Millennial-scale vegetation changes in the tropical Andes using ecological grouping and ordination methods

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Author's response

Includes:

- Point-by-point response to the reviews,
- List of all relevant changes made in the manuscript, and
- Marked-up manuscript version

Interactive comment on “Rapid millennial-scale vegetation changes in the tropical Andes” by D. H. Urrego et al.

S. Metcalfe (Referee)

This paper by Urrego and co-authors goes back to eight published pollen records from the tropical Andes (between 6o29’N and 16o20’S) and reinterprets them using both ecological groupings (with a particular focus on AP%) and ordination scores from DCA. The DCA axis scores are also used to estimate rates of change (RoCs). Except for the case of Llano Grande in Columbia, the authors have used the published age models. The paper is set out to look at millennial scale variability, specifically Heinrich stadials and what are called Greenland interstadials (D/O interstadials). In practice, however, the paper says more about the stadials (including the YD) than the interstadials, pre- sumably because only three of the records actually extend back beyond 25 ka.
I think that this is an interesting paper, but have concerns about the emphasis in the text on moisture sources when in fact most of the responses seem to be driven by temperature.
>> We have reshaped the manuscript to emphasize the air temperature signal extracted from the records. The paper now focuses on the last 30 ka and discusses both the signature of HS and GI as far as the chronologies allow.

MAJOR COMMENTS
Environmental setting. I found this quite confusing in places in terms of a) modern climatology (linking to Fig. 1) and b) setting. a) The description of this in section 2 and Fig. 1 need to be linked together more effectively.
>> The environmental setting section now includes a part on vegetation, and we have revised it to link more effectively different aspects of climate and environmental variability. We have also modified Figure 1, including two panels to illustrate the seasonal variability of atmospheric systems.

At a basic level Fig.1 has no latitudes or longitudes marked on it.
>> The Figure now includes coordinates.

It isn’t clear whether the LLJ that is marked on the figure is the South American Low level jet referred to on p. 1707 (presumably it is).
>> We have replaced the term Low Level Jet with South American Low Level Jet (SALLJ) in the text.

The Choco Jet referred to on p. 1706 isn’t shown on the figure at all. The ITCZ is shown in only one location, with no indication of its seasonal shift and the label for the SASM seems to be located a long way to the east.
>> We have modified the Figure and now include average monthly precipitation data for the period 1998 to 2007. The Figure also includes one panel for the boreal summer and one for the boreal winter. We think this solves potential issues with the incorrect location of SASM and ITCZ. The approximate locations of the Choco Jet, SALLJ and ENSO are depicted in the Figure.

The text on cold front outbreaks (p. 1705) is rather confusing as it refers to the impact of these fronts from both north and south, but then reports that cold fronts (from

which direction?) can make a significant contribution to summertime (SH or NH?) precipitation in western Amazonia. It would be helpful to clarify this.
>> This refers to southern-hemisphere cold fronts and it is now clarified in the text, line 248.

P. 1706 line 9 – based on Fig. 1 it isn't clear how the Choco Jet affects the western flank of the Andes, this feature really needs to added to Fig. 1. It will then make sense.
>> We have added the approximate location of the Choco Jet to the Figure.

In the text on Millennial scale variability, trends and climatic mechanisms it would be good to clarify the relationship between the ITCZ and the SASM (see top of p. 1704).
>> The potential link between ITCZ and SASM is mentioned lines 305 and 307.

The signature of stadials in Cariaco and the northern sites in this transect is dry. b) The text contrasts sites in the northern and central/southern Andes (p. 1706) but this categorisation isn't shown in Table 1 or Fig. 1. This could also be picked up in the first paragraph of 3 Methods. In this paragraph I would help the reader by inserting a bit more explanation in line 8 e.g. 'Lakes Chochos, Pacucha and Consuelo also lie on the eastern flank of the Andes, but further south'.
>> Table 1 now includes a categorisation of northern, central and southern Andean sites. We have also added a sentence to the first paragraph of the methods, lines 357-359: "For the purpose of this paper, sites are classified according to their latitudinal position into northern (latitude north), central (latitude < 10ºS) and southern (latitude > 10ºS) Andean sites (Table 1)"

What is meant by mid- to high-elevation in this context? (p. 1704 last line, 1705 top line).
>> We have clarified this aspect in line 355

Methods. I'm afraid that I am not convinced by the use of a ratio between aquatic pollen types classified as deep water taxa and shoreline/shallow water taxa, to reconstruct lake level change. The authors record that the Holocene D/SS is nearly zero for LakeTiticaca when it has been shown that there was a major drop in lake level in the early Holocene followed by recovery (e.g. Baker et al., 2001). Given their own caveats about the D/SS ratio at the top of p. 1719 and the fact that there are often more reliable lake level indicators for the sites discussed in this paper, I suggest that the authors think carefully about removing this element.
>> We have retained the D/SS ratio because we consider that it provides meaningful environmental information despite the caveats. We have added a more clear explanation for the lack of change in Lake Titicaca in lines 739-743.

Although lake level/moisture balance is referred to in Section 5.2 (Orbital scale environmental changes), it isn't referred to very much in relation to millennial scale change. If the authors do want to retain this, then they need a clearer definition of what is meant by shallow and deep (p. 1710, line 6) and make more use of other water balance indicators.
>> Unfortunately water balance indicators like diatoms are not available for all the records, as a result the aquatic vegetation is the best alternative to compare potential moisture availability changes among sites. We have added more information on the

classification of shoreline and aquatic taxa in lines 452-455.

Discussion. The anti-phasing of responses (in relation to moisture balance) to both Holocene orbital forcing and to millennial events between the northern part of tropical South America and the southern part is quite well established. The possible east – west variation suggested by Cheng et al. (2013) based on their speleothem work is a newer idea. If the authors wish to continue to make this a focus of their paper, then these complex patterns warrant more discussion and could be linked much more closely to moisture sources (see above).
>> Our north-to-south network of sites does not allow conclusions about east-west gradients of moisture/precipitation. However, we have included some inferences of north-south anti-phasing of moisture availability during the Pleistocene-Holocene transition (lines 946-951).

Conclusions. These say nothing about warm events (your Greenland Interstadials). I'm not sure there is that much to say given the records available, but they seem less consistent. See previous comments about moisture sources.
>> We have added more discussion on the Greenland interstadials, in particular GI1 (lines 993-1006). The conclusions and abstract also include information on GI1.

MINOR COMMENTS
Abstract. See comment above re moisture sources. I do not see this as the emphasis of the paper.
>> The revised manuscript now emphasizes the role of temperature rather than moisture source.

p. 1703 lines 13 and 14 add some non-ice core references
>> We have added non-ice core references

p. 1707 line 7 Do you really mean eastward transport of Amazonian moisture?
>> We have rephrased

p. 1708 The text on age models isn't very elegant. Can you re-phrase?
>> We have rephrased

p. 1709 line 1, insert 'the' before 'original authors'; line 7, insert 'a' before 'pollen taxon' p. 1710, line 13 aimed
>> Corrections incorporated.
p. 1713, line 2, study based on what?
>> Based on inverse modelling. This has been included in lines 550-551

p. 1714, line 3 What do you mean by high resolution in relation to the Chochos record?
>> We have rephrased

p. 1716, line 19 difference; line 20 insert 'the' before La Cocha
>> Corrections incorporated.
p. 1718, line 25 can you suggest some specific proxies? Leaf waxes? GDSTs?

>> Examples included in Line 1238

p. 1721 line 9, please check whether the YD has been mentioned previously; line 25 give the date for G1
>> Corrections incorporated. Timings of GI and HS have been added to the discussion.

p. 1722 line 17 either ‘directions differ’ or ‘direction differs’; lines 19-21 contrast with speleothem records from the east.
>> Rephrased

Interactive comment on Clim. Past Discuss., 11, 1701, 2015.

Interactive comment on "Rapid millennial-scale vegetation changes in the tropical Andes" by D. H. Urrego et al.

