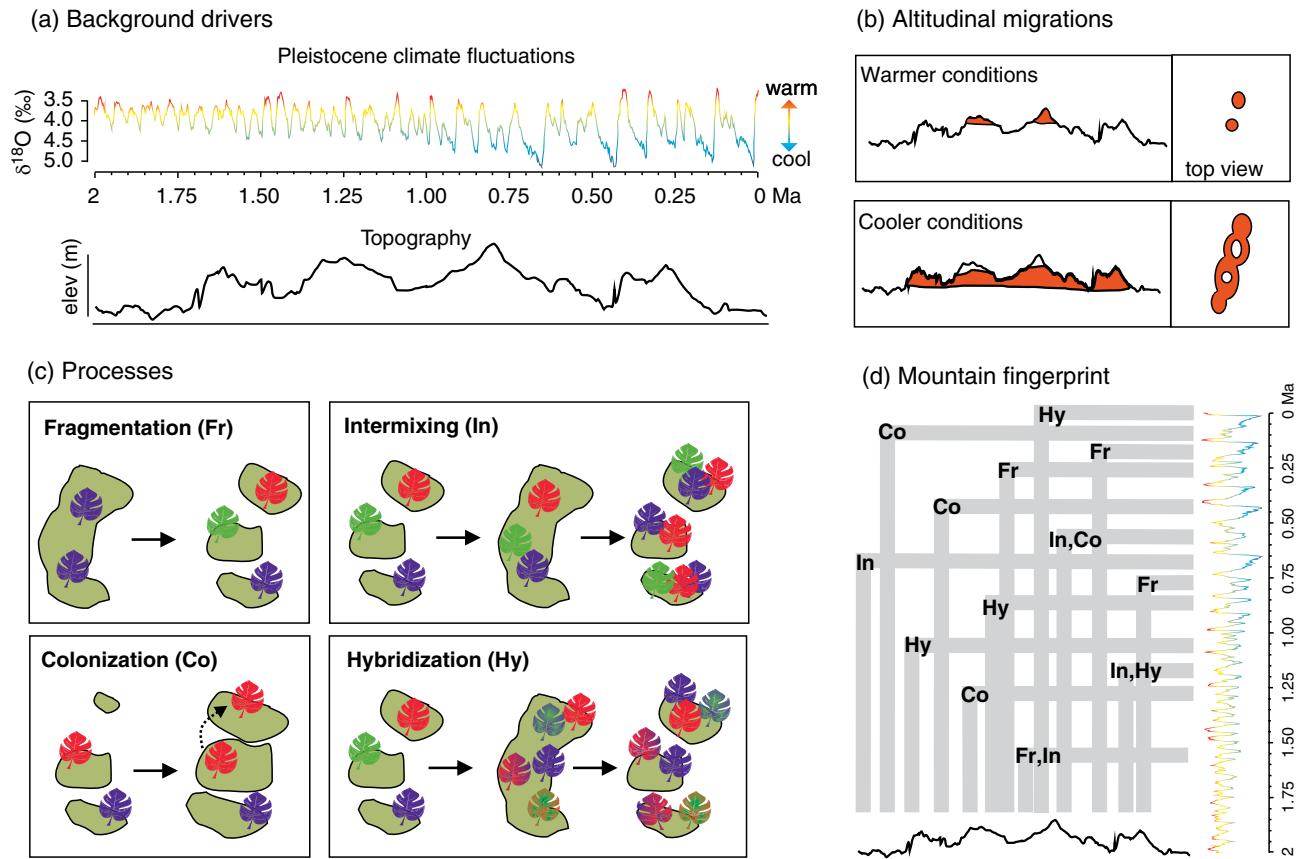
There has been an increased appreciation of the importance of the historical processes that foster the spatial patterns of modern diversity (Chapter 14; Duncan et al. 2015), but few studies have explored the mechanistic processes from a dynamic landscape perspective. Mountain biodiversity most likely accumulated over several climatic cycles during the Pleistocene (see the simulations by Colwell & Rangel 2010), through the consecutive processes of connecting core areas, internal species mixing, disconnecting of refugia into cradles of endemism and local extinction (Rull 2005). Therefore, we propose here that rapid diversification and high

species richness can be explained and understood through a framework we call the “flickering connectivity system” (FCS). This concept describes the multi-episodic diversification of species during the last 2.6 My through cyclical phases of connectivity and isolation of mountain ecosystems. It builds on a “ghost from the past” that suggests that historical connectivity left a strong imprint on present diversity of species and that areas that have been more connected in the past have higher species richness today.

The FCS is 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 12.1a). The “flickering” refers to a system that moves back and forth between states with rapid or gradual change. In our case, the “flickering” refers to the climate oscillations driven by variations in Earth’s orbit (Chapter 9; Hays et al. 1976).

The duration and frequency of climate states did not alternate equally throughout the Pleistocene. Only 15% of its duration consisted of warm and relatively moist interglacial conditions, as cool-to-cold and relatively dry climatic conditions (glacials) prevailed, while only ~10% involved extremely cold conditions, such as the Last Glacial Maximum (LGM). Most of the Pleistocene (75%) was characterized by slowly cooling to full glacial conditions (Figure 12.1a). During these conditions, millennial-scale climate variability of stadial (colder) to interstadial (mild) couplets occurred worldwide (Dansgaard et al. 1993; Labeyrie et al. 2007; Bogotá-Angel et al. 2011; Urrego et al. 2016). Before 1 Ma, glacial–interglacial cycles lasted ca. 40 ky, while after 1 Ma the cyclic duration slowed to ca. 100 ky. The latter cycle had a higher temperature amplitude and reached warmer and cooler temperatures than before (Figure 12.1a).

