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Colombia in the Quaternary: An Overview of Environmental and Climatic Change

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Abstract We provide an overview of environmental and climatic change in Colombia during the Quaternary, the last ca. 2.58 million years (Ma) before present. This period is characterised by a suite of glacial–interglacial cycles which are remarkably well documented in Colombian sediments. The distribution of Colombia's main ecosystems has changed repeatedly driven by orbital forcing at 21, 41, and 100 ky frequencies which were superimposed by millennial–scale (ca. 2.5 ky) climate oscillations. Fossil pollen records have detected biome dynamics through time but records vary in length: the shortest comes from the Chocó rainforest (extending back to ca. 7 thousand years before present, ka) and dry inter–Andean forest (ca. 12 ka), followed by the savannas of the Llanos Orientales (ca. 20 ka), the Amazonian rainforests (ca. 40 ka), and lower montane forest (ca. 40 ka). The longest records are from the deep sedimentary basins Bogotá (Funza09, last 2.25 Ma) and Fúquene (last 284 ka), alternatingly located in the upper montane forest and páramo during interglacial and glacial conditions, respectively. Climate change caused shifting biome distributions: mainly latitudinally in the lowlands and elevationally in the mountains. Extrinsic drivers (e.g., mean annual precipitation, length of dry season, atmospheric pCO_2, mean annual temperature, freezing days) of migration and changes in vegetation composition and intrinsic drivers (such as interspecies competition and legacy effects) are still insufficiently understood, and thus hamper meaningful projections of the effect of future environmental change on biomes. Multi–site Pleistocene and Holocene information has been spatially synthesised by developing the Latin American Pollen Database. Multi–site information has been analysed by the biomisation method to serve palaeodata–model comparisons and projections about the future of biomes in Colombia. A new method in which pollen–based palaeo–reconstructions are spatially analysed with digital elevation models improved our understanding of spatial and elevational shifts of ecotones, for example the upper forest line, in the northern Andes. In the supplementary information we highlight the strengths and weaknesses in current Quaternary palaeoecological research and provide suggestions for future research.

Keywords: *climate change, Colombia, environmental change, pollen records, quantitative analyses, Quaternary non–analogue environments.*

Resumen Presentamos una visión general del cambio ambiental y climático en Colombia durante el Cuaternario, últimos ca. 2,58 millones de años antes del presente (2,58 Ma). Este período se caracteriza por un conjunto de ciclos glaciales e interglaciales que se encuentran bien registrados en los sedimentos colombianos. La distribución de los

Supplementary materials:

S1: https://www.sgc.gov.co/LibroGeologiaColombia/tgc/sgcpubesp38201902s1.pdf

S2: https://www.sgc.gov.co/LibroGeologiaColombia/tgc/sgcpubesp38201902s2.pdf

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principales ecosistemas de Colombia ha cambiado repetidamente debido al forzamiento orbital a frecuencias de 21 000, 41 000 y 100 000 años que fueron superpuestas por oscilaciones climáticas a escala milenaria (ca. 2500 años). Los registros de polen fósil han detectado la dinámica del bioma a través del tiempo; sin embargo, estos registros varían en duración: los registros más cortos provienen de la selva húmeda tropical del Chocó (extendiéndose hasta ca. 7000 años antes del presente, ka) y del bosque seco interandino (ca. 12 ka), seguidos por las sabanas de los Llanos Orientales (ca. 20 ka), las selvas tropicales amazónicas (ca. 40 ka) y los bosques montanos bajos (ca. 40 ka). Los registros más largos corresponden a las cuencas sedimentarias profundas Bogotá (Funza09, últimos 2,25 Ma) y Fúquene (últimos 284 ka), ubicadas alternativamente en el bosque montano superior y el páramo durante las condiciones interglaciares y glaciales, respectivamente. El cambio climático provocó cambios en la distribución de los biomas: sobre todo latitudinalmente en las tierras bajas y altitudinalmente en las montañas. Los factores extrínsecos de la migración (p. ej. la precipitación media anual, la duración de la estación seca, la $p\mathrm{CO}_2$ atmosférica, la temperatura media anual y los días de congelación) y los cambios en la composición de la vegetación y los factores intrínsecos (entre ellos la competencia interespecie y los efectos heredados) no son lo suficientemente comprendidos y, por lo tanto, dificultan las proyecciones del efecto de los cambios ambientales futuros en los biomas. La información pleistocena y holocena de múltiples sitios se ha sintetizado espacialmente mediante el desarrollo de la base de datos palinológicos de América Latina. La información palinológica de múltiples sitios se ha analizado mediante el método de biomización para contribuir a los modelos basados en datos paleontológicos y proyecciones sobre el futuro de los biomas en Colombia. Un nuevo método en el que las paleoreconstrucciones basadas en datos palinológicos se analizan espacialmente con modelos digitales de elevación mejoró nuestro entendimiento sobre los cambios espaciales y altitudinales de los ecotonos, por ejemplo, la línea forestal superior en los Andes del norte. En el material suplementario de este capítulo destacamos las fortalezas y debilidades en la investigación paleoecológica cuaternaria y ofrecemos sugerencias para futuras investigaciones.

Palabras clave: *cambio climático, Colombia, cambio ambiental, registros palinológicos, análisis cuantitativos, ambientes cuaternarios sin análogo.*

1. Introduction

1.1. Colombia in the Quaternary

The Quaternary is defined in the geological record as the last 2.58 million years (Ma) before present (Gibbard et al., 2010). This period is characterised by glacial–interglacial cycles with increasing amplitude during the last 1 Ma. By fitting together palaeoecological records, a continuous story of Quaternary terrestrial climatic and environmental change has been established (e.g., van der Hammen, 1961; van der Hammen et al., 1971; Zagwijn, 1975). For South America in particular, among others Troll (1968), Troll & Lauer (1978), Flenley (1979a, 1979b), van der Hammen (1979) and van der Hammen et al. (1973) present early pioneering work on the Quaternary of the Neotropics. Marine sediment archive V28–238 (Shackleton & Opdyke, 1973) provided an early key record of Pleistocene climate change based on oxygen isotopes (∂^{18}O), which formed the basis of a system of oxygen isotope stages, later named marine isotope stages (MIS). The start of the Quaternary coincides with MIS 100. Lisiecki & Raymo (2005) developed a ∂^{18}O stack record based on 57 of the best oxygen isotope records which now serves as a global yardstick of Quaternary climate change in the marine environment. This record is also a valuable reference of environmental change in terrestrial environments at the scale of ice ages and a measure of Pleistocene time.

Orbitally driven changes in climate conditions (Abels & Ziegler, 2018; Cronin, 2009) prevailed during pre–Quaternary times (Zachos et al., 2001), although differences between cool and warm intervals were less pronounced. During the late Miocene and Pliocene, the uplift of the northern Andes was completed (Bermúdez et al., 2017; Graham, 2009; Helmens & van der Hammen, 1995; Hoorn & Wesselingh, 2010; Hoorn et al., 2010, and references therein) and the Great American Biotic Interchange had started (Leigh et al., 2014; Stehli & Webb, 1985; Woodburne, 2010; see also Hooghiemstra, 2006; Hooghiemstra et al., 2006). An understanding of the prelude to the Quaternary in terms of geology and climate is important to understand better the biogeographical and evolutionary consequences for biomes during the Quaternary. However, records covering the Pliocene and earliest Quaternary times are fragmentary (e.g., van der Hammen et al., 1973; Wijninga, 1996a, 1996b, 1996c;

Wijninga & Kuhry, 1990, 1993) or the facies are unsuitable for the extraction of palynomorphs.

In Colombia, the deep sedimentary basins of Bogotá and Fúquene contain unique series of sediment accumulation in which much of Colombia's environmental and climate history of the Quaternary has been preserved. The subsidence of the floor of the Bogotá Basin has allowed a thick sediment accumulation. One core—Funza–2—reaches 586 m depth. The Funza09 record is based on a composite in which the Funza–1 and Funza–2 cores are combined. The upper 485 m has been astronomically tuned and spans an age of 27 ka to 2250 ka. This means the deepest part of the Bogotá Basin (from 485 to 586 m) should be older than 2.25 Ma. An absolute age of an ash layer of 2.58 Ma in the lower part of the Funza–2 core indicates that the sediments at 586 m core depth are of latest Pliocene age (Andriessen et al., 1993; Torres et al., 2013). This unparalleled record is instrumental in understanding long–term changes in elevational vegetation distribution from which Quaternary climate change and the evolutionary composition of the north Andean mountain flora has been inferred (Flantua & Hooghiemstra, 2018; Hooghiemstra, 1984; Torres et al., 2013).

For the Quaternary of the tropics, and for the Neotropics in particular, only a few overviews (Clapperton, 1993; Flenley, 1979a, 1979b; Heine, 2018; Heusser, 2003; Hoorn et al., 2010; Livingstone & van der Hammen, 1978) or thematic collections of research papers (Bush et al., 2011; Hoorn & Wesselingh, 2010; Hoorn et al., 2010, 2018; Markgraf, 1993, 2001; Vimeux et al., 2009) are available. More general Quaternary palaeoclimatology and environmental change research is well presented in Bradley (2015), Cronin (2009), Ehlers et al. (2016), Elias (2007), Ruddiman (2008), and Veblen et al. (2007). The present–day flora and vegetation of Colombia has been studied in much detail, we mention here Cuatrecasas (1934), Espinal & Montenegro (1963), Pinto–Escobar (1993), (figures 1, 2), and for the wider Neotropics Graham (2010), Hueck & Seibert (1972) and UNESCO (1981). These studies serve to interpret pollen records into reconstruction of past vegetation change.

The objective of this paper is to provide an overview of the Quaternary history of Colombia's main biomes and to guide the reader through almost seven decades of palaeoecological research in this country. Issues of debate are identified and briefly discussed and references are provided for further reading. For each biome, we highlight the strengths and weaknesses of our current understanding: potential research questions for future studies are identified in the Supplementary Information S1. In this paper periods of time are expressed as "kiloyears" (ky), and ages of kiloyears before present either as "ky BP" or "ka".

1.2. Depositional Environments of Pollen Records

To collect lacustrine and fluviolacustrine sediments for pollen analysis, there is an overall sample bias towards extant lakes where the organic matter tends to be better preserved. Fluvial deposits have been less explored as frequent hiatuses in such records hamper age models, and fluvial redeposition of sediment and pollen content may impede the interpretation of the pollen spectra due to the mixed local, regional, and extra–regional influx (van der Hammen & Hooghiemstra, 2000). In

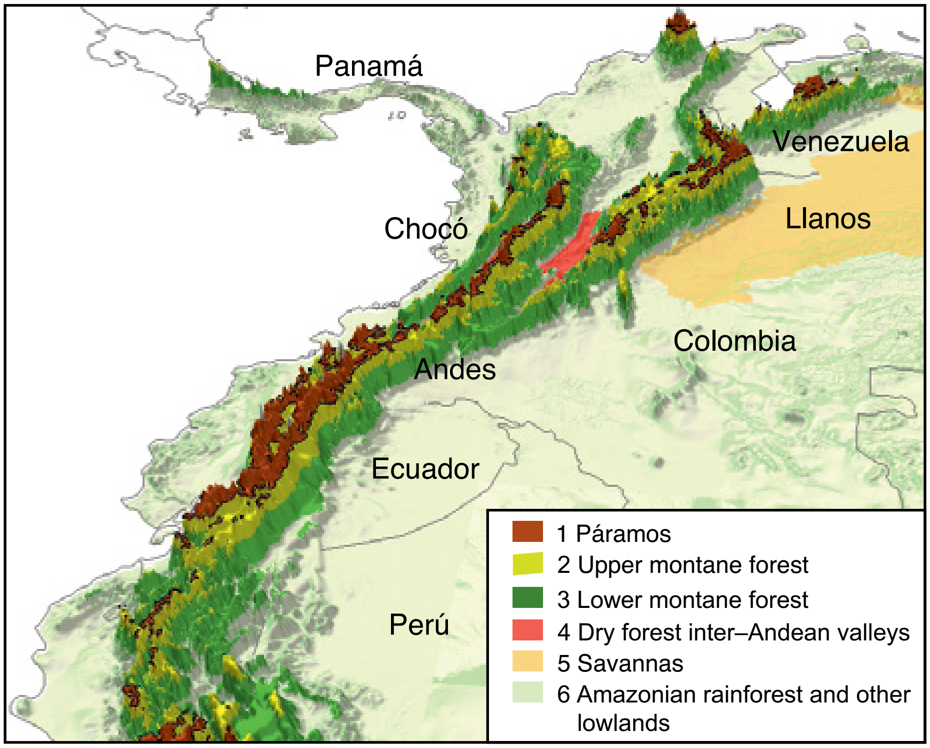

Figure 1. Overview of Colombia's ecosystems as distributed at present–day: **(1)** páramos, **(2)** upper montane forest, **(3)** lower montane forest, **(4)** dry forest of the inter–Andean valleys, **(5)** savannas of the Llanos Orientales, and **(6)** Amazonian rainforest and other lowlands.

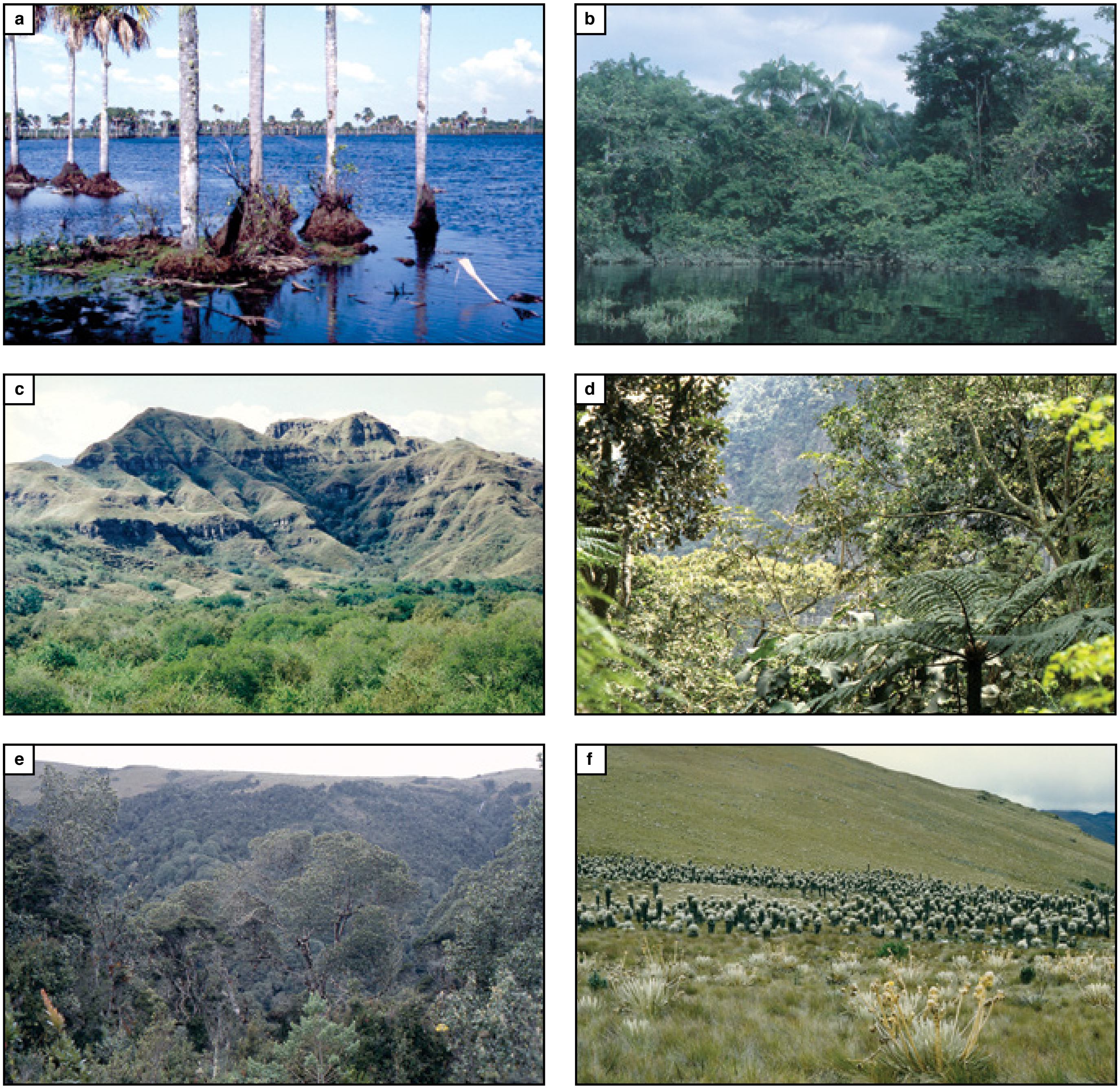

Figure 2. Representative vegetation of six selected biomes discussed in the text: **(a)** savanna of the Llanos Orientales at Lake El Piñal (ca. 180 m a.s.l.); **(b)** rainforest of Chocó at Lake Caimito (ca. 50 m a.s.l.); **(c)** dry forest vegetation at swamp Quilichao (1020 m a.s.l.); **(d)** lower montane forest at Parque Chicaque in the Eastern Cordillera at 2250 m a.s.l.; **(e)** upper montane forest in Guandera (northernmost Ecuador) showing an almost undisturbed upper forest line (UFL) at 3600 m a.s.l.; **(f)** grasspáramo with flowering *Espeletia* sp. near Bogotá at 3600 m a.s.l. (Photographs by Henry HOOGHIEMSTRA).

such cases, performing a multiproxy analysis can provide a much–needed complementary interpretation (Castilla–Beltrán et al., 2018; Hooghiemstra et al., 2018). For example, in the southern Magdalena River valley, a climatic reconstruction of the intra–Andean valley of the last 67.7 ka was done based on both sedimentology and palynology (Bakker, 1990; see also Wille et al., 2001). In the northern Magdalena River valley a 10 ka record was developed of the frequently flooded wetlands based on pollen, lithology, clay mineralogy, soil and sediment geochemistry, and ∂^{13}C values (Berrío et al., 2001).

Environmental histories from fossil pollen records often reflect the dynamics of a single biome (e.g., most records from the Llanos Orientales and Chocó) and do not go further back in time than the start of the Holocene (Flantua et al., 2015). Many records reach the Lateglacial, but not beyond the Last Glacial Maximum (Flantua et al., 2015). For instance, records from the savannas of the Llanos Orientales cover the last ca. 20 ka, those of the Amazonian rainforest the last ca. 40 ka, the Chocó rainforest the last ca. 7 ka, and the dry forest biome the last ca. 12 ka. There are a handful of records from the lower montane forest though that cover the last ca. 40 ka, and from the upper montane forest and páramo biomes that even cover the last 2.25 Ma. Here we will synthesise for each separate biome the current knowledge of its biogeographical setting, availability of records, and environmental dynamics during the Quaternary to provide an overview of the biome history in Colombia.

2. Quaternary Histories of Colombian Biomes

2.1. Savannas of the Llanos Orientales

Setting: The savannas of the Llanos Orientales are bordered by the rivers Vichada in the south, Orinoco in the east, and Arauca and Meta in the north (Romero–Ruiz et al., 2012). Climate is warm and humid during the rainy season (April to November) and warm and dry during the dry season. Mean annual precipitation varies from ca. 800 to 2500 mm. The mean annual temperature is 26–27 °C with annual variation of less than 3 °C between the monthly means. Daily temperature variation is 10–15 °C (Blydenstein, 1967; Botero, 1999; Müller, 1988). The vegetation consists of an open layer of trees and shrubs mainly along the drainage system in combination with a continuous herbaceous cover (Mistry, 2000; Romero–Ruiz et al., 2012). Vegetation cover varies from treeless savanna grassland to savanna–woodland with up to 80% tree cover (Sarmiento, 1984) (Figure 3). *Curatella* and *Byrsonima* are the most characteristic trees of woody savanna and their potential presence is well recognized in pollen records.

Evidence: The first pollen records were published by Wijmstra & van der Hammen (1966). HOOGHIEMSTRA and BEHLING explored the Llanos in 1997 and collected cores from lakes and swamps in the departamentos del Meta and Vichada. Between 1998 and 2003, pollen records were published from lakes El Angel, Sardinas, El Piñal, Carimagua, Carimagua–Bosque, Loma Linda, Chenevo, Mozambique, and Las Margaritas. The long and dry period in the departamento de Arauca causes a sparse accumulation of sediments and poor pollen preservation. Lake floors consist of hard "sun baked" clayey sediments, hampering the archiving of regional environmental history in the sediments.

Results: Pollen diagrams show a competition between palm forest (*Mauritia* and *Mauritiella*), open herbaceous vegetation, and woody vegetation of shrubs and trees which may develop dense vegetation in gallery forests along the drainage system (Figure 4). From the Last Glacial Maximum at 20 ka to ca. 7 ka, dry herbaceous vegetation prevailed. Depending on the location, woody vegetation increased between ca. 7.1 and 5.3 ka. In most sites the proportion of palms increased rapidly between 4 and 3.6 ka, possibly driven by higher mean annual precipitation and/or a longer wet season, causing an increase in the area with stagnant water (Figure 5). The start of human occupation in the savanna area, however, may have coincided with this change to more mesic climate conditions. Palms provide food and services to local communities (e.g., construction material), and the significant increase in palm cover may reflect a form of agroforestry of the earliest inhabitants of the savanna region (Rull & Montoya, 2014; Rushton et al., 2012).

2.2. Amazonian Rainforest

Setting: The Colombian part of the Amazonian rainforest is located in the concave area of the Andes where Atlantic moisture is forced to ascend and causes orographic rains. Rainforest needs a minimum mean annual precipitation of 1500–1800 mm y^{-1} and a short (<3 months) dry season. Rainforest is not as monotonous as often thought as changes in drainage quality, annual flood frequency by rivers, and soil nutrients (nutrient rich vs. poor) can host a variety of forest types (Duivenvoorden & Lips, 1995). Sandstone plateau experience continuously relatively dry soils resulting in geologically driven islands of savanna–like vegetation (Berrío et al., 2003).

Evidence: Urrego (1994) discusses three pollen records from abandoned sediment–filled meanders covering the last ca. 7 ka. Behling et al. (1999) interpret three pollen records from the swamp area Pantano de Monica on the lower terrace of the Caquetá River, jointly covering the last 11 ka. Apart from sediment–filled meanders that mostly reflect Holocene sediments, long sediment records that include the Last Glacial Maximum are rare and are still lacking in the Colombian part of Ama-

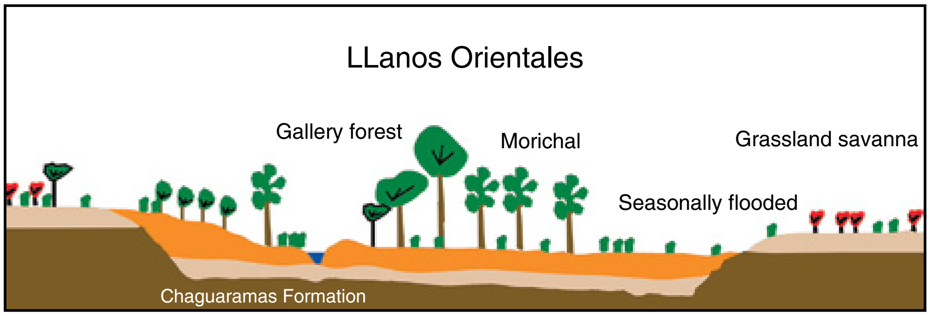

Figure 3. Schematic cross–section through the Colombian savanna area showing the relationship between landscape topography, drainage system, and vegetation. (Reproduced with permission from Hooghiemstra & Berrío, Encyclopedia of Quaternary Science, Vol. 4 (2007): p. 265., Copyright Elsevier).

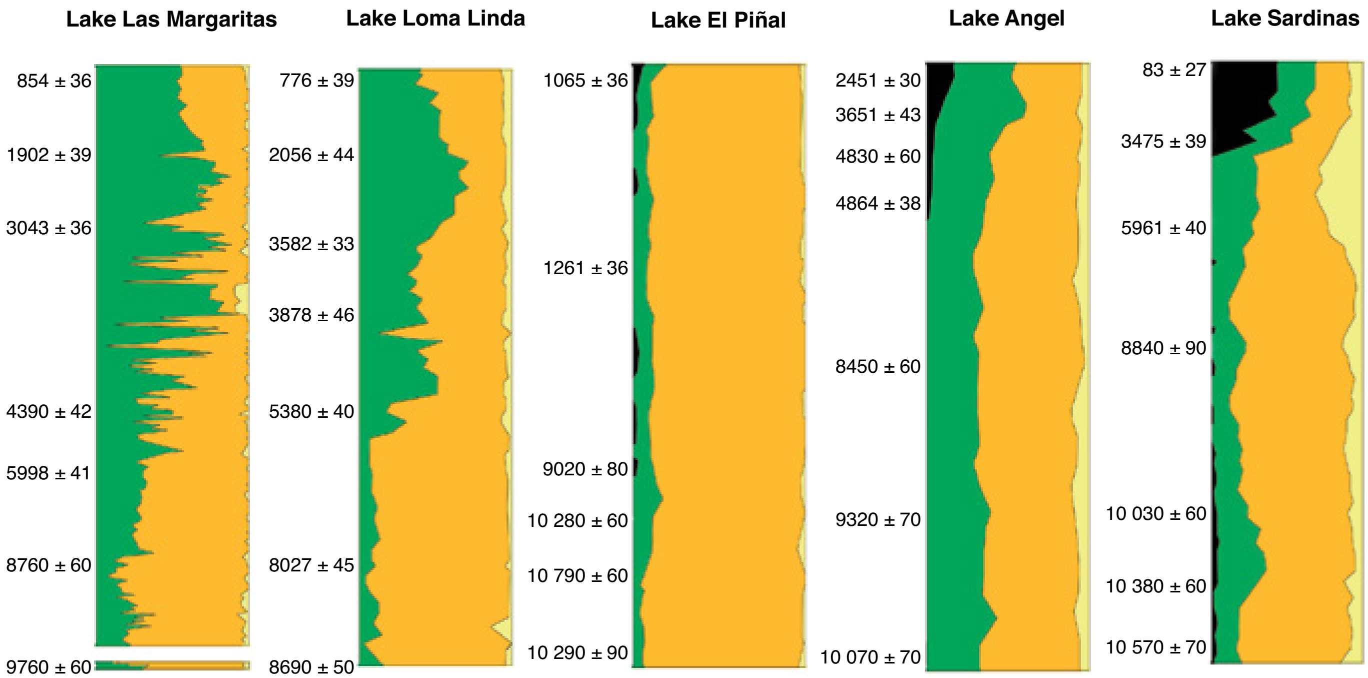

Figure 4. Holocene vegetation change in the savanna of the Llanos Orientales. The precipitation—dependent competition between wooded—savanna (in green) and open savanna herbs (in orange) and savanna herbs (in yellow) is shown. Black: proportion of Mauritia and Maritiella palms. Main pollen diagrams from 5 lakes from a west (near the foot of the Andes; left in the figure) to east (central part of the savanna area; right in the figure) transect Lake Las Margaritas, Lake Loma Linda, Lake El Piñal, Lake Angel, and Lake Sardinas. Data are plotted along the time scale (radiocarbon y BP). After Behling & Hooghiemstra (2000), Berrío et al. (2002a), and Wille et al. (2003). (Reproduced with permission from Hooghiemstra & Berrío, Encyclopedia of Quaternary Science, Vol. 4 (2007): p. 2655, Copyright Elsevier).

zonia. Modern pollen rain studies in Amazonian forest types have been insufficiently developed but tall *terra firme* forest in Bolivia has been characterised by Gosling et al. (2005).