Anonymous Referee #2

OVERVIEW

The present manuscript reports a reanalysis of some of the most important records for the tropical Andes, in West of South America, and focus on the vegetation changes de- tected at sub-millennial scale to study environmental variability. Given the uncertainty of the research question debated and the novel approach, the authors have nicely ex- plained the objectives of the present work and the advantages compared to previous attempts, as have discussed the potential problems of the techniques used. Regarding the objectives proposed however, the paper ends a bit shallow in its present form, lacking further discussion about the meaning of the results found, i.e., the potential drivers that have caused synchronicities/asynchronies between the records.
>> Discussion.

MAJOR COMMENTS

Abstract. The inference of precipitation changes (line 7) based on aquatic and shore-line vegetation is a bit risky as shifts in these taxa provide very local scale information and may be related to different drivers including precipitation, but also temperature through an increase in evaporation. I suggest the use of different terms such as moisture availability, P/E balance or similar throughout the text.
>> This is indeed a very good point that we had tried to address in the methods and discussion of the D/SS ratio. To avoid overstating the results we have now changed "inferred precipitation changes" from aquatic taxa to "moisture availability" and "lake level changes" throughout the text.

Environmental setting.
Section 2.1 is entitled "Geography, vegetation and climate" but I haven't found any information about vegetation so far. Although the study area will imply large variation of the taxa occurrence and distribution, some basic information is required that will help the readers not familiarised with the tropics.
>> We have added a paragraph on Andean vegetation to the Environmental setting section.

Methods.
1) Although the use of AP% as proxy for temperature shifts has been explained, some clarification would be appreciated. This proxy is especially useful in high steep loca-tions (mountain range) that includes a close ecotone between a forested and a non-forested plant community. This would be the case to some extent for the seven Andean records, but please clarify why using AP% in Lake Consuelo should work taken into account that puna is located almost 2000 m upwards and changes in communities promoted by temperature shifts might be unnoticed by AP%.
>> We clarify that AP% in Lake Consuelo is less sensitive than in high-elevation lakes sitting closer to the ecotone. We have added a section on the discussion on the low sensitivity of AP% in mid-elevation sites (Lines 967 to 992).

2) Given the data showed in Table 1, there are some records without a very high res-olution. This might be problematic for comparing the level of details that for instance

La Cocha record is going to provide. Please provide further details in how you are avoiding these potential issues.
>> We state that our regional comparison is constrained by the differences in temporal resolution among records (Lines 391 and 397). We consider that this issue is unavoidable and therefore refrain from drawing conclusions beyond the chronological resolution of individual records. The discussion also includes caveats on this, e.g. lines 1197-1198.

Table 1. Please add the number of radiocarbon dates obtained in each record for building the age-depth model.
>> The number of radiocarbon dates have been added to Table1.

Figure 1. Please check the right location of Lake Pacucha and re-draw SASM (maybe as a shade or with bars?) to clarify the real extent of the atmospheric pattern and include the season for the ITCZ etc.. Some coordinates would be much appreciated.
>> We have redrawn this figure and it now includes two panels of average precipitation during January and July depicting the position of the ITCZ and the development of SASM. The Figure includes coordinates.

Figure 2. Where are the lowland taxa? Were not important at all, including in Lake Consuelo?
>> We chose to show the sub-Andean and puna taxa for Lake Consuelo to allow comparisons with other sites. The Puna taxa in Lake Consuelo are also more sensitive to temperature change as they relate to the position of the upper forest line. This is now clarified in section 4.7.

SPECIFIC COMMENTS
Page 1704, lines 25-26: I would rephrase this including some potential mechanisms responsible for the lack of consistent signature found to date in time and/or space (differences in analysis resolution, proxy sensitivity, climate system operating. . .).
>> After the revision of the introduction this sentence is no longer in the text.

Page 1705, line 22: Please change “unmarked set by Dunia” for a proper reference.
>> Removed

Page 1712, lines 7-10: Please include the reference for the elevation of subAndean forests in the interglacials (or how they obtained the information).
>> This information was obtained from the original publication of the pollen record from Lake Fuquene. We have added a citation to support the statement.

Page 1713, lines 3-4: This sentence is saying just the opposite of the previous one (page 1712, lines 26-27). Please, clarify.
>> This information was indeed conflicting. The idea has been clarified.

Page 1713, line 11: There is a typo in Surucucho.
>> Corrected.

Page 1714, line 3: Please define “relatively high resolution” taken into account the record data (almost 300 years of sampling resolution).

>> We have removed this idea as it was an overstatement.

Page 1718, line 20: Please see comment on Methods above.
>> Clarified above.

Page 1721, line 11: Please avoid the term “precipitation changes” based on aquatic taxa, it will promote misunderstandings (despite you might be right in some cases, but this proxy cannot provide this type of evidence).
>> We have replaced ‘precipitation changes’ with moisture availability.

Interactive comment on Clim. Past Discuss., 11, 1701, 2015.

Millennial-scale vegetation changes in the tropical Andes using ecological grouping and ordination methods

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Prepared for publication in: Climate of the Past
Track record of manuscript: 29 April 2013 skeleton text by HH **version-1;** August 2013, added notes on methods, key questions and results DHU; 17 July 2014 **version-2** by DH Urrego; 22-23 July HH; 5Sep **version-4** by DHU; 9Sept HH input; 17thOct **version-6** by DHU; HH input 20Oct-4Nov; **version-7** by DHU 21Nov2014; 1Dec2014 LT, OR-C and BM input; HH input 30Nov-3Dec; **version-8** by DHU 23Jan15. HH input 26Jan15. BM input 28Jan15. **Version-9** by DHU 29Jan2015. BM feedback 30Jan. **Submission**: 31 Jan 2015 (**version-10**). Reviews May-July 2015. HH input 5Nov2015. Revised manuscript **version-11 by DHU** on 2-4Dec 2015. LT input 7Dec2015. Re-submission: 8 Dec 2015 (**version-12**).

Abstract

We compare eight pollen records reflecting climatic and environmental change from northern and southern sites in the tropical Andes. Our analysis focuses on the last 30,000 years, with particular emphasis on the Pleistocene to Holocene transition. We explore ecological grouping and downcore ordination results as two approaches for extracting environmental variability from pollen records. We also use the records of aquatic and shoreline vegetation as markers for lake level fluctuations, and moisture availability. Our analysis focuses on the signature of millennial-scale climate variability

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in the tropical Andes, in particular, Heinrich stadials (HS) and Greenland interstadials (GI).

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. We identify rapid responses of the vegetation to millennial-scale climate variability in the tropical Andes. The signature of HS and the Younger Dryas are generally recorded as downslope UFL migrations in our transect, and are likely linked to air temperature cooling. The GI1 signal is overall comparable between northern and southern records and indicates upslope UFL migrations and warming in the tropical Andes. Our marker for lake level changes indicated a north to south difference that could be related to moisture availability. The air temperature signature recorded by the Andean vegetation was consistent with millennial-scale cryosphere and sea surface temperature changes, but suggests a potential difference between the magnitude of temperature change in the ocean and the atmosphere.

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Keywords: arboreal pollen sum, detrended correspondence analysis, millennial-scale climate variability, pollen records, tropical Andes

1. Introduction

The signature of millennial-scale climate variations is recorded in ice cores, and in marine and terrestrial sediment archives both in the northern and southern hemispheres (NGRIPmembers, 2004; EPICA, 2006; Baker et al., 2001; Harrison and Sanchez Goñi, 2010; Hessler et al., 2010). The clearest manifestations of millennial-scale climate events are observed in Greenland ice core records (Wolff et al., 2010) and North-Atlantic marine sequences (Sánchez Goñi and Harrison, 2010). The Greenland interstadials (GI) are characterised by rapid warming in ice core records and can last up to 2500 years (Wolff et al., 2010). A second type of millennial-scale climate events are the Heinrich events (HE) (Heinrich, 1988), which are marked by an abrupt increase in the proportion of ice-rafted debris (IRD) from iceberg discharges in the Ruddiman Belt (Ruddiman, 2001). These iceberg discharges deliver fresh water into the North Atlantic and disrupt the Atlantic Meridional Overturning Circulation (Hemming, 2004) resulting in global climate changes. The intervals associated with North-Atlantic iceberg discharges are termed Heinrich Stadials (HS) (Sánchez Goñi and Harrison, 2010) and have been linked to temperature and precipitation changes in other regions of the world.