The flickering state of the Pleistocene climate caused substantial changes to plant distributions and was undoubtedly crucial in shaping contemporary biogeography (Comes & Kadereit 1998; Dynesius & Jansson 2000; Svenning et al. 2015). When rates of evolutionary adaptation are slow relative to environmental rates of change, niche conservatism prevails (Wiens 2004; Pyron et al. 2015), in which species tend to retain similar environmental niches over time and therefore follow temperature oscillations by shifting their geographic range. Species responded individualistically but similarly to changing environmental constraints, forming altitudinally restricted associations, variously called ecosystems (Golley 1993), biomes (Woodward & Cramer 1996), altitudinal belts (Tosi 1964; Van der Hammen 1974) or life zones (Holdridge et al. 1971). These associations were influenced by changing temperature, precipitation and atmospheric  $p\text{CO}_2$  during the Pleistocene’s alternating glacial and interglacial intervals.



**Figure 12.1** Conceptual framework of the flickering connectivity system (FCS). (a) The background drivers of speciation are the large Pleistocene climate fluctuations and highly complex montane topography. The  $\delta^{18}\text{O}$  curve is based on composite stable oxygen isotope ratios from benthic foraminifera and is an indicator of global ice volume and temperature (Lisiecki & Raymo 2005). (b) Altitudinal migrations of hypothetical high-mountain biota, shown in a simple two-phase setting reflecting warmer and cooler conditions. (c) Schematic representation of the intrinsic processes of the FCS as a result of changes in connectivity: fragmentation (Fr), colonization (Co), intermixing (In) and hybridization (Hy). (d) The “mountain fingerprint” is defined by the interaction between climate and topography. It is a unique mountain identifier in which the processes of (a) occur in a spatially and temporally complex way, and therefore causes different timings and patterns of species diversification when comparing between mountains. See also Plate 25 in color plate section.

Subsequently, cold-adapted species and alpine ecosystems shifted downslope during glacial periods and upslope during interglacials (Figure 12.1b). Thus, the turbulent climate history of the Pleistocene was the pacemaker for repeated altitudinal migrations.

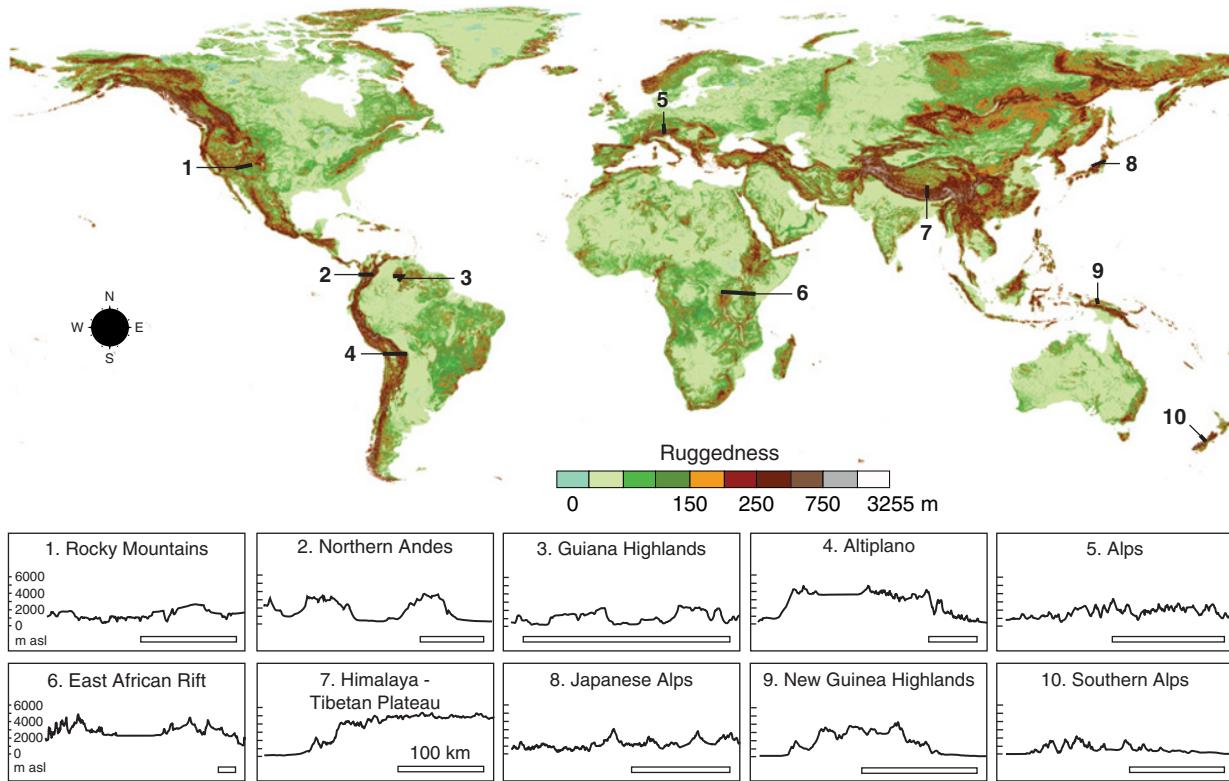
The mountain landscape imposed an additional set of opportunities and challenges for species' survival during the Pleistocene. The high variability of ridges, valleys, peaks and high-elevation plateaus at different elevations (Figure 12.2) creates, when pressured by climate fluctuations, a complex pattern of barriers and pathways for species to disperse around. Hence, past climate change and topographic complexity have been identified as the key extrinsic drivers of species diversification (Bouchenak-Khelladi et al. 2015), and together they form the domains of the biogeographical theatre of the Pleistocene. Therefore, the FCS builds upon these

background drivers for the integration of spatial and temporal dynamics (Figure 12.1a).

