Climate variability and human impact in South America during the last 2000 years: synthesis and perspectives from pollen records

Running title: Climate variability and human impact in South America during the last 2000 years.

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Abstract

An improved understanding of present-day climate variability and change relies on high-quality data sets from the past two millennia. Global efforts to model regional climate modes are in the process of being validated against, and integrated with, records of past vegetation change. For South America, however, the full potential of vegetation records for evaluating and improving climate models has hitherto not been sufficiently acknowledged due to an absence of information on the spatial and temporal coverage of study sites. This paper therefore serves as a guide to high-quality pollen records that capture environmental variability during the last two millennia. We identify 60 vegetation (pollen) records from across South America which satisfy geochronological requirements set out for climate modelling, and we discuss their sensitivity to the spatial signature of climate modes throughout the continent. Diverse patterns of vegetation response to climate change are observed, with more similar patterns of change in the lowlands and varying intensity and direction of responses in the highlands. Pollen records display local scale responses to climate modes, thus it is necessary to understand how vegetation-climate interactions might diverge under variable settings. We provide a qualitative translation from pollen metrics to climate variables. Additionally, pollen is an excellent indicator of human impact through time. We discuss evidence for human land use in pollen records and provide an overview considered useful for archaeological hypothesis testing and important in distinguishing natural from anthropogenically driven vegetation change. We stress the need for the palynological community to be more familiar with climate variability patterns to correctly attribute the potential causes of observed vegetation dynamics. This manuscript forms part of the wider LOng-Term multi-proxy climate REconstructions and Dynamics in South America – 2k initiative that provides the ideal framework for the integration of the various palaeoclimatic sub-disciplines and palaeo-science, thereby jumpstarting and fostering multi-disciplinary research into environmental change on centennial and millennial time scales.

Key words: Pollen records, South America, last 2000 years, climate modes, LOTRED-SA, PAGES-2k, LAPD

Abbreviations:

2k: Last 2000 calibrated years (short writing for: 2000 cal yr BP)
AD: Anno Domini (equivalent to CE: Current Era)
ALLJ: Andean Low-Level Jet
AMO: Atlantic Multidecadal Oscillation
BP: Before Present, present defined as AD 1950
C: Central
cal kyr BP: Thousand calibrated years before present
Cheno/Am: Chenopodiaceae/Amaranthaceae
DJF December-January-February
ENSO: El Niño – Southern Oscillation
GS: Gran Sabana
IPO: Interdecadal Pacific Oscillation
ITCZ: Inter-Tropical Convergence Zone
JJA: June-July-August
ka: In this paper: thousand calibrated years before present, cal kyr BP
LAPD: Latin American Pollen Database
LIA: Little Ice Age
LOTRED-SA: LOng-Term multi-proxy climate REconstructions and Dynamics in South America
masl: meters above sea level
MCA: Medieval Climate Anomaly
NE: Northeast(ern)
NW: Northwest(ern)
PAGES: Past Global Changes
P/E Precipitation/Evapotranspiration ratio
S: South(ern)
SA: South America
SACZ: South Atlantic Convergence Zone
SAM: Southern Annular Mode
SASM: South American Summer Monsoon
SE: Southeast(ern)
SON: September, October, November
SPA: Subtropical Pacific Anticyclone
SST: Sea Surface Temperature
SWWB: Southern Westerly Wind Belt
TNA: Tropical North Atlantic SST
TSA: Tropical South Atlantic SST
UFL: Upper forest line
W: West(ern)

1. Introduction

Accurately simulating the complexity of Earth's climate system is still a major challenge for even the most advanced Earth system models. One major obstacle for evaluating model performance in historical runs is the lack of long and reliable climate records from some regions of the Earth. Given the scarcity of instrumental records in many regions, alternative, proxy-based climate reconstructions therefore provide an excellent dataset against which to test models and their ability to accurately simulate longer-term features of climate change. Proxy data sets from sedimentary records (in particular pollen, charcoal and tephra from lake sediments and peat bogs) have been particularly underutilized in this regard.

Increasingly studies have demonstrated the integration of multiple proxies (Li *et al.*, 2010) in a climate reconstruction, with a special focus on the two millennia (in this paper abbreviated to "2 ka") before present (BP, present defined as AD 1950). This period could be considered a baseline to current conditions, as climate has been very similar to the present. This integration is still in its infancy in South America (SA), especially in the tropics. Since 2009, regional climate reconstructions from SA have gained momentum from compilations of multiple datasets and from fine-tuning of model reconstruction methods (Villalba *et al.*, 2009). However, an improved understanding of the spatial distribution of proxy data sets has been identified as necessary to make further progress (Villalba *et al.*, 2009; Flantua *et al.*, 2015a). Tree ring studies constitute a widely distributed and frequently used high-resolution climate archive that has fortunately recently expanded its spatial coverage (Boninsegna *et al.*, 2009; Villalba *et al.*, 2009). However, the tree ring records are limited compared to the spatial and temporal coverage provided by records obtained from sedimentary archives (e.g. pollen records). The newly updated inventory of palynological research in SA documents the extensive spatial and temporal coverage of pollen-based research available throughout the continent (Flantua *et al.*, 2015a. However, to integrate records from different sedimentary archives across SA a standard chronological framework is required. To this end an alternative recalibrated age models and evaluation of chronologies has been undertaken to facilitate the intergration of multi-proxy records in SA (Flantua *et al.*, 2015b). However, multi-proxy climate reconstructions from the last 2 ka have hitherto been focused mainly on southern SA (PAGES-2k Consortium, 2013), omitting input from the northern two thirds of the continent. Furthermore, palynological research has been underrepresented in most reconstructions of climate variability (Villalba *et al.*, 2009; Neukom *et al.*, 2010; Neukom and Gergis, 2012).

The lack of an adequate overview of available pollen records from the continent has been an impediment to the advancement of its use and inclusion in climate studies.

As a result, we identified the need to review and discuss pollen records in SA that can fulfil requirements for inclusion in 2 ka-palaeoclimate reconstructions, within the framework of *LOng-Term multi-proxy climate REconstructions and Dynamics in South America* (LOTRED-SA, this Special Issue) and the PAGES-2k Network (http://www.pages-igbp.org/ini/wg/2k-network/intro). This paper is structured following an assessment for individual regions in SA within the context of current climate modes. These modes are characterized by their precipitation and temperature fingerprint over SA and used as a baseline framework to identify past climatic changes from pollen records. Certain zones are more prone to particular climate signals; therefore comparison between the spatial expression of climate modes and highly correlated records from different regions strengthens the interpretation of palaeoecological findings. To use pollen as a palaeoclimate proxy, the degree of human impact on the vegetation needs to be considered at a minimum or absent over the last 2 ka. Therefore, drivers of vegetation change, both natural and anthropogenic, are discussed within the different regions to describe the general settings required for palaeoecological research in the last millennia. Records that identify significant human impact are identified and excluded from the proposed dataset for PAGES-2k when the climate signal is lost, but are considered useful within the regional purposes of LOTRED-SA (this Special Issue). We provide a qualitative translation from pollen metrics to climate variables based on expert knowledge. We finish by discussing the potential of including pollen-inferred climate information 2ka-climate model validation and emphasize the importance of multi-proxy working groups such as LOTRED-SA.

