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vegetation changes
in the tropical Andes**

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Rapid millennial-scale vegetation changes in the tropical Andes

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Received: 31 January 2015 – Accepted: 24 February 2015 – Published: 11 May 2015

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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in the tropical Andes (Urrego et al., 2009). Hessler et al. (2010) used biomisation and plant functional types (PFTs) in an attempt to extract the environmental signature of millennial-scale events. However, PFT classification is limited in the Andes as cool Andean forests (upper montane) and warmer sub-Andean (lower montane) forest are included within the same PFT. More recently, it has become clear that records from relatively dry inter-Andean valleys (Bogotá et al., 2011; Velásquez and Hooghiemstra, 2013) and from the eastern flank of the Andes continuously immersed in clouds (González-Carranza et al., 2012; Urrego et al., 2010) show different histories of environmental change.

10 **Millennial scale variability, trends, and climatic mechanisms**

The signature of millennial-scale climate variations such as Heinrich events (HE) and Greenland Interstadials (GI) is recorded in ice cores, and in marine and terrestrial sediment archives both in the northern (NGRIPmembers, 2004) and southern (Jouzel et al., 2007) hemispheres. These abrupt climate changes are characterized by a rapid onset and duration ranging between 200 and 2500 years (Wolff et al., 2010). The HEs are marked by an abrupt increase in the proportion of ice-rafted debris (IRD) from the Laurentide and Scandinavian ice-sheets forming the Heinrich layers in marine sediments from the North Atlantic (Heinrich, 1988). Iceberg discharges deliver fresh water into the North Atlantic, disrupting the Atlantic Meridional Overturning Circulation (Hemming, 2004). The climate-change intervals associated with these discharges are termed Heinrich Stadials (HS) (Sanchez Goñi and Harrison, 2010). Model simulations and climate reconstructions suggest that these events result in decreased SST in the North Atlantic and increased SST in the South Atlantic, shifting the thermal equator and the Intertropical Convergence Zone (ITCZ) southwards (Broccoli et al., 2006). Such an atmospheric and oceanic configuration is linked to a weakened North-American Monsoon (Lachniet et al., 2013), and reduced precipitation in central (Escobar et al., 2012; Correa-Metrio et al., 2012) and northern South America (Bogotá et al., 2011; González et al., 2008). Downslope migration of the upper forest line (UFL) in the tropical Andes

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(Bogotá et al., 2011) are also linked to HS cooling. The precipitation signature of HS in tropical South America is described as enhanced South American Summer Monsoon (SASM) activity in northeastern and southeastern Brazil (Cruz et al., 2006) and wet episodes in the Bolivian Altiplano (Baker et al., 2001; Fritz et al., 2010). In the Ecuadorian Amazon, precipitation change appears to be positively correlated with some HS, but not with others (Mosblech et al., 2012).

GIs follow abrupt warming events in the Greenland ice core records (Dansgaard et al., 1993), whose magnitudes of change are as large as 50% that of glacial–interglacial transitions (Wolff et al., 2010). The magnitude of tropical Atlantic sea surface temperature (SST) change at the onset of GI1 is estimated to be less than 1°C in the Tobago Basin (Rühlemann et al., 2003), 2°C in the Colombian basin (Schmidt et al., 2004) and 3.8°C in the Guyana Basin (Rama-Corredor et al., 2015). Precipitation changes during GI1 include wet conditions (Escobar et al., 2012) in Central America and decreased run-off in the Guyana Basin (Arz et al., 1998). In western Amazonia, some GI appear to be associated with reduced lake levels (Urrego et al., 2010), while increased humidity is recorded in the Bolivian Altiplano (Paduano et al., 2003; Baker et al., 2001; Placzek et al., 2013). High-resolution speleothem records from subtropical Brazil suggest a weakened SASM and reduced precipitation associated with the onset of some GI, while the signature of other GI is not clear (Cruz et al., 2005). Available pollen records suggest that the signal of vegetation change can be opposite between the northern and southern parts of the region influenced by the ITCZ, while in south-east Brazil and western South America the changes associated with GI appear to be inconsistent (Hessler et al., 2010).

Overall, a series of environmental changes in the American tropics appear to be coupled with HS and GI. However, whether there is a spatially and temporally consistent signature of these events in the tropical Andes remains unclear. The objective of this paper is to test whether the signature of millennial-scale variability in the tropical Andes is consistent among northern and southern sites. We re-analyse a suite of eight pollen records from the tropical Andes that reveal vegetation changes at mid to

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high-elevations during last 50 ka. We compare all records on a common timescale, and explore how records expressed as percentage data and as downcore detrended correspondence analysis (DCA) time series provide complementary information on environmental change. As far as the chronologies allow, we explore the degree of synchronicity of environmental change between terrestrial pollen records, and marine and ice-core markers from the region. This study differs from previous studies that have focused on vegetation changes and their palaeoecological meaning. Here, we use changes in the vegetation as markers for climatic change. We consider vegetation changes as one of the internal responses of the climate system (i.e. biosphere) and we integrate our observations with records that reveal the responses of the cryosphere and ocean.

2 Environmental setting

2.1 Geography, vegetation and climate

Topography is a key environmental variable in the American tropics (Graham, 2009). It determines temperature (Vuille and Bradley, 2000), and precipitation variability and its spatial distribution (Garreaud et al., 2009). Cold-air advection from the northern (Poveda et al., 2006) and southern (Garreaud, 2000) hemispheres reaches the tropical Andes year round and can have a great effect on air temperatures. Cold advection can significantly reduce air temperatures and lead to heavy precipitation due to convective cloudiness (Poveda et al., 2006; Garreaud et al., 2009). Garreaud and Wallace (1998) have estimated that cold-front outbreaks are associated with ca. 30 % of summertime precipitation in western Amazonia. These cold fronts travel mostly along the eastern side of the Andes (unmarked set by Dunia) and can produce freezing conditions down to 2500 m elevation in the tropical Andes (Gan and Rao, 1994).