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The signature of millennial-scale climate variability in the American tropics has mostly been linked to precipitation change, specifically to southward migrations of the

Intertropical Convergence Zone (ITCZ) and variations in the strength of monsoonal systems during HS. Model simulations and climate reconstructions suggest that HS result in a southward shift of the thermal equator and the ITCZ (Broccoli et al., 2006) linked to decreased sea surface temperature (SST) in the North Atlantic and increased SST in the South Atlantic. Such an atmospheric and oceanic configuration is associated with a weakened North-American Monsoon (Lachniet et al., 2013), and reduced precipitation in central (Escobar et al., 2012) and northern South America (Peterson et al., 2000). The precipitation signature of HS is also described as wet episodes in the Bolivian Altiplano (Baker et al., 2001; Fritz et al., 2010) and as enhanced South American summer monsoon (SASM) activity in southeastern Brazil (Cruz et al., 2005). In the Ecuadorian Amazon, precipitation change appears to be positively correlated with some HS (Mosblech et al., 2012).

GI have also been linked to precipitation changes in the American tropics. These include wet conditions during GI1 in Central America (Escobar et al., 2012) and decreased run-off in the Guyana Basin (Arz et al., 1998). Some GI appear to be associated with reduced lake levels in western Amazonia (Urrego et al., 2010) and decreased humidity in the Bolivian Altiplano (Baker et al., 2001). Weakening of SASM and reduced precipitation are also associated with the onset of some GI in speleothem records from subtropical Brazil (Cruz et al., 2005). The precipitation signals of HS and GI indicate that climatic conditions in the American tropics were far from stable during these millennial-scale climate events.

Estimates of temperature change during HS and GI in the American tropics differ in magnitude and are hindered by the number of available records. The magnitude of tropical Atlantic SST warming at the onset of GI1 for instance 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). The isotopic record from the Sajama ice core also indicates a large-magnitude change during GI1 that has been linked to precipitation but could also be associated with air temperature warming (Thompson et al., 1998). In the Colombian Andes, the best resolution vegetation-based reconstruction of air temperatures available to date suggests that the magnitude of warming associated with GI1 is as large as 9°C (Groot et al., 2011), twice the SST estimate. Similarly, the signature of HS in the same record suggests downslope forest migrations and large-magnitude temperature depressions (Bogotá et al., 2011). A regional synthesis suggests that the vegetation signature of HS and GI can be opposite between the northern and southern parts of the region influenced by the ITCZ (Hessler et

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al., 2010) and highlights the paucity of records. Overall, whether there is a consistent air and ocean temperature signature of millennial-scale climate events in the ocean and the American tropics remains unclear.

The main objective of this paper is to assess the signature of millennial-scale climate variability in the tropical Andes, and to test whether it is consistent among northern and southern sites. We re-analyse a suite of eight pollen records that reveal vegetation changes at mid to high-elevations during last the 30,000 years BP (ka), with particular emphasis on the Pleistocene to Holocene transition. 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 can provide different information on environmental change. This study differs from previous studies that have focused on vegetation changes and their palaeoecological meaning. Here, we use the Andean vegetation as a marker for climatic change. We consider vegetation change as one of the internal responses of the climate system and integrate our observations with records that reveal the responses of the cryosphere and the ocean to millennial-scale climate variability in the American tropics.

2. Environmental setting: vegetation and climate

Vegetation in the north and central Andes is dominated by lower montane forest above 1000 m elevation and up to c. 2300 m where there is absence of night frost. Upper montane forests are found where night frost may occur and extend up to the upper forest line (UFL). The UFL position, defined as the highest contour of continuous forest (Bakker et al., 2008), is instrumental in temperature reconstructions as it coincides with the c. 9.5°C mean annual temperature (Hooghiemstra, 1984). The UFL is found in the study area between 3200 and 3500 m elevation and depends amongst other factors on regional temperature, precipitation, ground-level cloudiness (cloud forest), and soil conditions. In the northern Andes of Colombia and Ecuador relatively humid Páramo (Luteyn and Churchill, 1999) is found between the UFL and the perennial snow at c. 4800 m. Much drier Puna vegetation occurs above the UFL in Perú and Bolivia. The Huancabamba Deflection (Weigend, 2002), a low elevation part of the Andes between Ecuador and Perú, forms the transition between wet Páramo and dry Puna.

Topography is a key environmental variable in the tropical Andes (Graham, 2009). It determines air temperature change (Vuille and Bradley, 2000), and precipitation variability and its spatial distribution (Garreaud et al., 2009). Air temperature decreases with elevation, with modern empirically derived lapse rates of 5.5°C per 1000 m (Bush et al., 2004). Air temperature in the tropical Andes can also be significantly reduced by

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cold-air advection funnelled through Andean valleys from the northern (Poveda et al., 2006) and southern (Garreaud, 2000) high latitudes. Cold fronts also affect precipitation regimes due to convective cloudiness (Poveda et al., 2006; Garreaud et al., 2009), in particular southern-hemisphere cold fronts have been linked to ca. 30% of summertime precipitation in western Amazonia (Garreaud and Wallace, 1998).

With respect to precipitation distribution, spatial differences between the eastern and western flanks are partly due to topography (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 and the altitudinal 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).

Several large-scale atmospheric and oceanic mechanisms modulate precipitation regimes in the tropical Andes (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).

The SASM (Fig. 1) 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). This low pressure system 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

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Werner, 2005). This moisture is transported across Amazonia by easterly trade winds (Vuille et al., 2000) and is linked to the South American low-level jet (SALLJ) (Zhou and Lau, 1998). Variations in the position of the Atlantic ITCZ are suggested to play a role in modulating the strength of the 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 SALLJ along the eastern flank of the Andes, and enhancement of the 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 30 ka (Fig. 1, Table 1). This temporal focus is driven by the time span of available records. Selected lakes form a north-to-south transect from 6°N to 16°S and lie at mid- (<3000 m) and high-elevations (>3000 m) in the tropical Andes. For the purpose of this paper, sites are classified according to their latitudinal position into northern (latitude north), central (latitude < 10ºS) and southern (latitude > 10ºS) Andean sites (Table 1). The sites are located in inter-Andean valleys partly lying in the rain shadow, the eastern flank of the Andes facing the Amazon lowlands, and 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 the SASM (Bush et al., 2005). The SASM also is the primary moisture source for Lakes Pacucha, Consuelo and Titicaca

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(Urrego et al., 2010; Valencia et al., 2010; Baker et al., 2001) (Table 1).

We selected pollen records where knowledge of regional vegetation was sufficient to allow a classification of pollen taxa into ecological groups. The selected records also met minimum requirements of stratigraphic consistency and chronology quality. We used records in which stratigraphic consistency allowed linear interpolations between radiocarbon-dated samples (Table 1). We also selected records that included in average 5 radiocarbon ages in 10 ka. Age models developed by the 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 temporal resolution of the records ranged from an average of ca. 26 years in La Cocha to 530 years in one of the sequences from Lake Titicaca (Table 1). Given the differences in temporal resolution among records, we only discuss major trends and refrain from drawing conclusions beyond the chronological constraints of each record.

To assess the regional signature of millennial-scale climate events, our analysis benefits from comparisons with direct proxies of tropical Atlantic SST (7°N, Guiana basin), and isotopic records from the Sajama ice cap (18°S). We explore the degree of consistency between these independent markers and changes recorded by the Andean vegetation as far as the chronological uncertainties allow.