Results: Pollen records register vegetation succession after a meander has been abandoned (Urrego, 1994). Vegetation develops from a *Cecropia*–dominated pioneer forest to a more diverse várzea (seasonal floodplain) forest, and subsequently changes into a palm forest dominated by *Mauritia*. Records from Pantano de Monica show changing forest composition with higher proportions of *Podocarpus* in Lateglacial times, which, according to some authors, is indicative of lower mean annual temperature. However, this increase can also be attributed to downslope fluvial transport of pollen from cool montane forest as evidenced by Berrío et al. (2002a) and discussed by van der Hammen & Hooghiemstra (2000). The interpretation of *Podocarpus* in the Amazonian lowlands is still much debated (D'Apolito et al., 2013, 2017; Punyasena, 2008; Punyasena et al., 2008, 2011). The montane tree *Podocarpus* reached higher abundance in last glacial Amazonian forests but the interpretation of this evidence varies from little temperature depression of 2–3 °C (van der Hammen & Hooghiemstra, 2000) to 5–6 °C cooling during glacial times (Bush et al., 2004; Cárdenas et al., 2011; Colinvaux et al., 1996; D'Apolito et al., 2013; see also Waelbroeck et al. 2009 and Loomis et al., 2017). Apart from competition between forest taxa, the abundance of palm vegetation (*Mauritia*, *Euterpe*) is also subject to change (Behling et al., 1999). Effects of climatic dryness and low atmospheric $p\mathrm{CO}_2$ on Amazonian vegetation are difficult to disentangle from temperature changes and the current data are inconclusive. The rainforest biome is mainly driven by changes in mean annual precipitation and the length of the dry season, whereas a suite of intrinsic factors such as drainage, flooding frequency, nutrient status, and legacy effects (Bürgi et al., 2017; Cavender–Bares et al., 2016; Cuddington, 2011) determines its taxonomic composition.

Palaeoecological research in Amazonia has long been driven by the debate to support or reject the "forest refugia hypothesis" of Haffer (1969) who postulated a hypothesis to explain the high biodiversity in this region. Ecologists and palaeoecologists engaged vigorously in the discussion but for a long time were unable to provide decisive evidence to prove or disprove Haffer's elegant hypothesis. Although Endler (1982) concluded that many of the assumptions of the refuge hypothesis were not justified, the debate continued for three decades (e.g., Haffer & Prance, 2001). In America, Haffer's hypothesis was discarded earlier (compare Figure 12.7 in Bush (1997) with Figure 15.8 in Bush 2000) than in Europe. The papers by Colinvaux et al. (2000) and van der Hammen & Hooghiemstra (2000) reflect well the state–of–the–art thinking on the matter at the turn of the century. The real breakthrough came with new lines of evidence from molecular phylogenies of plants and animals framed in an improved geological context (Hoorn & Wesselingh, 2010; Hoorn et al., 2010). These advances showed that much of Am-

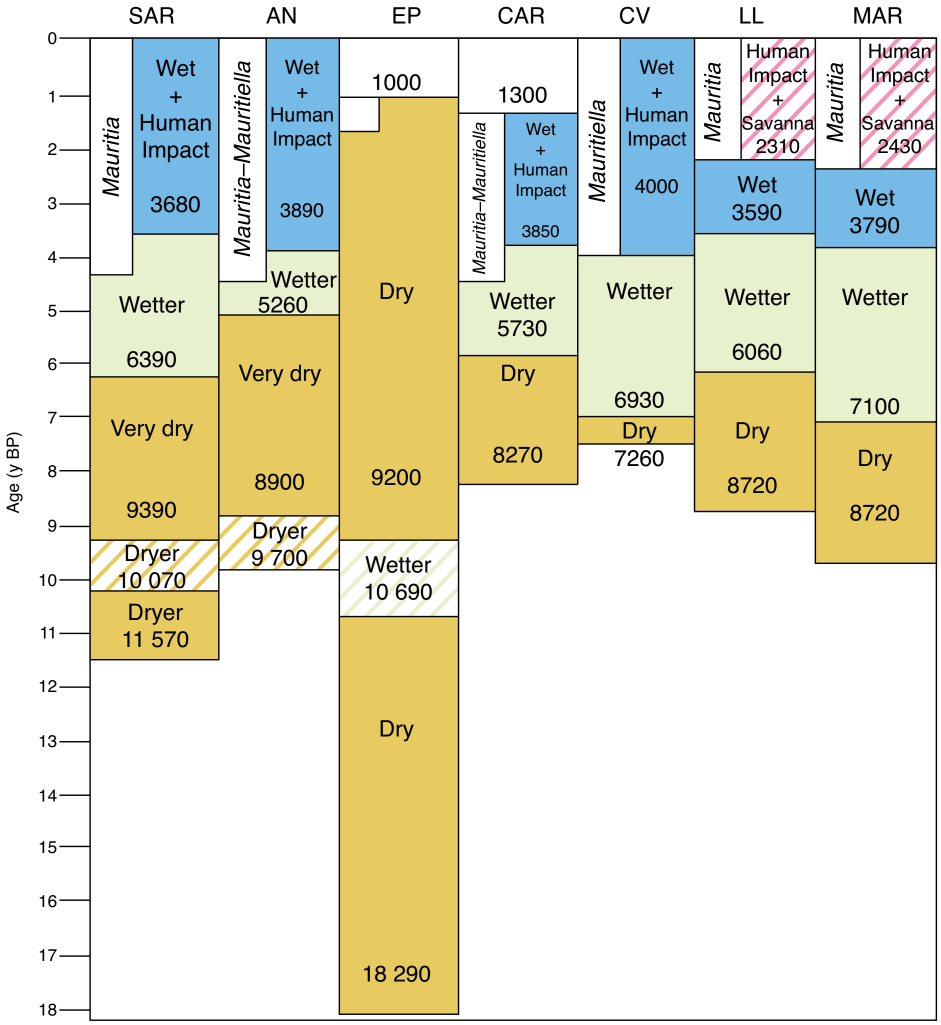

Figure 5. Synthesis of environmental changes in the savannas of the Llanos Orientales since the Last Glacial Maximum. Data are plotted on a linear time scale. From left (east) to right (west) are shown: SAR—Lake Sardinas, AN—Lake Angel, EP—Lake El Piñal, CAR—Lake Carimagua, CV—Lake Chenevo, LL—Lake Loma Linda, and MAR—Lake Las Margaritas. (Reproduced with permission from Hooghiemstra & Berrío, Encyclopedia of Quaternary Science, Vol. 4 (2007): p. 2656, Copyright Elsevier).

azonian biodiversity had appeared during the Oligocene and Miocene, and therefore the Quaternary ice ages were not the main drivers of the region's stunning diversity, although speciation continued during the Quaternary (Rull, 2011). Haffer's hypothesis that ice ages were the driving force behind speciation in Amazonian rainforest lost support in accordance with the early opinions of Paul A. COLINVAUX and Mark B. BUSH.

2.3. Chocó Rainforest

Setting: The upheaval of the northern Andes in the late Miocene separated the Chocó biogeographic area (Figure 6) from Amazonia (Hoorn et al., 2010; Mora et al., 2008). At Ecuadorian latitudes, relatively cold waters of the Humboldt Current deviate westwards and cause dry coastal vegetation in Perú and Ecuador to wet rainforest in the coastal area of Colombia. Characteristic is the extreme high mean annual precipitation from 7500 up to 15 000 mm y^{-1}. Mean annual temperature is 26–27 °C and the warmest and coldest month differ by only 1 °C. Substantial precipitation occurs during all months and mean annual values are far above the minimum values necessary for any biome shift to occur. Even a substantial reduction is not expected to affect the present distribution of the rainforest biome.

Evidence: The first pollen record from Chocó was published from the Darién in Panamá (Bush & Colinvaux, 1994). In Colombia, the first sediment records were collected in 1997 by BEHLING, HOOGHIEMSTRA, and NEGRET close to Tumaco (Lake Piusbi: last 7.67 ka), Guapi (Lake Caimito: last 3.85 ka), and Quibdó (Lake Jotaordó: last 4.2 ka; Berrío et al., 2000a). Lakes may originate from past changes to the drainage system. Relatively few pollen records are available from this region, as transport by small aircraft and canoe makes access difficult. Pollen spectra are very diverse: 200 different pollen and spore taxa were identified in the Holocene Piusbi sediments.

Results: The Chocó rainforest reflects a centre of high biodiversity (Barthlott et al., 1996; Myers, 1988) but its Pleistocene history is unknown. Pollen records show that plant composition was relatively stable during the Holocene. Changes in forest composition relate to the development of a sedimentary basin (Lake Jotaordó) or a migrating coast line (Lake Caimito). Human impact is evidenced for the last ca. 1700 y (Behling et al., 1998a) by the cultivation of maize and possibly also by the

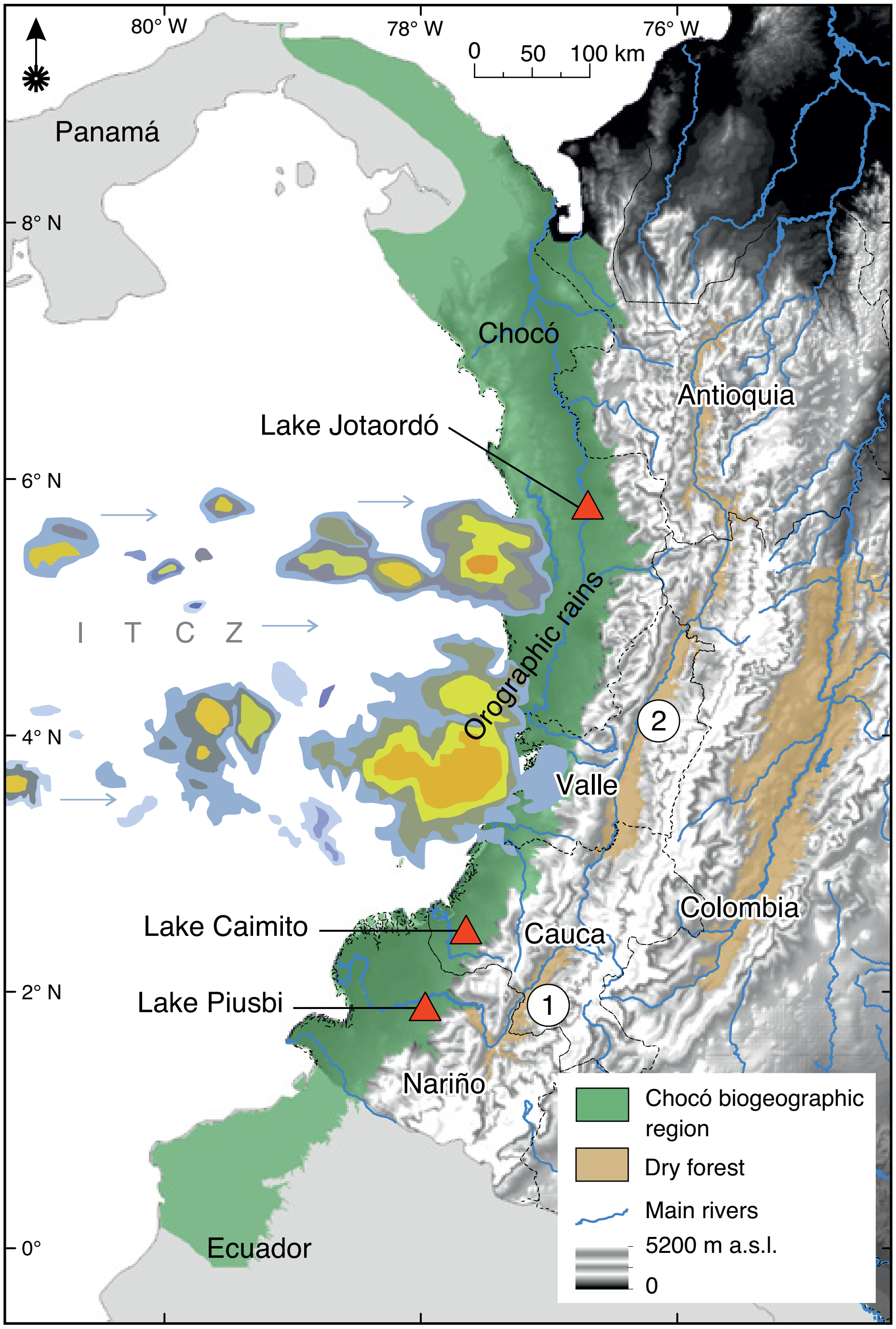

Figure 6. The rainforests of Chocó biogeographical area which extends along the Pacific coast from the Panamanian province of Darién to the Ecuadorian province of Esmeraldas. The locations of pollen sites Lake Piusbi, Lake Caimito, and Lake Jotaordó are shown. The intra–Andean valleys of the Patía and Cauca Rivers bear dry forest vegetation. 1—swamps Patía–1, Patía–2, and Potrerillo–2; 2—swamps Quilichao–1 and La Teta–2; ITCZ—intertropical convergence zone: rain bringing air masses.

increase of palms which play a central economic role in local indigenous communities.

2.4. Dry Forest of the Inter–Andean Valleys

Setting: Dry forest occurs mainly in inter–Andean valleys with substantial rain–shadow effects, for example the Cauca and Patía valleys (Figure 6), and climatologically dry areas in northern Colombia near Lake Maracaibo. Mean annual precipitation is ca. 1800 mm y^{-1} but high evaporation decreases plant–available moisture substantially. The valleys profit locally from periodic stagnant water leading to mosaics of herbaceous and dry arboreal vegetation. At some hundreds of metres above the valley floor a condensation belt allows a transition from dry forest to mesic montane forest, whereas elevations near the mountain tops are covered by grassy meadows. Rains are distributed over two rainy seasons from March to May and from September to December, controlled by the annual migration of the intertropical convergence zone. During El Niño events precipitation decreases and droughts ensue. Dry forest hosts high species richness and endemism (Banda et al., 2016); however, dry forest has been largely cleared due to a lack of protective status (Armenteras et al., 2003; Pizano & García, 2014), and patches of secondary forest are mixed with pasture and coffee plantations (Portillo–Quintero & Sánchez–Azofeifa, 2010).

Evidence: From the Cauca valley (1020 m a.s.l.) evidence comes from cores Quilichao–1 reflecting the periods 13.1–7.7 ka and 2.9–0 ka, and La Teta–2 reflecting the last 8.7 ka (Berrío et al., 2002b) (Figure 7). From the Patía valley (760 m a.s.l.) evidence comes from cores Patia–1 and Patia–2 reflecting the last ca. 7.8 ka (Vélez et al., 2005a) and Potrerillo–2 reflecting the last 9.5 ka (González–Carranza et al., 2008). All sedimentary archives were formed in abandoned parts of a former drainage system.

Results: In Lateglacial times (ca. 13.15 ka) the Cauca valley (Figure 7) was covered by dry forest at lower elevations. At higher elevations the condensation zone allowed the occurrence of montane forest. After 10.5 ka, climatic conditions became drier causing a change in the floral composition of dry forest and consequently its replacement by grassy vegetation. These cool and dry conditions possibly reflect the El Abra stadial (van der Hammen & Hooghiemstra, 1995). Around 8.8 ka dry climatic conditions intensified as seen in the Quilichao record between ca. 6 and 2.8 ka and at La Teta up until 2.7 ka. Maximum drought occurred between 7.5 and 4.3 ka when dry forest had maximally replaced montane forest, leading to abundant grassy vegetation in the Cauca valley around 2.3 ka. Since 2.3 ka, human presence is registered (Duncan et al., 2013). Evidence of depopulation is observed around 950 years ago and from about 400 years ago charcoal peaks point to more intense land–use, possibly related to European colonisation.

The Patía valley was covered by dry forest from ca. 8.3–7.7 ka reflecting mesic climate conditions. In the following millen-

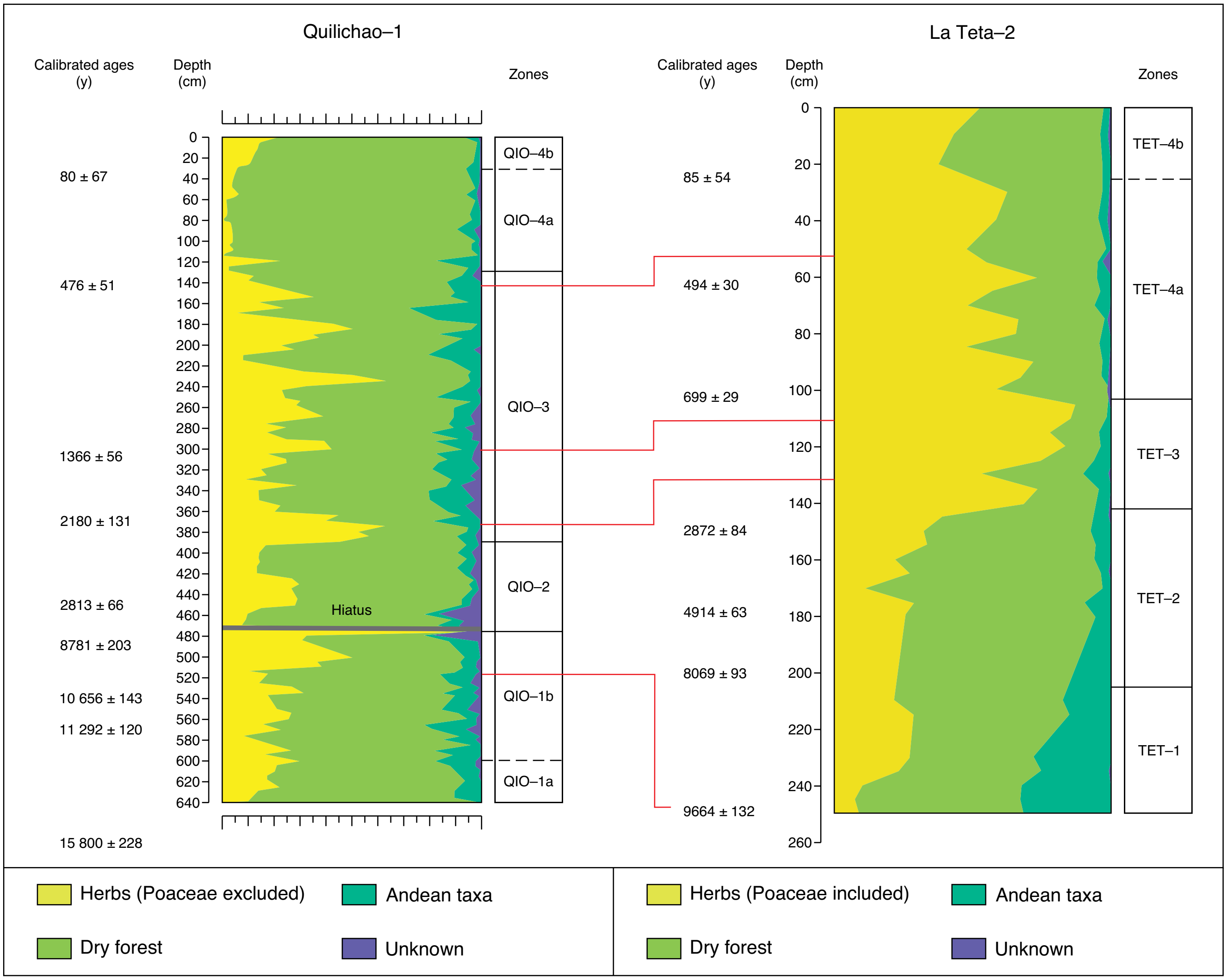

Figure 7. Holocene history of the dry forest biome in the Cauca valley, southern Colombia. Main pollen diagrams of cores Quilichao–1 and La Teta–2 from 1020 m elevation show the precipitation–driven competition between dry forest and dry herbaceous vegetation. The chronological relationship between both records based on calibrated radiocarbon ages is shown. Ages were recalibrated by Flantua et al. (2016b). (Modified after Berrío et al. 2002b).

nium, climate became drier and droughts were frequent, temporarily desiccating the lake and causing erosion. From 6.7 to 3.9 ka, dry forest was replaced by open herbaceous vegetation, suggesting that dry climatic conditions continued and intensified. In the period 3.9–2 ka signals of human interventions are apparent. After 2 ka, there are clear signals of agriculture and open herbaceous vegetation increased. In conclusion, the records in the Patía and Cauca valleys show a similar sequence from mesic to dry forest conditions in the early Holocene, a replacement of dry forest by grassy vegetation reflecting increasing drought in the mid Holocene, and human impact during the last four millennia in the Patía valley and the last 2300 y in the Cauca valley.

2.5. Lower Montane Forest (LMF)

Setting: Today, lower montane forest (LMF) occurs in Colombia from ca. 1200 to ca. 2300 m a.s.l. where a transition to upper montane forest (UMF) can be found. The environmental constraints of present–day LMF, as well as the changes LMF experienced since the Last Glacial Maximum, are poorly known. Steep slopes are frequent between 500 and 2400 m a.s.l. (Flantua et al., 2014) and as a consequence lakes and bogs with undisturbed sediments in this elevational interval are less frequent. Only a handful of pollen records provide insights into the dynamic nature of LMF (Flantua et al., 2015). The lowermost ecotone around 1200 m a.s.l. is climatologically, ecologically, and palynologically difficult to detect. In general, LMF consists of species not resistant to nightfrost. The elevational distribution of LMF taxa shows a species turnover around 2300 m a.s.l. (Behling et al., 1998b) (Figure 8). The Fúquene–9C pollen record (hereafter Fq–9C) demonstrates that, during events of rapid climate change, LMF trees with pioneer qualities can escape rapidly from low elevations and move upslope (Bogotá et al., 2011a; Groot et al., 2013) making the LMF and UMF forest intervals less distinct. Because of this insufficient distinctness between lower and upper montane forest, changing elevational and spatial distributions are often studied considering LMF and UMF as a single unit (e.g., Flantua & Hooghiemstra, 2018). Recent pollen–rain studies along the elevational gradient provide valuable insights into the LMF to UMF transition zone (Figure 9).