Because of the complex topography of the Andes, the spatial distribution of precipitation differs significantly between the eastern and western flanks, and between inter-Andean valleys (Poveda et al., 2011). Moisture on the eastern flank is primarily

sourced in the tropical Atlantic and Amazonia, while SST in the tropical Pacific modulates precipitation on the western flank (Vuille and Bradley, 2000). On the eastern flank, the Andean mountains form a barrier to moisture export from the Amazon basin to the Pacific coast. When Amazonian humid air encounters the eastern flank of the Andes, the temperature decline forces humidity to condense and form clouds (Poveda et al., 2006). In areas of the eastern flank where prevailing winds and topography are not favourable, cloud cover can be low and precipitation can be less than 1500 mm, forming relatively dry enclaves (Killeen et al., 2007). In contrast, moisture regimes on the western flank are linked to the westerly Chocó jet in the northern Andes (Poveda et al., 2006), and to upwelling and El Niño Southern Oscillation (ENSO) in the central and southern Andes (Vuille et al., 2000). Such a difference in moisture drivers results in a large precipitation gradient from north to south, with some of the rainiest areas on earth found on the Pacific coast of Colombia, and deserts found along the Peruvian coast. Rain shadow effects govern precipitation in inter-Andean valleys (Vuille et al., 2000).

2.2 Operating climate mechanisms and moisture sources

Current precipitation in the tropical Andes is influenced by large-scale atmospheric and oceanic mechanisms such as the ITCZ, SASM, and ENSO (Fig. 1). The position of the ITCZ is primarily forced by trade wind convergence and Atlantic and Pacific SSTs, and is linked to continental rainfall and seasonality at sub-annual timescales (Garreaud et al., 2009; Poveda and Mesa, 1997). At inter-annual to millennial timescales, the inter-hemispheric migration of the ITCZ seems to respond to multiple factors including insolation and the position of the thermal equator (Fu et al., 2001), high-latitude temperatures and land–sea ice extent (Chiang and Bitz, 2005) and high-latitude North Atlantic variability (Hughen et al., 1996). The ITCZ is in turn linked to the distribution of mesoscale convective systems in northwestern South America, contributing an average of 70 % of annual precipitation in the region (Poveda et al., 2006).

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SASM is linked to a large area of precipitation and convection that forms over most of Amazonia and subtropical Brazil during the austral summer (Garreaud et al., 2009). SASM delivers a large proportion of annual rainfall between December and February (Garreaud et al., 2009), and isotopic fingerprinting suggests that the tropical Atlantic is its main moisture source (Vuille and Werner, 2005). This moisture is transported across Amazonia by easterly trade winds until it encounters the Andes, causing significant orographic precipitation (Vuille et al., 2000). The eastward transport of Amazonian moisture is also linked to the South American low-level jet (LLJ), whose strength increases east of the Andes and reaches a maximum in subtropical South America (Zhou and Lau, 1998). Variations in the position of the Atlantic ITCZ, in response to SST gradients in the tropical Atlantic, are suggested to play a role in modulating the strength of SASM on interannual to decadal timescales (Zhou and Lau, 1998). SASM strength has also been linked to the mean state of the Pacific (Vuille and Werner, 2005), and interannual and long-term ENSO variability (Zhou and Lau, 1998).

ENSO drives a large portion of the interannual precipitation variability in the tropical Andes, despite regional differences in timing, magnitude and direction of change (Poveda et al., 2011). Warm ENSO events are associated with decreased rainfall and more prolonged dry seasons in the Colombian Andes (Poveda et al., 2006). Drought is also experienced in northeast Brazil during warm ENSO events, while southern Brazil and the Ecuadorian Pacific coast experience increased rainfall (Zhou and Lau, 2001). Warm ENSO events are also associated with strengthening of the low-level jet along the eastern flank of the Andes, and enhancement of SASM (Zhou and Lau, 2001).

3 Methods

We use eight pollen records from the tropical Andes to reconstruct environmental change at a regional scale over the past 50 000 years (50 ka) (Fig. 1, Table 1). Selected lakes form a north-to-south transect from 6° N to 16° S and lie at mid- and high-elevations in the tropical Andes. The sites are located in inter-Andean valleys partly

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lying in the rain shadow, the eastern flank of the Andes facing the Amazon lowlands, and one from the Peruvian-Bolivian Altiplano (Table 1). This latitudinal transect provides a large environmental gradient and includes sites with various moisture sources. In the two northernmost Colombian sites, the Atlantic ITCZ and ENSO modulate moisture (Velásquez and Hooghiemstra, 2013; Bogotá et al., 2011). Further south, Lakes La Cocha and Surucucho are located on the eastern flank of the Andes and receive most precipitation from Amazonian orographic rains (Colinvaux et al., 1997; González-Carranza et al., 2012). Lakes Chochos, Pacucha and Consuelo lie on the eastern flank of the Andes, and Lake Titicaca on the Peruvian/Bolivian Altiplano. Lake Chochos precipitation is sourced from Amazonian convection and SASM (Bush et al., 2005). SASM also is the primary moisture source for Lakes Pacucha, Consuelo and Titicaca (Urrego et al., 2010; Valencia et al., 2010; Baker et al., 2001) (Table 1).

We selected pollen records where knowledge of regional vegetation is sufficient to allow a classification of pollen taxa into ecologically meaningful groups. The selected records also met minimum requirements of stratigraphic consistency and quality of chronology. We used records in which the chronology was sufficiently robust to allow linear interpolations between radiocarbon-dated samples and where sample intervals were relatively short (Table 1). Age models developed by original authors were used, except for Llano Grande. For this record, we took the radiocarbon dates available in the original publication and generated an age model based on calibrated ages using Calib 7.1, IntCal13 (Reimer et al., 2013) and using linear interpolation between dated intervals. The age models developed by original authors were considered robust enough for our search of operating mechanisms.

3.1 Protocol to extract environmental information from pollen records

Raw pollen counts were obtained from the original authors or from the Latin American Pollen database (<http://www.ncdc.noaa.gov/paleo/lapd.html>). We calculated a pollen sum that included only terrestrial taxa, and re-calculated pollen percentages of individual taxa based on that sum. The ecological grouping of terrestrial taxa was defined

based on the ecological information published by original authors. For sites where this information was unavailable, we followed the author's interpretations of the pollen record, ecological knowledge of the regional vegetation, and information from modern pollen calibrations from the tropical Andes (Reese and Liu, 2005; Urrego et al., 2011; Weng et al., 2004). Ecological envelopes of Andean taxa at genus level may be wide, as more than one species may be reflected in one pollen taxon. Additionally, the ecological affinity of pollen taxon in a relatively dry inter-Andean valley may differ from that of the same taxon in a humid cloud forest. Our interpretations of fossil pollen spectra into past climate change included region-specific conditions. For example, presence of pollen of Cactaceae and *Dodonaea* reflected local rain shadow effects, rather than regional dry climates. Rare pollen taxa with unknown ecological affinity were excluded from this classification.