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 based on the ecological information published by the 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 (Reese and Liu, 2005; Urrego et al., 2011; Weng et al., 2004). We considered that ecological envelopes of Andean taxa at genus level may be wide, as more than one species may be reflected in one pollen taxon. We also took into account that the ecological affinity of a 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

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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, sub-Andean (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 sub-Andean 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 sub-Andean taxa. In Llano Grande at 3650 m, AP% only includes cold Andean taxa as pollen grains from sub-Andean forests hardly reach this high-elevation site. AP% is most sensitive when sites are located between the highest interglacial and the lowest glacial UFL positions. We therefore anticipate a lower sensitivity of the records from Lake Consuelo (1360 m) and Lake Titicaca (3800 m) as a consequence of site location. Using the ecotone of the upper/lower montane forest transition is not feasible yet as this ecotone is palynologically insufficiently constrained (Hooghiemstra et al., 2012). Changes in AP% relate to 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).

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. The shoreline group includes taxa found in the wet and seasonally flooded shores (i.e. *Plantago*, *Rumex* and *Typha*), shallow water taxa are found growing up to 1 m water depth (i.e. *Hydrocotyle* and *Ranunculus*), and deep water taxa include *Isöetes* ferns and other aquatic plants found up to 6 m water depth (González-Carranza et al., 2012). We calculate a ratio (D/SS) between taxa characteristic of deep water over taxa growing in shallow water and wet shores, and use it as an indicator of lake level changes and

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moisture availability. 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 untransformed terrestrial pollen percentages for each site. The first DCA was run on the entire pollen percentage matrices. A second DCA was run on reduced pollen percentage matrices after applying a filter that aimed to eliminate 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 only 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 standard deviation for each record. Rates of ecological changes (RoC) 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 (Fig. 2). 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 and moisture availability that appear to be registered at most studied sites (Fig. 4). In the following section we describe results from our re-analysis of each of eight selected pollen records.

4.1 Llano Grande (Velásquez and Hooghiemstra, 2013)

The Llano Grande 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. DCA1 z-scores (reversed) and AP% are remarkably similar (Fig. 3) suggesting that temperature, the driver of

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changes in AP%, is also the strongest driver of DCA1. The abundance of Andean taxa (AP%) shows a clear trough between ca. 12.5 and 10.5 ka (Fig. 2 and 3). Several AP% oscillations are observed during the Holocene. D/SS shows a peak after the onset of the pollen record at ca. 14.5 ka, and three increases of lesser magnitude during the Holocene (Fig. 4). The onset of the record and the largest D/SS peak are probably linked to the formation of the lake. D/SS increases occur between ca. 6 and 5 ka, and between ca. 4.5 and 2.5 ka.

4.2 Lake Fúquene (van der Hammen and Hooghiemstra, 2003)

The Fúquene2 record comes from an intra-Andean valley at 2540 m elevation, a position centrally located in the current altitudinal range of Andean forests. The location of Lake Fúquene makes this record highly sensitive to temperature-driven migrations of montane taxa. During glacial times this area was covered by cold Páramo vegetation, and during interglacials sub-Andean forest taxa reached up to ca. 2300 m (Groot et al., 2011). The short distance between sub-Andean forest and the lake explains pollen from sub-Andean taxa also being represented in AP%.

Páramo taxa show high percentages between ca. 30 and 17.5 ka, but also vary at several intervals (Fig. 2). Andean and sub-Andean taxa (AP%) show an overall increase starting around 15.6 ka, with a trough between ca. 13 and 11 ka, and showing 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 temperature-driven UFL migrations. Pleistocene downslope migrations of the UFL can be inferred from AP% decreases around 26, 18 and 13 ka (Fig. 3). AP% increases and upslope UFL migrations are observed at ca. 23.3 and 15 ka. D/SS also shows variations that suggest increases in lake levels after at ca. 22, 12, 8 and 3 ka (Fig. 4).

4.3 Lake La Cocha (González-Carranza et al., 2012)

Lake La Cocha sits in 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 sub-Andean 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 inverse hydrological modelling suggests that Holocene vegetation changes at this site are driven both by increased temperature and moisture (Van Boxel et al., 2014).

Andean and sub-Andean taxa (AP%) in this record increase consistently while

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Páramo taxa decrease at the Pleistocene-Holocene transition (Fig. 2). Short but clear increases of AP% are detected around 11.5, 9.5, 8 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 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 Surucucho (Colinvaux et al., 1997)

Lake Surucucho is located at 3180 m elevation. Sub-Andean forests reach up to 2800 m in this part of the Andes, while the subpáramo is found at 3500 m elevation. The Andean forest thus covers a vertical range of approximately 700 m. AP% values include Andean taxa at this site and reflect UFL shifts.

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 indicating that temperature is their common driver (Fig. 3). AP% decreases before 18 ka and increases again around 14.5 ka. At ca. 11.3 ka there is a two-fold increase in AP% and a shift in DCA1 z-scores. D/SS is relatively high during the late Pleistocene with a peak at ca. 17 ka. D/SS decrease after ca. 10 ka and are low throughout the Holocene (Fig. 4).

4.5 Lake Chochos (Bush et al., 2005)

Lake 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. AP% includes Andean taxa and is expected to reflect temperature-driven UFL shifts at this site.

Percentages of Andean forest taxa (AP%) are high at the end of the Pleistocene and gradually decrease between ca. 17 and 12 ka (Fig. 2). Andean taxa show some fluctuations during this interval, while Puna and subpuna taxa increase. Between ca. 12 and 9.5 ka, Andean taxa dominate the record again and Puna and subpuna taxa show relatively low proportions. Andean taxa decrease again between ca. 4.5 ka and 2.5 ka (Fig. 2). AP% and DCA1 z-scores show different trends, suggesting that different drivers affect these records (Fig. 3). D/SS are high between ca. 14 and 6 ka, with the highest peak centred at ca. 8.2 ka (Fig. 4).

4.6 Lake Pacucha (Valencia et al., 2010)

Lake Pacucha is located at 3095 m elevation in the Peruvian Andes. The vegetation

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around the lake is strongly influenced by small-scale topography with mesic forests on the windward slopes and xeric forests in the rain shadow areas. The natural UFL lies between 3300-3600 m, where vegetation changes into shrublands of 100 to 200 m vertical extension. Upslope, this shrubby vegetation transitions into herbaceous Puna up to 4300-4500 m. As the site is located ca. 300 m below the UFL, AP% changes are expected to be very sensitive to temperature-driven altitudinal shifts of the UFL. AP% at Lake Pacucha includes Andean taxa.

Puna and subpuna taxa dominate until ca. 15.6 ka. Andean forest taxa then show a three-fold increase and exceed Puna and subpuna taxa proportions by at least 10% (Fig. 2). Puna and subpuna taxa increase again at ca. 13, while the percentages of Andean forest taxa decrease approximately two-fold. Andean forest taxa percentages recover after ca. 11.8 ka. During the Holocene, both Andean forest and Puna taxa vary 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, with minima around 18 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 sub-Andean forest, the AP% record is mainly composed of sub-Andean taxa. Lowland taxa were grouped for Lake Consuelo, but showed less variation than sub-Andean 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 sub-Andean forests.

Sub-Andean forest taxa dominate the record and reach up to 80% (Fig. 2). Despite its mid-elevation location, the record shows over 30% of the subpuna vegetation during the Pleistocene. The trends of DCA1 z-scores and AP% are similar, but the signals seem more consistent during the Holocene (Fig. 3). D/SS are low between ca. 30 and 10 ka, and show a series of peaks centred around ca. 8 ka (Fig. 4).

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

Lake Titicaca is located at 3810 m elevation; the highest site 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. AP% includes

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Andean taxa and is expected to 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 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. Puna taxa fluctuate during the Pleistocene, and 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. D/SS could be calculated for the record collected closer to the shore, but given the lake's size and depth, the abundance of shoreline and shallow aquatics is very low. D/SS is mostly driven by deep-water indicators and is therefore not comparable with the other records (Fig. 4).