2. Climate settings

Continental overview climate zones and modes

We begin with an overview of the main climate ‘zones’ of SA to provide the climatological context for a discussion of pollen records covering the past 2000 calibrated years before present (cal kyr BP). Climate zones are regions of coherent seasonality and mean climate (intra-annual climate regime), while climate ‘modes’ are based on ocean-atmosphere interactions with often oscillatory behaviour affecting the interannual to multidecadal climate

variability in a region. The spatial influence of climate modes is assessed by documenting their role in driving interannual precipitation and temperature variability.

Continental SA extends from the tropics (12°N) to mid-latitudes (55°S). Three major noticeable climate zones can be distinguished: tropical, subtropical and extratropical SA. Atmospheric circulation and climate in all three zones is highly modulated and constrained by the orography of the Andes, the shape of the continent and interactions with the underlying land-surface, vegetation, soil moisture; furthermore ocean currents, such as the cold Humboldt Current affecting coastal climate along the South American west coast, also affect climate (Wang and Fu, 2002; Li and Fu, 2006).

The climate of tropical SA is dominated by the seasonal migration of the Intertropical Convergence Zone (ITCZ) over the Atlantic and Pacific, and the seasonal development of convective activity associated with the South American Summer Monsoon (SASM) over the interior of the continent (Fig. 1). The seasonal migration of the ITCZ affects primarily coastal areas and northernmost SA as it is characterized by a fairly well constrained narrow band of low level wind convergence over the equatorial oceans. The SASM is a seasonal phenomenon that develops between September and April and affects primarily the SA tropics and subtropics south of the equator (Garreaud *et al.*, 2009). During the austral spring (September to November, SON) moisture influx from the ITCZ contributes to the development of this monsoon system (Zhou and Lau, 2001; Vuille *et al.*, 2012). This monsoonal system reaches its mature phase (maximum development) during December to February (DJF) and is characterized by heavy rainfall advancing southward from tropical to subtropical latitudes. To the east of the tropical Andes a strong low-level wind, the Andean low-level jet (ALLJ), transports moisture in a southeasterly (SE) direction from the tropics to the subtropical plains (Cheng *et al.*, 2013), feeding the South Atlantic Convergence Zone (SACZ), extending from the SE Amazon basin toward the SE out over the S Atlantic. The extratropical region is characterized by a quasi-permanent westerly circulation embedded in-between the subtropical anticyclones located over the subtropical Pacific and Atlantic to the N and the circum-polar trough of low pressure to the S. Frequent northward propagation of extratropical cold air incursions E of the Andes provide for continued atmospheric interaction and heat exchange between mid- and low latitudes over the subtropical continent. The latitudinal extension of the westerlies over land displays limited variations across the year and covers southern and

central (C) Argentina and Chile. Additional information is presented in Supplementary Information.

Both precipitation and temperature exhibit significant variability on interannual to interdecadal time scales in all three climate zones of SA (e.g. Garreaud *et al.*, 2009). This variability is mainly caused by ocean-atmosphere interactions (Vuille and Garreaud, 2012) that lead to a reorganization of the large-scale circulation over SA and the neighbouring oceans. To quantify the influence and relative importance of these ocean-atmosphere coupled modes on the interannual precipitation and temperature variability over SA, spatial correlation and regression coefficients are calculated.

Gridded precipitation and temperature data were derived from the UDelaware data set V2.01 (Legates and Willmott, 1990) at 0.5° resolution. We limit our assessment to the six most relevant climate modes (Table 1). Other modes analyzed were either largely redundant or showed a much weaker influence over the SA continent. The resulting correlation maps indicate the correlation coefficient on interannual time scales between the mode in question and the local temperature and precipitation at each grid cell. Conversely, the regression maps indicate the local anomaly (in physical units of mm or °C) at each location that corresponds to a unit (one standard deviation) anomaly in the climate mode. The Southern Annular Mode (SAM) and all three Atlantic modes (Atlantic Multidecadal Oscillation - AMO), Tropical North and South Atlantic Sea Surface Temperature (TSA, TNA; Table 1) were detrended prior to analysis to ensure that correlation and regression coefficients account for co-variability on interannual timescales only and do not result from spurious common trends. More information on the methodology can be found in the Supplementary Information.

In all correlation maps (Figs. 2 and 4) we show correlations in excess of ± 0.2 only, which approximately corresponds to the 95% significance level. For the regression maps (Figs. 3 and 5) we used thresholds of ± 0.12 °C and ± 50 mm, respectively. The correlation maps can help inform whether a certain temperature or precipitation anomaly in the regression map is statistically significant. In our discussion we focus primarily on the impact of the positive phase from each of these modes, as these are the fingerprints presented in Figures 2-5. Since this is a linear analysis the negative phase of these modes would lead to the same changes in temperature and precipitation, but with the sign reversed. In general these outcomes are consistent with earlier analyses reported by Garreaud *et al.* (2009). However, some differences are apparent and most likely related to different time periods analyzed, our

choice of using the hydrologic year as opposed to the calendar year, and different definitions of the indices used (see Supplementary Information for more details). For example, Garreaud *et al.* (2009) used the Multivariate El Niño - Southern Oscillation (ENSO) Index, while here we focus on the Niño3.4 index to describe ENSO variability. Similarly Garreaud *et al.* (2009) used the Pacific Decadal Oscillation Index to describe Pacific interdecadal variability, while here we use the Interdecadal Pacific Oscillation (IPO).

Temperature

The largest and most significant influence on interannual temperature variability in SA is exerted by ENSO, with above average temperatures during El Niño and reduced temperature during La Niña (Figs. 2 and 3). A one standard deviation departure in the Niño3.4 index is associated with a change in temperature of up to 0.8°C along the Pacific coast of SA. In the Andes of Colombia the correlation between temperature and the Niño3.4 index is >0.8, indicating that more than two thirds of the temperature variability on interannual scales can be explained by ENSO. The largest increase in temperature is observed during austral summer (DJF, not shown) linked to the peak phase of ENSO, which tends to occur at the end of the calendar year.

The IPO has a similar, albeit slightly weaker, fingerprint over SA as ENSO, which is not surprising given that the Pacific decadal and multidecadal variability is often described as 'ENSO-like' (e.g. Garreaud and Battisti, 1999). The IPO impact extends further south along the west (W) coast of SA than ENSO, however, with a somewhat stronger influence on temperature in N-C Chile. It is noteworthy that the IPO impact over SA is almost identical to the influence of the Pacific Decadal Oscillation as described in Garreaud *et al.* (2009).