## 12.2.2 The FCS in the Andes

Altitudinal migrations are often displayed in a simplified two-stage framework of an alpine system in a fragmented state or a highly connected state (Figure 12.1b) (e.g., Ramírez-Barahona & Eguiarte 2013). Here, we expand on this framework by showing that the climate fluctuations and the topography considered in the FCS have a very dynamic character, creating a more diverse story than is represented by a simple two-state model.

Changes in alpine ecosystems have been reconstructed using fossilized plant material such as pollen (e.g., Van der Hammen et al. 1973; Hooghiemstra & Van der Hammen 2004; McCormack et al. 2009; Brunschön &



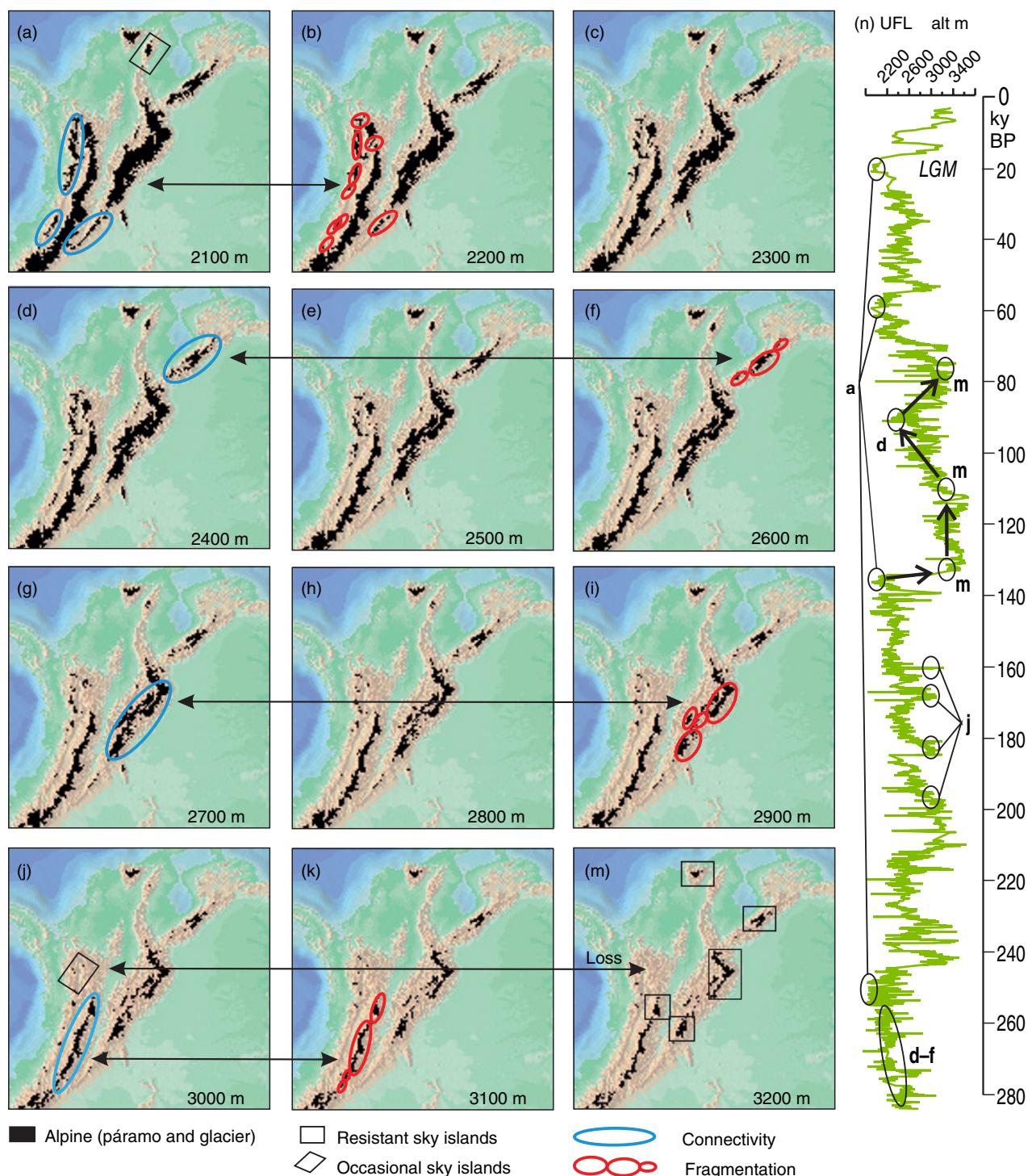
**Figure 12.2** Mountain areas based on ruggedness, as defined by Körner et al. (2011) (maximal elevational distance between nine grid points of 30" in 2.5' pixel; for a 2.5' pixel to be defined as "rugged" (i.e., mountainous), the difference between the lowest and highest of the nine points must exceed 200 m). Numbers indicate topographic profiles of selected mountain ranges around the world. The characteristic topography of a mountain directly relates to the potential impact and frequency of connectivity breaks caused by Pleistocene glacial cycles, and thus the expression of the flickering connectivity system. Bars below profiles indicate a 100 km distance proportional to the profile shown. Source: Adapted from Körner et al. (2011). Mountain ruggedness database downloaded from the Mountain Biodiversity Portal ([www.mountainbiodiversity.org](http://www.mountainbiodiversity.org)). See also Plate 3 in color plate section.