5. Discussion

5.1 Extracting climatic information from pollen records

Our comparison of AP% and DCA1 z-scores to extract climate change information from pollen records allows us to highlight differences between the two approaches. On the one hand, ordination analyses like DCA attempt to find the clearest relationships within the pollen dataset, both between pollen taxa and between time slices. The strongest source of variability in one dataset may be precipitation while it may be temperature in another. As a result, ordination scores are not always comparable between sites even after standardization. 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 with AP%, which uses modern ecology to group fossil taxa. On the other hand, ordination analyses produce results that require ecological knowledge for interpretation. The ordination results consist of axis scores for pollen taxa and for time slices that are non-dimensional, lack direction, and can

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be rotated as desired (Hill and Gauch, 1980). Additionally, information extracted from the ordination axes can only 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. Ordination-based interpretation of pollen records may be more appropriate for non-analogue species re-assortments, but still requires knowledge on modern species affinities to extract climate or environmental change information from ordination results.

Using *a priori* ecological knowledge to calculate AP% has been criticized due to potential subjectivity involved in the classification of pollen taxa (Colinvaux et al., 1997). This potential subjectivity relates to the fact that boundaries between vegetation formations are rarely clear-cut, therefore ecological grouping of transitional or wide-raging taxa is left to the palynologist's discretion. AP% has also been criticised because of the underlying assumption that species respond to change as an assemblage rather than individualistically (Urrego et al., 2010). The record from Lake La Cocha reveals individualistic changes in pollen abundance (González-Carranza et al., 2012), but also clear variations in AP% that may respond to shifting Andean and sub-Andean associations. The record of Lake La Cocha is therefore a good example of how ecological grouping associated with AP% allows for individualist migrations within groups.

The main advantage AP% has over ordination scores is that AP% gives a direction to the observed change from the start. AP% can be translated into temperature-driven UFL migrations (Hooghiemstra et al., 2012) and is comparable between sites. AP% is also particularly sensitive in high to mid-elevation sites. For instance in Fúquene and Pacucha, AP% is relatively high during the Holocene compared to the Pleistocene (Fig. 3) indicating the signal of post-glacial warming. The sensitivity of AP% can be low however where forest composition remains within one ecological group. In Lake Consuelo AP% remains high from glacial to interglacial periods, indicating that the area had a relatively stable forest cover. Site-to-site comparisons of ordination scores are not possible because DCA results are driven by the main source of variability within each site. On the other hand, AP% changes are comparable between sites regardless of differences in site sensitivity.

We also calculated RoC and D/SS ratios to explore their sensitivity to environmental change. RoC values appear to be sensitive to changes in sedimentation rate, while showing little difference when calculated based on DCA results vs. raw pollen percentages. As an example of this sensitivity we show RoC calculated for the La Cocha record (Fig. S1). We 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

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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 (for an example see Urrego et al. (2013)).

Another climate change indicator calculated here from pollen records is the D/SS ratio. Assuming that the lakes have minimal losses by underground leaks or outflow, D/SS values potentially indicate lake level changes due to fluctuations in precipitation and evaporation. Increases in D/SS are associated with high abundance of deep-aquatic taxa and likely indicate high lake-level stands. 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 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 comparisons among sites and samples within one record. Additionally, the sensitivity of D/SS may depend on water depth. In Lake Titicaca for instance where water depth is more than 200 m, the D/SS ratio is uninformative because no aquatic taxa were recorded.

5.2 Temperature and moisture availability during the Pleistocene to Holocene transition in the tropical Andes

The eight pollen records from the tropical Andes consistently record Pleistocene altitudinal migrations of Andean and sub-Andean forests linked to glacial cooling. Páramo and subpáramo, or Puna and subpuna vegetation characterize the Pleistocene, while the Holocene is characterised by sub-Andean and Andean forest (Fig. 2). Such forest migrations and inferred temperature change are consistent with other pollen records from the region (e.g. Hansen et al. (2003); Urrego et al. (2010)) and tropical air temperatures changes derived from 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 $\delta^{18}O$ records (Baker et al., 2001; Seltzer et al., 2000), and $\delta^{18}O$ 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.

The pollen records show an overall warming trend during the Pleistocene-Holocene

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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 are consistent with 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 ca. 17 ka (Rühlemann et al., 1999), and shifts in stable oxygen isotopes from the Sajama ice cap at ca. 15.5 ka (Thompson et al., 1998).

Changes in D/SS in the selected sites suggest that Pleistocene moisture availability differed 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 Pleistocene-Holocene transition (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 moisture availability through the Pleistocene-Holocene transition and up to 8 ka. D/SS in Lake Consuelo follows 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 and peaking around 8 ka (Fig. 4), analogous to D/SS increases observed in Northern Andean sites. Moisture in Northern Andean sites is mostly linked to the ITCZ, while southern sites are mostly influenced by precipitation from the SASM (Table 1). Overall, these data suggest a north-south difference in lake levels and moisture availability during the Pleistocene-Holocene transition that may be related to glacial-interglacial atmospheric reorganisations of the ITCZ (Haug et al., 2001) and the SASM (Cruz et al., 2006).

5.3 The signature of millennial-scale climate changes in the tropical Andes

The signature of millennial-scale climate variability is suggested in most pollen records used for our analysis (Fig. 3). AP% decreases in Fúquene, Surucucho and Pacucha approximately coincide with the timing of HS1 (18-15.6 ka, Sánchez Goñi and Harrison (2010). In Lake Titicaca AP% increases during HS1, but the direction of this change is

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comparable with the change in other records because of the altitudinal location of the site, i.e. above treeline. HS2 (26.5-24.3 ka, Sánchez Goñi and Harrison, 2010) is also insinuated in the low-resolution record from Fúquene by a slight decrease in AP%. In Llano Grande, two AP% decreases observed during the Pleistocene-Holocene transition are roughly consistent with the timing of the Younger Dryas (YD, 12.9-11.6 ka, (Rasmussen et al., 2006; Mangerud et al., 1974). Decreases in AP% during the YD are also apparent in Fúquene, Surucucho, Chochos, and Pacucha. The AP% fluctuations observed during North-Atlantic millennial-scale cooling events are best explained by downslope migrations of Andean vegetation and the UFL linked to air temperature cooling in the tropical Andes.

The AP% records from Lake La Cocha and Consuelo appear to be less sensitive to air temperature cooling at millennial timescales. In Consuelo in particular the signature of post-glacial warming is marked in the DCA1 z-scores but not in AP% (Fig. 3). DCA1 z-cores in Consuelo only show a few millennial-scale variations that seem unrelated to North-Atlantic cooling events. AP% in Consuelo remains largely unchanged and indicates continuous Andean and sub-Andean forest cover at this site throughout the record (Urrego et al., 2010). The low sensitivity of AP% in Consuelo may also be related to the distance between the site and the UFL as well as the buffering effect of ground-level cloud cover. In La Cocha, UFL sits closer to the site but millennial-scale and centennial-scale climate variability seem to be superimposed in the record (González-Carranza et al., 2012). La Cocha is also a site constantly influenced by ground-level cloud, which may buffer the effect of air temperature cooling on the vegetation.

The signature of GI warming events is best shown for GI1, while the signals of GI2, GI3 and GI4 are hardly recorded (Fig. 3). GI1 (14.6-12.7 ka, Wolff et al., 2010) is suggested by AP% increases in Llano Grande, Fúquene, Surucucho, Chochos and Pacucha. These AP% increases seem more conspicuous and of longer duration in Fúquene and Pacucha. Shifts in DCA1 z-scores are also apparent around the onset of GI1 in Chochos and Consuelo. In the record from Lake Titicaca, the signal of GI1 is either weak or not captured due to the elevation of the site. The onset of the records from Llano Grande and La Cocha probably indicates the formation of these two lakes during GI1 and may be due to increased regional moisture and/or glacial retreats. Differences between the signal of GI1 and other warming events may be related to the duration of this warming event in Greenland compared with other GI. Lasting 1900 years (Wolff et al., 2010), GI1 is more likely to be captured in records with the resolution available for this regional comparison (Table 1). Overall, GI1 potentially coincides with upslope UFL migration and regional warming in the tropical Andes, as well as the formation of some

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Andean lakes.