After *Quercus* immigrated into Colombia (e.g., Hooghiemstra, 2006) and arrived in the Bogotá area (ca. 430 ka; Torres et al., 2013), it expanded into a remarkably broad elevational interval. Pollen records show that the LMF tree *Alchornea* ex-

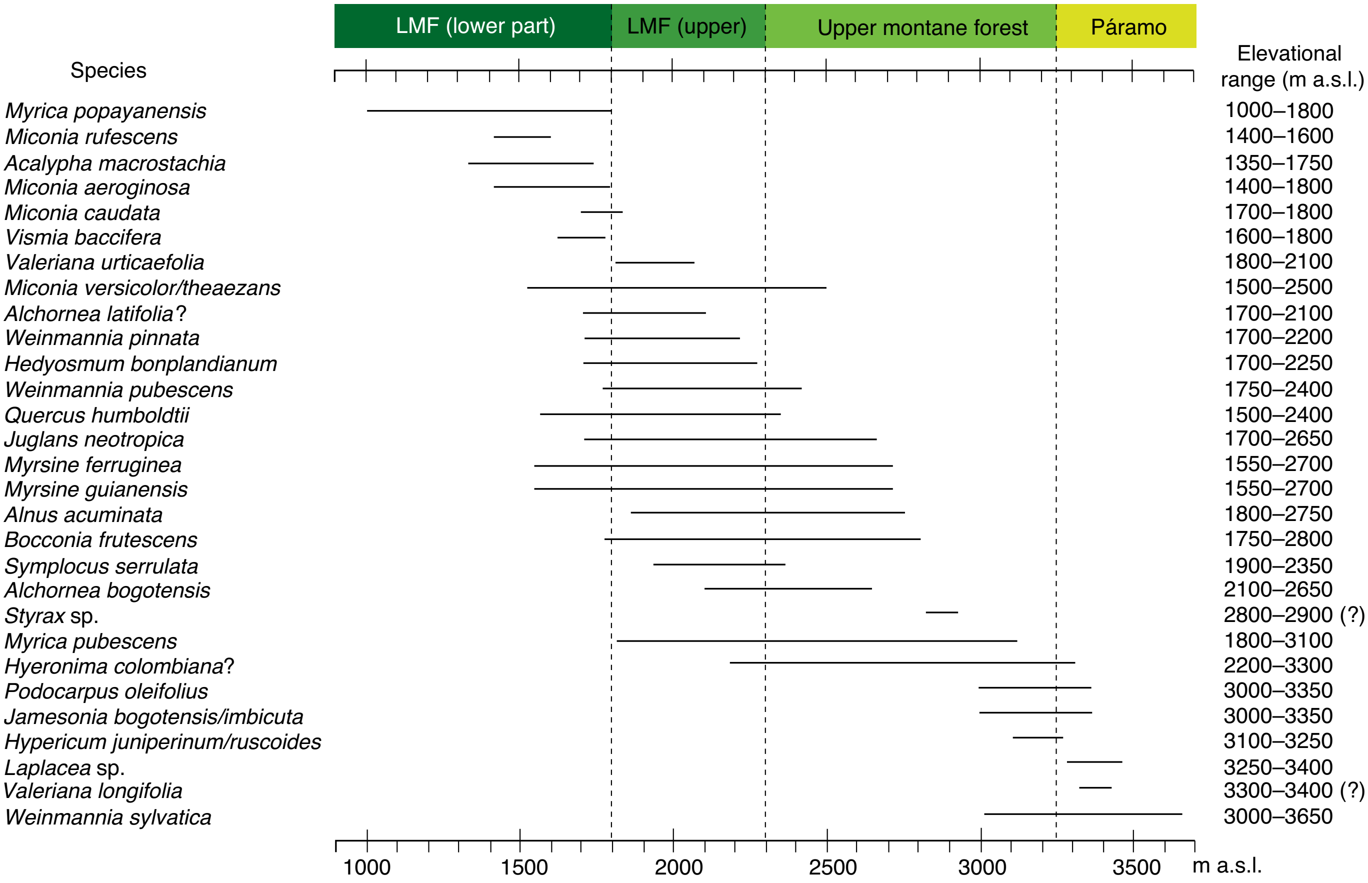

Figure 8. Elevational distribution of modern forest taxa showing the transition from sub–Andean to Andean forest composition based on botanical inventory studies by A. Negret near Popayán. Only taxa represented in the pollen records are shown. (Modified after Wille et al., Vegetation History and Archaeobotany 10, 2001).

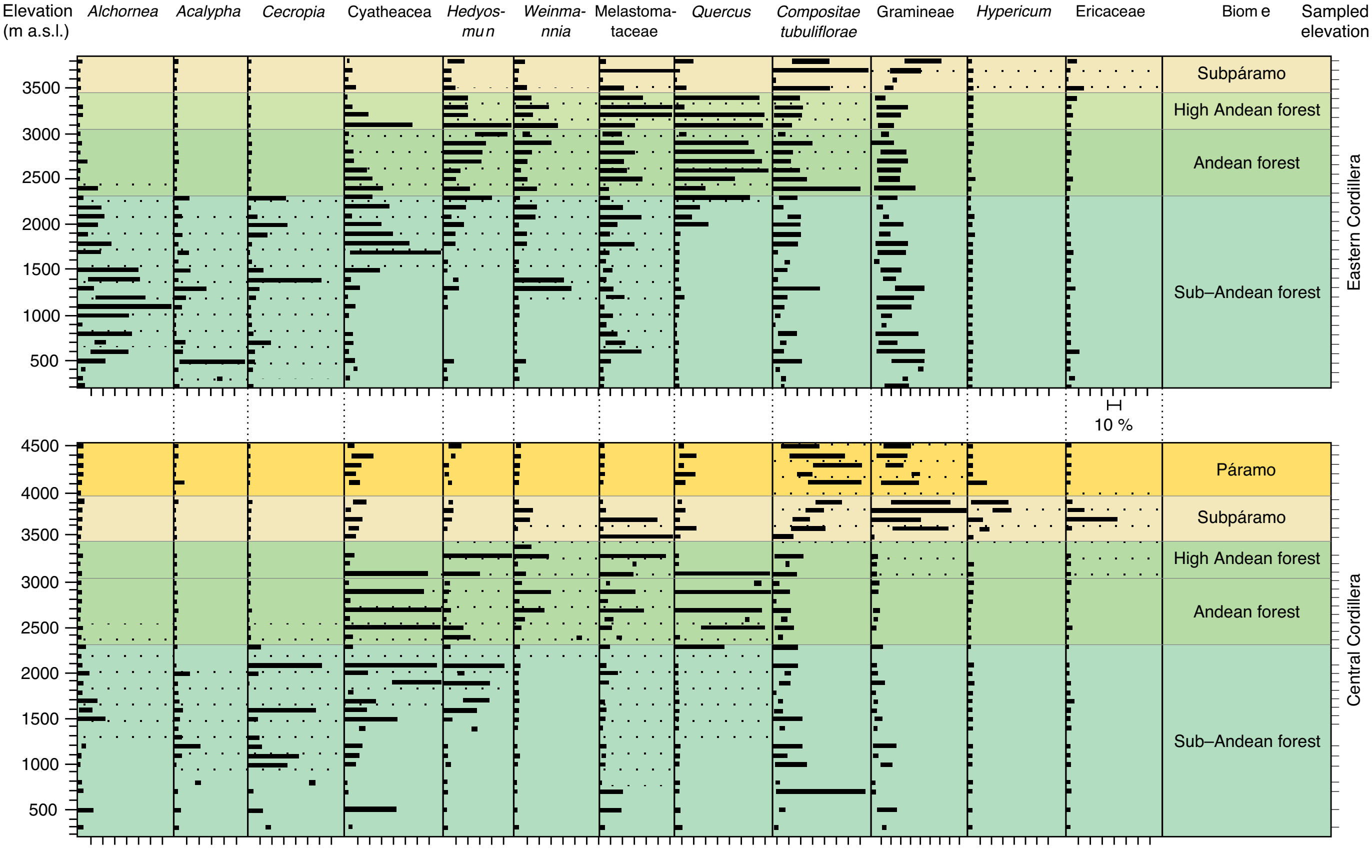

Figure 9. Elevational distribution of modern pollen–rain representation (bars) compared with the elevational range of arboreal taxa in the modern vegetation (shaded intervals). This data forms the basis to infer from pollen records information about the elevational position of the upper forest line (UFL) and other transitions (ecotones) in the palaeo–vegetation. Data are from the Eastern and Central Cordilleras at the latitude of Bogotá and shown in elevational intervals of 100 m. This synthesis is based on data presented in Grabandt (1980), Melief (1985), and Salomons (1986). Only the most important pollen producers are shown. (Modified after van 't Veer & Hooghiemstra, Journal of Quaternary Science 15, 2000).

panded its range to higher elevations when *Quercus* increased its proportions in the UMF. *Quercus* was successful in replacing the UMF trees such as *Weinmannia*, *Podocarpus*, and *Polylepis* (Torres et al., 2013). Today, *Quercus* occurs from 1100 m a.s.l. up to the upper forest line (UFL) at ca. 3200–3500 m under a wide spectrum of dry to humid climatological conditions. Currently, *Quercus*–dominated forest is mainly found as part of the UMF but it is expected that before the LMF was severely cleared for coffee and fruit plantations *Quercus* occurred in equal abundance in both elevational intervals.

Evidence: LMF dynamics are revealed in the pollen records from southern Colombia—Pitalito (1300 m), Piagua (1700 m), Genagra (1750 m), and Timbío (1750 m), and central Colombia—Lusitania (1500 m), Líbano (1820 m), Pedro Palo (2000 m), and Ubaque (2000 m). The most comprehensive synthesis of LMF dynamics is presented by Wille et al. (2001) who compared 11 pollen records from eight locations.

Results: Today, LMF covers a ca. 1300 m vertical interval from ca. 1000 to ca. 2300 m a.s.l. During the Last Glacial Maximum, LMF occurred from ca. 800 to 1400 m a.s.l., reducing the vertical extension by ca. 55% (Hooghiemstra & van der Hammen, 2004). Comparing the available surface area in the Colombian Andes of the 1000–2300 m interval with the 800–1400 m interval, we estimate that this represents a reduction of ca. 42%. Although the LMF shifted significantly in elevational range, it seems to have persisted since the Last Glacial Maximum in the 1000–1400 m vertical interval. This suggests that pollen records from the 1000–1400 m interval might be less sensitive to detecting climate change. To estimate temperature change at lower elevations, changes in the elevational position of the LMF–UMF ecotone can be used. A Last Glacial Maximum cooling of 6–7 °C at 1700 m a.s.l. compared to today has been inferred from a fossil pollen record at 1700 m a.s.l. by deducing changes in the elevational position of the LMF–UMF ecotone (Wille et al., 2001). This study suggests a steeper lapse rate of ca. 0.76 °C 100 m^{-1} compared to today's value of ca. 0.6 °C 100 m^{-1}, which concords with inferred drier air during glacial times (Loomis et al., 2017). After the Last Glacial Maximum, temperature increased around 14 ka from 6–7 °C to 2–3 °C lower than today. As a result the LMF–UMF ecotone could have been at ca. 1800 m a.s.l., ca. 500 m below the present–day level. After the Lateglacial oscillations (Wille et al., 2001), the LMF–UMF ecotone shifted to its maximum elevation of 2300–2400 m a.s.l. (ca. 1–2 °C warmer relative to today) reflecting the mid–Holocene hypsothermal (Kaufman et al., 2004). During the last 5 ka the presence of cultivated plants points to human colonisation of the lower montane zone in Colombia (Marchant et al., 2001a; Behling et al., 1998b).

2.6. Upper Montane Forest (UMF)

Setting: UMF stretches from ca. 2300 m a.s.l. to the upper forest line (UFL) at ca. 3200–3500 m a.s.l., an interval where night-frosts may occur. The lower boundary of the UMF is less distinct than the upper boundary: it is also more difficult to identify palynologically. However, the ecotone at the upper boundary is a distinct transition from continuous forest to dwarf–forest, shrub, and herbaceous vegetation (Moscol–Olivera & Cleef, 2009a). The physiological, climatological constraints are largely driven by mean annual temperature (Körner, 1998, 1999, 2012; Körner & Paulsen, 2004), but other climatological variables, such as $p\mathrm{CO_2}$ (Claussen et al., 2013; Grace et al., 2002; Groot et al., 2011; Harrison & Prentice, 2003; Hooghiemstra et al., 2012; Marchant et al., 2002a; Mayle et al., 2004), freezing (Rehm & Feeley, 2015), humidity (Cleef, 1981), and treeline form (Harsch & Bader, 2011) may also drive the UFL–position, although all individual contributions are difficult to express quantitatively. It is important to distinguish between the UFL (uppermost limit of continuous forest) and the upper tree line (highest position of individual trees). In the Colombian Andes both ecotones may be up to 800 m apart. The UFL can be inferred from a pollen record: the upper tree line not.

In the Americas the existence of elevational zones ("belts") in the vegetation distribution from low to high elevations (Figure 10) is still debated and is an issue in reconstructing elevational vegetation dynamics and inferred climate change. Elsewhere, this debate is non–existing and altitudinally constrained "vegetation belts" are widely applied, for example in the East African mountains (e.g., Flenley, 1979a; Hedberg, 1951; Knapp, 1973; White, 1983). The contrasting opinions about recognizing altitudinally (climatologically) constrained "vegetation belts" go back to the papers by Gleason (1926: species migrate individually) and Clements (1916: species migrate in clusters when they share environmental constraints). von Humboldt & Bonpland (1807), Cuatrecasas (1958), Troll (1968), and van der Hammen (1974) provided a helpful set of climatologically constrained vegetation belts. For example, Morueta–Holme et al. (2015) analysed changes in the position of vegetation zones at the Chimborazo (Ecuador) during the last 210 y and found evidence of strong upslope shifts since von Humboldt related to global warming. Modern elevational ranges of plant taxa and long–term changes in forest composition, as shown by the Fq–9C record, show support for both concepts. GLEASON's and CLEMENTS' concepts can be considered as the ends of a continuum (Keddy, 2007, p. 497). Other relevant contributions to this debate come from Bach & Gradstein (2011), Bush (2002), Depatta–Pillar (1999), Feeley et al. (2011), Keddy (2007), Kluge et al. (2006), Nicolson & McIntosh (2002), Rehm (2014) and Shipley & Keddy (1987). The overall conclusion is that working with elevationally constrained vegetation "belts" is useful, for example, when translating pollen data into past vegetation change (e.g., Flantua et al., 2014), and because some belts are much more pronounced (UMF vs. páramo) than others (UMF vs. LMF).

The interpretation of pollen records requires knowledge of a taxon's ecological preferences, elevational range, traits (pioneer vs. late–successional qualities), and pollination syndrome (Figure 11). Alternatively, in the absence of knowledge of the ecological constraints of individual plant taxa, principal component analysis may group pollen taxa into clusters with an assumed ecological preference (Birks & Gordon, 1985; Correa–Metrío et al., 2012a, 2012b, 2012c; Urrego et al., 2016). This cluster analysis approach has the advantage that field experience is less needed. Both approaches have advantages: knowledge from the field possibly better serves the interpretation of modern vegetation associations, whereas the more objective cluster analysis is expected to support better the analysis of non–analogue vegetation associations, which are abundant in long Quaternary records (see Urrego et al., 2016, for a comparison).

Evidence: Today, the UMF covers a 1000 m elevational interval (from ca. 2300 to ca. 3200–3500 m a.s.l.). This elevational interval includes many high–elevation plains (Flantua et al., 2014; Flantua & Hooghiemstra, 2018) where sediment can accumulate. The UMF zone is rich in lakes, mires, and peat bogs which offer excellent opportunities to collect informative sediment cores (Flantua et al., 2015). The updated Latin American Pollen Database shows numerous available pollen records (see interactive map from Flantua et al., 2015). For syntheses of past vegetation dynamics and the evolution of the high Andean flora we refer to Bush et al. (2011), Flantua & Hooghiemstra (2018), Livingstone & van der Hammen (1978), van der Hammen (1974), van der Hammen & Cleef (1986) and van der Hammen et al. (1973).

Results: During the Last Glacial Maximum, the UMF was probably reduced to a 600 m vertical interval from 1400 to ca. 2000 m a.s.l. (Hooghiemstra & van der Hammen, 2004). However, the lower position of the UMF implies a higher surface availability due to topographic characteristics (Flantua et al., 2014): since the Last Glacial Maximum the total surface of LMF changed by only a negligible 2.4%.

2.6.1. Exceptional Long Fossil Pollen Records from the Bogotá Basin

The Eastern Cordillera of Colombia offers several deep sedimentary basins where deep cores have been extracted during

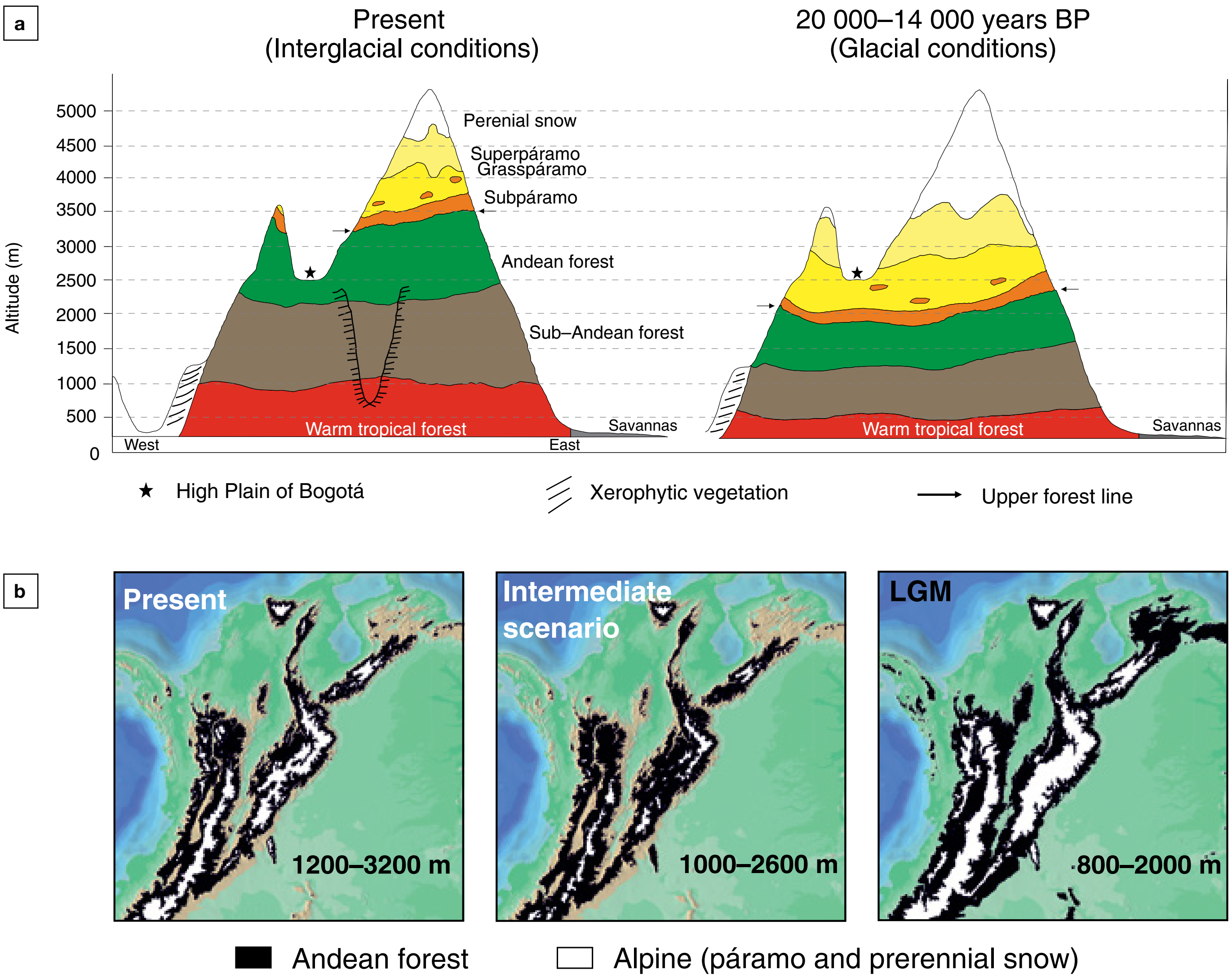

Figure 10. (a) Comparison of the elevational vegetation distribution in the northern Andes for today (left) and during the Last Glacial Maximum at ca. 20 ka (right) showing the maximum change in vegetation cover in a Pleistocene glacial–interglacial cycle. **(b)** Comparison of spatial vegetation distribution of the full montane forest biome, including lower montane forest (sub–Andean forest) and upper montane forest (Andean forest) showing the maximum change in vegetation cover in a Pleistocene glacial–interglacial cycle. Montane forest occurred from ca. 800–2000 m at the Last Glacial Maximum (LGM), from ca. 1200–3200 m at present–day, and from ca. 1000–2600 m during an intermediate scenario. (Modified after T. van der Hammen, Journal of Biogeography 1, 1974; Original figure by Torres, 2006).

the last five decades (Figure 12). The first deep cores of the Bogotá Basin (2550 m a.s.l.) were drilled at the campus of the Universidad Nacional: the 12 m deep core Ciudad Universitaria–X (CUX) (van der Hammen & González, 1960, 1963) and 195 m deep core Ciudad Universitaria–Y (CUY) (van der Hammen, 1968; see also Hooghiemstra, 1984, Figure 24). The CUX–CUY record was never fully published as the record is fragmentary because of its position at the border of ancient Lake Bogotá where sediment accumulation and erosion have alternated many times. The high potential of the Bogotá Basin (van der Hammen, 1968, 1998) as an archive of Quaternary environmental and climate change motivated researchers to continue further exploration of its sediments. In 1975, the Servicio Geológico Colombiano (INGEOMINAS) drilled the first deep core (357 m core depth) near Funza (labelled Funza–1), but unfortunately subterraneous water prevented further drilling. In a second attempt in 1988, a successful drilling operation collected a core of 586 m (labelled Funza–2), reaching the bedrock of the basin although subterraneous water prevented extraction of sediments between 160 and 205 m. Pollen preservation was poor below 540 m, but 2100 pollen samples were attained from the upper 540 m and analysed over the years by Henry HOOGHIEMSTRA, Eva RAN, and Vladimir TORRES (Figure 13).

Reconstructions of the sedimentary environments of ancient Lake Bogotá (van der Hammen, 1986) were further complemented by grain size distributions (Torres et al., 2005). This analysis provided key insights into how the ancient Lake Bogotá developed in its earliest stages (Montoya–Arenas &

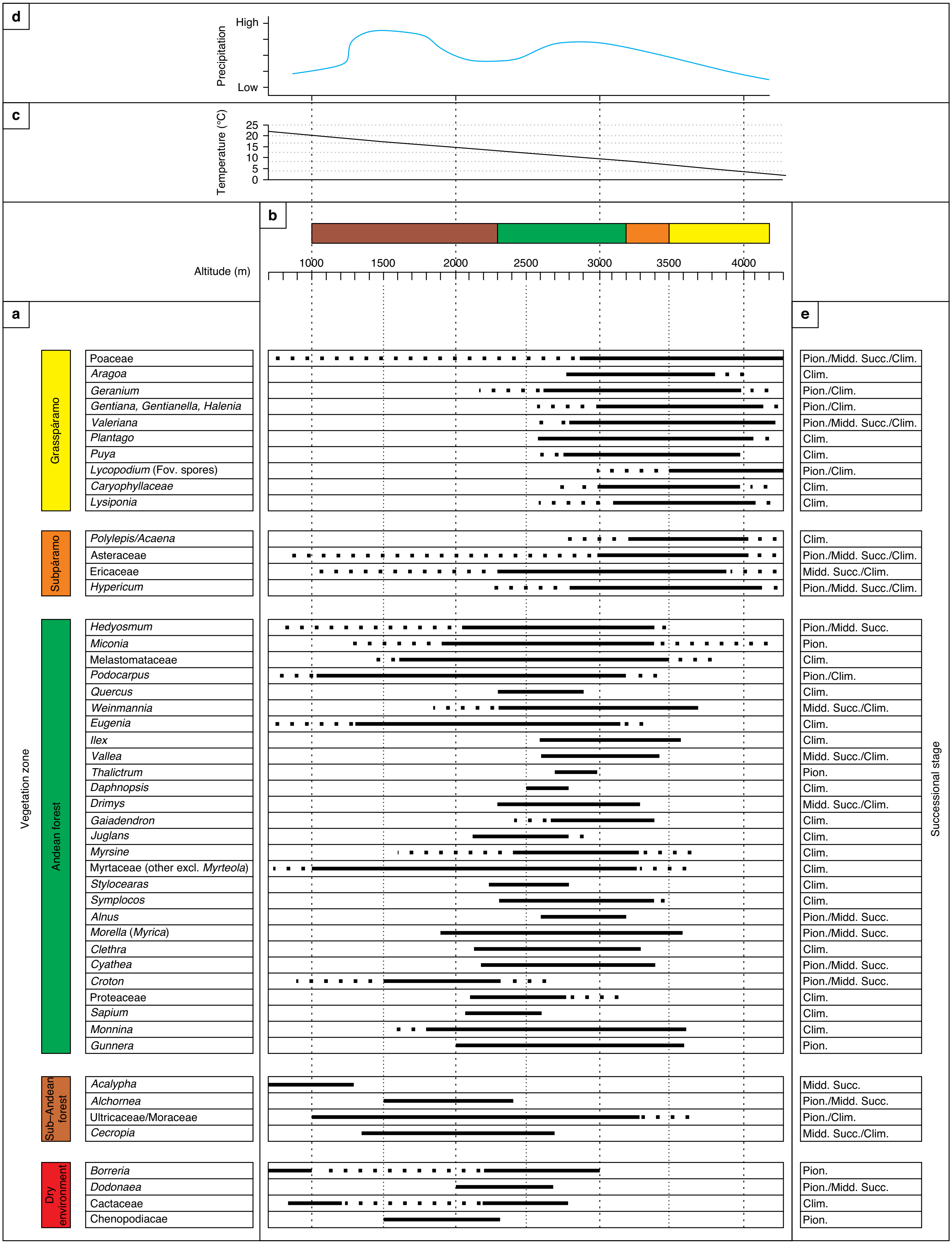
d
High
Precipitation
Low
c
Temperature (°C)
25
20
15
10
5
0
b
Altitude (m)
1000
1500
2000
2500
3000
3500
4000
a
e
Vegetation zone
Grasspáramo
Poaceae
Aragoa
Geranium
Gentiana, Gentianella, Halenia
Valeriana
Plantago
Puya
Lycopodium (Fov. spores)
Caryophyllaceae
Lysiponia
Subpáramo
Polylepis/Acaena
Asteraceae
Ericaceae
Hypericum
Andean forest
Hedyosmum
Miconia
Melastomataceae
Podocarpus
Quercus
Weinmannia
Eugenia
Ilex
Vallea
Thalictrum
Daphnopsis
Drimys
Gaiadendron
Juglans
Myrsine
Myrtaceae (other excl. Myrteola)
Stylocearas
Symplocos
Alnus
Morella (Myrica)
Clethra
Cyathea
Croton
Proteaceae
Sapium
Monnina
Gunnera
Sub-Andean forest
Acalypha
Alchornea
Ultricaceae/Moraceae
Cecropia
Dry environment
Borreria
Dodonaea
Cactaceae
Chenopodiacae
Successional stage
Pion./Midd. Succ./Clim.
Clim.
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Figure 11. Elevational ranges of selected pollen and spore taxa arranged after ecological preference. Data based on literature and field expertise of A.M. CLEEF. **(a)** Main ecological groups. **(b)** Modern elevational range in the study area; dotted line = full range; solid line = interval of optimum cover. **(c)** Mean annual temperature along the elevational gradient. **(d)** Estimated mean annual precipitation along the altitudinal gradient (compiled from modern vegetation studies; see Groot et al., 2013). **(e)** Main functional place of taxon in the vegetation succession (compiled from modern vegetation studies; see Groot et al., 2013). Pion.—pioneer taxon; Midd. Succ.—middle successional taxon; Clim.—climax taxon. (Reproduced with permission from Groot et al., Review of Palaeobotany and Palynology 197 (2013), Copyright Elsevier).