The N Atlantic modes, AMO and TNA are also quite similar, both featuring warming over tropical SA during periods when sea surface temperature (SST) in the N Atlantic domain are above average, most notably so over the southern C Amazon Basin (Figs. 2 and 3). In fact the warming associated with a unit variation in the AMO or TNA index is larger over most of the Amazon Basin than the warming associated with ENSO. The region of largest warming is co-located with an area of strong precipitation reduction during the warm phase of the TNA and the AMO (Figs. 4 and 5). This suggests that much of the warming is caused by cloud cover and soil moisture feedbacks associated with reductions in precipitation (reduced cloud

cover leading to enhanced solar radiation and reduced soil moisture limiting evaporative cooling).

The south (S) Atlantic counterpart, the TSA, is associated with a temperature dipole over subtropical SA, characterized by warming along a zonal band extending from the S-C Brazilian coast westward to Bolivia, while C Argentina contemporaneously experiences cooling (Figs. 2 and 3). The warming in the subtropical region coincides with a region of reduced precipitation during the TSA positive phase (Fig. 4), suggesting that the warming is at least in part caused by changes in the hydrological cycle (cloud cover and/or soil moisture feedbacks).

The SAM is positively correlated with temperature over Patagonia (Fig. 2) and also shows a weak negative temperature departure over western tropical SA during its positive phase (Fig. 3). The warming over Patagonia is strongest during austral summer (Garreaud *et al.*, 2009; not shown) and results from enhanced heat advection, combined with higher solar radiation receipts due to cloud free conditions (Gupta and England, 2006).

Precipitation

Given that ENSO is the source of the strongest interannual variability on Earth, it is not surprising that it also leads to the strongest modern precipitation anomalies over SA (Fig. 5). In general in the tropics, El Niño events lead to significant precipitation reductions over much of tropical SA, with the strongest signal seen in N Brazil along the Atlantic coast and in the Andes of Colombia. Over NE Brazil the precipitation reduction is the result of El Niño events inducing a delayed anomalous warming of the tropical N Atlantic in boreal spring (March-May) (e.g. Curtis and Hastenrath, 1995; Giannini *et al.*, 2001). Hence the ENSO influence in this region strongly projects onto the TNA pattern (Fig. 4). Over the N Amazon Basin the precipitation reduction is the result of a shifted Walker circulation, enhanced subsidence and reduced convective activity (e.g. Liebmann and Marengo, 2001; Ronchail *et al.*, 2002). In the subtropics on the other hand precipitation is enhanced during El Niño events, in particular over southeastern SA (see also Grimm *et al.*, 2000). The only tropical location that sees an increase in precipitation during El Niño is along the Pacific coast of Ecuador and northern Peru, where flooding is a common occurrence during these events (e.g. Takahashi, 2004). During La Niña events these precipitation anomalies are essentially reversed. The correlations

are weaker in our annual analysis over some regions where the ENSO influence is highly seasonal, such as the precipitation reduction over the C Andean 'Altiplano' (high plain) region in DJF (Vuille *et al.*, 2000) or the enhanced precipitation during El Niño in C Chile in June to August (JJA; Montecinos and Aceituno, 2003).

The largest change in the IPO in the period analyzed is related to the Pacific climate shift of 1976-77, when the tropical Pacific switched from its cold to its warm phase. Since El Niño events also became more frequent and stronger over this period (including the two extreme events of 1982-83 and 1997-98), it is no surprise that the observed changes in precipitation associated with the IPO are similar to the ENSO footprint, albeit somewhat weaker. Indeed the low-frequency modulation by the IPO may strengthen El Niño events during its positive phase and weaken La Niña events, while the opposite is the case during the IPO negative phase, a phenomenon known as 'constructive interference' (e.g. Andreoli and Kayano, 2005). Espinoza Villar *et al.* (2009) documented the influence of Pacific interdecadal variability on precipitation over the Amazon Basin and showed that its positive phase is related to a decrease in precipitation over the basin since 1975, consistent with our results.

Precipitation is reduced in the southernmost part of SA during the positive phase of the SAM (Fig. 4). This reduction extends N into the subtropics along both the Atlantic and Pacific coast to approximately 30°S (Silvestri and Vera, 2003; Gillett *et al.*, 2006). Most of this precipitation reduction is associated with reduced westerly moisture flux and moisture convergence from the Pacific (Garreaud *et al.*, 2013). The correlation (Fig. 4) and regression (Fig. 5) maps also suggest a significant influence of the SAM on precipitation in parts of the tropics. This signal, however, is not well documented and its physical mechanism is unclear. It may to some extent be related to teleconnections and an anticorrelation between ENSO and the SAM (e.g. Carvalho *et al.*, 2005), which is supported by the fact that the Niño3.4 index and the SAM correlation maps are almost mirror images of one another (Fig. 4).

The AMO and the TNA have a similar fingerprint on the hydrologic cycle of SA (Fig. 5). Both modes are characterized by a significant reduction in precipitation over much of the Amazon basin during their positive phase, with the amplitude of the changes being slightly larger associated with TNA forcing. This negative precipitation anomaly is associated with the northward displacement of convective activity in the ITCZ region due to warmer SST in the tropical North Atlantic and Caribbean during the positive phase of the TNA (and to a lesser extent also the AMO). This directly affects precipitation amounts over NE Brazil (e.g.

Hastenrath and Greischar, 1993; Nobre and Shukla, 1996), while the northward shift in the core region of convection also leads to anomalous subsidence, located over the Amazon basin. In fact the recent droughts in 2005 and 2010 in the Amazon Basin were both associated with such anomalously warm SST in the tropical N Atlantic (Marengo *et al.*, 2008; Lewis *et al.*, 2011). The only region where precipitation is enhanced is in the NW part of the Amazon belonging to Venezuela, Colombia and Peru (Fig. 4).

An anomalously warm tropical S Atlantic (positive phase of the TSA) leads to the exact opposite conditions, with the ITCZ displaced anomalously far south, causing copious rainfall over NE Brazil, with weaker positive anomalies extending inland as far as the Peruvian border (Fig. 5). Another region of enhanced precipitation is located in S Brazil, associated with a southerly movement of the SACZ (Fig. 1; e.g. Doyle and Barros, 2002).

3. Selection of pollen records covering 2 ka

Within the working groups of PAGES, the "2k-Network" was initially established in 2008 to improve current understanding of temperature variability across the Earth during the last 2 ka. To collate records across the Earth for this time period systematically a set of criteria that defined the suitability of individual records was required. The principle of the criteria was to ensure, as far as possible, consistency (and therefore comparability) in the chronological control and sampling resolution of fossil pollen records (Table 2). Of the six PAGES-2k criteria within this paper we regarded criteria A (peer-reviewed publication) as the base line criterion (all sites considered are from peer-reviewed studies). However, implementation of criterion B (resolution ≤50 years) was not possible for SA because such a criteria would leave only a handful of pollen records to discuss. The sparsity of samples that meet the stringent PAGES-2k resolution criterion occurs because sedimentary archives with long time spans (>10,000 yr) are typically sampled at coarser temporal resolution. Furthermore, many lowland sites have slow sedimentation rates, which preclude high-resolution sampling. Therefore we propose a more flexible temporal resolution, depending on the identified relevance of the case study.