Ecological groups include puna (or páramo), subpuna (or subpáramo), Andean (upper montane) forest, subAndean (lower montane) forest, and taxa from tropical lowland vegetation. The puna (relatively dry) and páramo (relatively wet) groups include taxa from cold vegetation above the UFL (Bakker et al., 2008; Groot et al., 2011). These groups also include transitional taxa between the UFL and puna or páramo. The Andean and subAndean groups reflect high-elevation and mid-elevation forests found today between ca. 1200 and 3200–3500 m elevation. Finally, tropical lowland taxa reflected warm and moist forests below ca. 1200 m elevation.

The arboreal pollen percentage (AP%) groups the regional vegetation for each site. Interpretation of AP% is dependent on the altitudinal location of a given site relative to the modern UFL (Hooghiemstra and van der Hammen, 2004). For instance, in Lake Fúquene at 2540 m, AP% includes Andean and subAndean taxa. In Llano Grande at 3650 m, AP% only includes cold Andean taxa as pollen from subAndean forests hardly reaches this high-elevation site. Changes in AP% are indicative of altitudinal migrations of montane vegetation and the relative position of the UFL, an ecological boundary relatively well established in climatological terms (Körner, 2007; Hooghiemstra, 2012).

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The terrestrial pollen sum excludes taxa of the aquatic and shoreline vegetation, such as *Cyperaceae*, *Isöetes*, *Myriophyllum* and other taxa described by original authors as aquatic and wet shoreline elements. We have followed the shoreline vegetation zonation detailed by González-Carranza et al. (2012), when information on aquatic vegetation was unavailable. We establish an “aquatic pollen sum” that includes taxa grouped into shoreline, shallow- and deep-water taxa, reflecting a gradient of water depth. Thus, we calculate a ratio between taxa characteristic of deep water, over taxa growing in shallow water and wet shores (D/SS), and use it as an indicator of lake level changes. D/SS is based on the sum of aquatic taxa and is independent of AP%.

Two DCA analyses (McCune and Grace, 2002) were performed on each untransformed pollen dataset. The first DCA was run on pollen percentage matrices, excluding aquatic and shoreline taxa. A second DCA was run on reduced pollen percentage matrices after applying a filter that aim to eliminate the noise caused by rare pollen taxa (Birks and Birks, 1980). This filter retained taxa with at least 1 % abundance and that were found in at least 5 samples per record. Taxa that met the latter requirement, but had abundances below 1 % were retained as such taxa likely reflected low pollen producers. Iterations were run until a stable solution was reached for all ordinations. To make DCA scores comparable between records, axis scores were standardized by calculating *z*-scores based on the mean and SD for each record. RoCs were calculated as the dissimilarity distance between two consecutive pollen time slices divided by the time interval in between (Urrego et al., 2009). Euclidean, Sorensen and Bray Curtis dissimilarity distances (McCune and Grace, 2002) were calculated based on raw pollen percentages. The DCA axis scores for the first four axes were also used to calculate RoC using a Euclidean distance. RoC calculated using raw percentages were compared with RoC based on DCA axis scores to evaluate the influence of DCA variance reduction.

4 Results and interpretation

The proportions of sub-Andean (lower montane) and Andean (upper montane) forest taxa vs. vegetation located above the UFL (puna and páramo) show temporal variations that appear synchronous between some sites, but opposite between others (Fig. 2).

5 The comparison of AP% vs. DCA1 z-scores demonstrates similar trends in three of the eight pollen records analysed (Fig. 3). In the remaining five records, AP% and DCA z-scores trends differ in at least part of the record, despite a few similarities. The record of D/SS potentially reflects lake level changes that appear to be registered at most studied sites (Fig. 4). In the following section we describe results from our re-analysis
10 of each of eight selected pollen records.

4.1 Llano Grande (Velásquez and Hooghiemstra, 2013)

This site is located near the current position of the UFL at 3650 m elevation. Changes in AP% at this elevation are expected to be sensitive to changes in the composition of the Andean forests found downslope today. The abundance of Andean taxa increases abruptly ca. 10.5 ka (Fig. 2). Five oscillations of AP% are observed during
15 the Holocene. DCA1 z-scores (reversed) and AP% are remarkably similar (Fig. 3) suggesting that temperature, the driver of changes in AP%, is also the strongest driver of DCA1. D/SS shows a peak after the onset of the pollen record at ca. 14.5 ka, and two increases of lesser magnitude during the Holocene (Fig. 4). The onset of the record
20 and the largest D/SS peak are linked to the formation of the lake after the Pleistocene-Holocene transition. D/SS increases occur between ca. 6 and 5 ka, and between ca. 4.5 and 2.5 ka.

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4.2 Lake Fúquene (Bogotá et al., 2011; Groot et al., 2011; van der Hammen and Hooghiemstra, 2003)

This record comes from an intra-Andean valley at 2540 m elevation, a position centrally located in the current altitudinal range of Andean forests, and between the highest (ca. 3400 m) and lowest (ca. 2000 m) positions of past UFLs. The location of Lake Fúquene makes this record highly sensitive to temperature-driven vertical re-organizations of montane taxa. During glacial times this area was covered by cold páramo vegetation, and during interglacials subAndean forest taxa reached up to ca. 2300 m. The short distance between subAndean forest and the lake explains pollen from subAndean taxa also being represented in AP%.

Páramo taxa show high percentages between ca. 38.3 and 17.5 ka, but also vary at several intervals. Andean and subAndean taxa show an overall increase starting around 15.6 ka, when páramo taxa start to decrease (Fig. 2). AP% decreases again between ca. 13 and 11 ka, and shows a few fluctuations during the Holocene. DCA1 follows remarkably well the variability of AP% (Fig. 3), indicating that this ordination axis is probably driven by UFL migrations. AP% and DCA1 z-scores consistently increase after HSs. The signature of cooling stadials is that of decreasing AP%, reflecting downslope UFL migrations (Fig. 2). D/SS also shows variations that suggest increases in lake levels after HS2 and HS1 (Fig. 4). D/SS increases between ca. 9 and 7.3 ka, and again between 4.5 and 2.5 ka.

4.3 Lake La Cocha (González-Carranza et al., 2012; Van Boxel et al., 2014)

This record comes from a valley at 2780 m elevation on the eastern flank of the Andes. Amazonian moisture causes abundant orographic rains at this site. Centrally located in the current altitudinal range of the Andean forest (2300 to 3650 m elevation), the AP% record also includes taxa from the subAndean forest. During the deglaciation, the UFL was below the elevation of the valley and páramo vegetation surrounded the lake. AP% reflects temperature changes in this record, although its location suggests that upslope

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UFL migration during most of the Holocene is also driven by increased moisture. The study of past precipitation changes at this lake has revealed that temperature change potentially has a significant impact on evaporation and lake levels. Hence, we may anticipate that AP% in this record has a weak relationship with temperature change.