Reyes–Torres, 2007). Here it was discovered that the lake developed later than previously suggested by Helmens & van der Hammen (1995) and Hooghiemstra (1984). It was shown that after ca. 1.4 Ma, subsidence of the basin floor accelerated and reached higher values than the rate of sediment infill, allowing the formation of a lake. The highest lake levels prevailed from 1.3 to 0.9 Ma. During the last 0.9 Ma, lake–level oscillations were driven by glacial–interglacial cycles with highest lake levels during the glacial periods and lowest stands during interglacial periods. Here, temperature–dependant evaporation must have played an additional role to precipitation changes in driving lake–level change (van Boxel et al., 2014).

2.6.2. Fitting a 2.25 Million Year Long Age Model

Establishing a chronology has been challenging for the records from the Bogotá Basin. Since the initial age model (Hooghiemstra, 1984), several alternative age models have been developed in an attempt to improve the temporal framework of the records derived from this basin. The age model by Andriessen et al. (1993) laid the foundation for subsequent studies by Torres et al. (2005) and Torres (2006). Later, the upper part of Funza–1 and the lower part of Funza–2 pollen records were merged into the composite record Funza09 by using, as a common event, the first appearance date of *Alnus* (located in Funza–1 and Funza–2 at 257.60 m and 255.20 m, respectively). Subsequently, Funza09 was correlated with the benthic $\delta^{18}O$ stacked record of ODP Sites 846 and 849 for the last 1 Ma and provided the necessary tie–points to build an astronomically tuned age model for the remaining record (Torres et al., 2013) (Figure 14). Although the age of the 540–586 m interval remains uncertain, the age of the start of the pollen record at 540 m composite depth is dated to 2.25 Ma (Torres et al., 2013). Nevertheless, earlier studies suggest absolute dates of Pliocene age for the deepest part of the core (Andriessen

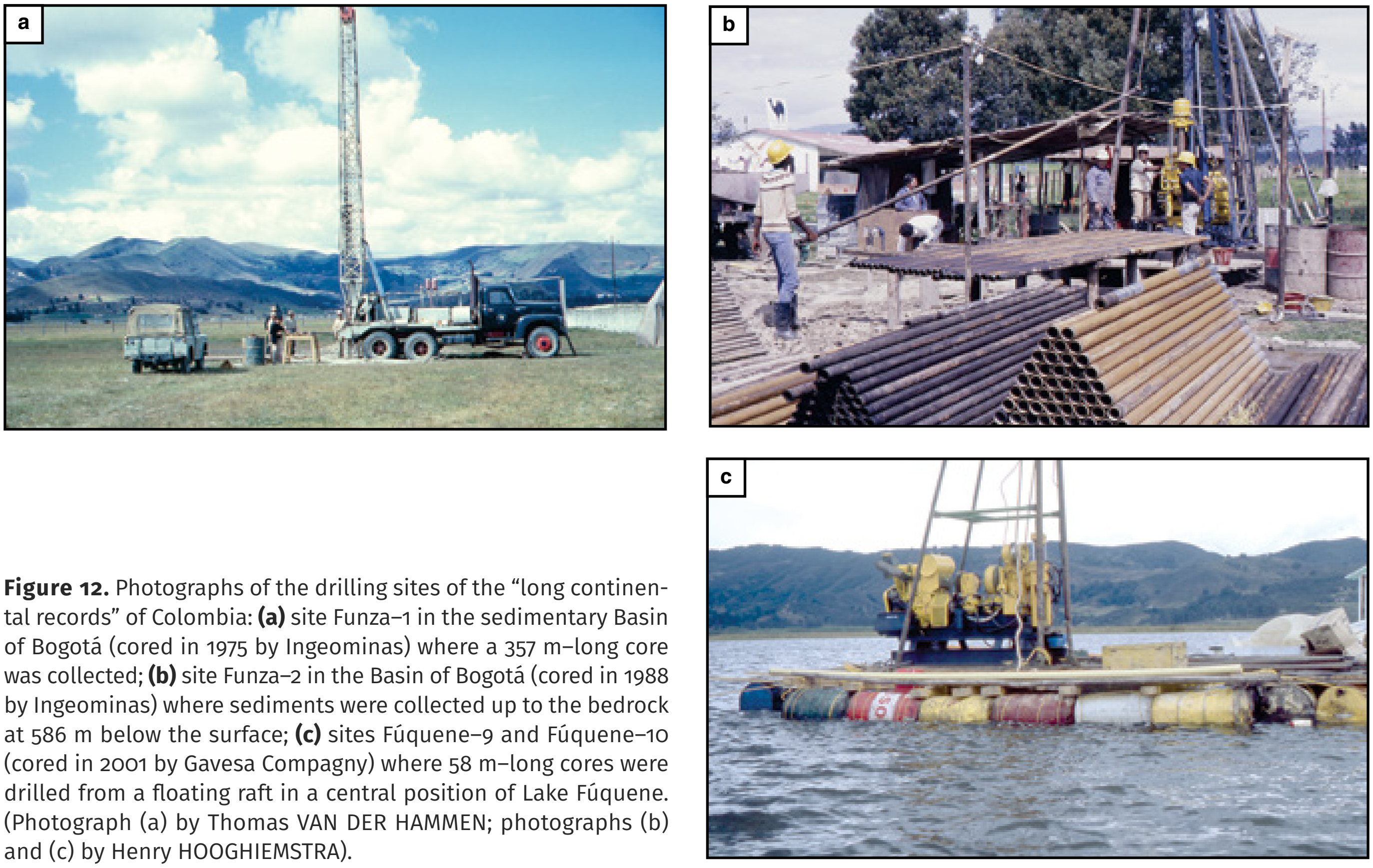

Figure 12. Photographs of the drilling sites of the "long continental records" of Colombia: **(a)** site Funza–1 in the sedimentary Basin of Bogotá (cored in 1975 by Ingeominas) where a 357 m–long core was collected; **(b)** site Funza–2 in the Basin of Bogotá (cored in 1988 by Ingeominas) where sediments were collected up to the bedrock at 586 m below the surface; **(c)** sites Fúquene–9 and Fúquene–10 (cored in 2001 by Gavesa Compagny) where 58 m–long cores were drilled from a floating raft in a central position of Lake Fúquene. (Photograph (a) by Thomas VAN DER HAMMEN; photographs (b) and (c) by Henry HOOGHIEMSTRA).

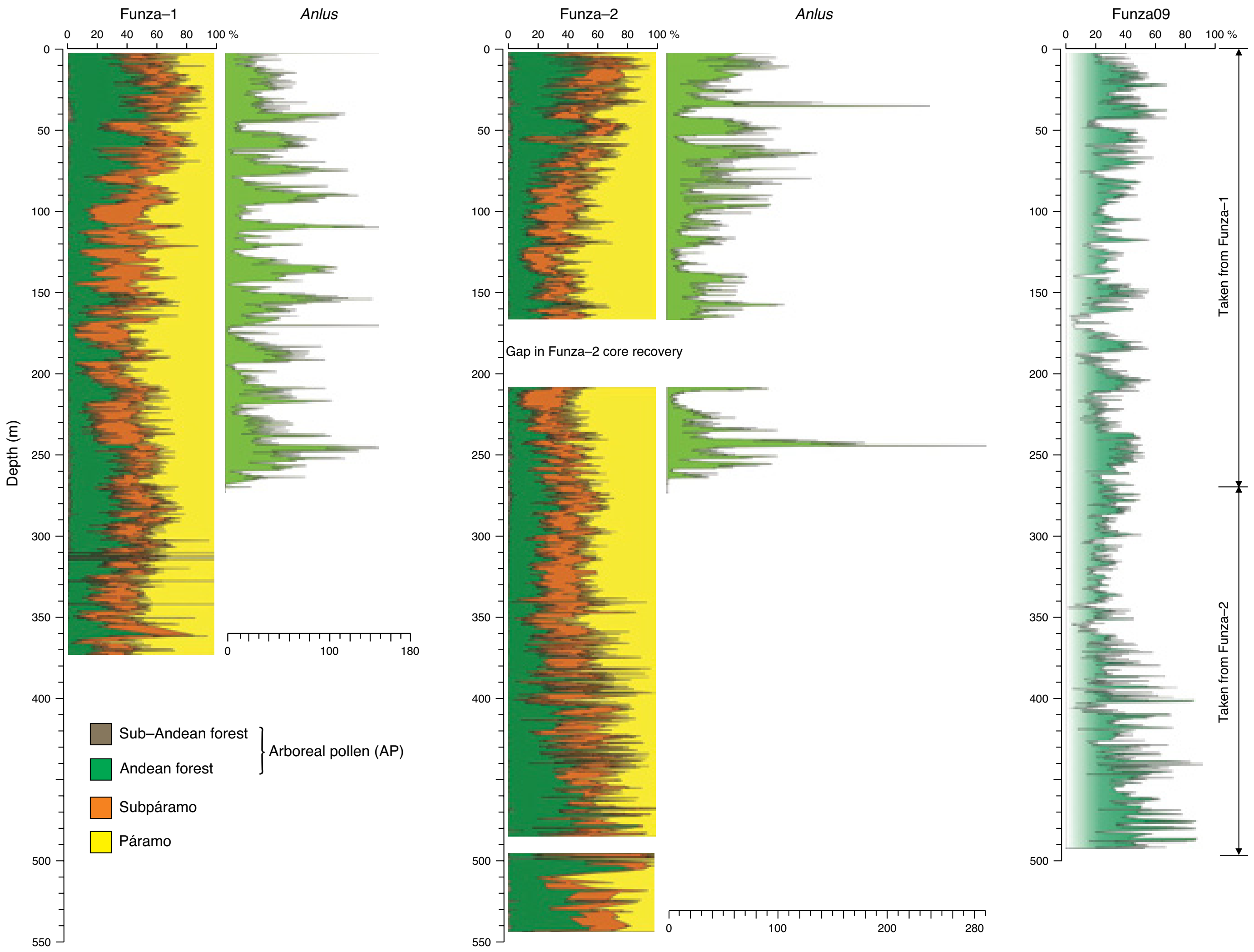

Figure 13. Main pollen percentage diagrams of the long continental records Funza–1 (357 m) and Funza–2 (upper 540 m) located at 2550 m elevation. Data are plotted on a linear depth scale. Interglacial periods are characterised by high percentages of trees of the Andean forest; glacial periods by high percentages of páramo herbs. The records of *Alnus* are shown separately. At the right the composite "Funza09" arboreal pollen % record is shown with *Alnus* excluded from the pollen sum. (Reproduced with permission from Torres et al., Quaternary Science Reviews 63, 2013, Copyright Elsevier).

et al., 1993) hinting at a sediment sequence in the Bogotá Basin that reflects the entire Quaternary.

2.6.3. Relatively Stable Floral Composition of Montane Forest during the Last Million Years

Immigration events, interspecific competition, and varying climatic constraints influenced the taxonomic composition of montane forest throughout the Pleistocene (Torres et al., 2013, Figure 10; Supplementary Information S2). In Europe, subsequent Pleistocene interglacial periods caused substantial loss of species and are the driving force behind taxonomic differences between the multiple interglacials (Tzedakis et al., 1997, 2001). Interestingly, the floral composition of montane forest in the northern Andes has been remarkably stable during the ten interglacials of the last 1 Ma (Felde et al., 2016). North Andean interglacial forest associations are shown to be of a similar floristic composition, and offer no clues to differentiate the interglacial periods (Felde et al., 2016). As a consequence, biostratigraphical dating of interglacial forest associations in the northern Andes is limited to immigration events of key species, such as of *Alnus* at 1.01 Ma and *Quercus* at 430 ka (Hooghiemstra, 1984; Torres et al., 2013; van der Hammen et al., 1973). A plausible reason for this apparent "stability" is that the upper forest line could have shifted over 1500 vertical metres during an interglacial–glacial cycle while, for instance in Europe, the northernmost forest line shifted over ca. 3000 km between northern Scandinavia (today) and the Alps (during the Last Glacial Maximum) (van der Hammen, 1979; van der Hammen et al., 1971; Willis & van Ander, 2004). Vertical shifts in mountainous areas where surface availability is not a restricting factor imply "a low risk to lose" taxa during migration, making the ecological legacy (Cavender–Bares et al., 2016; Cuddington, 2011) in the Andes strong.

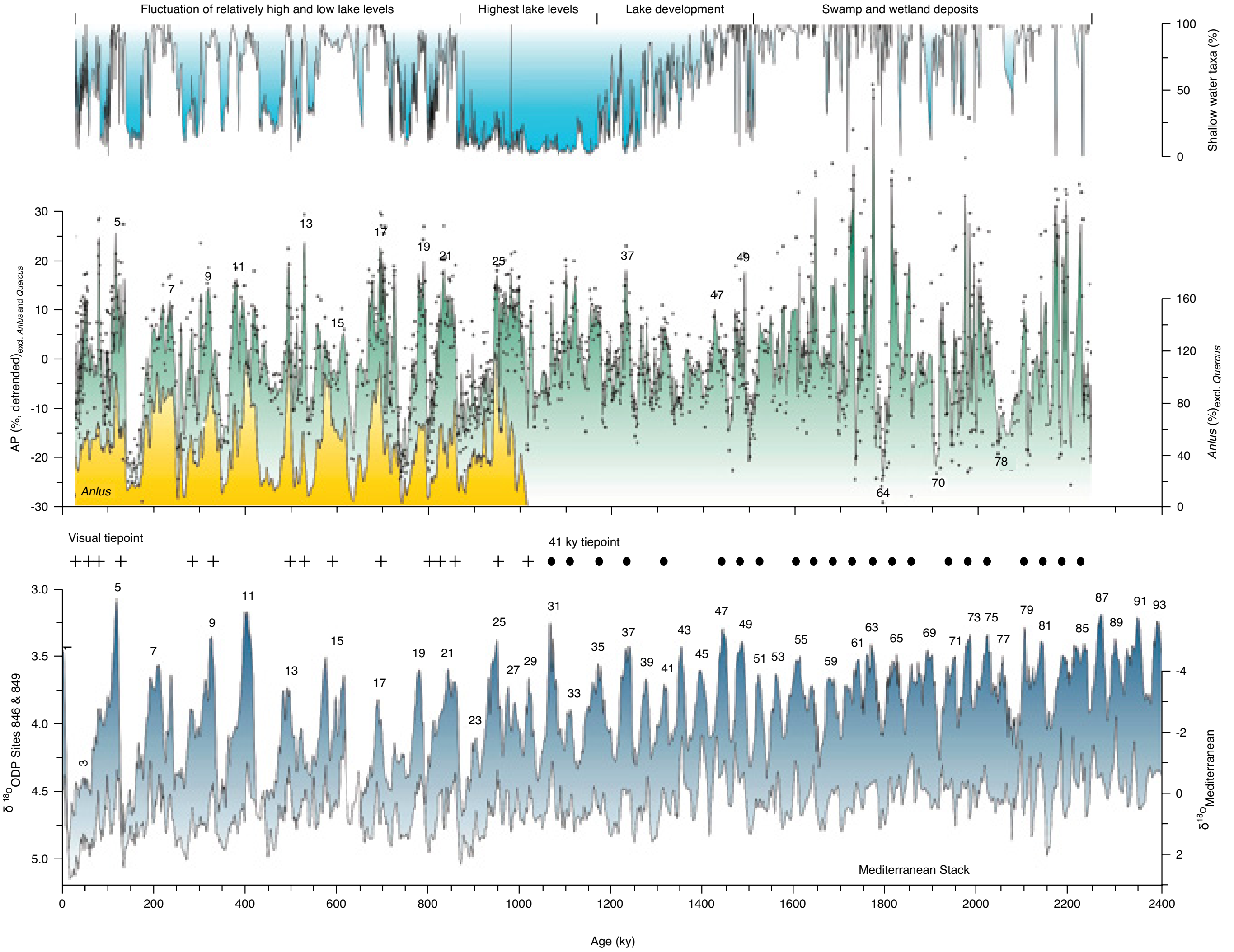

Figure 14. Lake development and climate change during the last ca. 2.25 Ma from palynological information in the sediments of the Bogotá Basin. The age model is based on **(1)** visual correlation of major glacial–interglacial cycles during the last million years (tie points shown as crosses), and **(2)** obliquity–tuning of the arboreal pollen % (AP %) record to the benthic $\partial^{18}O$ stacked record of ODP Sites 846 and 849 (Mix et al., 1995a, 1995b; Shackleton et al., 1995) and the Mediterranean plankton $\partial^{18}O$ stacked record (Lourens et al., 2004, tie points shown as bullets).
Central Panel: shows *Alnus* % record reflecting ice age cycles clearly since its immigration event at 1010 ka: extensive *Alnus* carr during warm interglacial periods with high evaporation and low average lake–levels vs. limited *Alnus* carr (high lake–levels) to absent (when the upper forest line (UFL) shifted below the elevation of Bogotá) during cold interglacial periods with low evaporation and high average lake–levels. Arboreal pollen % record (detrended) shows elevationally shifting UFL, with ancient Lake Bogotá immersed in montane forest (during interglacial periods) vs. ancient Lake Bogotá immersed in páramo (during glacial periods). Numbers reflect marine isotope stages).
Top panel: shows the record of Pleistocene lake–level fluctuations in ancient Lake Bogotá based on the calculated percentage ratio of *Isoetes* (reflecting water up to 8 m deep) vs. aquatics and wetland taxa (Cyperaceae, *Hydrocotyle*, *Ludwigia*, and *Myriophyllum*) reflecting shallow water. Ancient Lake Bogotá developed between 1400–1200 ka and lacustrine conditions continued up to the desiccation event around 27 ka. Before 1400 ka, swamp, swamp forest, and riverine conditions prevailed in the basin. During lacustrine conditions pollen source areas are at relatively large distance extending across the slopes of the Bogotá Basin; when the basin floor was covered by swamp forest, pollen source areas were close to the coring site: this explains peaks of high AP % before 1400 ka.
Bottom panel: shows the record of marine isotope stages for comparison. (Reproduced with permission from Torres et al. Quaternary Science Reviews 63, 2013, Copyright Elsevier).

2.6.4. The Environmental History of Lake Fúquene

After the turn of the century, a new generation multi–proxy pollen record was analysed from Lake Fúquene (2540 m a.s.l.) at an exceptionally high temporal resolution. This lake is a colluvial dam–blocked lake (Sarmiento et al., 2008) where sediment accumulation in the northern part of the basin serves as a plug to keep the water in the southern part of the basin. Along the borders of Lake Fúquene sediment accumulation continues up to the present–day (Mommersteeg, 1998; van Geel & van der Hammen, 1973). Two parallel cores Fq–9 and Fq–10 were drilled to 58 m depth from a floating raft in the centre of the lake (Figure 12). Lithological changes and x–ray fluorescence–based geochemical records of both cores formed the basis to develop the composite core Fq–9C (Bogotá et al., 2011b; Groot et al., 2011; Vriend et al., 2012). The core was sampled at 1 cm increments. Regional vegetation change was assessed via terrestrial pollen and spores (Bogotá et al., 2011a; Groot et al., 2013). Pollen and spores of aquatics and wetland taxa produced records of lake–level change, while four classes of grain size distributions (proportions of clay, fine silt, coarse silt, sand) provided insights into the production of organic matter in the lake and changing energy levels in the sedimentary environment and/or distance to the river inlet (Vriend et al., 2012) (Figure 15) (Supplementary Information S2).

The series of records extracted from Lake Fúquene provided the basis for a basin–wide temporal correlation of sediment sequences (Bogotá et al., 2011a) (Figure 16). A striking coincidence is observed when comparing cores Funza–1, Funza–2, and Fq–9C as the most recent sediments have all been dated to ca. 27 ka. We hypothesise that around 27 ka the Bogotá Basin became overfilled with sediments leading to the demise of ancient Lake Bogotá. In Lake Fúquene we postulate a change in the trajectory of a through–flow. The main water current from inlet to outlet of the lake may have passed over sites Fq–9 and 10 since ca. 27 ka, preventing at those sites a continuation of undisturbed sediment accumulation, while at the borders of the lake sediment accumulation continued up to recent times (Mommersteeg, 1998; van Geel & van der Hammen, 1973). Alternatively, the end of sediment accumulation in the Bogotá and Fúquene Basins had a common origin, potentially related to a tectonic event in the Eastern Cordillera that changed instantaneously the conditions of sediment accumulation in both basins. Frequency analysis of core Fq–3 strongly suggests that the lower part of the record reflects an unknown period of interglacial conditions different to what was previously thought to be MIS 5 (van der Hammen & Hooghiemstra, 2003).

2.6.5. Orbital Forcing Differs between Andean and Amazonian Biomes

Reconstruction of past temperatures can be done by estimating the UFL position (where mean annual temperature is around 9.5 °C) based on arboreal pollen (AP) percentages. In the area of Bogotá, Hooghiemstra (1984) found that a 40% representation of AP reflects the UFL and that a lapse rate of 0.6 °C 100 m^{-1} represents the UFL vertical displacement. A reconstructed palaeo–temperature record of Fq–9C for the last 180 ka has been compared to the ∂^{18}O–based temperature record from Greenland and the deuterium–based temperature record from Antarctica (Figure 17). From orbital to millennial scales, there is a remarkably good congruence between the palaeo–temperature records. Millennium–scale climate variability with oscillations of 2500–3500 y in Fq–9C corresponds in amplitude and timing with the Dansgaard–Oeschger cycles from the Greenland ice cores (Barbante et al., 2006). Further, it shows that environmental change in the high tropical Andes of Colombia is driven by similar mechanisms operating at high latitudes where the ca. 41 ky obliquity cycle and ca. 100 ky eccentricity cycle are dominant (Torres et al., 2013). In the high northern Andes, climate change is mainly temperature driven (contribution of atmospheric $p\mathrm{CO}_2$ seems relevant but is unquantified; Groot et al., 2011; Harrison & Prentice, 2003) with obliquity (41 ky) and eccentricity (100 ky) forcing as the main drivers. This contrasts with lowland Amazonia where environmental change is mainly driven by precipitation, modulated by the 21 ky precession and the 100 ky eccentricity cycles (Bush et al., 2002; Cruz et al., 2009), just as in the Bolivian–Peruvian highlands (Hanselman et al., 2011). This link is probably due to the significant influx of Northern Hemisphere air masses and moisture over the Amazon Basin during the South American summer monsoon with strong orographic rains along the central Andes (Baker & Fritz, 2015; Flantua et al., 2016a; Marsh et al., 2018). We postulate that differences in the albedo effect in the high Andes contribute to the significant temperature amplitude of 8–10 °C over a glacial–interglacial cycle compared to an estimated 3–5 °C in the Amazonian lowlands