Behling 2010; Flantua et al. 2014; Hao et al. 2016). Paleogeographical reconstructions based on very long pollen records, such as cores from the mountain lakes Fúquene in Colombia (last 284 ky) (Bogotá-Angel et al. 2011; Groot et al. 2011) and Titicaca in Bolivia and Peru (last 370 ky) (Hanselman et al. 2011), demonstrate shifting biotic distributions during the Pleistocene. Combining paleotopographical and paleoenvironmental reconstructions using Geographic Information System (GIS) software can provide insights into past migration routes, degrees of isolation due to topographic restrictions and the persistence of core areas through time (Rull & Nogué 2007; Flantua et al. 2014; Flantua 2017).

Here, we use a long pollen record from Lake Fúquene in Colombia (Fúquene-9C) to show the spatial complexity of the repeated connection and isolation of the páramo during the past ca. 280 ky (Figure 12.3). The páramo consists of an island-like biome located on the highest mountaintops of the northern Andes; it is the most species-rich tropical alpine ecosystem (Sklenář

et al. 2014), and is considered to be a relatively young ecosystem (Plio–Pleistocene), in which numerous recent radiations have been identified (Hughes & Eastwood 2006). The time period of the last ca. 280 ky includes two full glacial–interglacial cycles and is representative of the temporal dynamics of the last million years, with a strong glacial–interglacial amplitude and a dominant 100 ky rhythm. The lower limit of the páramo, the upper forest line (UFL: the maximum elevation at which continuous forest occurs; Bakker et al. 2008), shifted altitudinally over a maximum interval of 1500 m (Van der Hammen et al. 1973; Hooghiemstra 1984; Groot et al. 2011), creating a series of very different spatial configurations of páramo distribution in the past (Figure 12.3).

The cooler periods (low UFL) alternated variably with warmer periods (high UFL) during the Pleistocene (Figure 12.3a–m). As a result, some spatial configurations occurred several times over a longer period while others occurred within a relatively short period



**Figure 12.3** (a–m) Spatial reconstructions of tropical alpine systems (páramo and glaciers; black) in the northern Andes during the last 280 ky, showing the upper forest line (UFL) moving between elevations of 2100 and 3200 m. Each map represents a simplified reconstruction of the distribution of the alpine Andean ecosystem (the páramo) using a digital elevation model. (n) Estimated elevations of the UFL are inferred from the Fúquene-9C pollen record (Bogotá-Angel et al. 2011; Groot et al. 2011). Letters correspond to the maps. Low UFL reflects cooler periods, such as the Last Glacial Maximum (LGM), while a higher UFL reflects warmer periods (interglacial conditions, such as the present). Different regions experience alpine system connectivity and fragmentation at different moments in time. Some páramo areas persist continuously (resistant sky islands), while others appear and disappear (occasional sky islands). See also Plate 26 in color plate section.

(Figure 12.3n). Some transitions between configurations appear gradual (e.g., d–f ~260 ka in Figure 12.3n), while others are rapid (e.g., the progression a–m–d–m between 140 and 80 ka in Figure 12.3n). The contemporary páramo distribution lies above 3200 m. As can be seen from Figure 12.3, the present interglacial conditions are atypical compared to most of the Pleistocene, and extreme cold events, such as the LGM, occurred several times.

The topographic characteristics of the northern Andes allow the formation of several large sky islands and archipelagos (clusters of relatively small islands). “Sky islands” refers to a range of isolated mountain peaks separated by valleys and surrounded by a “sea” of hostile environment consisting of low-elevation habitat (Warschall 1994). By analogy with oceanic islands, the isolation of the alpine ecosystems facilitated the divergence between montane floras and faunas, creating isolated cradles of evolution.

However, sky islands such as the páramo alternated between isolation (present-day conditions) and the formation of connected islands or archipelagos with increased surface area. Lowering of the UFL facilitated páramo connectivity through the provision of ample surfaces at mid and high elevations (Flantua et al. 2014; Elsen & Tingley 2015). For instance, the extent of páramo habitat was at least three times larger during the LGM than it is under today’s interglacial conditions (Hooghiemstra & Van der Hammen 2004). Thus, the cyclic climate fluctuations caused phases with significant increases in surface area and created massive opportunities for historical connectivity.

### 12.2.3 Why is Historical Connectivity Relevant?

Until now, most research emphasis has been put on phases of isolation, locations of refugia and the identification of the role of biogeographical barriers on patterns of genetic differentiation. However, an increasing number of studies support the idea that connectivity may have contributed more than just vicariant barriers to modern species richness and genetic variation (Rull & Nogu   2007; Edwards et al. 2012; Fjelds   et al. 2012; Smith et al. 2014; Duncan et al. 2015; Cadena et al. 2016; Kol  r et al. 2016). In other words, diversification due to processes related to connectivity (e.g., colonization and episodic dispersal) could have had a bigger impact on mountain biodiversity than the isolation of populations. Here, we review how different processes intrinsic to the FCS triggered species diversification during the Pleistocene, discussing the consequences of increased and reduced connectivity and the triggers related to connectivity that stimulated diversification and species richness build-up.