Andean and subAndean taxa in this record increase consistently while páramo taxa decrease at the Pleistocene-Holocene transition (Fig. 2). Short but significant increases of AP% are detected around 12, 9.5, 8, 5 and 2 ka. The trend of DCA1 z-scores closely follows AP% (Fig. 3). AP% variability increases during the Holocene and displays a shift around 6 ka. Two gradual increases in D/SS suggest lake level increases between ca. 11 and 6 ka, and between ca. 4.5 and 2.5 ka (Fig. 4).

4.4 Lake Suruchucho (Colinvaux et al., 1997)

This lake is located at 3180 m elevation. SubAndean forests reach up to 2800 m in this part of the Andes, while the subpáramo starts around 3500 m elevation. The Andean forest thus covers a vertical range of ca. 700 m. AP% values reflect UFL shifts at this site.

Puna and subpuna taxa dominate the pollen record during the late Pleistocene (Fig. 2). Andean forest taxa increase gradually from ca. 13 ka and remain relatively abundant during the Holocene, despite the persistent abundance of puna and subpuna taxa. DCA1 z-scores and AP% follow a similar trend and show clear differences between the Pleistocene and Holocene (Fig. 3). At ca. 11.3 ka there is a two-fold increase in AP% and a shift in DCA1 z-scores. D/SS is high during the late Pleistocene, indicative of high lake level stands that persisted until ca. 10 ka. Holocene D/SS values are low (Fig. 4).

4.5 Lake Chochos (Bush et al., 2005)

Chochos is located at 3285 m elevation and sits on the eastern flank of the Andes. The record is centrally located in the altitudinal range of UFL glacial–interglacial migrations.

around 4 ka. During the Holocene, both Andean forest and puna taxa vary erratically and appear to follow the same trend. AP% varies independently from DCA1 z-scores, indicating little correlation between the two markers (Fig. 3). D/SS is high and shows several fluctuations until ca. 11.9 ka, while it is near zero during the Holocene (Fig. 4).

D/SS fluctuations include maxima around 19.3 and 16 ka, and minima around 18.8, 17.5 and 15 ka.

4.7 Lake Consuelo (Urrego et al., 2010)

Lake Consuelo is located at 1360 m on the eastern flank of the Andes. Amazonian moisture causes significant orographic rains at this site, covering the lake in semi-permanent ground-level clouds. Located in the lower part of the current altitudinal range of subAndean forest, the AP% record is mainly composed of warm subAndean taxa. The vertical distance from Lake Consuelo to the UFL is large, and even during glacial times the lake remained surrounded by cool Andean forests. Changes in AP% are expected to reflect temperature-driven shifts of subAndean forests.

SubAndean forest taxa reach up to 80 % (Fig. 2). Despite its mid-elevation location, the record shows over 30 % of the subpuna vegetation during the Pleistocene. Subpuna percentages peak around 39.7, 32.5, 27.2, 26, 24.2, 17 and 15.1 ka. Holocene subpuna percentages peak around 8.8, 7.3, 4.9 and 2 ka. The trends of DCA1 z-scores and AP% are similar, but the signal seems more consistent during the Holocene (Fig. 3). D/SS is high from the onset of the record and until ca. 35.5 ka, with at least six maxima (Fig. 4). Other peaks in D/SS are present around 10 ka and become small after ca. 5 ka.

4.8 Lake Titicaca (Paduano et al., 2003; Hanselman et al., 2011)

This lake is located at 3810 m elevation; the highest in our transect study. Today the lake is surrounded by puna vegetation, and Andean forests occur below 3200 m. Glaciers must have reached the lake basin during glacial times and vegetation comparable to the modern puna brava (4500–5300 m) probably surrounded the lake. Changes in AP%

reflect altitudinal shifts of the UFL. However, the significant distance between the UFL and the lake (between ca. 600 and 1500 m) potentially cause two sources of bias in the AP% values: (1) registered changes in AP% may not be sensitive to minor changes in UFL position and (2) AP% increases may lead by centuries the real migration of the UFL due to upslope aeolian pollen transport (Jansen et al., 2013).

Two pollen records are available from Lake Titicaca, and in both puna taxa dominate the pollen spectra (Fig. 2). Andean forest taxa account for less than 10% of the pollen sum, and reflect the downslope location of the UFL. Andean taxa show maxima around 29.5, 24.5, 21, and 17 ka. Puna taxa fluctuate during the Pleistocene, and sharply decrease between ca. 17.8 and 13.8 ka. DCA1 z-scores and AP% fluctuate differently during the Pleistocene, but are consistent during the Holocene (Fig. 3). The core from the centre of the lake did not record aquatic vegetation, hence D/SS was calculated only for the other record. D/SS shows large values between the onset of the record and ca. 17 ka (Fig. 4). Holocene D/SS is nearly zero.

5 Discussion

5.1 Environmental and climatic interpretation: percentage data vs. ordination scores

RoC values appear to be sensitive to changes in sedimentation rate, while showing little differences when calculated based on DCA results vs. raw pollen percentages. As an example we show RoC calculated for La Cocha record (Fig. S1 in the Supplement). We therefore refrain from using RoC in this paper as age uncertainties may be inflated when pollen records of varying quality are compared. One way to circumvent RoC dependency on age and sedimentation uncertainties is to preserve the ecological dissimilarity distances calculated between pollen assemblages as a measure of pollen taxa turnover.

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Comparison of the other two common methods to explore environmental change from pollen records shows that the information extracted from AP% and from ordination scores is seldom equivalent. This observation indicates that temporal changes in AP% and DCA1 z-scores may respond to different drivers and may not be comparable. Some differences between the two approaches may explain this lack of comparability. On the one hand, ordination analyses like DCA utilize the matrix of pollen percentages and time slices, and attempt to find the clearest relationships within the pollen matrix. Simultaneously, the ordination searches for relationships between time slices. Relationships between pollen taxa may be due to ecological affinities, and in this sense, this step of the ordination analysis is somewhat equivalent to the taxa grouping done for AP%. However, ordination analyses do not involve a priori information (i.e. ecological knowledge) and are only driven by the main sources of variability within the pollen dataset. This is why ordination analyses have been argued to have an advantage over AP% because each pollen taxon is free to be correlated with any other taxon (Urrego et al., 2005; Colinvaux et al., 1996; Bush et al., 2004). A taxon that today would be grouped as Andean is free to have more affinity with lowland taxa in the past. It is difficult to allow for this flexibility when using modern ecology to group fossil taxa.