One important question is whether the signature of millennial-scale climate variability is consistent in the northern and southern tropical Andes. The signature of HS and YD are generally recorded as downslope UFL migrations in our transect, and are likely linked to air temperature cooling. Based on the longer records, we also observe a temporal consistency between the signals of different HS. HS1 and HS2 are both linked to AP% decreases and cooling in Fúquene, although the magnitude of change differs. The GI1 signal is overall comparable between northern and southern records and indicates upslope UFL migrations in the tropical Andes. These trends are spatially consistent between northern and southern sites, and imply a common forcing. Air temperature cooling during HS and YD could potentially be linked to cold front advection from the Northern hemisphere reaching as far as 13ºS (Pacucha) or 16ºS if we take the record from Titicaca into account. Cold advection both from the northern and southern hemisphere are common in the tropical Andes and can produce freezing conditions down to 2500 m elevation (Gan and Rao, 1994). The air temperature cooling recorded by the Andean vegetation during YD and HS1 could be explained by increased intensity or frequency of northern hemisphere cold advection. On the other hand, upslope UFL migrations and air temperature warming during GI1 could be related to reduced intensity or frequency of northern hemisphere cold advection.

To address the consistency of air temperature change recorded by the Andean vegetation with changes recorded by the ocean and the cryosphere, we compare the pollen records from Fúquene and Pacucha with SST reconstructions from the Guyana Basin and the isotopic record from the Sajama ice cap (Fig. 5). Fúquene and Pacucha are used for this comparison as a northern and a southern Andean site, respectively. We also plot the NGRIP and EPICA isotope records in an attempt to assess the relative importance of northern-hemisphere versus southern-hemisphere forcing. Air temperature fluctuations recorded by the Andean vegetation both in the northern and southern Andes are consistent with changes in tropical Atlantic SST (Rama-Corredor et al., 2015) and the isotopic record from the Sajama ice cap (Thompson et al., 1998), especially during HS1, GI1 and YD (Fig. 5). When compared with the long-term variability within each record, the amplitude of change recorded by the Andean vegetation during GI1 and YD seems comparable to that of the Sajama ice core record. The vegetation records and the isotopic signal of the Sajama ice core are comparable despite differences in moisture sources, reiterating that together these changes are best explained by fluctuations in air temperature. The SST record from the tropical Atlantic suggests reduced amplitude of temperature changes during the same period compared to the Andean vegetation and the

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ice core record. This comparison suggests a potential difference between the magnitude of temperature change in the ocean and the atmosphere that could relate to the thermal inertia of the ocean. Additionally, the climatic trends observed in the Andean records are comparable to the Greenland ice core record (NGRIPmembers, 2004), and show fewer similarities with Antarctica (EPICA, 2006). The observed similarities point to northern-hemisphere climate variability forcing UFL migrations and air temperature cooling in the northern and southern tropical Andes.

Millennial-scale vegetation changes in the tropical Andes show great variability, and appear to be asynchronous to those of tropical Atlantic SST and the isotopic signal of Andean ice core records (Fig. 5). Vascular plant biomarkers preserved in the Cariaco Basin have suggested that tropical vegetation lagged climate change by several 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 and sampling resolution. However, our results suggest that vegetation responses to millennial-scale climate variability are overall very rapid.

6. Conclusions

Records of past vegetation change in the tropical Andes showed that altitudinal migrations of the Andean vegetation are best explained by millennial-scale cooling and warming of air temperatures linked to northern-hemisphere forcing. Taking into account differences in the sensitivity of individual sites, the signature of HS is overall consistent among northern and southern Andean 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. GI1 potentially coincides with upslope UFL migration and regional warming in the tropical Andes, as well as the formation of some Andean lakes. The air temperature change recorded by the Andean vegetation was consistent with millennial-scale cryosphere and ocean temperature changes, but suggests a potential difference between the magnitude of temperature change in the ocean and the atmosphere. Our analysis also suggests a north-south difference in the moisture availability during the Pleistocene-Holocene transition that can potentially be related to reorganisations of the ITCZ and SASM.

We showed that AP% and DCA scores, two approaches to extract environmental variability from pollen records, are complementary rather than divergent. Transforming

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raw pollen counts into percentages of ecologically meaningful groups (e.g. AP%) or into ordination values results in records that are seldom driven by similar factors. The two approaches rely on a reasonable understanding of ecological affinities and knowledge of the regional vegetation. This information is used *a priori* for AP% and *a posteriori* for ordination scores. AP% and DCA axis scores remain as vegetation markers and are not independent records of environmental change. Such records are still needed for most of the studied sequences. Along with the development of pollen records, independent markers of temperature or precipitation (i.e. biochemical or isotopic markers) are needed in the American tropics (Urrego et al., 2014), and future work should preferably generate combinations of proxies to disentangle differences between the magnitude of atmospheric and oceanic change. Integrated multi-tracer approaches will help minimize chronological uncertainty and may shed light on the underlying forcing of these rapid shifts in the climate system.

7. Acknowledgements

This paper is a result of the project 'Latin American Abrupt Climate Changes and Environmental Responses' (LaACER) funded by PAGES and INQUA. B.M. thanks CSIC-Ramón and Cajal post-doctoral program RYC-2013-14073. We would also like to thank the data contributors for sharing their raw pollen data.

The plot data of this manuscript can be found in:

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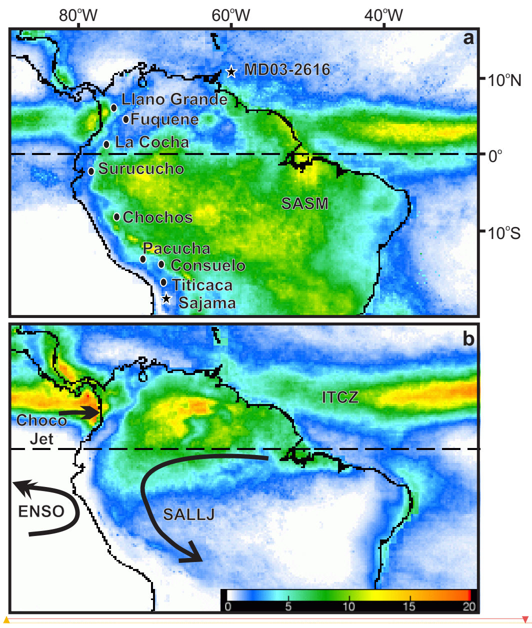

Figure 1. Average daily rainfall rates during the months of January (a) and July (b) from 1998-2007 from the Tropical Rainfall Measuring Mission. Black circles show the locations of pollen records described in Table 1. Stars indicate the location of the sea surface temperature record from the tropical Atlantic (MD03-2616) and the Sajama ice core. The rainfall distribution depicts the average southern and northern positions of the Intertropical Convergence Zone (ITCZ), and the South American Summer Monsoon (SASM). Arrows indicate the approximate location of relevant atmospheric and oceanic systems: South America Low Level Jet (SALLJ), El Niño Southern Oscillation (ENSO) and the Chocó Jet.