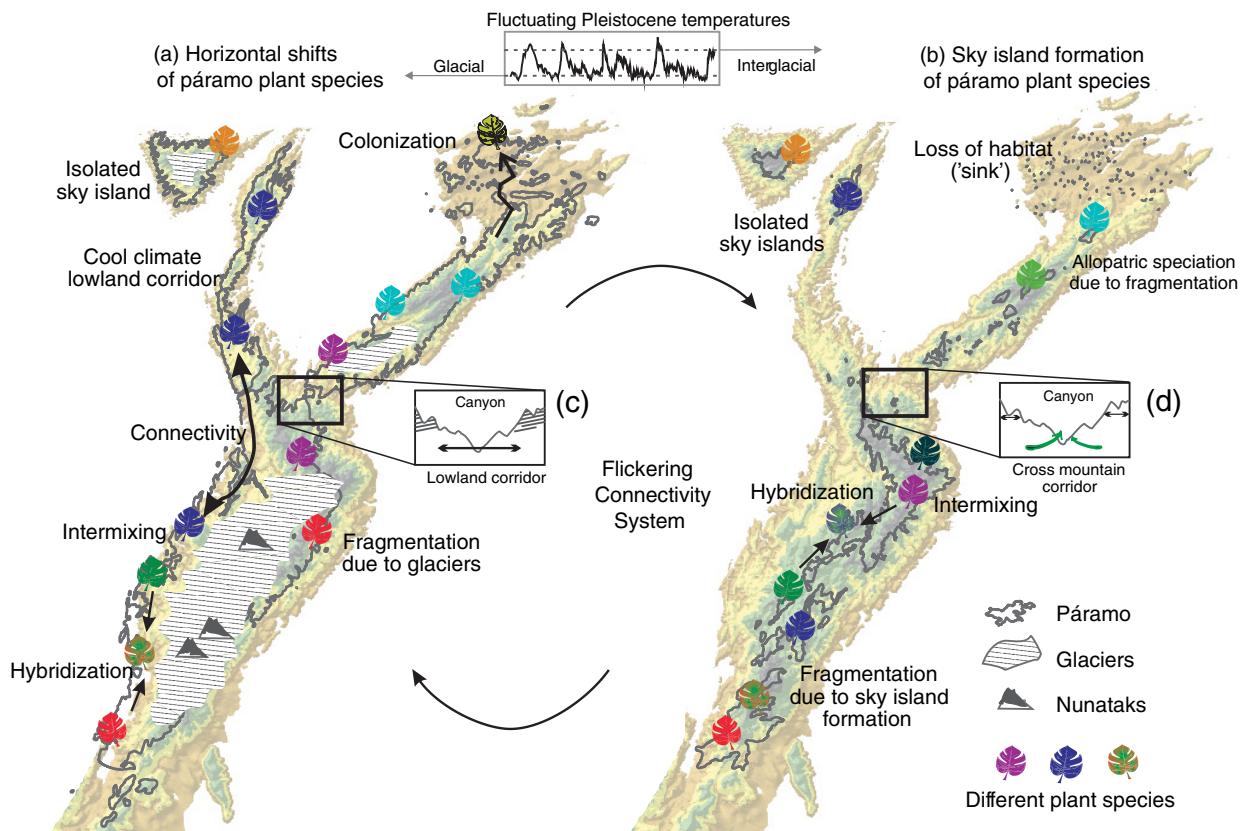
Signatures of past connectivity can be identified on short (decadal) time scales and long (millennial) time scales. For instance, patches of semi-natural grasslands that are currently in an isolated state but which were connected 50–100 years ago show a higher species richness than those patches that had a lower or no historical connectivity (Lindborg & Eriksson 2004). This legacy of historical connectivity has been observed on a spatial scale of only a few kilometers for species richness (Lindborg & Eriksson 2004) and genetic diversity (Ewers et al. 2013; M  nzbergov   et al. 2013), but on a global scale for freshwater fish biodiversity (Dias et al. 2014) and angiosperm diversity on islands (Weigelt et al. 2016). In the global cases, it is shown that the degree of historical connectivity thousands of years ago (LGM conditions) is still reflected in contemporary patterns of biodiversity. Hence, a key mechanism in explaining contemporary spatial patterns of species richness is the degree of past connectivity.

Evidence of historical connectivity is also scattered throughout the mountainous landscape. Previous states of mountain biome connectivity are evidenced by shared species in adjacent mountain regions, such as the highest part of the páramo (superp  ramo) (Luteyn 1999), that are currently highly isolated but still maintain a trans-Andean species distribution (Sklen  r & Balslev 2005). Likewise, contemporary disjunct populations in neighboring mountainous regions can have more genetic resemblance than those separated by elevation. This trans-mountain pattern is common and has been observed for butterflies (Hall 2005), mammals (Patterson et al. 2012) and birds (Arctander & Fjelds   1994; Fjelds   et al. 2012).

## 12.3 Components of the FCS

### 12.3.1 Processes and the Mountain Fingerprint

There are four processes inherent to the FCS that relate to the degree of connectivity: fragmentation, colonization (dispersal), intermixing and hybridization (Figure 12.1c). Each process plays a different and complementary role in maintaining richness or stimulating species diversification. They occur in a spatially and temporally dynamic manner, influenced by the local topography and the regional impact of climate fluctuations, and come together in what we call the “fingerprint” of a mountain (Figure 12.1d): the interaction between climate and topography, defining where and when each process of the FCS occurs. The mountain fingerprint can be considered to be a unique identifier, as mountains have different topographic profiles (Figure 12.2) and



**Figure 12.4** Spatial representation of the four intrinsic processes of the FCS in the Eastern Cordillera of the Colombian Andes. The potential distribution of páramo is shown during (a) cooler and (b) warmer conditions. The figure shows how different processes can occur at different locations throughout a mountain system, and as a result cause a spatially complex biogeographic pattern. The many possible intermediate configurations are shown in Figure 12.3. (c) Cool climate corridor of alpine species through a mid-elevation or lowland canyon. Glaciers are seen on the mountain tops. The arrow indicates the direction of connectivity. (d) Cross-mountain corridor between populations on either side of a mountain. Alpine species are restricted here to high elevation, and connectivity is reduced. See also Plate 27 in color plate section.

experience different degrees of climate fluctuations, and as a result the FCS is expressed in a distinctive manner for each mountain system. Figure 12.4 exemplifies the four processes of the FCS in the Eastern Cordillera of Colombia in order to highlight the mountain fingerprint in two different climate settings.