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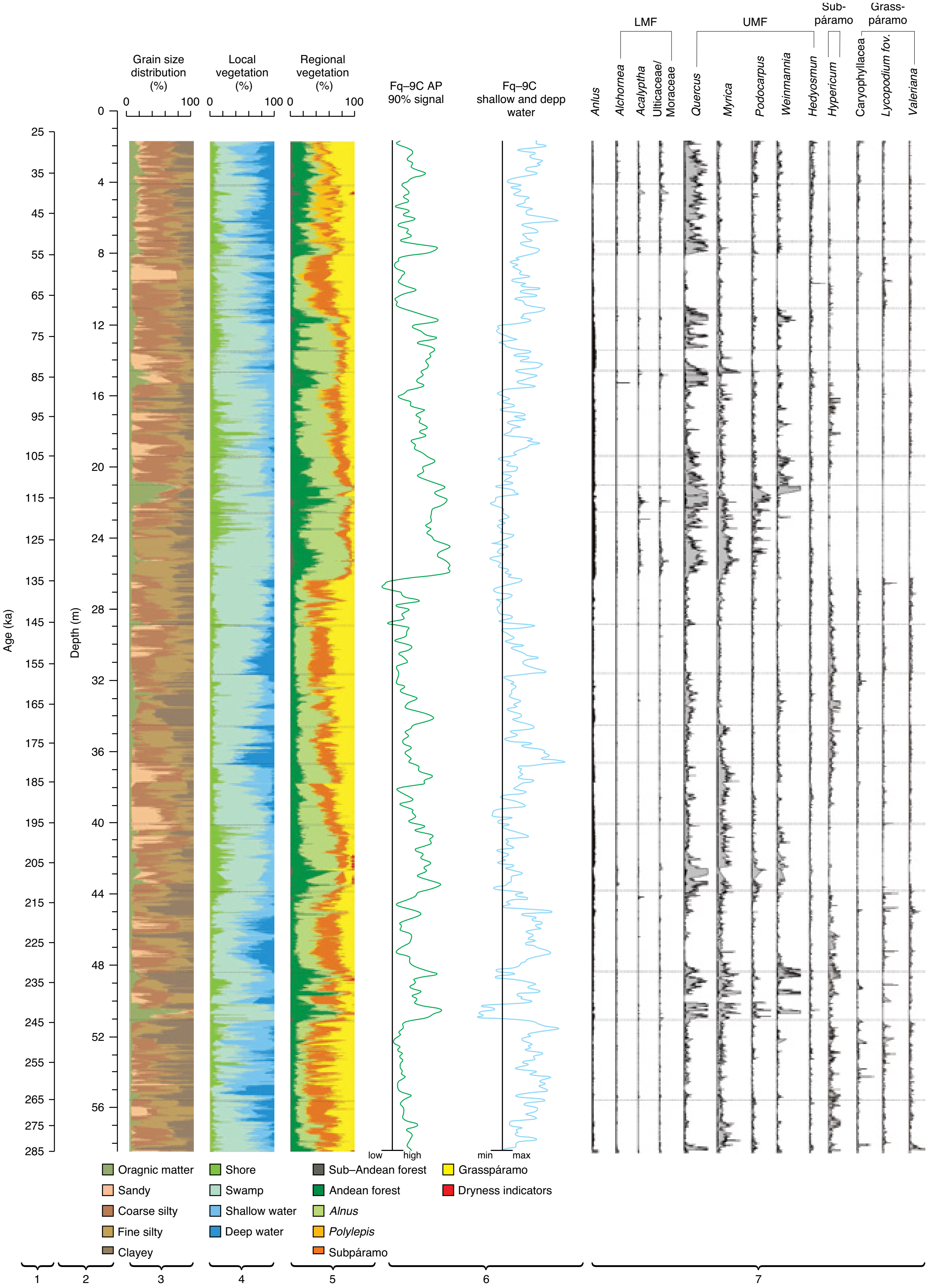
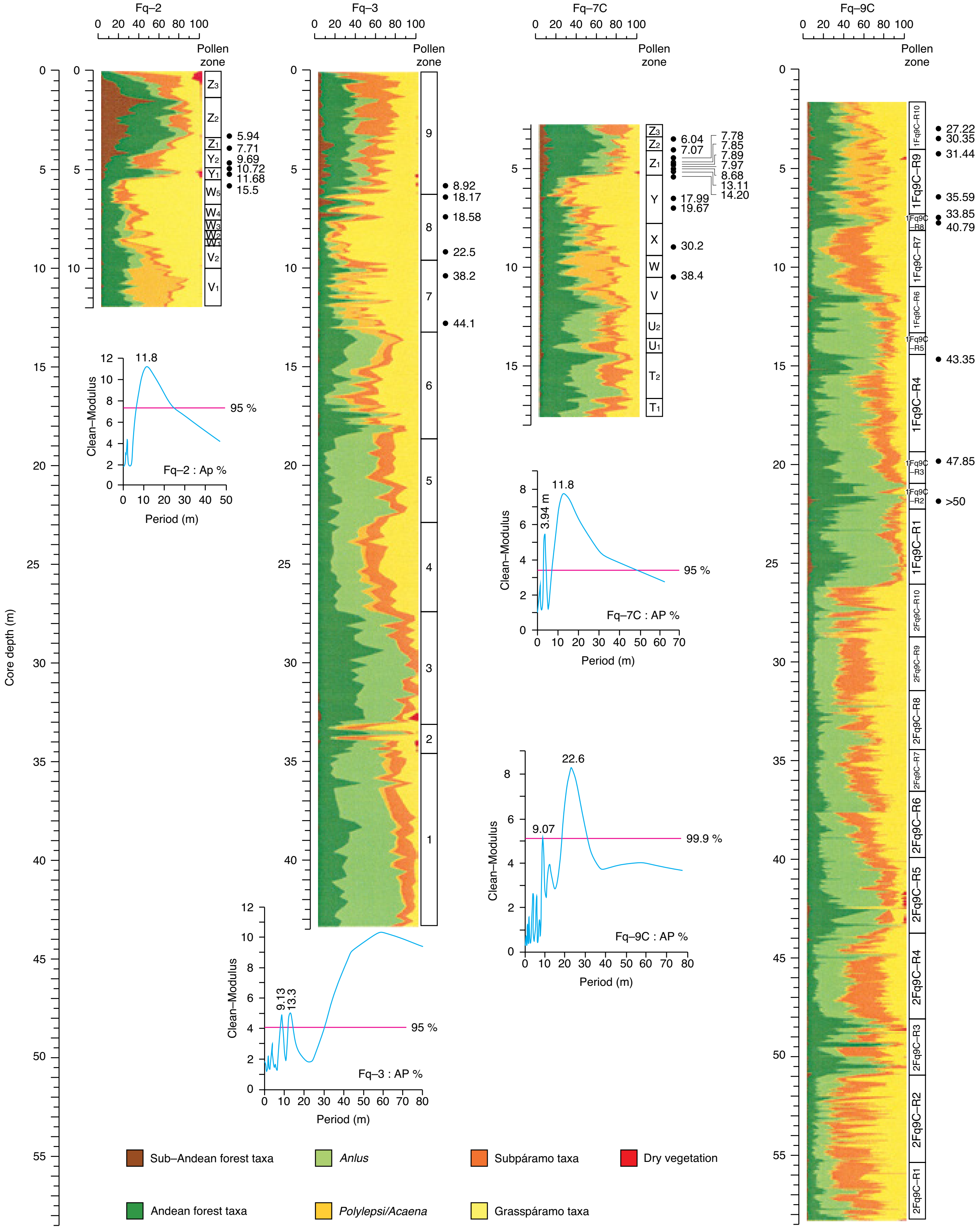
Figure 15. Synthesis of late Quaternary records of sediment accumulation, water level changes, and regional vegetation change from core Fúquene–9C for the interval 58–1.8 m composite depth reflecting the period 284–27 ka. From left to right: **(1)** inferred age scale (ka); **(2)** linear depth scale; **(3)** grain size distributions shown in 5 classes: proportions of four end–members–1 (EM–1 to EM–4) produced by the end member model algorithm (EMMA). EM–5 (organic matter and peat) was developed from the loss–on–ignition data; **(4)** aquatic vegetation shown in four groups reflecting vegetation from shallow to deep water conditions; **(5)** regional vegetation showing Lake Fúquene immersed in montane forest (green) of páramo (orange and yellow) reflecting temperature–driven shifts of the upper forest line; **(6)** arboreal pollen 90 % significance signal compared to maxima (deep–water conditions) and minima (shallow–water conditions) in the record of aquatic taxa; **(7)** records of individual pollen taxa organised by ecological preference. At 2550 m elevation lower montane taxa are only reflected during the warmest intervals of an interglacial. Most of the time Lake Fúquene is surrounded by upper montane forest. Highest representation of páramo taxa coincide with periods when Lake Fúquene was immersed in páramo vegetation reflecting glacial periods. The column for *Alnus* is 100% wide; columns of all other taxa are 10% wide (Original figure by M. Vriend).


Grain size distribution (%)
Local vegetation (%)
Regional vegetation (%)
Fq–9C AP 90% signal
Fq–9C shallow and depp water
LMF
UMF
Sub-páramo
Grass-páramo
Anlus
Alchornea
Acalyptha
Ulticaceae/ Moraceae
Quercus
Myrica
Podocarpus
Weinmannia
Hedyosmun
Hypericum
Caryophyllacea
Lycopodium fov.
Valeriana
0
100
Age (ka)
Depth (m)
25
35
45
55
65
75
85
95
105
115
125
135
145
155
165
175
185
195
205
215
225
235
245
255
265
275
285
0
4
8
12
16
20
24
28
32
36
40
44
48
52
56
low
high
min
max
Oragnic matter
Sandy
Coarse silty
Fine silty
Clayey
Shore
Swamp
Shallow water
Deep water
Sub–Andean forest
Andean forest
Alnus
Polylepis
Subpáramo
Grasspáramo
Dryness indicators
1
2
3
4
5
6
7


Fq–2
0 20 40 60 80 100
Pollen zone
Z3
Z2
Z1
Y2
Y1
W5
W4
W3
W2
W1
V2
V1
5.94
7.71
9.69
10.72
11.68
15.5
Fq–3
0 20 40 60 80 100
Pollen zone
9
8
7
6
5
4
3
2
1
8.92
18.17
18.58
22.5
38.2
44.1
Fq–7C
0 20 40 60 80 100
Pollen zone
Z3
Z2
Z1
Y
X
W
V
U2
U1
T2
T1
6.04
7.07
7.78
7.85
7.89
7.97
8.68
13.11
14.20
17.99
19.67
30.2
38.4
Fq–9C
0 20 40 60 80 100
Pollen zone
1Fq9C–R10
1Fq9C–R9
1Fq9C–R8
1Fq9C–R7
1Fq9C–R6
1Fq9C–R5
1Fq9C–R4
1Fq9C–R3
1Fq9C–R2
1Fq9C–R1
2Fq9C–R10
2Fq9C–R9
2Fq9C–R8
2Fq9C–R7
2Fq9C–R6
2Fq9C–R5
2Fq9C–R4
2Fq9C–R3
2Fq9C–R2
2Fq9C–R1
27.22
30.35
31.44
35.59
33.85
40.79
43.35
47.85
>50
Core depth (m)
0
5
10
15
20
25
30
35
40
45
50
55
Clean–Modulus
11.8
95 %
Fq–2 : Ap %
Period (m)
0 10 20 30 40 50
Clean–Modulus
3.94 m
11.8
95 %
Fq–7C : AP %
Period (m)
0 10 20 30 40 50 60 70
Clean–Modulus
22.6
9.07
99.9 %
Fq–9C : AP %
Period (m)
0 10 20 30 40 50 60 70 80
Clean–Modulus
9.13
13.3
95 %
Fq–3 : AP %
Period (m)
0 10 20 30 40 50 60 70 80
Sub–Andean forest taxa
Anlus
Subpáramo taxa
Dry vegetation
Andean forest taxa
Polylepsi/Acaena
Grasspáramo taxa

⟵

Figure 16. Pollen records from Lake Fúquene, including the 12 m long Fq–2 record (van Geel & van der Hammen, 1973), the 43 m long Fq–3 record (van der Hammen & Hooghiemstra, 2003), the 17.5 m composite Fq–7C record (Mommersteeg, 1998), and the 58 m composite Fq–9C record (Bogotá et al., 2011a; Groot et al., 2011) record plotted with a normalised pollen sum on a linear depth scale. Record Fq–9C is most complete and shows a resolution of ca. 60 y over the period from 284–27 ka. The original pollen zones and available ^{14}C ages are shown. Power spectra of arboreal pollen % (AP %) time series above confidence levels of 95 % and 99.9 % show the main periodicities in the depth domain and were used to re–calibrate the originally published age models. (Reproduced with permission from Bogotá et al., Quaternary Science Reviews 30, 2011a, Copyright Elsevier).

(Annan & Hargreaves, 2013; Bush & Philander, 1999; Bush et al., 2001; Clark et al., 2009; Schneider von Deimling et al., 2006). The LMF zone includes the transition between climate regimes from lowlands (precession driven, precipitation most important) and highlands (obliquity driven, temperature most important), making reconstructions of climate change from records between 1000 and 2000 m a.s.l. even more challenging to understand in terms of driving mechanisms.

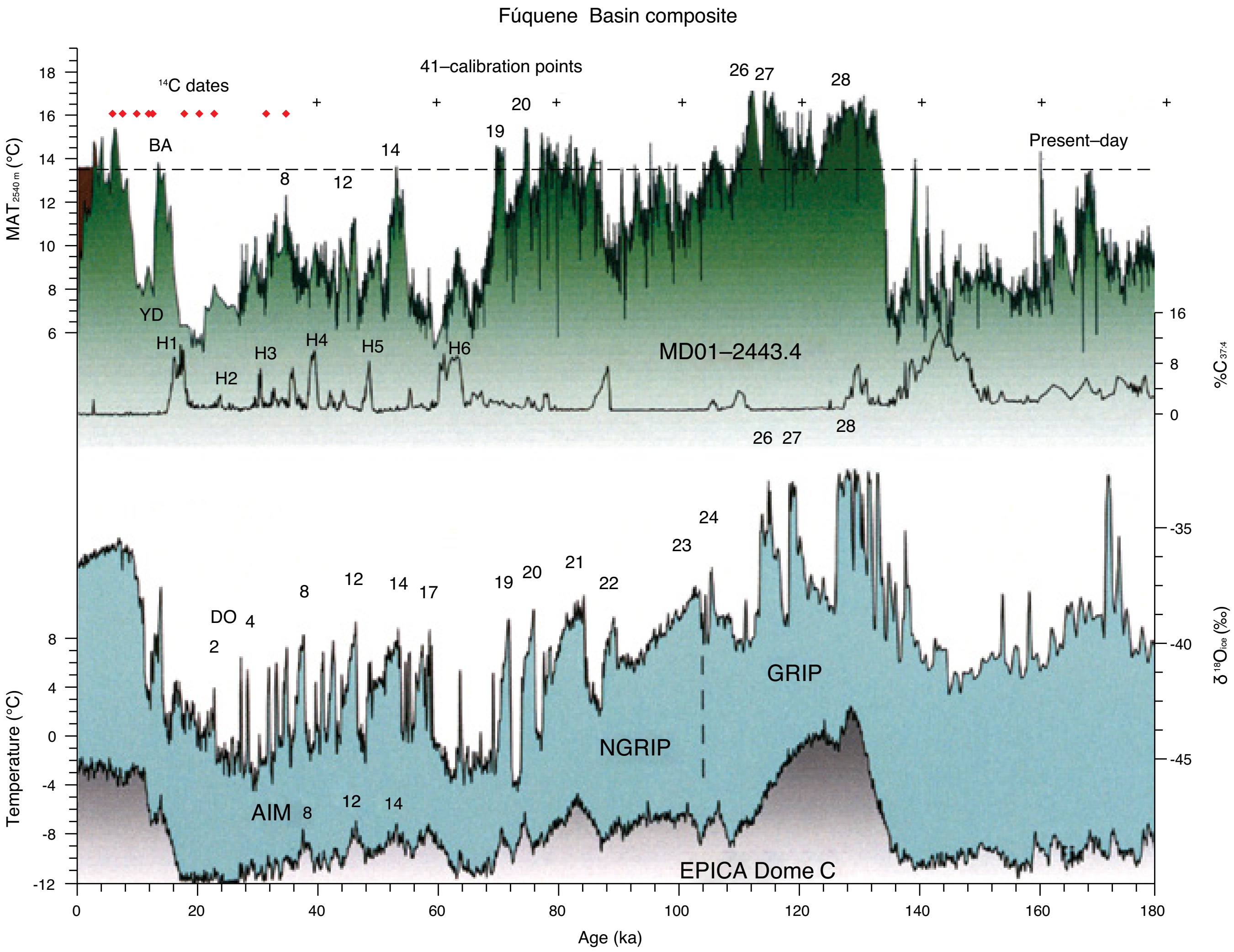


Figure 17. Comparison of palaeotemperature records from Colombian Andes, Greenland and Antarctica for the last 180 ka. Top panel: shows reconstructed mean annual temperatures at Lake Fúquene located at 2550 m a.s.l. Bottom panel: shows the combined Greenland ∂^{18}O ice core records (Anklin et al., 1993) and the Antarctica temperature record of EPICA Dome (Jouzel et al., 2007; Parrenin et al., 2007). In the top panel numbers H1–H6 reflect "Heinrich events", BA—Bølling–Allerød interstadial, and YD—Younger Dryas. In the bottom panel DO numbers indicate "Dansgaard–Oeschger (DO) cycles" 28 to 2; AIM numbers indicate the "Antarctic Isotope Maxima". The combined Greenland ∂^{18}O record includes (1) the Greenland Ice Core Chronology 2005 (GICC2005) (Andersen et al., 2004) based on annual layer counting for the past 60 ka; (2) the original NGRIP data (Andersen et al., 2004; Svensson et al., 2008) between 60 ka and 103 ka; and (3) the data from GRIP below 103 ka. The above "forest–green" color indicates MAT and the "green–blue–ish" color on the bottom the Delta 18O, and the grey–white area indicates the temperature by the EPICA Dome C curve (Reproduced with permission from Open Access paper Groot et al., Climate of the Past 7, 2011, Copyright Copernicus Publications).

2.6.6. Late Quaternary Environments in Southern Colombia: Lake La Cocha

An 11 m–long sediment core representing 14 ka of environmental history at a temporal resolution of ca. 25 y was retrieved from Lake La Cocha (2780 m a.s.l.), southern Colombia (Figure 18). This lake is located on the Andean slope facing the Amazon Basin and therefore continuously receives orographic rains. Present–day mean annual temperature is lower than expected as evaporation has a cooling effect in the area (van Boxel et al., 2014). The UFL shifted remarkably slowly from ca. 2200 m during the Lateglacial to 3550 m around 2.8 ka. This 8000 year–long rise of the UFL is thought to reflect increasing climatic moisture during the Holocene related to the southward migration of the intertropical convergence zone (Haug et al., 2001). Millennial– and centennial–scale variability is superimposed on this trend. The intertropical convergence zone–modulated trans–Amazonian moisture flow is thought to be an important driver of elevational forest dynamics but after 7 ka El Niño Southern Oscillation variability may also have played a role (see operating climate modes in Flantua et al., 2016a). The La Cocha record shows many intervals in which arboreal taxa show different proportions than today, suggesting that non–analogue vegetation associations occurred throughout most of the Holocene. Upslope forest shifts of up to 300 m 100 y^{-1}, reflecting ca. 1.5 °C temperature increase, were common during the Holocene.

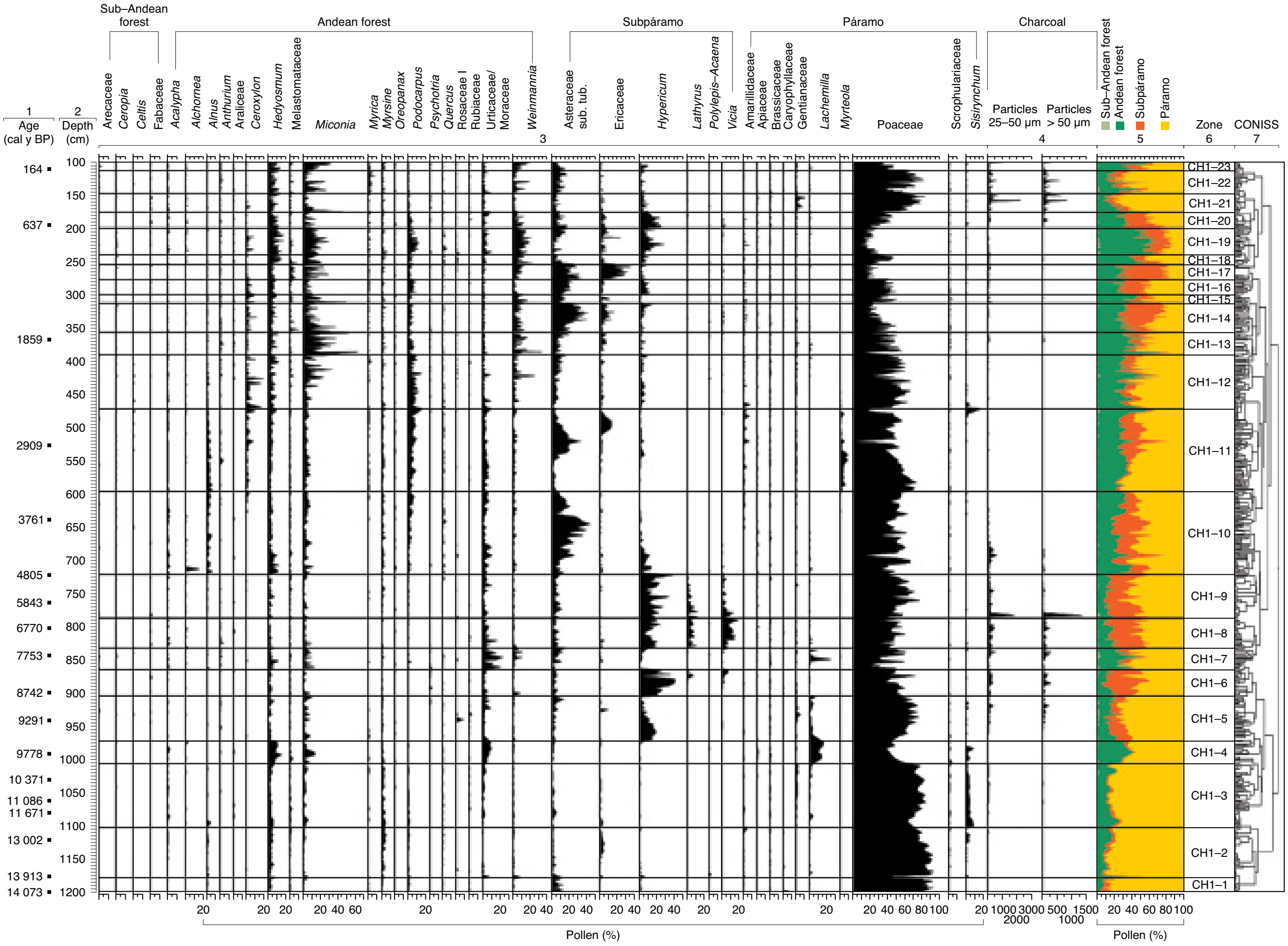


Figure 18. Vegetation and inferred climate change of the last 14 ka from a 12–m deep core from Lake La Cocha, located at 2780 m a.s.l. in southern Colombia. The pollen percentage diagram shows the records of the most important taxa arranged after ecological preferences; data are plotted on a linear time scale. From left to right: **(1)** interpolated age scale from calibrated radiocarbon ages; **(2)** depth scale (cm); **(3)** records of selected individual pollen taxa; **(4)** record of charcoal particles shown in two size classes reflecting periods of substantial burning. Burning is related to natural forest turnover (much dead biomass available as fuel) at the Lateglacial–Holocene transition, and during the period of anthropogenic deforestation during the last ca. 1400 y; **(5)** main pollen diagram showing changes in the contribution of sub–Andean forest, Andean forest, subpáramo, and grasspáramo. Note that cool growing subpáramo temporarily disappeared when montane forest rapidly shifted upslope; **(6)** pollen zones; and **(7)** the CONISS dendrogram as the basis for the zonation of the record. (Modified after González–Carranza et al., The Holocene 22, 2012).

Fast–growing trees with pioneer qualities are able to shift more rapidly upslope (Pearson, 2006) than slowly growing woody páramo shrub, which might cause subpáramo to become overrun immediately after a rapid warming. However, as shown in Flantua et al. (2014) habitat connectivity can facilitate the return of subpáramo from other locations after decades to centuries of absence. Signals of forest clearance are evident in the Lake La Cocha record during the last 1400 y.

2.7. Páramo

Setting: The páramo is a tropical alpine herbaceous vegetation located between the UFL and permanent snow (Cleef, 1981; Cuatrecasas, 2013; Guhl, 1982; Luteyn, 1999; Monasterio, 1980; Sklenář et al., 2005). The lowermost boundary varies between ca. 3200 m a.s.l. (Eastern Cordillera) and ca. 3500 m (Western Cordillera), and the uppermost boundary lies at ca. 4800 m a.s.l. where perennial snow covers mountain tops. Regional elevational differences exist (Hooghiemstra & van der Hammen, 2004; Moreno et al., 2016) but human impact on the páramo and the UMF often makes it difficult to recognise the elevation of the natural lower limit of the páramo. Páramo may have abundant shrubs in the lowermost 200–300 m interval (subpáramo), a dominance of grasses and other herbaceous vegetation in the next ca. 700 vertical metres (grasspáramo; in the Eastern Cordillera ca. 3500–4200 m), and an uppermost zone characterised by harsh climatic conditions and an incomplete vegetation cover (superpáramo; in the Eastern Cordillera ca. 4200–ca. 4800 m; Cleef, 1981; Crawford, 2008; Guhl, 1982; Luteyn, 1999; Silva et al., 2011; Sklenář et al., 2005; Vareschi, 1970). Dry páramo often occurs in inter–Andean valleys where the rain shadow prevails. Wet páramo, characterised by the bamboo *Chusquea*, occurs on slopes with orographic rains (Cleef, 1981). The elevational position of the lowermost boundary of the zone with páramo vegetation, the UFL, is driven by temperature and an unknown contribution of atmospheric $p\text{CO}_2$, whereas the proportions of subpáramo, grasspáramo, and superpáramo seem to be driven mainly by humidity and the number and intensity of frost days (Cleef, 1981; Troll, 1968). Páramo vegetation is characterised by mosaic structures and therefore transitions between the three páramo zones are difficult to constrain by climatological parameters (Hooghiemstra et al., 2012). In pollen–based vegetation reconstructions we mostly recognise a 300 m vertical interval for the subpáramo, a 700 m vertical interval for the grasspáramo, and a 700 m vertical interval for the superpáramo.

Evidence: Numerous lakes, mires, and wetlands can be found in the present–day páramo. As a consequence, palynological studies are relatively abundant compared to other biomes (see Figure 10 in Flantua et al., 2015). Pollen records often start in the Lateglacial or early Holocene when glaciers retreated to higher elevations. Ice extent and the elevational position and age of moraines were studied in Colombia by Helmens (1990, 2004, 2011; Helmens & van der Hammen, 1995).

The pollen record of La Cocha (2780 m a.s.l.) shows that during the Holocene the UFL resided mainly at four different elevations: around 2000 m a.s.l. during the Last Glacial Maximum, around 2400 m between 14 and 8 ka, around 2800 m between ca. 8 and 3 ka, and around 3550 m under modern conditions (González–Carranza et al., 2012). Using a digital elevation model, the surface area of páramo was calculated for these four frequent UFL positions (Flantua et al., 2014). The modern surface area of páramo covers only a remarkable ca. 5% of what it had been during the Last Glacial Maximum. Palaeo–record evidence is lacking that páramo lost diversity due to these dramatic surface reductions, which must have been repetitive during the Quaternary. A quantitative reconstruction of UFL position during the last 1 Ma shows evidence that the current surface of the páramo biome is close to being the smallest of the last 1 Ma (Flantua & Hooghiemstra, 2017). It is expected that current changing environmental conditions, including greenhouse gas concentrations, may drive the archipelago of páramo islands to even smaller surface areas (Anderson et al., 2011; Morueta–Holme et al., 2015; Tovar et al., 2013; Young et al., 2011), a scenario that occurred only a few times during the last million years (Flantua & Hooghiemstra, 2018; Flantua et al., 2019).