The ordination results consist of axis scores for pollen taxa and for time slices that are non-dimensional and lack direction, and can be rotated as desired (Hill and Gauch, 1980). Information extracted from the ordination axes can be used in relative terms. As a result, a posteriori ecological knowledge of the taxa with the highest loadings is necessary to interpret the main sources of variability within the pollen dataset (e.g. Urrego et al., 2010). Ordination-based interpretation of pollen records may be more appropriate for non-analogue species re-assortments, but still requires ecological knowledge on modern species affinities to extract environmental-change information from ordination results.

Calculating AP% uses prior knowledge of the regional vegetation to classify pollen taxa into ecological groups. Hence, AP% has the advantage of giving a direction to the observed change from the start. Using a priori ecological knowledge to calculate

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AP% has been criticized due to potential subjectivity involved in the classification of pollen taxa (Colinvaux et al., 1997). The potential subjectivity derives from the fact that boundaries between vegetation formations are never sharp. Ecological grouping of transitional or wide-ranging taxa is left to the palynologist's discretion. Grouping pollen taxa into regional vegetation also requires detailed knowledge of the current vegetation, and this is not always available at the necessary detail. Modern pollen calibrations are useful to understand how vegetation cover translates into the pollen rain, and finally how these translate into the fossil pollen record. Unfortunately, such calibrations remain scarce and underdeveloped in the tropical Andes and Amazonia.

The sensitivity of classifications like AP% can be low where forest composition remains within one ecological group. For instance, in Lake Consuelo AP% remains high from glacial to interglacial periods (Fig. 3), indicating that the area had a relatively stable forest cover while individual taxa are indeed changing in abundance (Urrego et al., 2010). The record from Lake La Cocha also reveals individualistic changes in pollen abundance (González-Carranza et al., 2012), but also clear variations in AP% that may respond to shifting Andean and subAndean associations. The record of Lake La Cocha is a good example of how ecological grouping associated with AP% may be sensitive to both individualistic and community-based migrations. Therefore, the ecological grouping associated with AP% allows for individualist migrations within groups, but may be less sensitive in low-elevation sites.

In conclusion AP% and ordination axis scores may be complementary, rather than contradictory. The two approaches necessitate a reasonable understanding of ecological affinities and knowledge of the regional vegetation. Both remain vegetation markers, and as such cannot provide independent information about climatic change. Along with the development of pollen records, independent markers of temperature or precipitation are needed in the American tropics and subtropics (Urrego et al., 2014), and future work should preferably generate combinations of proxies to disentangle differences between AP% and ordination-based environmental reconstructions.

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Changing values of the D/SS ratio potentially indicate lake level changes due to fluctuations in precipitation and evaporation, assuming that the lakes have minimal losses by underground leaks or outflow. Increases in D/SS are associated with increases in deep-aquatic taxa and likely indicate high lake-level stands. Similarly, low D/SS indicates abundant aquatic vegetation from shallow waters and reduced water bodies. A potential bias for D/SS is that some taxa included in the “aquatic pollen sum” have different growth forms. For instance, *Isöetes* is an aquatic fern growing up to ca. 6 m water depth in lakes and is indicative of relatively deep-water conditions. However, in fluvial and fluvio-lacustrine environments *Isöetes* species may also occur on sand banks (Torres et al., 2005). The ratio is based on relative abundances and is calculated in the same way for all sites. Therefore, calculating D/SS makes differences in pollen/spore production a systematic bias, and allows meaningful comparisons among sites and samples within one record.

5.2 Orbital-scale environmental changes in the tropical Andes

The eight pollen records from the tropical Andes consistently record Pleistocene altitudinal migrations of Andean and subAndean forests linked to cooling. Páramo and subpáramo, or puna and subpuna vegetation characterize the Pleistocene, while the Holocene is characterised by subAndean and Andean forest (Fig. 2). Such orbital-scale forest migrations and inferred temperature change have been documented in pollen records from the region (e.g. Hansen et al. 2003; Urrego et al. 2010). Records of tropical air temperatures changes between the late Pleistocene and the Holocene also exist from other markers, including Andean ice-core isotopic signals (Thompson, 2005), dating of Andean moraines (Smith et al., 2008; van der Hammen et al., 1980/1981), high-elevation Andean lake $\delta^{18}\text{O}$ records (Baker et al., 2001; Seltzer et al., 2000), and $\delta^{18}\text{O}$ from Andean speleothems (Cheng et al., 2013). SST reconstructions from the western tropical Atlantic similarly document large fluctuations between the Late Pleistocene and Holocene (Rühlemann et al., 1999), but their magnitude is believed to be less than air-temperature changes recorded by the vegetation and other terrestrial

markers. Differences between SST and terrestrial records of temperature change are probably associated with the oceans' thermal inertia.

The pollen records show an overall warming trend during the Pleistocene-Holocene transition, but the onset of post-glacial warming differs in timing among records. Taking the Fúquene record as an example for the northern Andean sites, the first post-glacial warming occurred around 15.6 ka (Fig. 2), but is interrupted by a cooling period between ca. 13 and 11 ka. In Lake Surucucho, the record of Andean forest taxa suggests a steady increase in air temperatures starting around 13 ka. On the other hand, the record of Lake Pacucha in the southern Andes shows a clear trend towards warming starting around 15.6 ka, with a relatively short-lived cooling between ca. 13 and 11.5 ka, followed by another warming. These differences in the onset of post-glacial warming in the Andes have been documented from reconstructions of snowline depressions starting ca. 21 ka in the Peruvian Andes (Smith et al., 2005), the onset of SST warming in the tropical Atlantic around 17 ka (Rühlemann et al., 1999), and shifts in stable oxygen isotopes from the Sajama ice cap at 15.5 ka (Thompson et al., 1998).

Changes in D/SS in the selected sites suggest a Pleistocene humidity different from that of the Holocene. D/SS in Northern Andean sites (i.e., Llano Grande, Fúquene, and La Cocha) may indicate increasing lake levels during the mid-Holocene ca. 5–2 ka (Fig. 4). Another increase in lake levels is recorded at Fúquene and La Cocha around 8 ka, but not in Llano Grande. Central and Southern sites (i.e. Surucucho, Pacucha, Titicaca and the onset of the pollen record in Lake Chochos) indicate large water bodies and probably high precipitation through the Pleistocene-Holocene transition and up to 8 ka. D/SS in Lake Consuelo follow a different trend to that observed in other central and southern Andean sites during the late Pleistocene. These differences may be due to the buffering effect of semi-permanent ground-level cloud cover during the last glacial (Urrego et al., 2010). D/SS in lakes Consuelo and Chochos suggest high lake-level stands between ca. 10 and 6 ka, peaking around 8 ka (Fig. 4), analogous to D/SS increases observed in Northern Andean sites.