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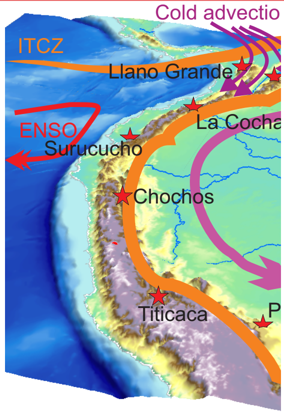

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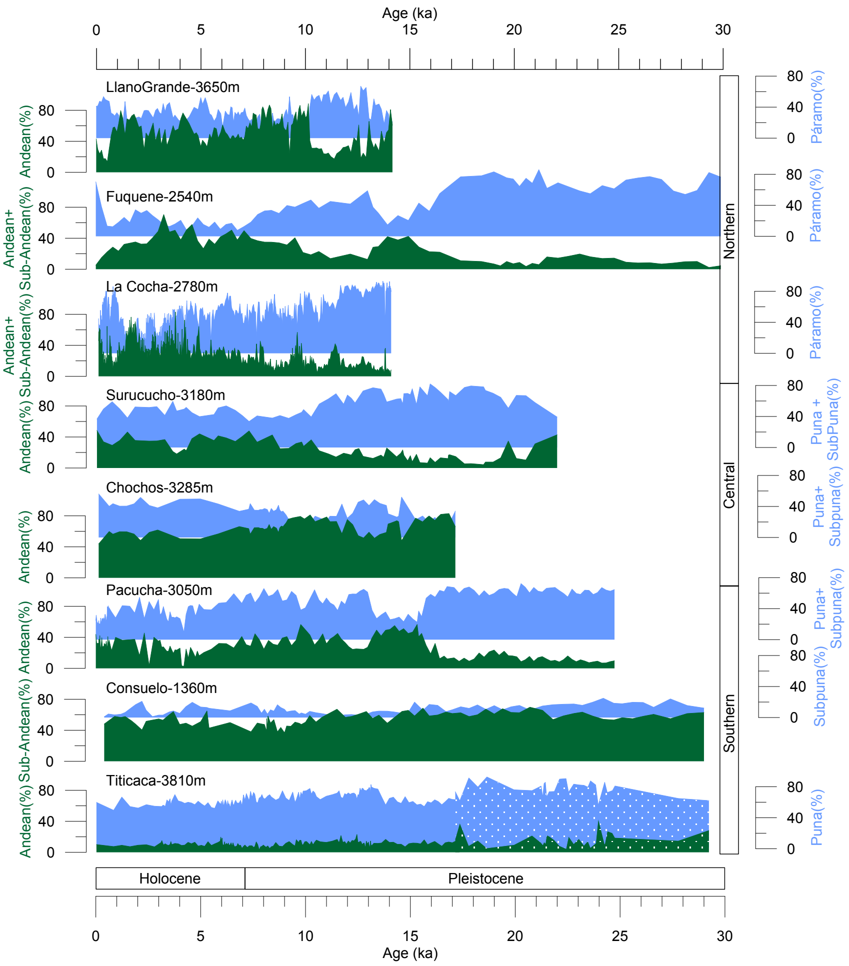

Figure 2. Summary pollen diagrams of selected pollen records from the tropical Andes (Fig. 1, Table 1) plotted on against time in thousands of years (ka). Pollen taxa are grouped into Andean and sub-Andean taxa (green) and Páramo, Puna or subpuna taxa (blue). Taxa groupings follow original papers when available. For sites published without ecological groups, taxa have been grouped for the first time. Two pollen records are available from 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.

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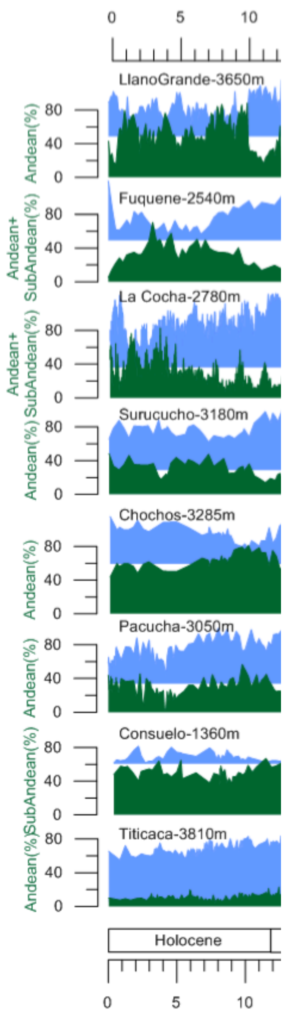

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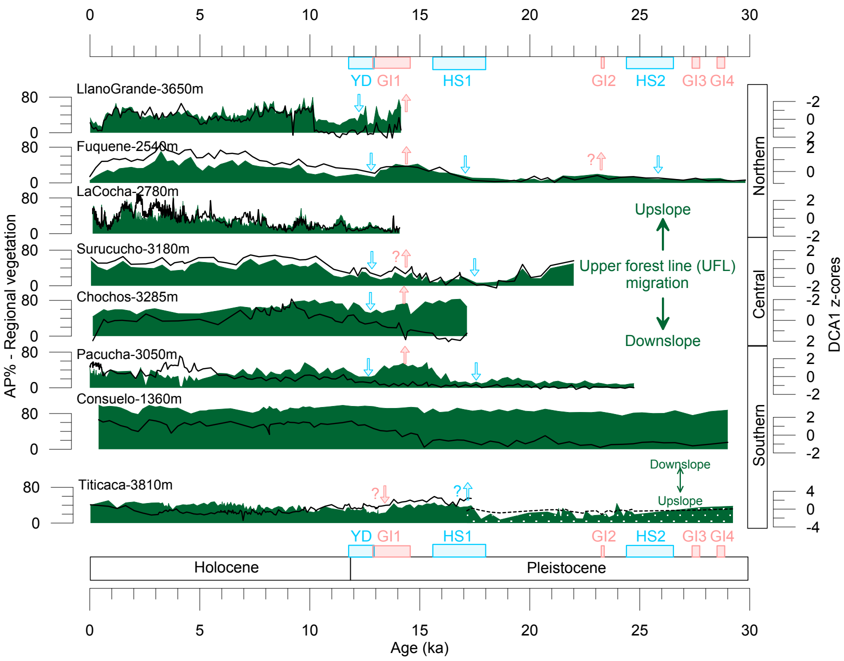

Figure 3. Temporal changes in regional vegetation AP% (green polygons) and DCA1 z-scores (black line) plotted on a linear time scale for selected pollen records from the tropical Andes (Fig. 1, Table 1). Two pollen records are available from Lake Titicaca, and here they are differentiated with a dotted 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 & 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). The timing of Greenland interstadials (GI) is based on Wolff et al. (2010).

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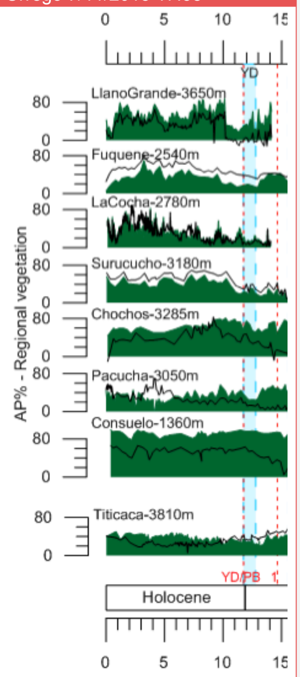

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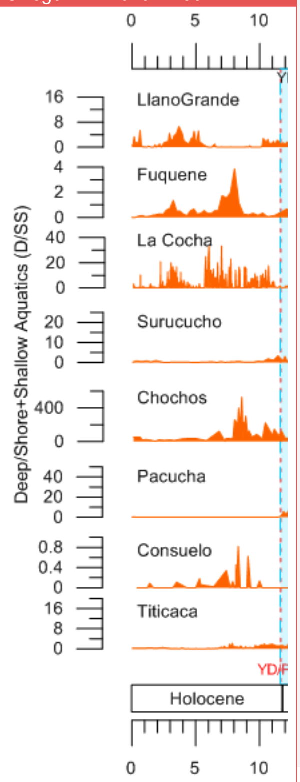