Changing atmospheric $p\text{CO}_2$ influences the relative abundances of C3 and C4 plants (Ehleringer et al., 1997). Boom et al. (2001, 2002) shows that during glacial times, when atmospheric $p\text{CO}_2$ was ca. 180 ppmv instead of the 280 ppmv for pre–industrial time, the proportion of C4 plants in the páramo was substantially larger than today (Figure 19). Marchant et al. (2006) explore the transition from montane forest to páramo and conclude that montane forest is replaced by páramo under conditions of lowering atmospheric $p\text{CO}_2$ conditions as well as under lower mean annual temperature. Experiments using a simplistic climate model assessed which climatic drivers mimic temperature fluctuations in the Fq–9C record (M. Ziegler in Groot et al., 2011) and showed $p\text{CO}_2$ to be a major player in influencing environmental changes. Thus, $p\text{CO}_2$ is a potential driver of a changing composition of páramo vegetation but mechanisms of C3 vs. C4 dynamics are complicated and still little understood (Cavender–Bares et al., 2016; Reich et al., 2018).

Results: The Funza09 pollen record shows unprecedented insights into the páramo evolution during the Quaternary (see Figure 10 in Torres et al., 2013; Supplementary Information S2). The páramo biome experienced a very dynamic history of changes in surface area, elevational interval on mountain slopes, and degree of connectivity and fragmentation. These aspects are further elaborated in section 3.3.

Hypericum is common in the current páramo but was abundant during the period from 1.9 Ma to 1.5 Ma. *Aragoa* is a stable, but minor component during the last 2.25 Ma. The rosaceous tree *Polylepis* forms ecotone forest at the UFL and occurs

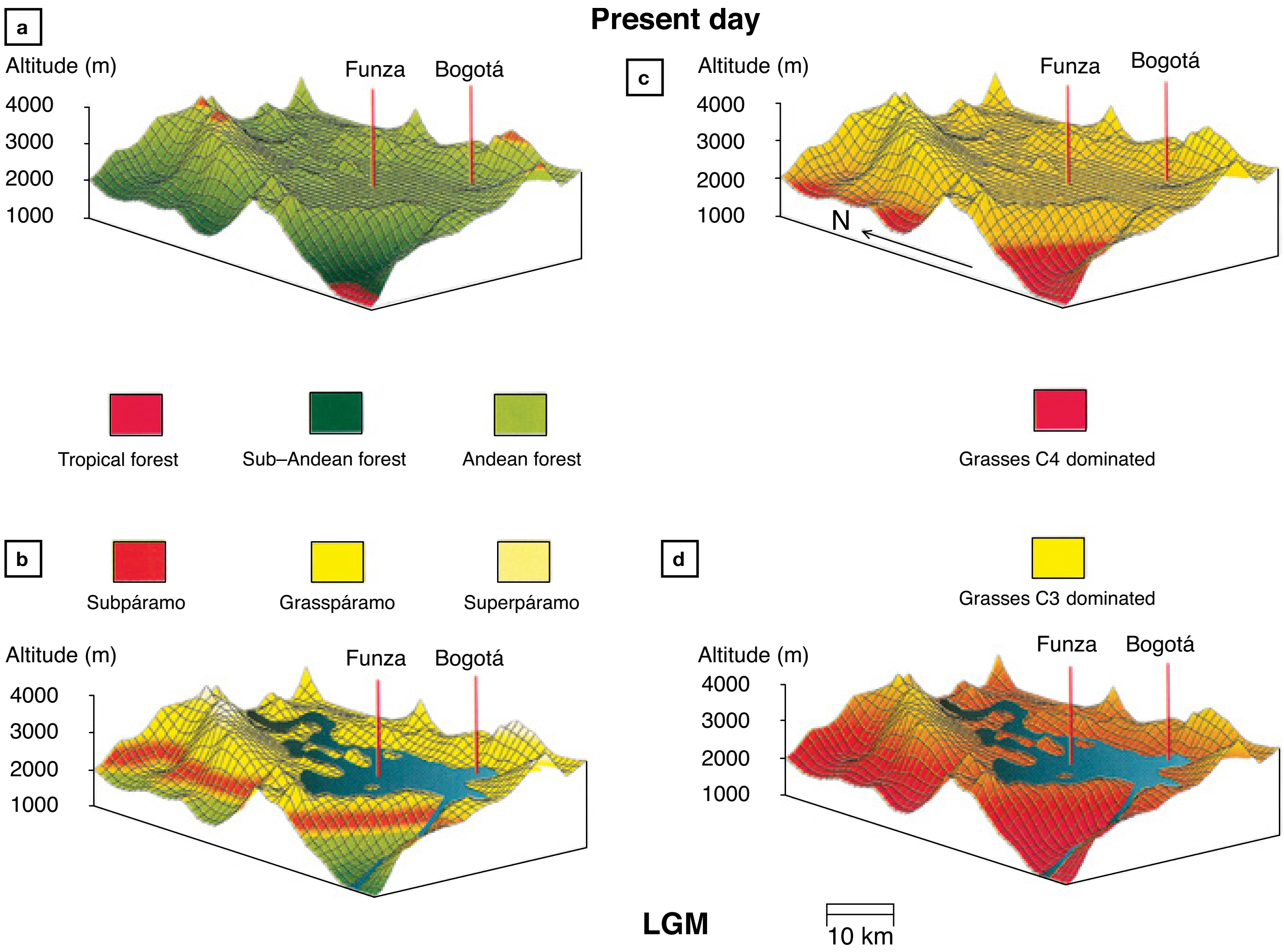


Figure 19. Vegetation distribution in the area of the High Plain of Bogotá for elevational vegetation zones. **(a)** Observed present–day elevational vegetation distribution; **(b)** reconstructed elevational vegetation distribution for the Last Glacial Maximum (LGM) (ca. 20 ka); **(c)** observed present–day elevational distribution for C3 and C4 plants; **(d)** hypothesised elevational distribution for C3 and C4 plants for the Last Glacial Maximum (ca. 20 ka).
(a) the Bogotá Basin is immersed in cool Andean forest and the upper forest line (UFL) is at ca. 3200 m a.s.l. Areas above 3200 m (mountain peaks) are covered by páramo.
(b) Vegetation distribution based on >30 pollen record from locations between 2000 and 3800 m. The presence of ancient Lake Bogotá is shown (although this lake drained already at ca. 27 ka, just before the Last Glacial Maximum. The UFL is estimated at 2000 m mainly based on the pollen record of Lake Pedro Palo (Hooghiemstra & van der Hammen, 1993). Ancient Lake Bogotá is immersed in grasspáramo.
(c) Distribution of plants with a C3 or C4 photosynthetic metabolism is based on dates from the literature, own observations (Boom et al., 2001) and unpublished data. The boundary reflects the elevation where C3 and C4 plants are both represented by 50%; this level is temperature ($T_{50\%}$) and $p\text{CO}_2$ bound and under modern conditions located below the High Plain of Bogotá.
(d) The maximum extent of C4 grass distribution is based on Ehleringer et al. (1997) model, using today's temperature constraint $T_{50\%}$ predicted at 10 °C, and using an atmospheric $p\text{CO}_2$ of 180 ppmv. It suggests that most of the páramo may have been dominated by C4 plants and thus, potentially, differs substantially from its modern floral composition. Only mountain peaks may have been covered by C3 plants as temperatures are too low for C4 plants. This setting of parameters illustrate that changes in atmospheric $p\text{CO}_2$ potentially contribute to the reconstructed shifts of the UFL. (Reproduced with permission from Boom et al., Palaeogeography Palaeoclimatology Palaeoecology 177, 2002, Copyright Elsevier).

as isolated patches of dwarf forest in the páramo. This tree is ecologically categorised as part of the subpáramo and is a good example of a dwarf tree with a substantial representation in the uppermost UMF. In the early Quaternary, presence of *Polylepis* was low but its share increased substantially during the last 1.3 Ma. Peaks in the *Polylepis* record are observed within a 150 ky period from 1.05 Ma to 0.9 Ma and, during the last 0.6 Ma, *Polylepis* became a common element of dwarf forest at the UFL and in the páramo.

Research on the páramo from northern Ecuador has been valuable for a better understanding of the Colombian páramo. The natural elevational position of the UFL was established on the basis of Holocene pollen records located on both sides of the UFL (Bakker et al., 2008) and vegetation studies along elevational gradients (Moscol–Olivera & Cleef, 2009a, 2009b). Although the present–day landscape is deforested, evidence is strong that the natural UFL is around 3600 m a.s.l. In the frame of this same objective, Jansen et al. (2013) used molecular biomarkers, which are not wind–transported and better reflect in situ evidence, to support the estimation of the UFL position. An important observation was that in a pollen site located several hundreds of metres above the UFL, and well immersed in the grasspáramo, the percentage of arboreal pollen was biased and much higher than expected due to upslope wind–transport. The combination of pollen and biomarkers evidence suggests that the UFL reached the studied coring site centuries later than assumed based on the pollen record alone (Jansen et al., 2013). This implies that reconstructions of the UFL from sites at high elevations in the páramo may systematically interpret upslope shifts of the UFL, reflecting warming conditions, too early. This outcome requires careful consideration for palaeoreconstructions of páramo, with potentially relevant consequences for UFL and land–cover models through time.

3. Multi–site Syntheses

3.1. Latin American Pollen Database

Setting: The Latin American Pollen Database (LAPD) was initiated by Vera MARKGRAF (Markgraf et al., 1996) at the University of Colorado (USA). Between 1998 and 2003, the management of the LAPD was based at the University of Amsterdam, where Robert MARCHANT served as the main coordinator and additional support was provided by Juan Carlos BERRÍO. The invaluable contributions of numerous researchers from Central and South America, the Caribbean, and México (see overview of collaborators at http://www.latinamericapollendb.com/) supported the LAPD throughout the years. Overviews have been published by Marchant et al. (2001a, 2001b, 2002b, 2004a), followed by Flantua (2017) and Flantua et al. (2013, 2015, 2016a, 2016b), after a thorough update between 2010 and 2014 by Suzette Flantua.

Evidence: The updated list of palaeoecological records in Latin America (status of 2014) shows that there are at least 1379 cores and over 4800 modern pollen–rain samples from virtually all countries in Central and South America, the Caribbean, and México (Flantua et al., 2015) (Figure 20). The metadata database and full list of literature is accessible online (www.latinamericanpollendb.com), as well as recalibrated age models from the northern Andes and R scripts to estimate temporal uncertainty of age models (Flantua et al., 2016b; https://doi.org/10.6084/m9.figshare.2069722.v2). Freely accessible raw pollen counts are available at NEOTOMA (https://www.neotomadb.org/).

Results: An overview of pollen records and recent pollen–rain data, and a spatial and temporal analysis of the data are provided by Flantua et al. (2015). Due to a relatively long history of palaeoecological research (first studies were published in the late 1950s, e.g., van der Hammen, 1959, 1961; van der Hammen & González, 1965a), Colombia has long been among the leading countries in vegetation and climate reconstructions based on fossil pollen records. Nowadays, countries such as México and Brasil are rapidly enriching their spatial and temporal coverage of palaeo–sites investigated. Within Colombia, biomes with a relatively high density of sites are the páramos and UMF, with an increasing number of sites from mangrove systems along the Caribbean coast (e.g., Urrego et al., 2009, 2010, 2018).

3.1.1. Improving the Temporal Framework of Colombian Fossil Records

Multi–site and multi–proxy studies require that chronologies of fossil pollen records are as robust as possible to test hypotheses such as whether vegetation responses to climate change are synchronous over space and time, or whether there are significant leads and lags between atmospheric, marine and terrestrial systems. To be able to answer these kinds of hypotheses, it is crucial to have accurate age models that provide the temporal backbone of palaeo–records in the best possible way. This means that age models should be plotted using calibrated dates (^{14}C dates only represent measured values of radiocarbon from a sample submitted to a laboratory: they are not calendar dates and are of less use for age estimates), the most recent calibration curve should be used, a more advanced polynomial rule should ideally be applied (instead of linear regression), and additional sedimentation information be considered, such as hiatuses and slumps (for further recommendations see Grimm et al., 2014 and Flantua et al., 2016b).

Chronologies accompanying Colombian fossil pollen records are derived from a number of different proxies, including radiocarbon, biostratigraphy, and tephra. Unfortunately, there are still a significant number of pollen records that lack chronologies or do not use calibrated ages along the depth scale. To support temporal analysis based on multi–site and multi–proxy synthesis work in Colombia, Flantua et al. (2016b) present new age models for pollen record sites without chronologies or recalibrated existing models with updated calibration curves (e.g., Intcal13 instead of Intcal98). Additionally, the temporal quality (uncertainty) of each age model and sample with a record was assessed based on a method proposed by Giesecke et al. (2014). To stimulate reuse for new analyses and capacity building on age modelling, all outcomes, R scripts, and manuals (English and Spanish) to create age models using the freely available age–modelling package CLAM in R (Blaauw, 2010), and to perform the temporal uncertainty analysis are available from figshare at: http://dx.doi.org/10.6084/m9.figshare.2069722.v4

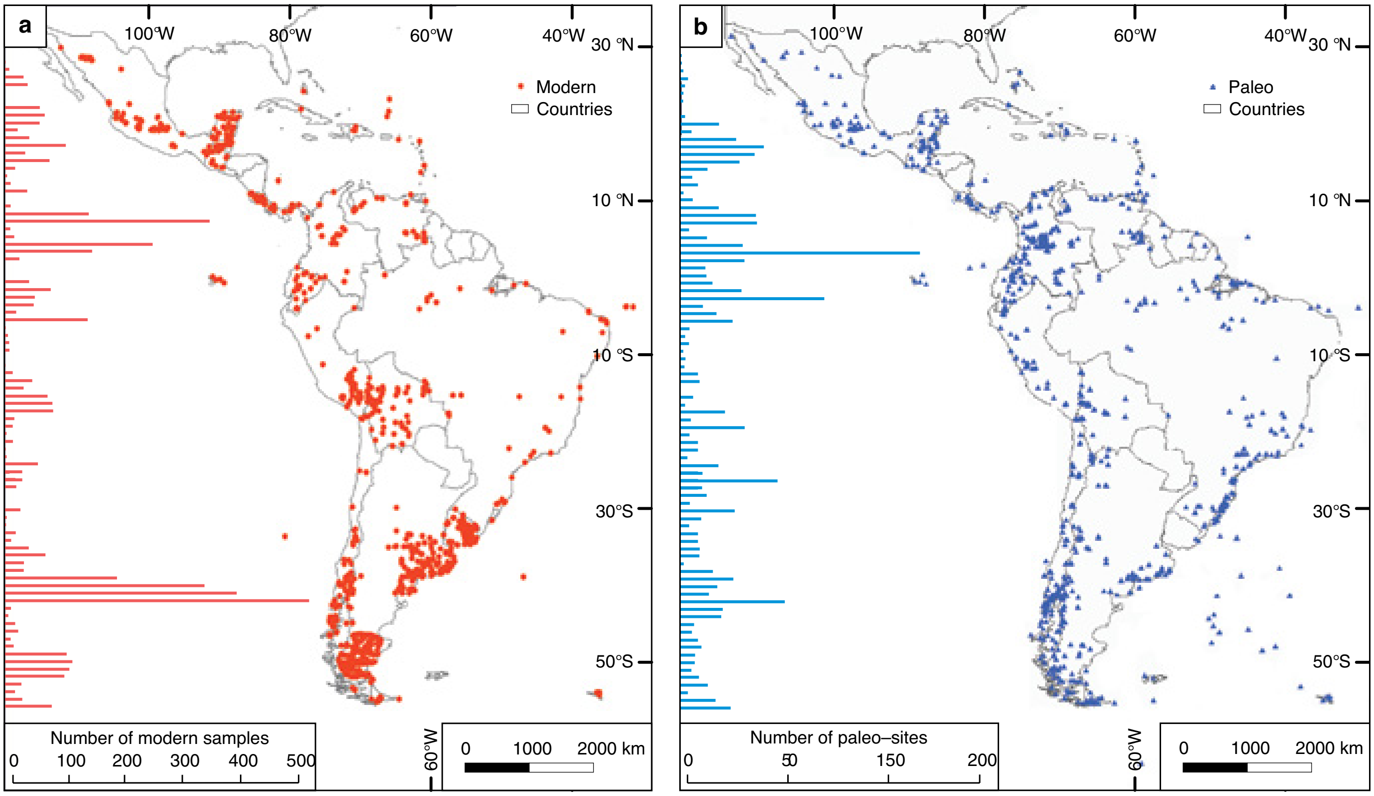


Figure 20. Overview of sites with palynological information lodged in the 2014 update of the Latin American Pollen Database (Flantua et al., 2015). **(a)** Locations with modern pollen–rain data from core tops, pollen traps, and surface sediment samples shown (red dots). **(b)** Locations of drilled sediment cores and exposed sediment sections (blue triangles). (Reproduced with permission from Open Access paper Flantua et al., Review of Palaeobotany and Palynology 223, 2015, Copyright Elsevier).

3.2. Palaeodata–Model Comparisons: the Biomisation Method

Setting: The biomisation method was developed to convert palynological data into a "*reconstructed*" vegetation map with the aim to validate a climate model–based output. Validation means that the projected vegetation map from the model is compared with the multi–site pollen–based reconstructed vegetation map of the same study area. In this procedure plant functional types (PFTs) are a necessary device for reducing the complex and often uncharted characteristics of species diversity in function and structure when attempting to project the nature and function of species assemblages into future environments (Woodward & Cramer, 1996). In the biomisation method, pollen data are treated in three matrices (Figure 21). In the first matrix, the data generated from microscope analyses are shown as the identified pollen types and their counts. In the second matrix, pollen taxa are classified according to their plant physiological constraints and assigned to groups characteristic of specific climatic variables; these groups are called PFTs (Marchant et al., 2001a, 2001b; Woodward & Cramer, 1996). Thus, the second matrix shows the pollen taxa vs. PFTs. A pollen type may belong to more than one PFT. To prepare the third matrix, biomes are "grown" out of the suite of PFTs, showing that the biomisation method is a "data–up" method. A PFT may belong to more than one biome. The third matrix shows biomes vs. PFTs. Based on matrix 3, the affinity score for each biome is calculated and the biome with the highest affinity score is considered the dominant vegetation. The advantage of the biomisation method is that the dominant vegetation is calculated via a reproducible procedure, while a palynologist interprets the data subjectively with arguments to identify the dominant vegetation, sometimes leading to debate.

Evidence: Assignments of pollen taxa to PFTs requires a good knowledge of the habitats where the parent plants of the pollen taxa occur and of growth forms. Assignment of PFTs to various biomes also requires ample field experience and knowledge of the variety of habitats in a biome. Thus, vegetation reconstructions based on floristic knowledge as shown in Figure 11, or biome reconstructions following the biomisation method as shown in Figure 21 both require input from field experience, but at a different moment in the procedure.

Results: We present here two examples of data analysis: the first based on biomisation of pollen data to reconstruct spatial–temporal changes in the vegetation of Colombia, the second based on using a vegetation model to reconstruct past changes in vegetation cover in the areas of 12 Colombian cities that reflect a variety of environments.

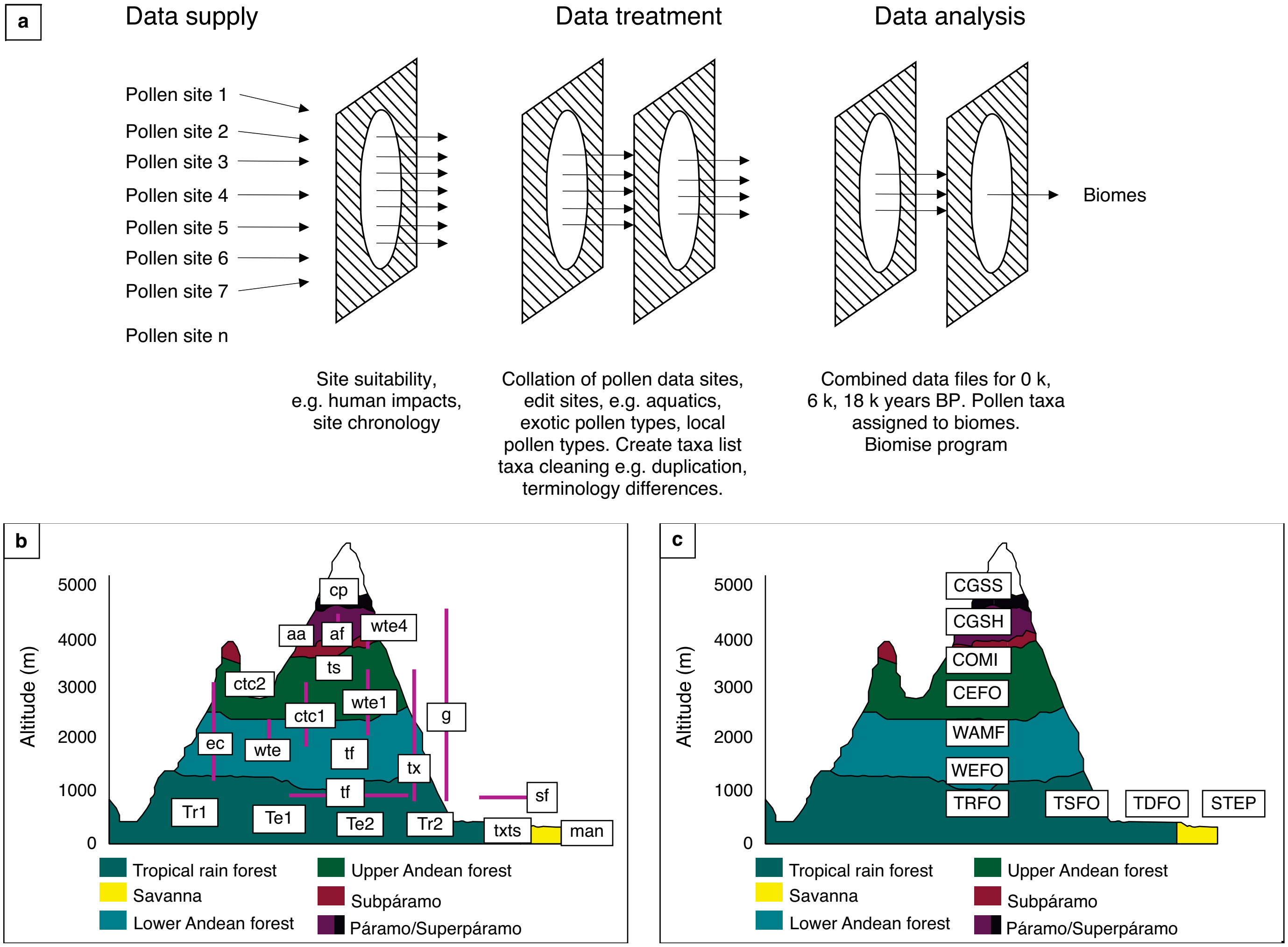
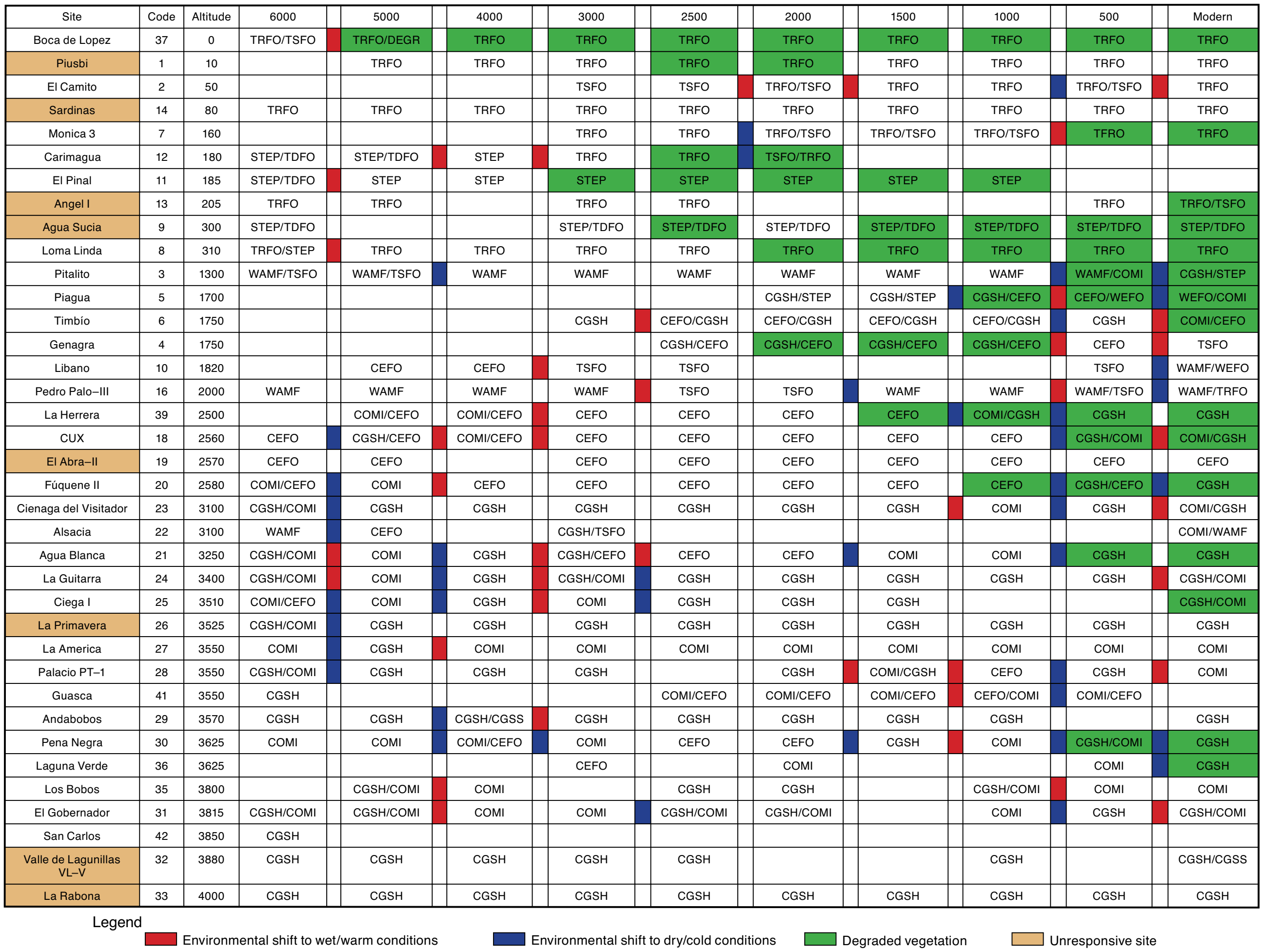


Figure 21. Data treatment in the "biomisation" procedure to prepare multiple–site pollen data as geological evidence to verify climate model output. Verification is based on comparing a *reconstructed* vegetation map based on multiple pollen sites for a particular time interval of the past with a *predicted* vegetation map for the same time interval based on climate model output.
(a) Data are collected, quality assessed, collated for specific time intervals, pollen taxa are assigned to plant functional types (PFTs) or traits, PFTs are assigned to biomes or ecosystems, and dominant biomes are plotted as biome–specific dots on a map. Such a *reconstructed* map is compared to the *predicted* map of a climate model in order to assess the climate model's quality.
(b) Cross section through the Andes near Bogotá showing in acronyms the variety of identified PFTs (traits), and the location of these PFTs in the Andes. The main elevational vegetation zones (plant formations) are shown in the background: aa—alpine shrub; af—alpine forb; cp—cushion forb; ctc1—cold temperate conifer; ctc2—maritime evergreen conifer; ec—eurythermic conifer; g—graminoid; man—mangrove; sf—eurythermic forb; Te1—tropical broad–leaved evergreen tree; Te2—tropical xeric broad–leaved evergreen tree; tf—tropical forb; Tr1—tropical raingreen tree; Tr2—dry tropical raingreen tree; ts—temperate summer green tree; tx—tree fern; txts—tropical xerophytic tree–shrub; wte—warm temperate evergreen broad–leaved tree; wte1—temperate cool deciduous broad–leaved tree; wte4—temperate cold–deciduous broad–leaved tree.
(c) Cross section through the Andes near Bogotá showing in acronyms the variety of identified biomes, and the location of these biomes in the Andes: CEFO—cool evergreen forest; COMI—cool mixed forest; CGSS—cool graslands; CGSH—cool grass shrublands; STEP—steppe–páramo; TDFO—tropical dry forest; TRFO—tropical rainforest; TSFO—tropical seasonal forest; WAMF—warm temperate mixed forest; WEFO—warm evergreen forest. (a: Reproduced with permission from Marchant et al., Quaternary Science Reviews 20, 2001b, Copyright Elsevier; b and c: Reproduced with permission from Open Access paper Marchant et al., Climate of the Past 5, 2009, Copyright Copernicus Publications).