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5.3 Millennial-scale vegetation changes in the tropical Andes

The signature of millennial-scale environmental variability is revealed in virtually all records, although the timing can differ along the studied transect. Most records show AP% increases during HS, indicating downslope migrations of the UFL and cooling during HS (Fig. 3). In Lake Titicaca AP% decreases during HS, but the direction of this change also indicates UFL downslope migrations and cooling, as the lake is located above the UFL. DCA z-scores also record shifts around the timing of HSs, although these are not as conspicuous as AP% changes. Lakes Fúquene and Pacucha show a decrease in AP% during YD. The signature of this event in other sites is either opposite (e.g. Llano Grande, Chochos) or not recorded (e.g. Consuelo).

The record of aquatic taxa reveals potential precipitation changes in the tropical Andes during HS1 and the YD (Fig. 4). Northern sites show decreased lake levels during these periods. Lake Fúquene suggests lake level reductions during HS4, HS3 and HS2 but the resolution of the record used here is probably too low to allow further conclusions. A future assessment could evaluate these hypotheses by calculating D/SS in the high-resolution Fúquene record (Bogotá et al., 2011). Most of the high elevation lakes formed after HS1, probably as a result of glacial retreat and increases in regional moisture. Sites located south of the Equator show high lake level stands during HS1, but reduced water bodies during YD. Overall, our data suggest a north–south difference in the signature of millennial-scale events that can potentially be related to differences in moisture sources. Moisture in Northern Andean sites is mostly linked to ITCZ influence, while southern sites are mostly influenced by SASM (Table 1). Observed differences coincide with previous work suggesting a southward migration of the ITCZ (Cruz et al., 2006), and strengthening of SASM during HS (Broccoli et al., 2006).

The signature of GI is suggested by changes in AP%, DCA1 axis and D/SS in the studied transect. The onset of GI1 appears to be followed by a sharp AP% increase in Chochos and Consuelo, while in Fúquene and Pacucha the AP% increase pre-dates GI1 (Fig. 5). The AP% changes linked to other GI are less clear. A sharp shift in DCA1

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decades (Hughen et al., 2004). A similar time lag between the response of vegetation and marine markers in northeastern South America is estimated to be 1000 to 2000 years during HS (Jennerjahn et al., 2004). Our explorations with regard to the asynchronicity of these signals remain within the constraints of available dating resolution. However, our results suggest that vegetation responses to millennial-scale climate variability are overall rapid, and that differences in signature may result from differences in moisture sources, marker sensitivity and location (e.g. vegetation vs. stable isotopes, continental vs. marine).

6 Conclusions

Transforming raw pollen counts into percentages of ecologically meaningful groups (e.g. AP%) or into ordination values result in records that are seldom driven by similar factors. Our analysis showed that these approaches are complementary rather than contradictory. Both approaches rely on ecological knowledge, a priori or a posteriori, respectively. AP% and DCA axis scores remain vegetation markers and are not independent records of environmental change. Such records are still needed for most of the studied sequences.

Records of past vegetation change showed that rapid altitudinal migrations of the Andean vegetation may be linked to millennial-scale climate variability. Taking into account differences in the sensitivity of individual sites, the signature of HS is overall consistent among records and indicates downslope shifts of the UFL and cooling. The air temperature cooling needed to produce such migrations could potentially have resulted from increased intensity and duration of cold advection from the Northern Hemisphere. The SST, reflectance and ice core records evidence temperature decreases during HS and YD, which are consistent with UFL downslope migrations and cooling recorded in the tropical Andes. Our analysis also suggests a north–south difference in the moisture signature of millennial-scale events that can potentially be related to differences in moisture sources.

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The Supplement related to this article is available online at
doi:10.5194/cpd-11-1701-2015-supplement.

Acknowledgements. This paper results from the project “Latin American Abrupt Climate Changes and Environmental Responses” (LaACER) which held workshops in Bogotá (Colombia) in November 2012, and in Natal (Brazil) in August 2013. We thank PAGES and INQUA for funding support. We also thank the data contributors for raw data. B.M. thanks CSIC-Ramón and Cajal post-doctoral program RYC-2013-14073.

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Table 1. Site description and details on temporal resolution and time span for eight selected pollen records in the tropical Andes. Sites are listed in a latitudinal order from North to South.

Site	Coordinates	Elevation (ma.s.l.)	Andean position	Main moisture source	Time span (ka)	Mean temporal resolution \pm SD	Source
Llano Grande	6°29' N 76°6' W	3650	Inter-Andean	Atlantic ITCZ, ENSO	26	99 \pm 35.6	Velásquez et al. (2013)
Fúquene2	5°27' N 73°46' W	2540	Inter-Andean	Atlantic ITCZ, ENSO	36	433 \pm 167	Bogotá et al. (2012)
La Cocha	1°06' N 77°9' W	2780	Eastern flank	Amazonian convection	14	26.7 \pm 16.6	González-Carranza et al. (2012)
Surucucho	2°51' S 79°08' W	3180	Eastern flank	Amazonian convection	21.9	318 \pm 175	Colinvaux et al. (1997)
Chochos	7°38' S 77°28' W	3285	Eastern flank	Amazonian convection, SASM	17.5	270 \pm 210	Bush et al. (2005)
Pacucha	13°36' S 73°19' W	3050	Eastern flank	SASM, LLJ	24.9	198 \pm 57	Valencia et al. (2010)
Consuelo	13°57' S 68°59' W	1360	Eastern flank	SASM, LLJ	43.5	365 \pm 303	Urrego et al. (2010)
Titicaca	16°20' S 65°59' W	3810	Altiplano	SASM	19.7, 350	113 \pm 100, 710 \pm 1040	Paduano et al. (2003), Hanselman et al. (2011)