From the newly updated Latin American Pollen Database (LAPD, Flantua *et al.*, 2015a) we initially selected all records that cover the last 2 ka (Fig. 6). Good chronological control is required for PAGES-2k, but the youngest ages in pollen records are typically constrained by

geochronological data. An assessment of the pollen records by the authors with expertise in each SA sub-region has revealed 585 records with pollen samples within the 2ka-range (Fig. 6), of which 337 and 182 records, respectively, contain one or more geochronological date within that time period. In total, 182 studies were checked to confirm its suitability for palaeoclimate reconstruction as outlined by the PAGES-2k criteria. Records with a resolution of 200 to 300 yr are included in our discussion, while records along coastlines influenced by sea level changes were not included. Within the regional assessments, only records that fulfil more than three criteria are discussed, unless the records are considered particularly valuable for regional climate assessments.

4. Results

Regional assessments

Pollen records are discussed according to their regional and geographical settings: (i) Venezuelan Guayana highlands and uplands (Fig. 6A), (ii) Northern Andes (Fig. 6B), (iii) Central Andes (Fig. 6C), (iv) lowland Amazon Basin (Fig. 6D), (v) Southern and Southeastern Brazil (Fig. 6E), (vi) Pampean plain (Fig. 6F), and (vii) Southern Andes and Patagonia (Fig. 6G). The references to all records discussed are presented in Table 3.

Climate-vegetation interaction in the Venezuelan Guayana highlands and uplands

The study area, also known as the Gran Sabana (GS), is located in SE Venezuela between the Orinoco and Amazon basins (Fig. 6A; Huber and Febres, 2000). Huber (1995) recognized three main elevational levels on the Venezuelan Guayana: lowlands (0-500 meters above sea level, masl), uplands (500-1500 masl) and highlands (1500-3000 masl). Lowlands are absent in the GS, which is mainly characterized by a continuous upland peneplain spiked with isolated highlands (table-mountains, ‘tepuis’). The GS highlands are part of the so-called Pantepui phytogeographical province, which is characterized by unique biodiversity and endemism patterns, encompassing all the tepui summits above 1500 masl (Huber, 1994; (Berry *et al.*, 1995). The tepuian vegetation is characterized by a mosaic of bare rock, pioneer vegetation, tepuian forests, herbaceous formations and shrublands (Huber, 1995b). Additional background information is provided in the Supplementary Information.

In the GS, 22 pollen records cover the last 2 ka. There are 4 records with a chronology based on one control point and an additional 10 records from which most, or all, control points lie outside 2 ka. Three potentially suitable records originate from the highlands, Eruoda PATAM6-A07, Churí Chim-2 and Apakará PATAM9-A07, and only 1 is found in the uplands, Laguna Encantada PATAM4-D07 peatland (Fig. 7A; Table 3). Of the 3 records of the highlands, just Eruoda provides sufficiently high resolution to explore the objectives proposed here. However, only Churi Chim-2 and Apakará contain several age control points within the last 2 ka, and Laguna Encantada presents a relatively low sampling resolution of 200 to 300 yr.

The criteria for chronological control excluded some of the most relevant work for the research questions posed by this paper. For example, the vegetation at the Eruoda summit has persisted unchanged during the last ~2.5 ka. This constancy can be extended to all the tepuian summits studied so far during the last 6 ka (except Churí). Equally of high importance is the Urué record in the uplands, which does not meet the dating control constraints but the sampling resolution is high enough to provide important insights into the vegetation-climate dynamics during the last 2 ka, and will be therefore be presented here.

The Eruoda summit represents an important reference to which almost all the tepuian summits vegetation dynamics can be compared (Fig. 7B). Based on the absence of human activities in these summits, it can be assumed that the vegetation dynamics observed in the fossil records are fully climate driven and therefore valuable for LOTRED-SA. In general, these summits are insensitive to temperature change (for 2 ka), whereas moisture variations potentially may cause small internal reorganisations of plant associations although these shifts are considered to be of minor ecological significance. Shifting river courses are considered to influence local vegetation patterns through the lateral movement of gallery forests in landscapes (Rull, 2005a; b).

The Urué sequence spans the last 1.6 ka and records the vegetation dynamics after an important fire event dated ~1.6-1.8 ka. Three main vegetation stages were reported coeval with high charcoal abundances at the bottom of the sequence, corresponding to plant communities' transitions from open secondary forest to fern-dominated associations transitional to savanna. Savannas were fully established around 0.9 ka, coinciding with the beginning of a phase of lower charcoal values, and continued as the dominant plant association until present-day. Savannas were accompanied by *Mauritia flexuosa* palm

swamps ('morichales') that established a phase that was likely more humid. These palm swamps greatly varied in extent through time, showing a parallel between the lowest palm abundance and two drought intervals' occurrence. These two drought intervals were centered during the 0.65-0.55 ka and 0.15-0.05 ka coeval to the Little Ice Age (LIA) signal observed in the Venezuelan Andes (Rull *et al.*, 1987; Rull and Schubert, 1989; Polissar *et al.*, 2006). Generally, the vegetation dynamics recorded so far in the Venezuelan Guayana uplands have shown a higher sensitivity to changes in the available moisture than to potential shifts in the average temperatures. The last 2 ka have been mainly characterised by vegetation change at a local scale.

Climate-vegetation interaction in the Northern Andes

The region of the N Andes consists in political terms of Colombia, Ecuador and Venezuela and includes a wide range of different ecoregions (Fig. 6B). Sharing both the Caribbean and the Pacific coastline and various climate influences, Colombia has a unique pattern of different ecosystems shared with neighbouring countries. Pollen records are found throughout a wide range of biomes and elevations (Flantua *et al.*, 2015a), from the tropical rainforest and mangroves along the coast to the high Andean 'páramos'. The complex formation of the Andes with the three mountain ridges characterizes this region with numerous valleys and watersheds.

A total of 64 records are available that present pollen data within the last 2 ka. Unfortunately, 14 were presented in publications without a peer-review procedure or presented only as a summary diagram (7 records with four positive criteria). An additional 5 records, which fulfilled all criteria, suggested human presence from before 2 ka, and were therefore excluded for climate reconstructions. From the remaining records, only 4 lakes lack human interference during the last 2 ka. The others describe human indicators over limited periods of time and are considered valuable for PAGES-2k purposes (Table 3).