Pollen data from 37 Colombian records located between 0 and 4000 m a.s.l. were assigned to PFTs and biomes. From all pollen records, samples were extracted representing ten time–windows between 6 ka and the present (Marchant et al., 2001b) and affinity scores were calculated for the 10 time–windows in the 37 records, producing a matrix of dominant vegetation in each of the 370 fields. Elevational variation in vegetation in the Colombian Andes is well reflected (Figure 22). At 6 ka, the biomes are mainly characteristic of warmer conditions relative to today (Kaufman et al., 2004). This trend continues until between 4 and 3 ka when there is a shift to more mesic vegetation, likely due to higher precipitation. The period between 2.5 and

1 ka reflects little or no change and is interpreted as a period of environmental stability. Human–induced impact on the vegetation (green fields in Figure 22) is recorded since 5 ka, but is particularly important from 2 ka (see also Flantua et al., 2016a). The extent of human impact increases over the late Holocene and becomes apparent at increasingly higher elevations, today up to ca. 3800 m a.s.l. Despite human interference, a number of sites do not change their biome assignment throughout the series of time–windows, pointing to an asynchronous vegetation response. Directions of change (to warmer and wetter or colder and drier conditions) may be opposite depending on elevation, mainly demonstrating that precipitation regimes can change suddenly and are not necessarily synchronous across a region (Flantua et al., 2016a). Multi–site biomisation of pollen data shows a wealth of results in concise form and stimulates a better understanding of past vegetation change and its drivers.

In another example, we show how biomes in the Last Glacial Maximum are assessed by applying the BIOME–3 vegetation model, set to operate at levels of 200 ppmv and with climatic data from 12 meteorological stations that encompass a range of environments within Colombia (Marchant et al., 2004a). At lower elevations, it is apparent that moisture is the dominant control on driving vegetation change, whereas temperature becomes more important at higher elevations. These results are in support of the model experiments with the Fq–9C data from 2540 m a.s.l. (Groot et al., 2011). Figure 23 shows, in



Site	Code	Altitude	6000		5000		4000		3000		2500		2000		1500		1000		500		Modern
Boca de Lopez	37	0	TRFO/TSFO	🟥	🟩 TRFO/DEGR		🟩 TRFO		🟩 TRFO		🟩 TRFO		🟩 TRFO		🟩 TRFO		🟩 TRFO		🟩 TRFO		🟩 TRFO
🟫 Piusbi	1	10			TRFO		TRFO		TRFO		🟩 TRFO		🟩 TRFO		TRFO		TRFO		TRFO		TRFO
El Camito	2	50							TSFO		TSFO	🟥	TRFO/TSFO	🟥	TRFO		TRFO	🟦	TRFO/TSFO	🟥	TRFO
🟫 Sardinas	14	80	TRFO		TRFO		TRFO		TRFO		TRFO		TRFO		TRFO		TRFO		TRFO		TRFO
Monica 3	7	160							TRFO		TRFO	🟦	TRFO/TSFO		TRFO/TSFO		TRFO/TSFO	🟥	🟩 TFRO		🟩 TRFO
Carimagua	12	180	STEP/TDFO		STEP/TDFO	🟥	STEP	🟥	TRFO		🟩 TRFO	🟦	🟩 TSFO/TRFO								
El Pinal	11	185	STEP/TDFO	🟥	STEP		STEP		🟩 STEP		🟩 STEP		🟩 STEP		🟩 STEP		🟩 STEP				
🟫 Angel I	13	205	TRFO		TRFO				TRFO		TRFO								TRFO		🟩 TRFO/TSFO
🟫 Agua Sucia	9	300	STEP/TDFO						STEP/TDFO		🟩 STEP/TDFO		STEP/TDFO		🟩 STEP/TDFO		🟩 STEP/TDFO		🟩 STEP/TDFO		🟩 STEP/TDFO
Loma Linda	8	310	TRFO/STEP	🟥	TRFO		TRFO		TRFO		TRFO		🟩 TRFO		🟩 TRFO		🟩 TRFO		🟩 TRFO		🟩 TRFO
Pitalito	3	1300	WAMF/TSFO		WAMF/TSFO	🟦	WAMF		WAMF		WAMF		WAMF		WAMF		WAMF	🟦	🟩 WAMF/COMI	🟦	🟩 CGSH/STEP
Piagua	5	1700											CGSH/STEP		CGSH/STEP	🟦	🟩 CGSH/CEFO	🟥	🟩 CEFO/WEFO	🟦	🟩 WEFO/COMI
Timbío	6	1750							CGSH	🟥	CEFO/CGSH		CEFO/CGSH		CEFO/CGSH		CEFO/CGSH	🟦	CGSH	🟥	🟩 COMI/CEFO
Genagra	4	1750									CGSH/CEFO		🟩 CGSH/CEFO		🟩 CGSH/CEFO		🟩 CGSH/CEFO	🟥	CEFO	🟥	TSFO
Libano	10	1820			CEFO		CEFO	🟥	TSFO		TSFO								TSFO	🟦	WAMF/WEFO
Pedro Palo–III	16	2000	WAMF		WAMF		WAMF		WAMF	🟥	TSFO		TSFO	🟦	WAMF		WAMF	🟥	WAMF/TSFO	🟦	WAMF/TRFO
La Herrera	39	2500			COMI/CEFO		COMI/CEFO	🟥	CEFO		CEFO		CEFO		🟩 CEFO	🟦	🟩 COMI/CGSH	🟦	🟩 CGSH		🟩 CGSH
CUX	18	2560	CEFO	🟦	CGSH/CEFO	🟥	COMI/CEFO	🟥	CEFO		CEFO		CEFO		CEFO		CEFO	🟦	🟩 CGSH/COMI	🟥	🟩 COMI/CGSH
🟫 El Abra–II	19	2570	CEFO		CEFO				CEFO		CEFO		CEFO		CEFO		CEFO		CEFO		CEFO
Fúquene II	20	2580	COMI/CEFO	🟦	COMI	🟥	CEFO		CEFO		CEFO		CEFO		CEFO		🟩 CEFO	🟦	🟩 CGSH/CEFO	🟦	🟩 CGSH
Cienaga del Visitador	23	3100	CGSH/COMI	🟦	CGSH		CGSH		CGSH		CGSH		CGSH		CGSH	🟥	COMI	🟦	CGSH	🟥	COMI/CGSH
Alsacia	22	3100	WAMF	🟦	CEFO				CGSH/TSFO												COMI/WAMF
Agua Blanca	21	3250	CGSH/COMI	🟥	COMI	🟦	CGSH	🟥	CGSH/CEFO	🟥	CEFO		CEFO	🟦	COMI		COMI	🟦	🟩 CGSH		🟩 CGSH
La Guitarra	24	3400	CGSH/COMI	🟥	COMI	🟦	CGSH	🟥	CGSH/COMI	🟦	CGSH		CGSH		CGSH		CGSH		CGSH	🟥	CGSH/COMI
Ciega I	25	3510	COMI/CEFO	🟦	COMI	🟦	CGSH	🟥	COMI	🟦	CGSH		CGSH		CGSH						🟩 CGSH/COMI
🟫 La Primavera	26	3525	CGSH/COMI	🟦	CGSH		CGSH		CGSH		CGSH		CGSH		CGSH		CGSH		CGSH		CGSH
La America	27	3550	COMI	🟦	CGSH	🟥	COMI		COMI		COMI		COMI		COMI		COMI		COMI		COMI
Palacio PT–1	28	3550	CGSH/COMI	🟦	CGSH		CGSH		CGSH				CGSH	🟥	COMI/CGSH	🟥	CEFO	🟦	CGSH	🟥	COMI
Guasca	41	3550	CGSH								COMI/CEFO		COMI/CEFO		COMI/CEFO	🟥	CEFO/COMI	🟦	COMI/CEFO		
Andabobos	29	3570	CGSH		CGSH	🟦	CGSH/CGSS	🟥	CGSH		CGSH		CGSH		CGSH		CGSH				CGSH
Pena Negra	30	3625	COMI		COMI	🟦	COMI/CEFO	🟦	COMI		CEFO		CEFO	🟦	CGSH	🟥	COMI	🟦	🟩 CGSH/COMI	🟦	🟩 CGSH
Laguna Verde	36	3625							CEFO				COMI						COMI	🟦	🟩 CGSH
Los Bobos	35	3800			CGSH/COMI	🟥	COMI				CGSH		CGSH				CGSH/COMI	🟥	COMI		COMI
El Gobernador	31	3815	CGSH/COMI		CGSH/COMI	🟥	COMI		COMI	🟦	CGSH/COMI		CGSH/COMI				COMI	🟦	CGSH	🟥	CGSH/COMI
San Carlos	42	3850	CGSH																		
🟫 Valle de Lagunillas VL–V	32	3880	CGSH		CGSH		CGSH		CGSH		CGSH						CGSH				CGSH/CGSS
🟫 La Rabona	33	4000	CGSH		CGSH		CGSH		CGSH		CGSH		CGSH		CGSH		CGSH		CGSH		CGSH

Legend
🟥 Environmental shift to wet/warm conditions
🟦 Environmental shift to dry/cold conditions
🟩 Degraded vegetation
🟫 Unresponsive site

Figure 22. Reconstruction of the dominant biomes at 37 Colombian sites located between 0 and 4000 m elevation, and for 10 time slices from 6000 ^{14}C y BP to today. Where the biomes change from one time window to the next, this is classified into one or two different responses: when there is a shift to a biome indicative of wetter and/or warmer environment it is indicated in red; when there is a shift to a biome indicative of a drier and/or cooler environment it is indicated in blue. Sites that do not change their biome assignment throughout the last 6000 y are highlighted in light brown. In order to make an experimental link between palaeoecology and archaeology an introduced artificial PFT reflects "anthropogenic degraded" vegetation. When sites demonstrate an affinity to the degraded vegetation category this is highlighted in green. The flow of green fields suggest that ancient people arrived around 6 ka in northern Colombia, migrated into the Andes between 3 and 1 ka in particular, and recently expanded agricultural activities up to 3850 m a.s.l. TRFO—tropical rain forest; TSFO—tropical seasonal forest; TDFO—tropical dry forest; WEFO—warm evergreen forest; CEFO—cool evergreen forest; WAMF—warm mixed forest; COMI—cool mixed forest; STEP—steppe; CGSH—cool grasslands; CGSS—cool grassland shrub; DEGE—degraded vegetation. (Reproduced with permission from Marchant et al., Quaternary Science Reviews 20, 2001b, Copyright Elsevier)

a mean annual temperature vs. mean annual precipitation space, the biome reconstructions for 12 cities in Colombia. In Quibdó no vegetation change is observed since the Last Glacial Maximum: here excessive high precipitation prevents any change. In Villavicencio, (orographic) rainforest prevails today whereas drier Last Glacial Maximum conditions caused seasonal forest to be dominant (current pollen records from this location are yet unable to confirm this model–based prediction). Nowadays, Cali is surrounded by seasonal forest but at this location xeric woodland shrub prevailed during the Last Glacial Maximum. In Arauca, xeric woodland shrub and tall grassland dominate the current landscape, while the vegetation model calculates moist savanna during the Last Glacial Maximum. In conclusion, the BIOME–3 vegetation model potentially offers insights into vegetation change and pollen–based reconstructions can provide the necessary validation of the model output.

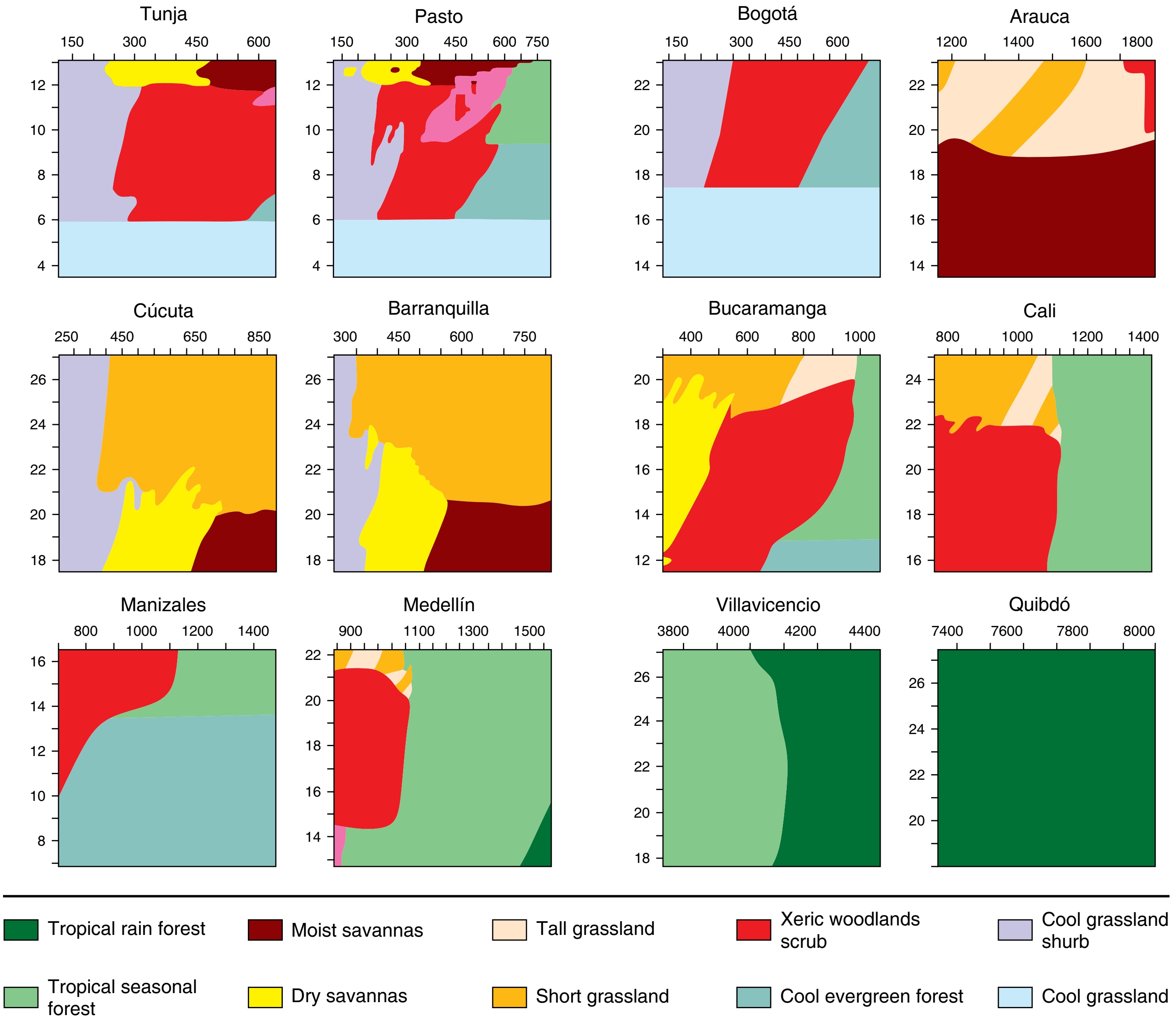


Figure 23. Reconstruction of vegetation change since the Last Glacial Maximum (ca. 20 ka) for 12 major Colombian cities. Biome reconstructions derived from the BIOME–3 vegetation model. Plots show a "climate space" with the mean annual temperature (°C) shown along the Y–axis and the mean annual precipitation (mm y^{-1}) shown along the X–axis. In each plot the present–day climate space is shown in the top right hand corner and the Last Glacial Maximum conditions in the bottom left hand corner. To simulate Last Glacial Maximum conditions we assumed an atmospheric $p\mathrm{CO}_2$ of 200 ppmv, a mean annual temperature of 8 °C cooler than today, and a mean annual precipitation of 600 mm y^{-1} lower than today. The sequence of potential vegetation change during the last 20 ka follows the diagonal from bottom–left to top–right. Note that, for example, Quibdó is constantly immersed in "rainforest", Villavicencio shows a change from "tropical seasonal forest" to "tropical rainforest", the vegetation in Arauca is changing from "moist savanna" to "tall grassland", and in Cúcuta different sequences of vegetation change may have occurred from cool grassland at 20 ka to "short grassland" today. (Reproduced with permission from Marchant et al., Journal of Quaternary Science 19, 2004a, Copyright Wiley–Blackwell).

3.3. Pollen–Driven Distribution Areas in a Digital Elevation Model

Setting: Pollen records intrinsically provide site–specific information and deriving spatial patterns remains challenging. The biomisation method brings together multi–site evidence, whereas in this example, evidence from a single site (the position of the UFL) is assumed to be representative of a larger area and extrapolated. Using a digital elevation model of the Colombian Andes the UFL contours are mapped for different elevations and at different time windows (Figure 24). The degree of isolation of páramo habitat varies with the elevational position of the UFL, and the varying degree of connectivity can be calculated. In addition, it is shown at which elevational interval and during how much time connections were potentially available between páramo islands, potentially allowing gene flow (Flantua & Hooghiemstra, 2017; 2018).

Evidence: For the northern Andes, elevational positions of montane forest (LMF and UMF together) and páramo during the last 1 Ma have been estimated from the Funza09 pollen record (Torres et al., 2013) and the Fq–9C record (Groot et al., 2011). For the pilot study in southern Colombia we used the pollen record from Lake La Cocha–1 (González–Carranza et al., 2012).

Results: Lake La Cocha reflects a suite of biomes along an altitudinal and climatic moisture gradient. We used a digital elevation model with pollen–inferred UFL positions (section

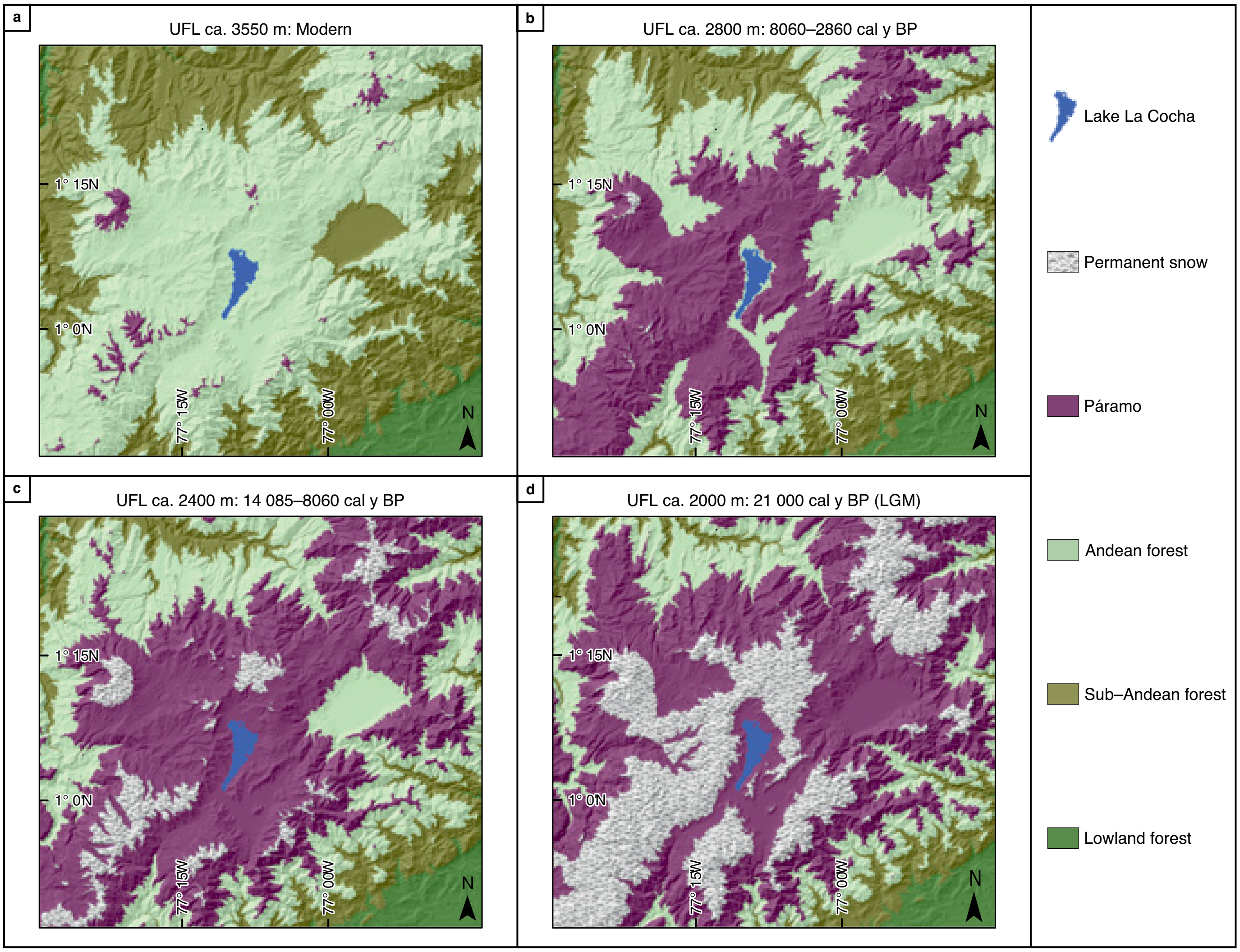


Figure 24. Changes in vegetation distribution since the Last Glacial Maximum around Lake La Cocha (2780 m a.s.l.) based on the pollen record by González–Carranza et al. (2012). Four periods are recognised with a characteristic elevational position of the upper forest line (UFL): **(a)** UFL at 3550 m reflecting the present–day conditions; **(b)** UFL at 2800 m reflecting the period from 8060 to 2860 y BP; **(c)** UFL at 2400 m reflecting the period from 14 085 to 8060 y BP; **(d)** UFL at 2000 m reflecting the Last Glacial Maximum at ca. 21 000 y BP. Using a digital elevation model the surface of "lowland forest", "sub–Andean forest", "Andean forest", "páramo" (including subpáramo, grasspáramo, and superpáramo), and "permanent snow" was calculated. Note that in this selected study area the present–day surface of páramo is ca. 5% of its Last Glacial Maximum surface highlighting the dramatic changes in surface of this high montane ecosystem. Isolation and connectivity between "páramo islands" depend on the roughness of the mountains, presence of plateau, and the elevation of thresholds (mountain passes). (Reproduced with permission from Flantua et al., 2014, Copyright The Missouri Botanical Garden Press).