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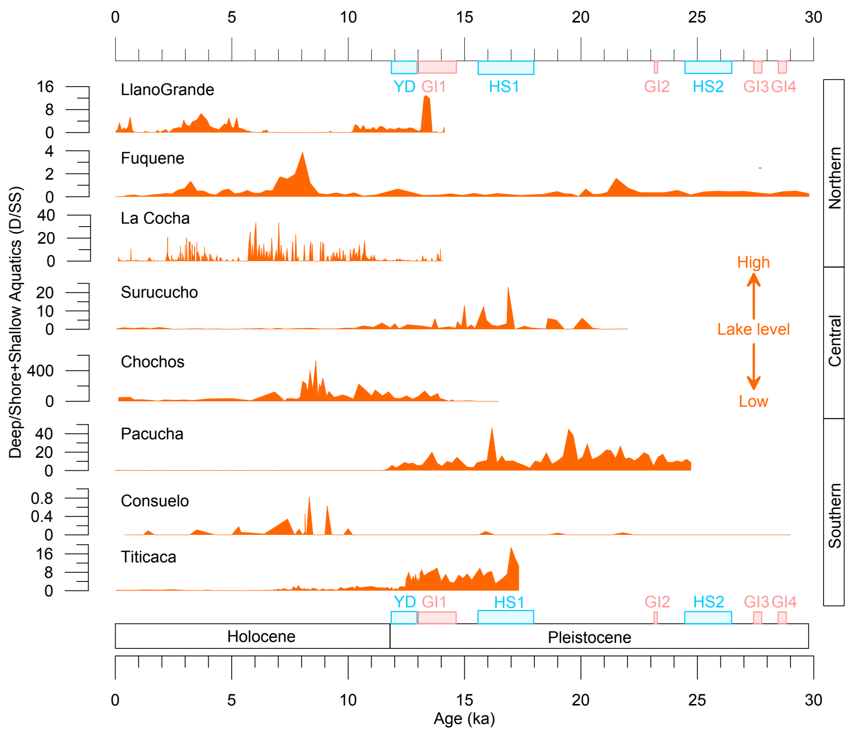

Figure 4. Temporal changes in the ratio of aquatic taxa characteristic of deep water to taxa from shallow water and wet shores (D/SS) for selected sites in the tropical Andes (Fig 1, Table 1). Heinrich stadials (HS) are drawn for reference as defined by Sánchez-Goñi & Harrison (2010). The Younger Dryas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

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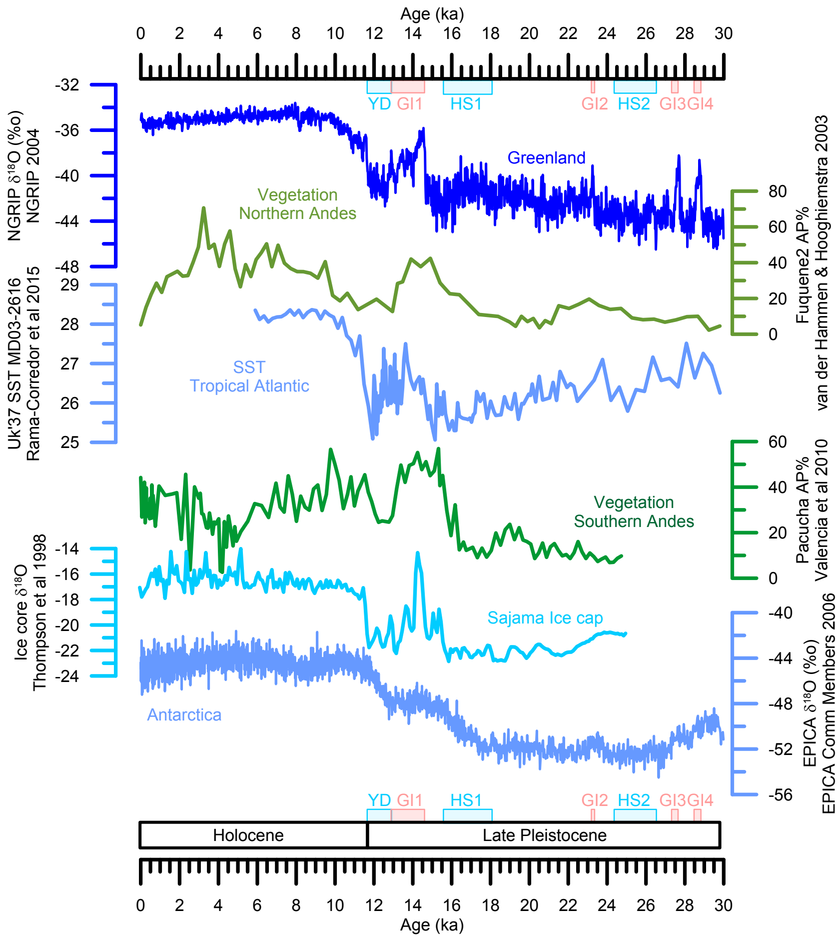

Figure 5. Millennial-scale vegetation changes in the northern and southern tropical Andes over the past 30 ka compared with other records: North Greenland (NGRIPmembers, 2004), EPICA Dome C (EPICA, 2006), and Sajama ice core record (Thompson et al., 1998), and sea surface temperatures (SST) from the Guyana Basin, tropical Atlantic (Rama-Corredor et al 2015). Heinrich stadials (HS) are drawn for reference as defined by Sánchez-Goñi & 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). The timing of Greenland interstadials (GI) is based on Wolff et al. (2010).

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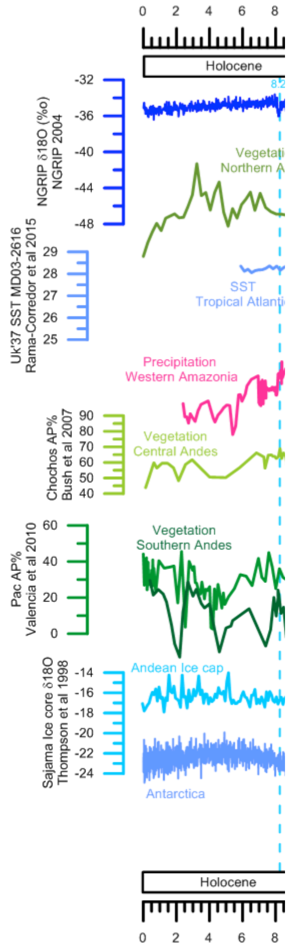

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Table 1. Site description and details on temporal resolution and time span for eight selected pollen records in the tropical Andes. Sites are listed in a latitudinal order from North to South.

Site	Coordinates	Elevation (m asl)*	Andean position	Main moisture source	Time span (ka)	Number of ^{14}C dates	Mean temporal resolution ± SD**	Source	Latitudinal position
Llano Grande	N 06°29′ W 76°6′	3650	Inter-Andean	Atlantic ITCZ, ENSO	14	6	99±35.6	Velásquez et al. (2013)	Northern
Fúquene2	N 05°27' W 73°46'	2540	Inter-Andean	Atlantic ITCZ, ENSO	36	10	433±167	van der Hammen & Hooghiemstra (2003)	Northern
La Cocha	N 01°06' W 77°09'	2780	Eastern flank	Amazonian convection	14	18	26.7±16.6	González-Carranza et al. (2012)	Northern
Surucucho	S 02°51' W 79°08'	3180	Eastern flank	Amazonian convection	21.9	9	318±175	Colinvaux et al (1997)	Central
Chochos	S 07°38'S W 77°28'	3285	Eastern flank	Amazonian convection, SASM	17.5	9	270±210	Bush et al. (2005)	Central
Pacucha	S 13°36' W 73°19'	3050	Eastern flank	SASM, LLJ	24.9	18	198±57	Valencia et al. (2010)	Southern
Consuelo	S 13°57' W 68°59'	1360	Eastern flank	SASM, LLJ	43.5	26	365±303	Urrego et al. (2010)	Southern
Titicaca	S 16°20' W 65°59'	3810	Altiplano	SASM	19.7, 350	17 18	113±100, 530±720	Paduano et al. (2003), Hanselman et al. (2011)	Southern

* m asl: metres above sea level; **SD: standard deviation

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