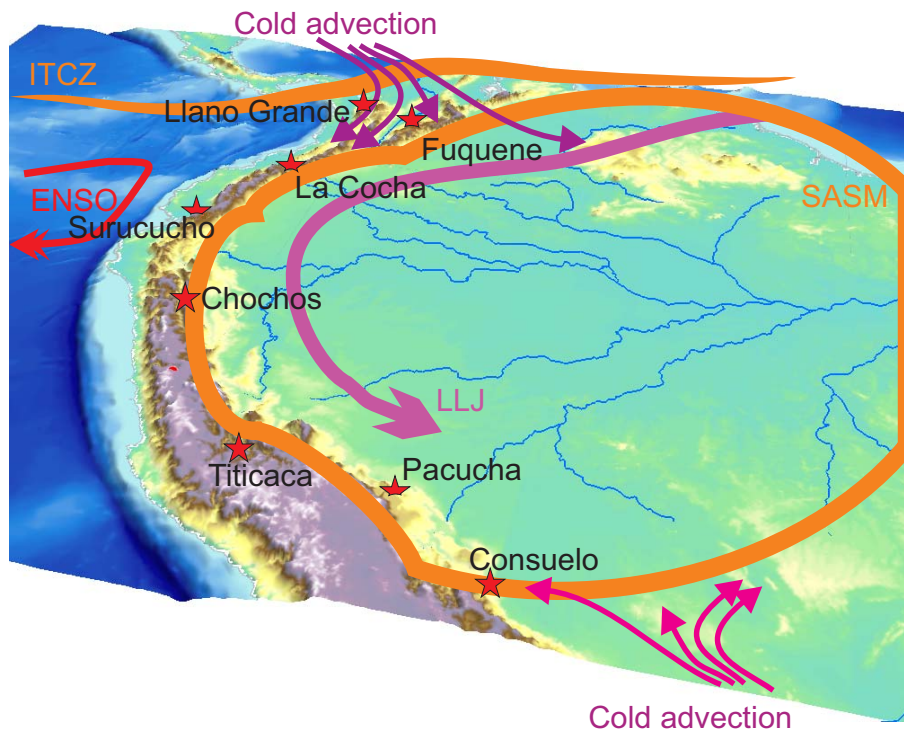


Figure 1. Map showing the Northern and Central Andes and major atmospheric patterns and oceanic systems controlling environmental conditions in the region. ITCZ: intertropical convergence zone, SASM: South American summer monsoon, ENSO: El Niño southern oscillation, LLJ: Low level jet. Red stars show the locations of sites mentioned in the text and described in Table 1.

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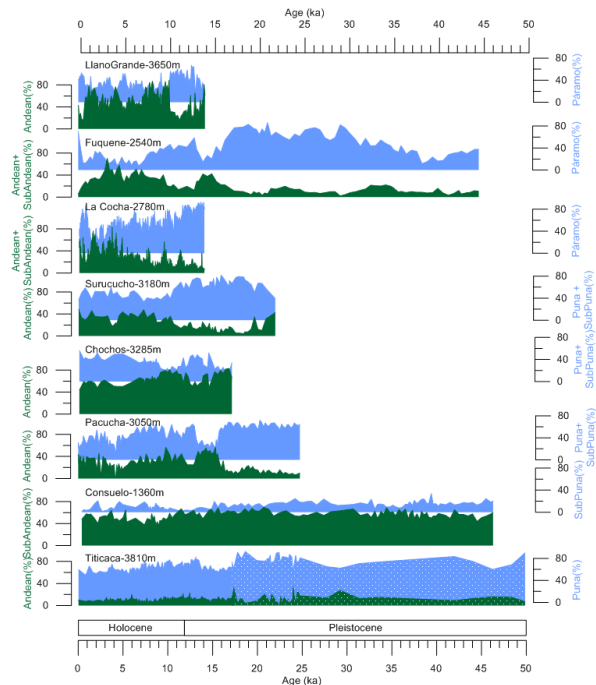


Figure 2. Summary pollen diagrams of selected pollen records from the tropical Andes (Fig. 1, Table 1) plotted on against time in thousands of years (ka). Pollen taxa are grouped into Andean and subAndean taxa (green) and Puna or Páramo taxa (blue). Taxa groupings follow original papers when available. For sites published without ecological groups, taxa have been grouped for the first time. Two pollen records are available for Lake Titicaca, and here they are differentiated with a dotted pattern for the Hanselman et al. (2011) record, and solid pattern for the Paduano et al. (2003) record.

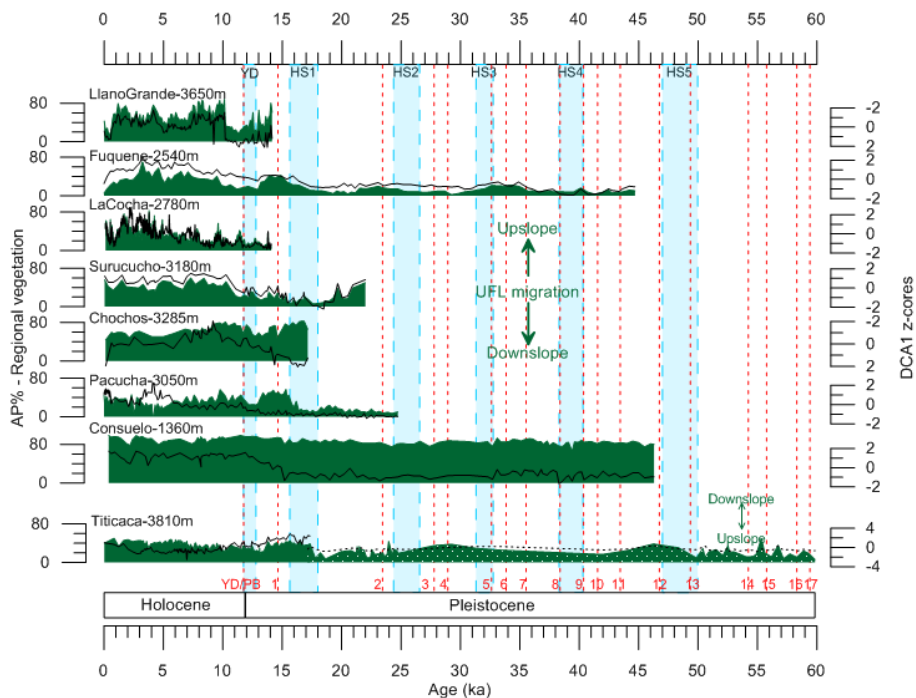


Figure 3. Temporal changes in regional vegetation or AP% (green polygons) and DCA1 z-scores (black line) plotted on a linear time scale for selected pollen records from the tropical Andes (Fig. 1, Table 1). Two pollen records are available for Lake Titicaca, and here they are differentiated with a dotted pattern for the Hanselman et al. (2011) record, and solid pattern for the Paduano et al. (2003) record. Heinrich stadials (HS) are drawn for reference as defined by Sánchez-Goñi and Harrison (2010). The Younger Dryas (YD) follows the timing of Greenland stadial 1 (Rasmussen et al., 2006) and the chronozone defined by Mangerud et al. (1974). Red dotted lines and numbers indicate the onset of Greenland interstadials (GI) in Greenland ice cores (Wolff et al., 2010).