<u>Lake Valencia</u> (Fig. 6B and Fig. 8), is represented by three cores with varying quality in chronology and resolution. The last 2 ka are characterised by a decline of forest cover, attaining the lowest values of the Holocene, at the expense of savannas. Aquatic proxies indicate declining lake levels and increasing nutrient input, a trend that accelerated during the last 0.5 ka, when human activities were more intense around the lake. Considering the entire

Lateglacial-Holocene record, the Lake Valencia catchment has shown to be more sensitive to moisture variations than to temperature, as known from tropical lowlands.

In the Andean region, changes of the altitudinal position of the upper forest line (UFL) are instrumental in reconstructing temperature changes. This ecotone is defined as the highest elevation contour of continuous forest and marks the boundary between the forest and high Andean páramo biome (Moscol-Olivera and Hooghiemstra, 2010; Groot *et al.*, 2013). The Andean sites in Venezuela and Colombia show indications of colder climates by decreased arboreal pollen at higher elevations. In the Venezuelan Andes, the only available pollen record is Piedras Blancas. There is no indication of human activity; hence changes should be attributed mostly to climatic shifts, notably temperature and moisture. Expansion of superpáramo vegetation suggests a response to the warm and moist Medieval Climate Anomaly (MCA, ~ 1.15-0.65 ka), while a period of scarce vegetation might be related to the LIA (~ 0.6-0.1 ka) (Ledru *et al.*, 2013a). The absence of tree pollen in several samples indicates significantly depressed UFL in comparison to today.

Along the transitional zone between savanna and tropical rainforest in the E Colombian savannas, three pollen records fulfil at least three criteria. Since 2 ka gradual increase in savanna vegetation is observed, suggesting a period of progressively drier conditions, e.g. Loma Linda and Las Margaritas). However, the expanding *Mauritia* palm forest observed in several records is considered to reflect increased local water availability and precipitation (Fig. 8B), and/or human impact (Behling and Hooghiemstra, 1998, 1999; Rull and Montoya, 2014).

Along the N Andean Pacific slopes, Jotaordó, El Caimito, Guandal and Piusbi document vegetation changes related to the precipitation regime in the C and S Chocó biogeographic region. Settings differ, as the first is located in a broad river valley with a meandering drainage system while El Caimito and Guandal are located in the coastal plain receiving signals from shifting mangrove forests. These shifts were considered not to be climate related but explained by tectonic events in the region and/or dynamic shifts of the river deposition patterns. Frequent erosion events, various seismic shifts and disturbance indicators from mixed origin during the last 2 ka hinder consistent conclusions for the region. Changes in vegetation composition around 0.65 ka were assigned in El Caimito to reduced flooding and possible human intervention, while similar changes at Jotaordó were ascribed to

endogenous dynamics. Only the multi-proxy approach of El Caimito suggests a possible relationship between periods of higher riverine dynamics and the frequency of long term ENSO variability. Within this region, *Cecropia* is used as natural disturbance indicator due to fluvial-marine dynamics, while in the other Colombian regions this fast-growing species is considered characteristic of human interference; both settings have disturbance as a common factor.

In the Colombian Andes there are no undisturbed pollen records during the last 2 ka suitable for climate reconstructions. Before the human disturbances, the La Cocha-1 record in the far S of Colombia (Fig. 8B) indicated generally wetter conditions similar to the N Ecuadorian pollen records of Guandera-G15 and Guandera-G8. A different kind of index to highlight vegetation-climate interaction was used in the E Ecuadorian Andes at Papallacta PA1-08. Established to characterize the SASM and ENSO, the index interprets cloud transported arboreal pollen grains and Poaceae as a proxy for upslope cloud convection. Supported by a high resolution (~15 yr), a high frequency of dry and humid episodes is detected during the last 1.1 ka. In this alternation of convective activity, the MCA, LIA and current warm period are considered detectable.

In S Ecuador 4 pollen records suitable for PAGES-2k purposes are found within a relatively small sub-region. Tres Lagunas suggests a cold phase, possibly the LIA, as one of several warm and cold phases detected during the last 2 ka (Fig. 8B). At Laguna Zurita, the decrease of *Isoëtes* was considered an indication of increased precipitation after ~ 1.2 ka, observed similarly in other fossil pollen records in the C Peruvian Andes. On the other hand, chemical analyses from the same core suggested drier conditions during the last millennium, confirmed by a different set of palaeoclimatic records. Unknown human interference in the last millennium could be related to these divergent patterns, as the nearby ECSF Refugio and Laguna Daniel Álvarez detected *Zea mays* around 0.8 ka and 1.4 ka, respectively.

Climate-vegetation interaction in the Central Andes

The C Andes includes the high elevation plateau of the Altiplano, above 3000 masl, in S Peru, Bolivia and N Chile (Fig. 6C). The Altiplano is an area of internal drainage within the Andes that contains multiple peaks over 5000 masl. The vegetation of the Altiplano is characterized

by different grassland types, collectively known as 'puna' (Kuentz *et al.*, 2007). Within the grassland matrix are patches of woodland dominated by trees of the genus *Polylepis* (Fjeldså and Kessler, 1996). To the E and W of the Altiplano are the steep flanks of the Andes.

In total 57 pollen records covering the last 2 ka were identified from the Altiplano in Peru and Bolivia. Only 4 of the Altiplano records met all PAGES-2k criteria: (i) Cerro Llamoca, (ii) Marcacocha, (iii) Chicha Soras, and (iv) Pacucha (Fig. 9A; Table 3). From the surrounding regions 2 additional records are also considered here because of their importance and fit to the PAGES-2k criteria: (i) Consuelo on the E Andean flank, at mid-elevation (1370 masl), and (ii) Urpi Cocha on the Pacific coast at sea-level (within the archaeological site of Pachacmac). Of the seven sites considered in this review only 2 records (Cerro Llamoca and Consuelo) show no human interference, while the others indicate human impact during different periods of time throughout the last 2 ka.

Discerning a climate signal from the pollen records of the last 2 ka in the C Andes is a challenge due to the long legacy of human occupation and landscape modification (Bennett, 1946; Dillehay *et al.*, 2005; Silverman, 2008). However, some idea of vegetation-climate relationships can be gained from modern pollen studies within the puna, e.g. Kuentz *et al.* (2007) use the ratio of Poaceae:Asteraceae (Coropuna), or Schittek *et al.* (2015) focus on the abundance of Poaceae (Cerro Llamoca) as an indicator of moisture availability. In the other records, where there is no direct relationship between vegetation and climate discernible, some authors look at the relationship between the pollen records and other indicators to disentangle climate and human induced vegetation change; such as independent evidence of farming activity (e.g. oribatid mites), or association with archaeological evidence for abandonment/occupation (Chepstow-Lusty, 2011).