2.6) to estimate changes in biome surface (Flantua et al., 2014) (Figure 24). Results show how changing climatic conditions give rise to connection or disconnection and at which locations. For specific areas, connectivity dynamics can be forecast: a relevant instrument in the conservation of mountain reserves. One of the most salient results is that the present–day páramo covers only ca. 5% of the Last Glacial Maximum surface area. Such dramatic reductions in biome surface may coincide with species loss, but for the páramo biome there is no evidence of species loss during the Pleistocene. On the contrary, from molecular phylogenetic analyses there are strong signals of Pleistocene speciation (Diazgranados & Barber, 2017; Nevado et al., 2018). We extended the study of spatial páramo distribution to the northern Andes, including Venezuela, Colombia, and Ecuador (Flantua & Hooghiemstra, 2017, 2018). Upslope shifts of the UFL provoke different histories of fragmentation and isolation of páramos in different cordilleras (Figure 25) and different connectivity histories under lowering UFL positions (Flantua & Hooghiemstra, 2017, 2018).

4. Human Impact on the Environment

Setting: The spread of early cultures during the late Quaternary receives much attention as a window into the development of civilisations, the earliest human impact on the environment (e.g., Bellwood, 2005; Dodson, 2010; Laws, 2010; Pearsall & Stahl, 2012; Reichel–Dolmatoff, 1965), and to what degree "natural" forest is pristine (e.g., Heckenberger et al., 2003; Willis & Birks, 2006). Palaeoecological evidence in Colombia of early human impact on the environment comes from the El Abra rock–shelters on the high plain of Bogotá (van der Hammen & Correal–Urrego, 1978) dated to ca. 12 ka. At a national scale, human impact is especially apparent during the last 3 ka (Marchant et al., 2001b).

Evidence: Evidence on climate variability and human presence during the last 2000 y was reviewed in detail by Flantua et al. (2016a). Metadata from the Latin American Pollen Database (Flantua et al., 2015) were used in combination with the originally published interpretations of the pollen records.

Results: Numerous Colombian pollen records show evidence of human impact during the late Holocene (Figure 26; Table 1): for instance, sites in the savannas of the Llanos Orientales during the last ca. 3500–2500 y (see section 2.1), in the Eastern Cordillera record of Fq–2 during the last 3000 y (van Geel & van der Hammen, 1973), in the Western Cordillera record of Llano Grande–2 over the last ca. 2300 y (Muñoz et al., 2017) and of Llano Grande–1 during the last 600 y (Velásquez–Ruiz & Hooghiemstra, 2013), and in the southern Central Cordillera Lake La Cocha during the last ca. 1400 y (González–Carranza et al., 2012). Evidence of human impact includes pollen grains from crop plants (e.g., maize), crop associated weeds (e.g., *Rumex*), pioneer species after disturbance (e.g., *Cecropia*), and also sudden decreases of arboreal pollen percentages (in combination with peaks of charcoal) (Figure 27). Biomisation–based evidence in Marchant et al. (2001b) illustrates for Colombia the progressive expansion of human occupation: starting around 5 ka in the lowlands of northern Colombia, and over the last 3000 y expanding into the savannas of the Llanos Orientales and into the high Andes in modern times where potatoes are cultivated up to >3800 m a.s.l. Flantua et al. (2016a) suggest north–south corridors in the Andes of early human migration as well as expansions of early settlements into regionally favourable environments. The Andes, especially, has been a region of long human occupation.

5. Discussion, Conclusions, and Perspectives

Sixty years of palynological research, gradually extending into multi–proxy synthesis work, has provided Colombia with a remarkably large volume of documentation and understanding of its Quaternary history. We presented here a comprehensive overview of available data and results within a defined number of topics. Quaternary pollen analysis developed a century ago (Birks & Berglund, 2017; Edwards 2018; Edwards & Pardoe, 2018) and was brought to Colombia in the 1950s by Thomas van der Hammen. Still today, palynology has a central position in palaeoenvironmental research. Understanding mechanisms of climate change and how modern environments came into existence after a long history of human interference is of high relevance for society, politics, and the national economy (Dodson, 2010; Matthews et al., 2012).

A better understanding of human impact on the landscape during the last 2000 y of the Quaternary may fuel better strategies in conservation initiatives. Assessing past environmental and climate change during two full glacial–interglacial cycles (the last ca. 200 000 y) is of imminent importance to interpret current effects of global change properly. Colombia can provide two, globally unique, long Pleistocene records of vegetation and climate change, which serve as a rich source of evidence. Apart from the straightforward interpretations of these large pollen data sets, numerical data analysis may help provide answers to otherwise intractable questions (e.g., Felde et al., 2016). The idea of how knowledge of the past can help us to conserve the future is pivotal in current societally relevant research (Nogué et al., 2017; Rangel–Churio, 2006; Willis & Birks, 2006; Willis & MacDonald, 2011; Willis et al. 2007a, 2007b, 2010a, 2010b). Baseline information is required on the potential of the elevationally shifting forests (Bakker et al., 2008) to sequester and store carbon in soils (Lal et al., 2015) and how ecosystem services can be conserved in the future (e.g., Jeffers et al., 2015). A growing notion in Colombia of these aspects was demonstrated in 2010 at the "Congreso Internacional de los 180 años de la Procuraduría General de la Nación de Colombia" in Santa Marta where this paper found its

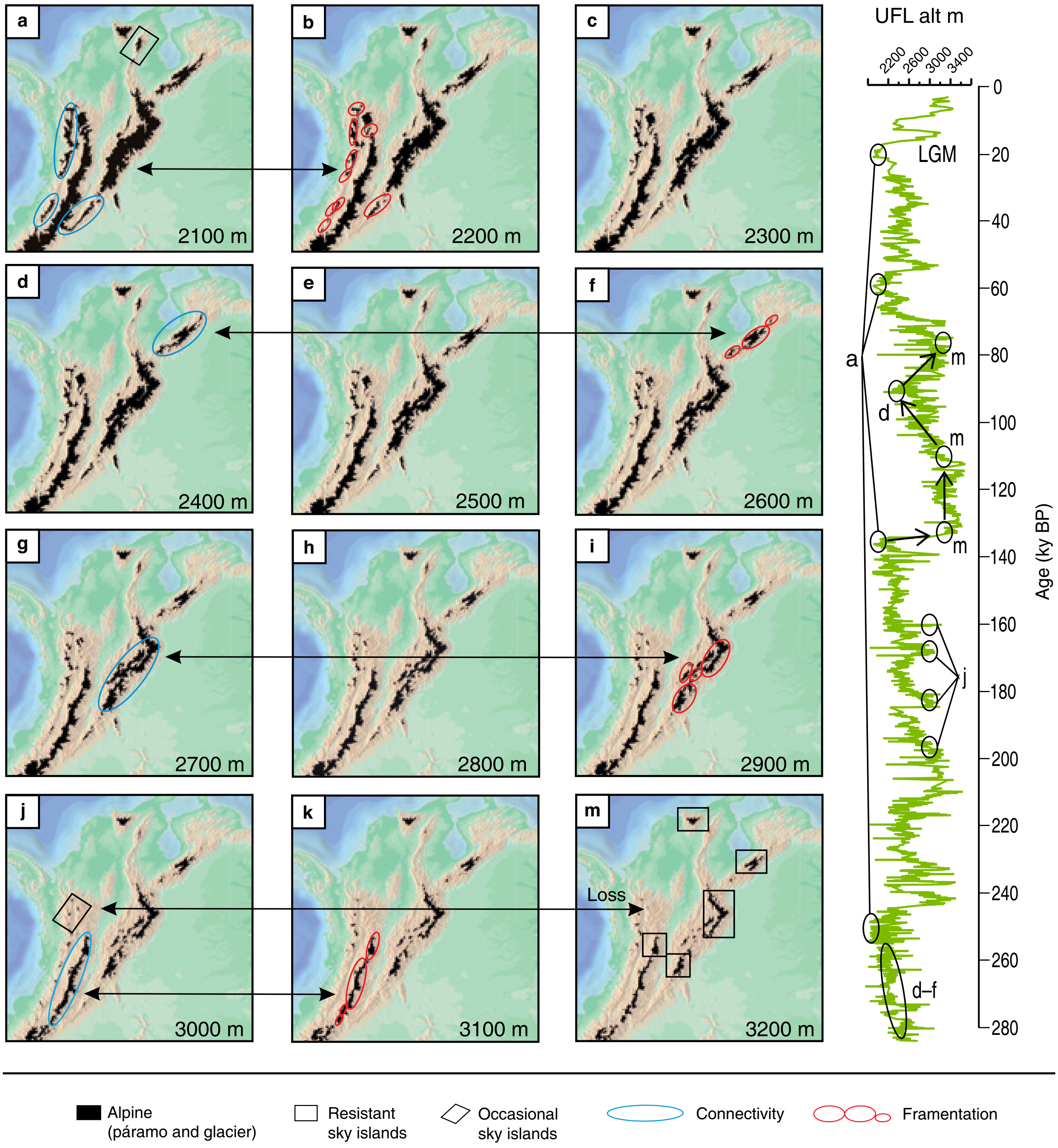


Figure 25. Spatial reconstructions of the extension of páramo and glaciers (in black) in the northern Andes during the last 280 ka shown for upper forest line (UFL) positions between 2100 and 3200 m (maps a to m). Each map represents a simplified reconstruction of the distribution of páramo and glaciers using a digital elevation model. Estimated elevations of the UFL are inferred from the Fúquene–9C pollen record shown in the right hand panel (Bogotá et al., 2011a; Groot et al., 2011). Letters in the right hand panel correspond to the panels with different UFL elevations. Low UFL positions reflect cool periods (stadials) to cold periods (such as the Last Glacial Maximum). Higher UFL positions reflect mild periods (interstadials) to warm periods (interglacial conditions, such as today). Different regions experience páramo connectivity and fragmentation at different moments in time, and at different elevational intervals depending on the roughness of the mountains. Note that some páramo areas persist continuously (resistant sky islands) whereas other appear and disappear (occasional sky islands). (Reproduced with permission from Flantua & Hooghiemstra, 2018, in Hoorn et al., 2018 (eds.), Mountains, climate, and biodiversity, Copyright Wiley–Blackwell).

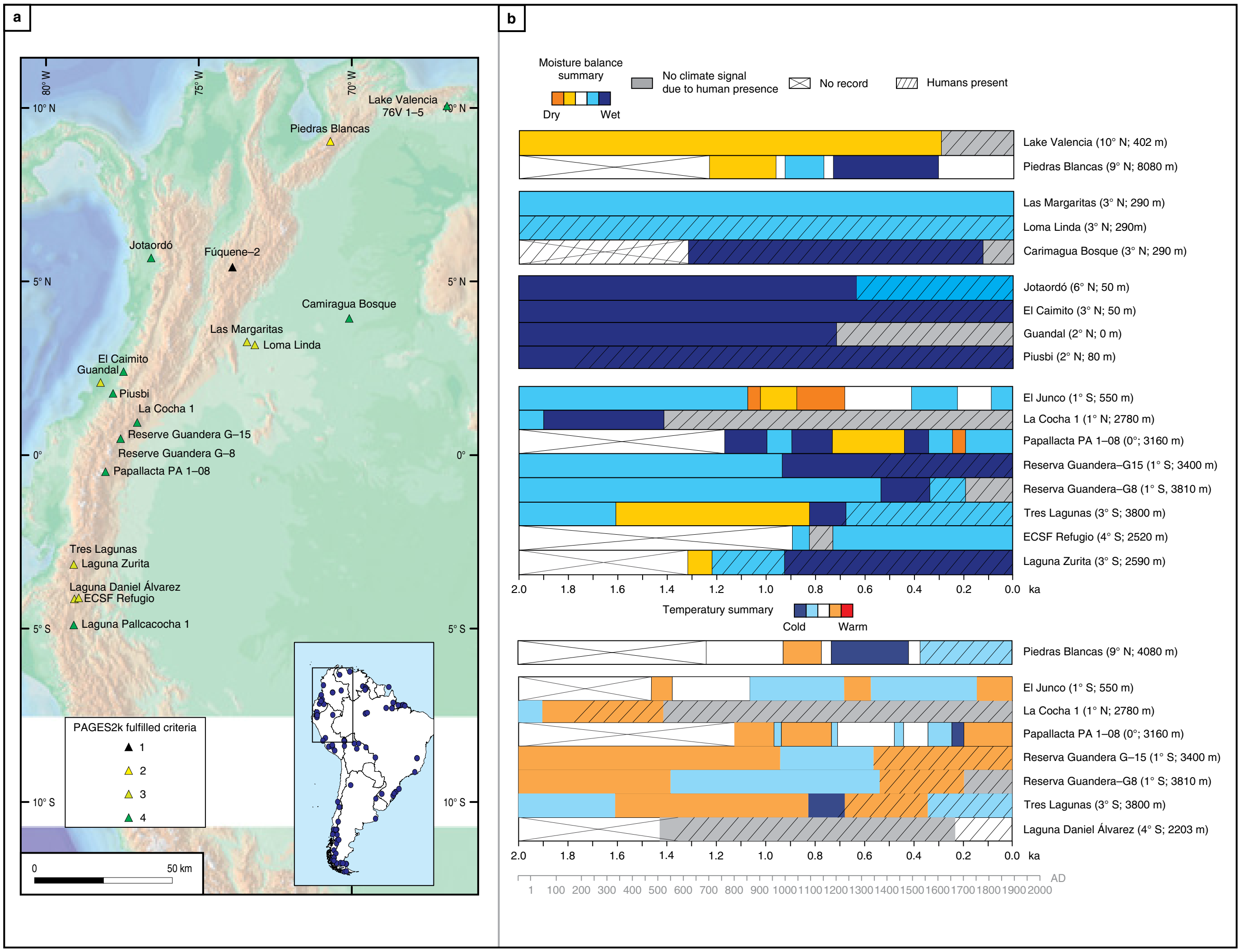


Figure 26. Selected site locations of Colombian pollen records with substantial anthropogenic influence in the last 2000 y. Ecuadorian and Venezuelan sites are shown for comparison. Panel **(a)** shows the location of the selected pollen records and the "PAGES–2k criteria" on the temporal quality these records fulfil on a scale of 1–4 (see Table 1). Panel **(b)** shows a summary of pollen–inferred moisture balance and temperature including human interference for the selected pollen records. Not all records are suitable for deriving both a moisture and a temperature signal. Climate and human presence are shown as overlapping when the pollen record is not conclusive regarding the derived signal. Bars are shaded grey when the climate signal is obscured by human interference. Records fulfilling one or two criteria are marked by a star. (Reproduced with permission from Open Access paper Flantua et al., Climate of the Past 12, 2016a, Copyright Copernicus Publications).

origin. As the pressures on the environment continue to grow, there is a need for policies and practice to promote successful strategies of adaptation based on an understanding of the past. Before this can occur, an appreciation is needed on how people perceive climate change, currently implemented adaptation measures, and other factors that may influence people's decisions to adapt their current practices (Marchant et al., 2018). Salutary lessons can be learned from a historical perspective. Conserving ecosystems and communities as they currently still exist, or intervening to restore them to a previous state, has almost become redundant. Instead, dynamic adaptive strategies are required as these allow different types of conservation that accommodate climate change and embrace concepts that encapsulate networks and connectivity as these can support fluidity and change (Hannah et al., 2002a, 2002b). Developing a notion of climatic and environmental change of the past, and how change could potentially develop into the future, should be part of any curriculum at high schools and universities. Colombia has the great advantage that Quaternary climatic and environmental change can be demonstrated with Colombian data. Hopefully, this motivates us to consider knowledge of Colombia's past, to understand better its present conditions, and to take the necessary measures required to offer an over–populated Earth a prosperous future.

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Table 1. List of pollen records checked for human impact indicators in Colombia, Venezuela and Ecuador. PAGES–2k criteria are used to selects records suitable for temporal and spatial comparison (further detailed in Flantua et al., 2016a). DUR500: Minimum duration of record >500 y; CONTROL2: More than two chronological tie points within the last 2 ky; TOP_END: Tie points near the end part (most recent) of the records and one near the oldest part; 1000_MIS3: Records longer than 1 ky must include minimum of one additional age midway between the other two. Yes: 1; No: 0. (Adjusted from Open Access paper Flantua et al., Climate of the Past 12, 2016a, Copyright Copernicus Publications).

Site Name	LAPD ID	Potentially suitable for 2k climate modelling	Potentially suitable for human studies	Criteria fulfilled	DUR 500	CONTROL2	TOP_END	1000_MID3	Human Indicators	First human indicator (cal y BP)	Precipitation Sensitive	Temperature Sensitive	References	Latitude	Longitude
Piedras Blancas	1665	1	0	2	1	1	0	0	No				Rull et al. (1987)	9.17	–70.83
Carimagua Bosque	851	1	1	4	1	1	1	1	*Mauritiella*, savanna, *Cecropia* increase	200	X		Berrío et al. (2000b)	4.07	–70.22
Las Margaritas	938	1	1	3	1	1	1	0	Savanna increase				Wille et al. (2003)	3.38	–73.43
Loma Linda	941	0	1	3	1	1	1	0	Savanna increase		X		Behling & Hooghiemstra (2000)	3.30	–73.38
Jotaordó	907	1	1	4	1	1	1	1	*Zea mays* and palm increase	1000	X		Berrío et al. (2000b); Urrego & Berrío (2011)	5.80	–76.70
El Caimito	877	1	1	4	1	1	1	1	*Cecropia* and palm trees (Arecaceae)	580	X		Vélez et al. (2001)	2.53	–77.60
La Cocha 1	910	1	1	4	1	1	1	1	Logging, preferentially *Podocarpus*, frequent fires, forest disturbance and changes of the diatom flora	1405–1100	X	X	González–Carranza et al. (2012)	1.06	–77.15
Reserve Guandera–G15	1867	1	1	2	1	1	0	0	R*umex*	100	X		Bakker et al. (2008)	0.60	–77.70
Reserve Guandera–G8	1176	1	1	4	1	1	1	1	*Dodonaea* presence	300			Moscol–Olivera & Hooghiemstra (2010)	0.60	–77.70
Laguna Daniel Alvarez	1751	0	1	3	1	1	1	0	Zea mays	1400			Niemann et al. (2013)	–4.02	–79.21
Laguna Pallcacocha 1	1158	1	0	4	1	1	1	1	No		X		Rodbell (1999)	–4.77	–79.23
Papallacta PA 1–08	2143	1	0	4	1	1	1	1	No		X		Ledru et al. (2013)	–0.36	–78.19
Tres Lagunas	1181	1	1	4	1	1	1	1	Zea mays	300			Jantz & Behling (2012)	–3.03	–79.23
Laguna Zurita	1160	0	1	3	1	1	1	0	Zea mays	900			Niemann & Behling (2010)	–3.03	–79.23
ECSF Refugio	1749	1	0	3	1	1	1	0	Decrease *Isoetes* & Cyperaceae (due to moisture increase or humans)	1200			Niemann & Behling (2010)	–3.99	–79.07

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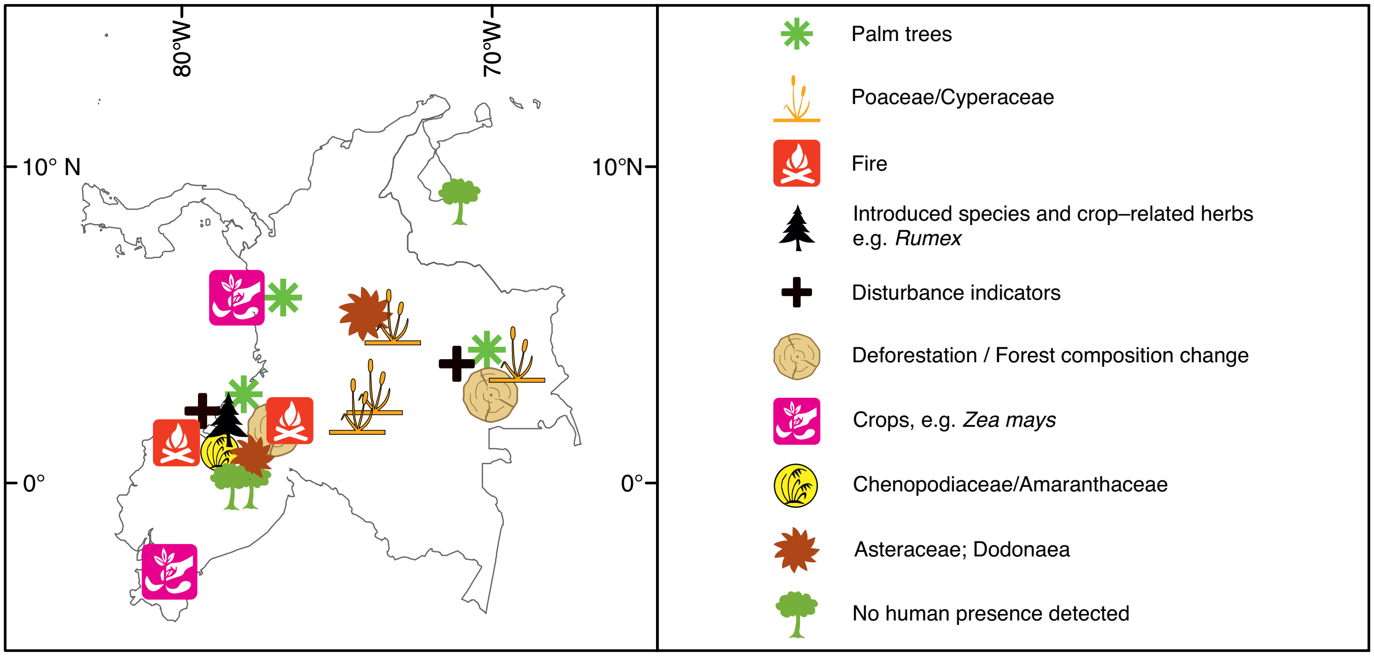

Figure 27. Human indicators observed in pollen records in Colombia. Ecuadorian and Venezuelan sites are shown for comparison. A pollen record can have different human indicators, and therefore the symbols may show an offset relative to their exact location to avoid overlapping point symbols. (Adjusted from Open Access paper Flantua et al., Climate of the Past 12, 2016a, Copyright Copernicus Publications).

(Colombian Andes), Peter KUHRY (Colombian Andes), Karin HELMENS (geology and glaciology of the Andes), Sonia SALAMANCA–VILLÉGAS (Colombian Andes), Gustavo SARMIENTO–PÉREZ (pre–Quaternary Andean geology and palaeoecology, Colombia), Ligia URREGO–GIRALDO (Colombian Amazonia), Eva RAN (Colombian Andes), Joost F. DUIVENVOORDEN (Amazonian vegetation and data analysis), Carina HOORN (pre–Quaternary geology and palaeoecology, origin of biodiversity), Henk WITTE (Colombian Andes & data analysis), Vincent WIJNINGA (Colombian Andes), Gerald ISLEBE (Colombian Andes; mainly Central America), Ron VAN ‘T VEER (Colombian Andes), Hermann BEHLING (Colombian Andes and lowlands), Herman MOMMERSTEEG (Colombian Andes), Rob MARCHANT (palaeodata–model comparisons), Michael WILLE (Colombian Andes), Juan–Carlos BERRÍO–MOGOLLÓN (Colombian Andes and lowlands), Jan–Jacob KEIZER (Colombian elevational vegetation gradients), Maria–Victoria ARBEAEZ–VELASQUEZ (Colombia Amazonia), Maria Isabel VÉLEZ–CAICEDO (diatoms; Colombian Andes and lowlands), Arnoud BOOM (geochemistry; Colombian Andes), Vladimir TORRES–TORRES (Colombian Andes), Johan BAKKER (Ecuadorian Andes), Marjolein VAN DER LINDEN (Colombian Andes), Catalina GIRALDO–PASTRANA (Colombian Andes and 3D–vizualisation), Marcela MOSCOL–OLIVERA (Ecuadorian Andes), Giovanni BOGOTÁ–ANGEL (Colombian Andes), Mirella H.M. GROOT (Colombian Andes), Mirjam VRIEND† (Colombian Andes), Vivian FELDE (numerical data analyses, Colombian Andes), Suzette FLANTUA (LAPD & GIS, northern Andes and lowlands, design of figures and maps), and Zaire GONZÁLEZ–CARRANZA (Colombian Andes).

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Explanation of units and acronyms:

Fq	Fúquene
ka	thousand years before present
ky	any period of a thousand years (e.g., frequency lengths, response delay time)
y	years
LMF	Lower montane forest
Ma	million years before present
MIS	Marine isotope stage
PFT	Plant functional type
UFL	Upper forest line
UMF	Upper montane forest

Biographic Authors Notes

Henry HOOGHIEMSTRA (1948) is a tropical paleoecologist. He studied biology at Amsterdam University. His PhD thesis (1984) focused on the Pleistocene environmental and climatic history of Colombia. At Göttingen University (1983–1987) he used marine palynology and earth–sciences to reconstructed the history of Saharan Africa. He was appointed professor at Amsterdam University (1991). His research and teaching focused on the (Neo)tropics, Colombia in particular. Apart from studying the dynamic histories of tropical ecosystems, studying the long records from the basins of Bogotá, Fúquene and La Cocha is ongoing for 40 y. He was involved in developing the LAPD, paleodata–model comparisons, global change studies, and Big History.

Suzette FLANTUA (1980) is a tropical biogeographer. She studied biology at the University of Groningen (2000–2003) and Amsterdam University (UvA; 2004–2008). Much of her workexperience in spatial analysis and Geographic Information System (GIS), she obtained during her years at the UvA and the time that followed which she spent in Venezuela and Colombia working in a range of different topics from the Amazonian lowlands up to the Andean glaciers. Between 2009 and 2012, she updated the inventory of the LAPD setting with this the basis for the start of her PhD at the UvA in 2012, which she completed in 2017.