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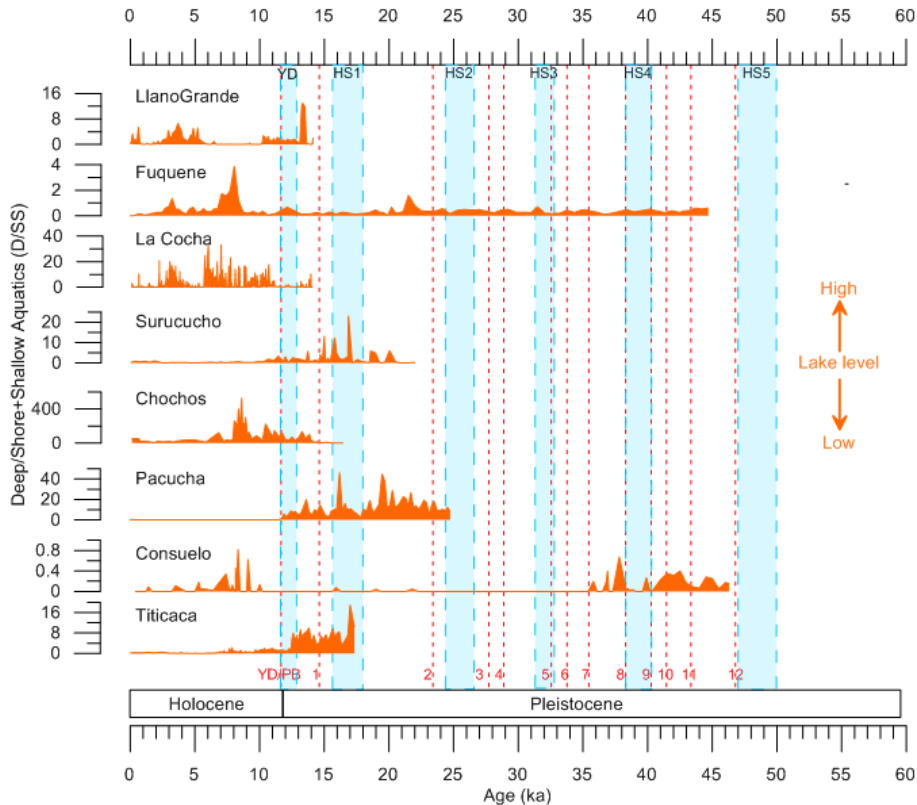


Figure 4. Temporal changes in the ratio of aquatic taxa characteristic of deep water to taxa from shallow water and wet shores (D/SS) for selected sites in the tropical Andes (Fig. 1, Table 1). Heinrich stadials (HS) are drawn for reference as defined by Sánchez-Goñi and Harrison (2010). The Younger Dryas (YD) follows the timing of Greenland stadial 1 (Rasmussen et al., 2006) and the chronozone defined by Mangerud et al. (1974). Red dotted lines and numbers indicate the onset of Greenland interstadials (GI) in Greenland ice cores (Wolff et al., 2010).

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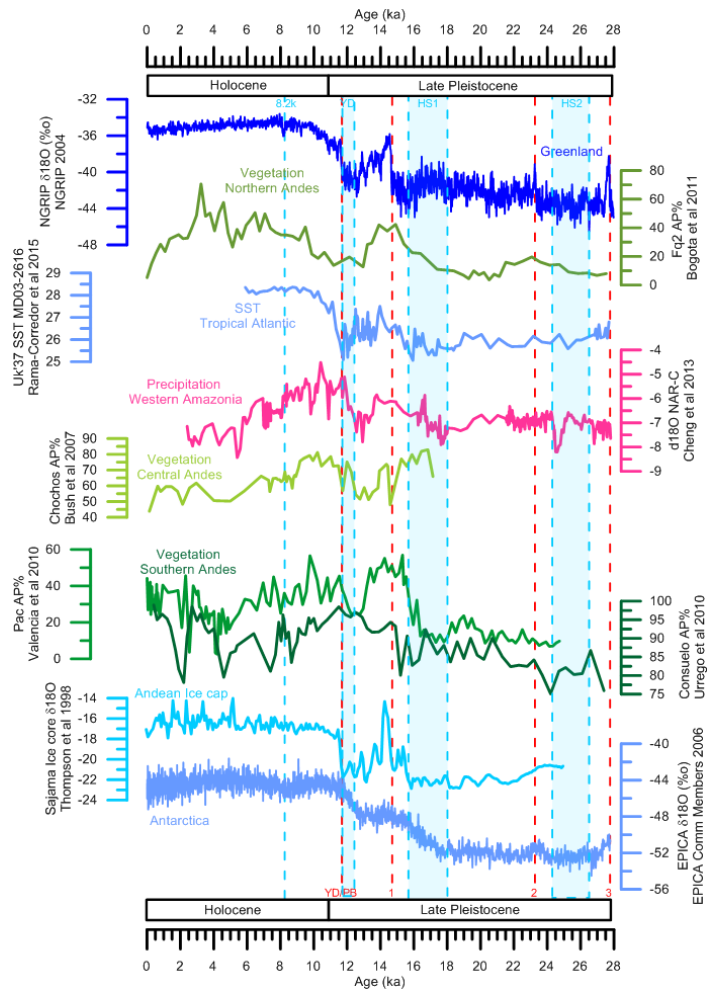
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Figure 5. Millennial-scale vegetation changes in four chosen pollen records from the tropical Andes during the Late Pleistocene and Holocene, compared with records from other climate components. Cryosphere: North Greenland (NGRIPmembers, 2004), EPICA Dome C (EPICA, 2006), and Sajama ice core record (Thompson et al., 1998). Atmosphere: Cueva del Diamante cave (Cheng et al., 2013); and ocean MD03-2616 (Rama-Corredor et al., 2015). Heinrich stadials (HS) are drawn for reference as defined by Sánchez-Goñi and Harrison (2010). The Younger Dryas (YD) follows the timing of Greenland stadial 1 (Rasmussen et al., 2006) and the chronozone defined by Mangerud et al. (1974). Red dotted lines and numbers indicate the onset of Greenland interstadials (GI) in Greenland ice cores (Wolff et al., 2010).

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