In this section, we discuss each of the different FCS processes and their implications for mountain biodiversity, looking particularly at the Andean páramo.

### 12.3.2 Fragmentation

Fragmentation of species distributions in mountain systems can occur in different ways. The many river valleys, intra-mountain valleys and high-elevation ridgelines form a labyrinth of potential hurdles and pathways for species to navigate. This complexity influences species

diversity. For instance, canyons influenced Andean bird (e.g., Weir 2009) and frog (e.g., Muñoz-Ortiz et al. 2015) diversity by imposing a physical barrier for the species to overcome. Similarly, mountain ridges, such as the dry forest patches in the Central Andes, capture species within geographically isolated patches, forming long-lasting isolated populations at high elevations (Pennington et al. 2010; Särkinen et al. 2012).

An additional mechanism of fragmentation in mountain ecosystems, which is often overlooked in the literature, is the glacial extent of ice caps on mountain tops and ridges during glacial periods (Osborne & Benton 1996). Mountainside populations may have differentiated due to the lack of cross-mountain gene flow, further stimulating intra-mountain endemism and diversification. For instance, periods with extensive ice caps have been linked to bird diversification events in the Southern

Alps of New Zealand (Weir et al. 2016) and to mammal diversification in various places (Chapter 14), showing the effect of recurring glacial fragmentation during the Pleistocene. Diversification rates of New Zealand birds increased fivefold due to the cyclical character of the Pleistocene climate – a pattern also observed for Neotropical birds (Weir 2006).

Small populations could have persisted on nunataks within ice shields, further contributing to the genetic variation of a region. Evidence for in situ survival exists for species in the European Alps (Stehlik et al. 2001; Schneeweiss & Schönswetter 2011). This means that allopatric speciation in alpine ecosystems such as the páramo probably occurred during both glacial (cross-mountain isolation) and interglacial (island top isolation) periods. This dual role of Andean topography, summarized in Figure 12.4, likely was a doubly reinforcing factor of Pleistocene páramo species radiations.

Restricted gene flow due to topographic barriers led to reproductive isolation and genetic drift. As a result, geographically isolated allopatric populations acquired unique and high genetic variation among populations, giving rise to high levels of endemism (Steinbauer et al. 2016). For example, refugia identified in the Alps show patterns consistent with areas known for their high levels of endemism and disjunct plant species (Schönswetter et al. 2005). In contrast to the Andean páramo, which expanded during glacial episodes (Figure 12.3), European mountain plant habitats were pushed into restricted peripheral sky islands towards the border of the European Alps (Schönswetter et al. 2005). Without a doubt, glacial refugia in the Alps played a key role in shaping biogeographical patterns of montane species endemism (Chapter 27) (Tribsch & Schönswetter 2003; Tribsch 2004).

The isolation of populations on multiple mountain tops, forming sky islands for short or extended periods during the Pleistocene, stimulated parallel radiations, population differentiation and inter-mountain endemism. A fragmented landscape is a key driver of radiations (Qian & Ricklefs 2000; Hughes & Eastwood 2006). Unsurprisingly, radiations of many plant lineages have occurred in topographically heterogeneous regions, such as the European Alps (*Gentiana*, *Globularia* and *Soldanella*: Kadereit et al. 2004), the Andes (*Lupinus*: Hughes & Eastwood 2006; *Campanulaceae*: Lagomarsino et al. 2016), the Rocky Mountains (*Penstemon*: Wolfe et al. 2006), the Himalaya (*Saussurea*: Wang et al. 2009) and the Drakensberg (*Macowanias*: Bentley et al. 2014). However, fragmentation and isolation alone are not enough to explain the evolutionary dynamics during the Pleistocene or the contemporary high species richness (Benham & Witt 2016).

### 12.3.3 Colonization

New habitat or space becoming available for colonization (the establishment after dispersal) is a key precursor of recent and rapid radiations (Linder 2008), and is therefore an important process of the FCS. New habitat can appear due to geologically recent mountain uplift and climate fluctuations, which facilitates (re)colonization. Due to the periodic nature of Pleistocene climate variations, colonization and subsequent population expansions occurred as episodic or cyclical events. Temporary connectivity facilitated colonization of new areas, and allopatry subsequently further induced differentiation (Smith et al. 2014; Cadena et al. 2016). Species may also respond to new habitat with increased diversification rates, as has been observed for the high rates of radiation in Ericaceae (Luteyn 2002). Thus, colonization played a significant role in stimulating diversification (Pennington & Dick 2004).

Just as Weir et al. (2016) were able to relate cold conditions and glacial fragmentation to diversification events in birds, so colonization events and diversification can be linked to climate conditions becoming optimal for connectivity, as shown by Collevatti et al. (2015) in the Brazilian highlands. Also, cross-Andean movements of bird taxa were facilitated by shifting climatic conditions (Figure 12.4d), and as a result each episodic dispersal across the Andes caused the formation of independent lineages on either side of the mountains (Miller et al. 2008). Similarly, Collevatti et al. (2015) observed an increase in the number of plant lineages within the short time frame of the Pleistocene due to connectivity driven colonization. Thus, climate change was a driver of species diversification not only because it led to habitat fragmentation, but also because it connected habitats and created new habitats to be colonized.

Interestingly, mountains that are old (e.g., Cape Fold Mountains, South Africa and the Great Dividing Range, Australia) display only a few or no recent and rapid radiations (Linder 2008). Due to the fact that there have been no active geological processes during geologically recent times to create new topographies, and as the topography itself has become eroded, the mountain fingerprint (Figure 12.1d) is “flattened,” and fluctuating climate conditions lack the topographic complexity pairing needed to stimulate radiations through new habitat and colonization.