The two records considered here that are purported to have no local human impact (Cerro Llamoca and Consuelo) provide the best opportunity of extracting a clear insight into past climatic change in the C Andes during the last 2 ka. The record from Cerro Llamoca indicates a succession of dry and moist episodes (Fig. 9B). After 0.5 ka sediments are composed of re-deposited and eroded material and consequently interpretation of the latter half of the record is difficult. In contrast little compositional change is evident in the Consuelo record, with the most significant variance during the last 2 ka being a rise in *Cecropia* sp. pollen after 1 ka. *Cecropia* pollen is typically interpreted as an indicator of disturbance (Bush and Rivera, 2001) and therefore, in the absence of humans signal, the rise

in *Cecropia* could be interpreted as an elevated level of natural disturbance. The switch to very dry conditions at Cerro Llamoca in the western Andean cordillera and the rise in *Cecropia* at Consuelo on the E Andean flank are broadly coincident (~ 0.85 ka); however, it is not possible to say if this pattern results from a common climatic mechanism.

Archaeological evidence from Chicha-Soras does not show any evidence of human occupation of the valley between ~ 1.9 ka and ~ 1.4 ka. Between 1.4 and 1 ka and between 1 and 0.65 ka, high abundance of Chenopodiaceae/Amaranthaceae (Cheno/Am) could be interpreted as either indicating arid conditions or expansion of *quinoa* crops (Ledru *et al.*, 2013b). However, a drop in charcoal fragments (fire activity) coupled with the absence of archaeological evidence (~1.9-1.4 ka), suggests that people abandon the valley during 1.5-0.5 ka and, consequently, that the aridity signal from the pollen could be interpreted as a climatic one.

Some climate information has been inferred from the four remaining sites (Marcacocha, Pacucha, Nevado Coropuna and Urpi Cocha) despite the strong human influence on the vegetation. At Nevado Coropuna humid conditions persisted until a short dry episode occurred 0.97-0.82 ka (Fig. 9B). During the last 2 ka at Marcacocha successive peaks in Cyperaceae pollen have been interpreted as indicative of three periods of elevated aridity while elevated *Plantago* at ~1.9 ka is suggested to indicate cooler conditions, and *Alnus* at ~1-0.5 ka could indicate warmer and drier conditions; although discerning the climate signal related to *Alnus* is difficult due to its utilisation in agro-forestry practices (Chepstow-Lusty and Jonsson, 2000). At Pacucha and Urpi Kocha significant changes to the pollen assemblage in the last 2 ka are attributed to human activity rather than climate. Although the pollen records are likely to be somewhat obscured by the agricultural activities and irrigation of the crops, all high elevation records with a moisture balance signal suggest generally drier conductions occurred in the C Andes between 1.2 and 0.7 ka when compared with the rest of the last 2 ka.

Generally the pollen records from the Altiplano tend to show a greater sensitivity to precipitation, rather than temperature. The greater sensitivity to precipitation is because moisture availability is in most areas the limiting factor for both vegetation and human occupation. However, human occupation provides hints on changes in temperature: (i) Marcacocha when the sudden stop in agricultural activities is attributed to colder

temperatures, and (ii) at Coropuna when the increase of human occupation (expansion of Inca culture) at higher elevation shows that there was no glacier and warmer temperatures.

Climate-vegetation interaction in the lowland Amazon basin

For the purpose of this review, the lowland Amazon basin constitutes those regions of the Amazon drainage < 500 masl and extends to the lowland Guianas (Fig. 6D). This encompasses the evergreen rainforest, which covers most of Amazonia, as well as the S transitional/seasonally-dry tropical forests located in NE Bolivia and S Rondônia, N Mato Grosso and N Para State, Brazil. It also includes the Llanos de Moxos savannas of NE Bolivia, the ecotonal rainforest-savanna areas of N Roraima State, Brazil, and extends to the coastal swamps/grasslands of N Brazil and French Guiana.

In total 42 published pollen records that cover the last 2 ka were identified from the lowland Amazon basin. By applying the dating constraints of the PAGES-2k criteria, the majority of pollen records from the Amazon basin are discounted from any analysis of climate-vegetation interaction for the past 2 ka. Only 5 records complied with all four of the criteria and 11 records met with three criteria (Fig. 10A; Table 3;). One of these records, lake La Gaiba, is situated just outside the Amazon basin, in the Pantanal region of central Brazil/SE Bolivia. However, the record and its hydrological catchment reflect Holocene precipitation in the S Amazon basin (Whitney *et al.*, 2011), and therefore was included as part of this review.

Lake Quistococha in the NE Peruvian Amazon is surrounded by *Mauritia flexuosa*-dominated palm swamp. Vegetation has undergone several significant species compositional changes over the past 2 ka. The broad pattern of vegetation change was from *Cecropia*-dominated riverine forest at ~2.2 ka, to abundant Cyperaceae and floating grasses/ferns and the commencement of peat formation ~2.1 ka, then to seasonally-inundated riverine forest, with abundant Moraceae and Myrtaceae from ~1.9 ka, and finally, the development of closed-canopy, *Mauritia*-dominated swamp from ~1 ka until present. Superimposed on this broad pattern of change were rapid, centennial-scale shifts in forest composition and degree of openness. However, these rapid shifts were attributed by the authors to hydrological dynamics, rather than climate change or human impact.

Lake Werth belongs to a collection of sites (also Gentry, Vargas and Parker) in the

'Madre de Díos' region of the SE Peruvian Amazon. The lake formed ~3.4 ka and records continuous evergreen rainforest throughout, with little evidence of burning. The records from the surrounding three lakes concur, suggesting that, regionally, rainforest (and climate) has been stable over the last 2 ka.

Laguna Granja is located on the edge of the Pre-Cambrian Shield in NE Bolivia. The record has a maximum age of 6 ka and indicates that savanna characterised the landscape from 6 ka. This is in agreement with a regional scale reconstruction from the much larger Lake Orícore (not shown, Carson *et al.*, 2014), which is located < 20 km away from Granja, and shows climate-driven expansion of evergreen rainforest in this region between ~2 and 1.7 ka. However, forest expansion does not occur on the Granja site until 0.5 ka. The distribution of forest vs. savanna around Granja was shown to be heavily influenced by human land use between 2.5 and 0.5 ka (Carson *et al.*, 2014; Carson *et al.*, 2015), therefore, it is not suitable for analysis of naturally-driven vegetation dynamics.

The Fazenda Cigana record is in the savanna-gallery forest mosaic landscape in the N Brazilian Amazon. The core was taken as one of a pair, along with the Terra Indígena Aningal record, which was cored from the same *Mauritia* swamp. The pollen records are dominated by *Mauritia* throughout, attributed to continuously wet climate in this region in the late Holocene. There are however centennial-scale periods of gallery forest reduction and grassland expansion, accompanied by increased charcoal concentrations. Da Silva Meneses *et al.* (2013) inferred that these periods of high burning were anthropogenic in origin, and compare them to modern day prescribed burning practices used by indigenous people in the northern Amazon to maintain an open savanna landscape. Despite the potential human interference, these records demonstrate natural stability of the forest-savanna ecotone over the last 1.5 ka in this particular part of the N Amazon.