New habitats are important for radiations but are not sufficient preconditions on their own (Linder 2008). Even if new habitat is potentially available through physical connectivity, differences in dispersal ability result in different biogeographic patterns among species (Dobrovolski et al. 2012; Papadopoulou & Knowles 2015a). Such differences, the degree of connectivity and

the directionality of patterns of dispersal all contribute to the complex patterns of beta diversity and phylobetadiversity (phylogenetic relatedness across space) (Graham & Fine 2008). Additionally, the randomness of long-distance dispersal events, independent of propagule type, adds to the intricacy of the biogeographical picture researchers try to assemble (Pennington et al. 2006). What is clear is that within the FCS, a vast number of colonization opportunities arise, fuelling diversification.

#### 12.3.4 Intermixing

Many sky islands formed, separated and reconnected through repeated pulses of expansion and contraction. This spatial effect is comparable to the shifting areas and connectivities of oceanic islands driven by sea level change, emphasizing the high resemblance between oceanic islands and sky islands. Interestingly, both systems are known to show rapid and recent radiations (see overview in Hughes & Atchison 2015). Furthermore, both boundaries are sharply defined, causing dispersal limitations, and are temperature-dependent: higher temperatures during Pleistocene interglacial periods correspond to a high sea level and high UFL position. During glacials, sea levels were roughly 120 m lower than they are at present (e.g., Rijsdijk et al. 2014; Spratt & Lisiecki 2016), while the UFL was between ca. 900 m (New Guinea) and ca. 1800 m (East Africa) lower (Coetzee 1967; Flenley 1979). These glacial–interglacial shifts in elevation and isolation have been widely identified as key features of the biogeographical history of insular systems, but their relationship to modern biodiversity and evolutionary radiations remains incompletely understood.

The isolation and fusion of oceanic islands caused multiple episodes of allopatric speciation and intermixing of species composition (Ali & Aitchison 2014; Gillespie & Roderick 2014). Intermixing (Figure 12.1c) facilitated by increased connectivity after isolation has been shown to be an important predictor of present diversity patterns on islands. Historical connectivity between islands facilitated intermixing of once single-island endemics into archipelago endemics, increasing the overall species richness of connected islands (Weigelt et al. 2016). Especially in clusters of islands, species diversity benefitted from parallel radiations on isolated islands during interglacial isolation, while subsequent reconnection during glacial periods had intermixing and possibly also hybridization as a consequence (Ali & Aitchison 2014). Thus, previously connected islands are characterized by higher total species richness, lower single-island endemism and higher levels of compositional similarity.

The described effect of historical connectivity on endemism has been observed for freshwater fish diversity (Dias et al. 2014) and sky islands. An example of the latter

is seen in the Andes: in Ecuador, the downward shift during glacial periods connected most superpáramo, possibly causing the relatively low number of single-sky island endemics and the high number of trans-Andean species (Sklenář & Balslev 2005). In the same shift in Colombia, topographic barriers inhibited an increase of connectivity between sky islands, and as a consequence a high number of single-sky island species can now be observed. The lack of historical connectivity in Colombian superpáramo is confirmed by the extremely low genetic diversity within populations and the high genetic differentiation among them (Sklenář & Balslev 2005).

The spatial configuration of islands in the past contributes to a higher species richness today than would be expected from current settings. Small islands located between two larger islands or that were once part of a larger connected island can still display the legacy of the historically connected state, and thus disobey the expected species-area relationship. As a result of historical connectivity, small sky islands can be more species-rich than their larger counterparts, which can confound relationships between endemism and montane land area that do not account for historical effects (Adams 1985; Sklenář & Balslev 2005).

#### 12.3.5 Hybridization

Historical connectivity increases plant species richness not only through intermixing, but also through hybridization after reconnection (Ali & Aitchison 2014; Gillespie & Roderick 2014). Hybridization (Figure 12.1c) can contribute to overall species richness through the formation of new hybrid taxa and thus new lineages alongside the parental taxa. A causal relationship between Quaternary climatic changes and the secondary contact of previously isolated populations and sympatric speciation via hybridization is observed in mountain regions such as the Alps (Comes & Kadereit 1998; Kadereit 2015). Evidence is also found for the emblematic stem-rosette plants of the Asteraceae family, for which the columnar life form of the genus *Espeletia* (also known by its local name, “frailejon”) stands as an example. Together with seven other genera, *Espeletia* forms the Espeletiinae (Cuatrecasas 2013; Hooghiemstra et al. 2006), which has undergone many radiations (Madriñán et al. 2013) and frequent hybridization at numerous contact zones (Diazgranados 2012; Diazgranados & Barber 2017). Importantly, there is evidence of extensive gene flow and hybridization in páramo plant species (e.g., *Loricaria*: Kolář et al. 2016; *Espeletia*: Diazgranados 2012; Diazgranados & Barber 2017), suggesting a relationship between connectivity, hybridization and radiation.

Hybridization at contact zones (the melting pots of genetic material between former isolated populations)

leads to high species richness and facilitates species radiations (Petit et al. 2003; Grant 2014). Clusters of these contact zones between connecting refugia are concentrated in mountain ridges, cross-mountain passes and mid-elevation corridors; such clusters have been identified for mountains in North America (Swenson & Howard 2005) and Europe (Hewitt 1996, 1999). For example, based on contemporary floristic evidence, it can be inferred that biogeographical boundaries in the Alps are remnants of refugia reconnection points (Schönswitter et al. 2005).

High levels of genetic diversity in refugia may reflect more stable population dynamics and larger population sizes. This diversity may also have accumulated over several climatic oscillations, not necessarily because they were stable climatically (see the páramo example, which was highly dynamic), but because they concentrated diversity from previously connected larger systems. This emphasizes the need to identify not only the locations of past refugia, but also where historical connectivity allowed exchange of genetic material between previously isolated populations, possibly enabling hybridization and consequent co-evolution.

In summary, the FCS incorporates four different processes, all of which have been identified as drivers of diversification, and which together have led to the accumulation of species in biodiverse ecosystems. Assessing the northern Andes in light of this framework shows repeating patterns of historical connectivity of sky-island archipelagos, which may have significantly contributed to the high species richness and radiations there. The reason that many sky-island complexes have high species richness and recent diversification (Hughes & Atchison 2015) is postulated to be due not only to phases of isolation but also to the opportunities provided through historical connectivity.

## 12.4 Perspectives on Paleogeographic Reconstructions and Historical Connectivity

Reconstructing evolutionary history and the governing processes behind diversification in complex landscapes is a difficult task, but through interdisciplinary approaches and techniques the biogeographic history can slowly be untangled. A complete review of future guidelines on paleoreconstructions goes beyond the scope of this paper, but it is clear that many opportunities and challenges lie ahead (see review on Neotropical plant evolution in Hughes et al. 2013). Here, we will briefly mention the value of spatial reconstructions in assembling the biogeographical picture of mountain

areas on a global scale and the possible role historical connectivity plays through time.

Spatially explicit models that consider historical connectivity have strong explanatory power for species turnover dynamics across a region (Graham et al. 2006). Differences in plant species richness between tropical sky islands (Andes, East Africa and New Guinea; Sklenář et al. 2014) and oceanic islands (Japanese archipelago; Wepfer et al. 2016) have already been attributed to their degrees of historical connectivity. When habitat connectivity is calculated across a series of time periods under different environmental conditions, a significant relationship with contemporary biodiversity emerges (Graham et al. 2010). Assessing alpine ecosystems from different mountain regions in light of this framework can provide crucial insights into the legacy of climate and topography as summarized by the system's mountain fingerprint (Figure 12.1d).

Due to the uniqueness of each mountain's topography (Figures 12.1d and 12.2), the divergence times of radiations during the Pleistocene are mountain-, biome- and probably even sky island-specific. Expectations of concordant timing and patterns of diversification among mountain systems are unrealistic, due to the inherent heterogeneity among sky-island systems (Papadopoulou & Knowles 2015b). Genetic diversity patterns are expected to be dissimilar depending on which sky-island species survived the Pleistocene (Bidegaray-Batista et al. 2016). Therefore, it is expected that different diversification histories exist for different biomes as well (Pennington et al. 2006; Hughes et al. 2013).

Creating paleogeographic maps for different moments during the Pleistocene, as has been done for oceanic islands (Warren et al. 2010; Ali & Aitchison 2014; Rijsdijk et al. 2014), is key to understanding a region's degree of connectivity through time and space. Paleogeographic reconstruction along different altitudinal gradients also improves our understanding of the differences in diversification between lower- and upper-elevation biomes, as has been suggested by studies in the Alps (Kropf et al. 2003) and in Venezuelan tepuis (Rull & Nogué 2007; Nogué et al. 2013; see Chapter 23).

Paleo-niche reconstructions can provide additional insights into historical connectivity and increase our understanding of supposed dispersal barriers. Paleo-niche models can show where and under what climatic conditions topographic barriers were removed. For example, genetic flow has been reconstructed between sister clades on either side of a steep topographic depression between the Venezuelan and Colombian Andes (Gutiérrez et al. 2015). Furthermore, the combination of paleo-niche modeling with phylogeography is a powerful approach to reconstruct historical connectivity

(Maguire et al. 2015), and recent studies are rapidly adding to our understanding of the current biodiversity in relation to past connectivity (e.g., Sobral-Souza et al. 2015; Melville et al. 2016; Thomé et al. 2016).

## 12.5 Conclusion

Climate change and topography are key abiotic, extrinsic variables that influence species diversification (see Chapters 16 and 18). In this chapter, we have focused on the consequences of the reshuffling of species distributions in mountain landscapes, emphasizing how historical connectivity plays an important role in species diversification.

The present interglacial patterns of diversity and environments often serve as the implicit or explicit backdrop to most hypotheses developed to explain contemporary biodiversity. However, historical connectivity played an important role in contemporary spatial biogeographic patterns, particularly in terrestrial and oceanic systems characterized by repeated changes between high and low connectivity. The fact that different disciplines are increasingly discussing the importance of historical mechanisms in mountain diversity opens up the possibility of more interdisciplinary hypothesis-building. In this chapter, we showcased historical connectivity as an important mechanism underlying Pleistocene radiations, and posited that the combination of environmental heterogeneity, topographic complexity and Pleistocene climatic fluctuations created a “flickering connectivity system” (FCS) in which alpine sky islands

connected and disconnected at different moments in time and at different locations. In particular, the taxa from the Andean alpine biome, the páramo, have shown exceptionally recent evolutionary radiations, which we link to past extended phases of high connectivity. The dynamics of historical connectivity in archipelago formations are powerful forces in creating and explaining the spatially complex patterns of biodiversity (Gillespie & Roderick 2014).

Due to topographic complexity, the effect of climate oscillations on diversification is not expected to be spatially or temporally synchronous between or within mountains or between species. Insights derived from paleotopographic reconstructions, as exemplified here, provide the necessary platform for new hypothesis development with regard to biological evolution in sky islands and the intriguing interplay between climate and geology.

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