The French Guiana K-VIII record was taken within a landscape of pre-Columbian mounded agricultural fields, with the principal aim of investigating ancient human land use associated with these earthworks on a local scale. From this earliest part of the record, the fossil pollen spectra indicate seasonally-inundated savanna, dominated by Cyperaceae and Marantaceae until 0.8 ka when human inference is detected. In the post-European period after ~0.5 ka, charcoal abundance increases, probably reflecting more intensive use of fire by colonial populations.

Climate-vegetation interaction in Southern and Southeastern Brazil

The landscape in S and SE Brazil is diverse from lowlands to high mountains, from subtropical regions with frost to tropical regions. Due to this heterogeneity distinct vegetation types occur throughout the region. The vegetation in S-SE Brazil includes forest ecosystems such as the tropical Atlantic rainforest, Araucaria forest, semi-deciduous forest, 'Cerrado' (savanna woodland) and different grassland ecosystems such as 'Campos' and 'Campos de Altitude' (high elevation grassland) (Fig. 6E). There is a gradient from no or short dry seasons in the coastal lowland up to 6 months in the hinterland (northernmost part of the highland in SE Brazil), marking the vegetational gradient from moist Atlantic rainforest to semi-deciduous forest and to Cerrado. Additional background information is provided in the Supplementary Information.

There are approximately 50 pollen records known from S-SE Brazil, but many sites have not been published in peer-reviewed journals and were therefore not considered. Unfortunately, the 2 records that agree with all criteria show human interference (Table 3). Therefore a general overview of climate-vegetation interaction from the region is presented, considering 7 records that fulfil some of the criteria (Table 3, Fig.11A).

In S Brazil pollen records indicate vegetational changes that reflect a change from relatively dry climate during early and mid Holocene to wetter conditions after about 4.3 ka, and in particular after 1.1 ka (Fig.11B). Increasing moisture is clearly indicated on the S Brazilian highlands by the expansion of *Araucaria* forests in form of gallery forests along rivers and a pronounced expansion of *Araucaria* forest into the Campos after about 1.1 ka (e.g. Cambara do Sul and Rincâo das Cabritas). The expansion of gallery forests at similar time periods (5.2 and 1.6 ka, respectively) is also recorded in the southernmost lowland in S Brazil by the São Francisco de Assis record. Study sites that reflect changes in the Atlantic rainforest area indicate an expansion during the Holocene where overall wetter conditions prevailed compared to highland and southernmost lowland areas, e.g. Ciama 2 (Fig.11B).

In contrast to other sites and regions, a relative humid and warm phase during the LIA is interfered from the high resolution Cambara do Sul record as an expansion of *Weinmannia* in the *Araucaria* forest is observed. In SE Brazil the Lago do Pires and Lagoa Nova record indicate that a dense and closed semi-deciduous forest existed in the region only during the late Holocene period under the current climatic conditions with a ~ 3 month dry season. In the

mountains of SE Brazil (e.g. Serra dos Orgâos record) a reduction of Campos de Altitude occurred 0.9 ka indicating a change to wetter conditions that is broadly coeval with a similar trend in the Lago do Pires record (Fig.11B).

Climate-vegetation interaction in Pampean plain

This region extends E of the Andes, between 30 and 40°S (Fig. 6F) and is characterized by aeolian landforms marking the climatic gradient of the landscape. The natural vegetation of the Pampa is a tree-less grassland, dominated by Poaceae in terms of both species number and abundance. Asteraceae shrubs (e.g. *Baccharis* and *Eupatorium*) are present locally in S Pampa, Cyperaceae characterize aquatic and wet-ground communities of temporary flooded depressions and shallow lakes mainly from the E Pampa, and Chenopodiaceae characterize edaphic communities such as salt marshes and alkaline flat areas (Tonello and Prieto, 2008). Additional background information is provided in the Supplementary Information. In total 9 pollen records were assessed for the last 2 ka. All four dating criteria were met in one record only (Lonkoy) and three criteria were matched at Sauce Grande (Table 3). The pollen record of site Hinojales-San Leoncio does not fulfil the four dating criteria, however the record shows important hydrological signals for the last 2 ka and is therefore briefly discussed.

Aquatic ecosystems are considered sensitive to climatic and/or hydrological variations, and exhibit frequent fluctuations in their water level and extension, leaving flooded and/or exposed plains. Pollen together with non-pollen palynomorphs and plant macrofossil analysis present similar trends in SE Pampa that support climate to be a regional trigger of change (Stutz *et al.*, 2015). From 2 to 0.7-0.4 ka an unstable regional environment with drier climatic conditions than present is inferred from the region (Fig. 12B), based on halophyte plant communities (Chenopodiaceae) surrounding the lakes whereas *Chara* and other aquatic plants (e.g. *Myriophyllum*, *Potamogeton*) characterized the water bodies. Towards ~0.5 ka vegetation changed to Cyperaceae dominance and aquatic plant composition similar to modern associations. Thus, turbid conditions with higher water level and/or extension of surface lakes under more stable environmental conditions are inferred. These support humid conditions similar to present with a noticeable increase of precipitation after 0.4 ka, indicated by high Cyperaceae abundances. However, a integrative multi-proxy approach allow inferring stable conditions and higher salinity values between 1.9 and 0.9 ka and periods of water level

fluctuations after 0.9 ka, with high water levels between 0.66 and 0.27 ka. These changes may have been caused by fluctuations in precipitation (Fontana, 2005).

Climate-vegetation interaction in the Southern Andes and Patagonia

The study area comprises the S Andes, which includes subtropical and temperate regions (22°-56°S) on both sides of the Andes, including Patagonia (40°-56°S) which extends from the Andes eastwards to the Atlantic Ocean (Fig. 6G). The region has different geomorphological settings associated with glacial, volcanic and tectonic activities. Vegetation associations reflect the W-E precipitation gradient from the wet *Nothofagus* forest to the dry grass and shrub steppe towards the Atlantic coast. The S-N gradient along the Andes ranges from the *Nothofagus* temperate forest in the austral region to the *Nothofagus-Astrocedrus* forest, sclerophyllous forest and xerophytic woodland in the C region. In the northernmost end of the latitudinal gradient, the vegetation is adapted to extremely arid conditions characterized by small and dwarf shrubs and scarce cover (See Supplementary Information for additional descriptions).

In this region, there are 48 pollen records that cover the last 2 ka with at least one chronological control point during this period. Of these, the 19 records that fulfil PAGES-2k criteria are mostly concentrated in the temperate forests, while only few originate from xerophytic shrub steppe (1 record), subtropical forest - sclerophyllous forest (2 records) and grass steppe (4 records) (Table 3; Fig. 13A).

There are three sites at the far south of Patagonia: the 'Tierra del Fuego's Onamonte mire (54°S) located at the *Nothofagus* forest-grass steppe ecotone shows a gradual *Nothofagus* forest development between 1.5-0.5 ka followed by a major forest development up to the present, reflecting increased precipitation (Fig.13B). Puerto Harberton (55°S) at the mixed *Nothofagus betuloides–N. pumilio* forest shows *Nothofagus* dominance during the 2 ka, whereas the *Ericaceae* increase during the last 1 ka suggests local decrease of the water table. Similarly, at Valle de Andorra (54°S) in *Nothofagus pumilio* forest, *Empetrum*/Ericaceae fluctuations reflect changing water tables.

In S Patagonia (52-51°S) along E Andes, there are several sites at or near the forest-steppe ecotone. Of these ecotonal sites, Rio Rubens (52°S) shows a closed *Nothofagus* forest until 0.4 ka when European impact starts (Fig.13B). Similary, Lago Cipreses (51°S) and Lago

Guanaco (51°S) show dominance of *Nothofagus* forest, but with increase of non-arboreal pollen (and decrease of *Nothofagus*) associated with a reduction of precipitation induced by the Southern Westerly Wind Belt (SWWB) and the SAM phases. Furthermore, changes associated to dry/warm climate conditions appear to synchronize with N Hemispheric events such as the Industrial Revolution, MCA, Roman Warm Period and Late Bronze Age Warm Period (Moreno *et al.*, 2014), that alternate with wet/cool phases. Cerro Frias (50°S) shows open forest from 2.0-0.9 ka, followed by prevalent grass steppe that is punctuated by an increase in *Nothofagus* at 0.016 ka. Estimates of annual precipitation suggest similar or higher values than modern between 2-1 ka, lower values between 0.9-0.015 ka, followed by similar-to-modern precipitation in the last 0.015 ka. Currently located in mixed deciduous *Nothofagus* forest, the Peninsula Avellaneda Bajo (50°S) records an open forest from 2 ka, of which large expanses were replaced by grass steppe between 0.4-0.2 ka, associated with a decline in precipitation.

In C Patagonia (47-44°S) pollen records are located at the E of Andes (Fig.13A). At Parque Nacional Perito Moreno (47°S) a shrub-steppe expansion (Asteraceae and *Embothrium* dominance) suggests lower precipitation values between 1.2 and 0.25 ka compared to previous values, after which an increase in grass-steppe occurs due to higher moisture availability (Fig. 13B). However, the Mallin Pollux (45°S) record indicates an open canopy prior to 1.5 ka followed by a *Nothofagus* forest expansion associated to precipitation increase. Mallín El Embudo (44°S) within *Nothofagus* deciduous forest, shows unvarying forest composition during the last 2 ka. Located in the same valley, the Lago Shaman (44°S) record (*Nothofagus* forest-steppe ecotone) shows a more diverse pattern throughout the last 2 ka, with a forest retraction at ~1.7 ka, followed by an expansion around 1.5-1.3 ka and a major forest development around 0.5 ka. The forest decrease during the last 0.2 ka is associated to human intervention.

In N Patagonia (44-38°S), Lago Mosquito (42°S) is the only record in E Andes and it is located at the transition between *Austrocedrus* woodland and shrubland-steppe. The record shows an open *Nothofagus-Austrocedrus* forest with elements of steppe and grassland elements between 2-1.4 ka, changing to higher *Nothofagus* forest dominance, which is attributed to wetter conditions (Fig. 13B). From 0.225 ka to the present, *Nothofagus* shows a sharp decrease and *Cupressaceae* increases, together with rising introduced species, e.g.

Rumex and *Pinus*. At the same latitude, Lago Lepué (42°S) located in the Isla Grande de Chiloé and surrounded by evergreen rain forest, shows dominance of *Nothofagus* during the last 6 ka with an important reversal between 2-0.8 ka. This suggests a lower precipitation than before and after 0.8 ka, shown by an increase of *Weinmannia* and *Isoetes*. Lago Pichilafquen (41°S) record, under the domain of the SWWB and influenced by the Subtropical Pacific Anticyclone in summer, shows a series of warm/dry and cold/wet phases for the last 2 ka (Fig. 13B). These phases are inferred by the varying abundances of *Nothofagus* and *Eucryphia*/*Caldcluvia* and Poaceae. The last centuries are characterized by human intervention. At the temperate-subtropical transition, Laguna San Pedro (38°S) record shows dry-warm phases which were associated with the MCA period. Cold and wet conditions, inferred by the relation between *Nothofagus* and Poaceae, and changes in the depositional time, prevailed during the LIA, possibly related to El Niño and La Niña influencing these wet and dry phases respectively (Fig. 5).

To the N (westward Andes), the lake Aculeo record (34°S) shows dominance of Poaceae suggesting relatively steady conditions during the last 2 ka with exception of last 0.1 ka, when a trend towards warmer conditions or human disturbance is reflected by increase in Chenopodiaceae (Fig. 13B). Interestingly, the sedimentary record shows a series of turbidite layers associated with major ENSO frequency between 1.8-1.3 ka and 0.7-0.3 ka (Jenny *et al.*, 2002). The Palo Colorado (32°S) record shows dominance of Myrtaceae associated with wet conditions during last 2 ka alterating with several dry pulses. A major dry peak at 0.4 ka may be related to climate and/or human activity. Similarly at E Andes, Abra del Infiernillo (26°S) shows an increase in moisture between 2-0.75 ka inferred from Juncaceae, Poaceae, Cyperaceae pollen and fern spores; and a change to dry climatic conditions similar than modern from 0.75 ka on.

Lago Potrok Aike and Lago Azul (both 52°S) show a dominance of Poaceae since 2 ka, with long-distance transported pollen of *Nothofagus*. At Potrok Aike, reconstructed annual precipitation based on transfer function indicates rising values during the last 2 ka (Fig. 13B). Cabo Vírgenes (52°S), located at SE Patagonian grass steppe, shows a shrubland community between 1.2-0.7 ka, associated with drier conditions than at present. An increase in moisture after ~0.7 ka is indicated by Poaceae and Juncaginaceae pollen. Cabo Vírgenes CV22 shows a similar trend, with dry grass-shrub steppe between 1.05-0.6 ka, followed by a grass-dominated steppe suggesting higher moisture availability.

Indicators of human land use in 2 ka pollen records

In any past environmental change reconstruction concerning the last 2 ka, human land use must be considered as a potentially important agent of environmental change. However, where there is no direct evidence of human land use, such as cultigen pollen, distinguishing natural from anthropogenically induced burning and vegetation change can be difficult. In some cases anthropogenic deforestation and decreased moisture might result in similar signals in the pollen record and therefore complementary proxies of past environmental change can be used to support interpretations, such as Chironomids (Matthews-Bird et al., 2015; Williams et al., 2012) and geochemical records from speleothems.

There are six key aspects of fossil records (pollen and charcoal) that can be seen as indicators of past human activity, these are a: (i) decrease in forest taxa (degraded forest and deforestions) and/or forest composition, (ii) presence of crops, e.g. *Zea mays*, *Manihot esculenta*, *Phaseolus* and *Ipomoea*, (iii) presence of crop-related herbs, e.g. *Rumex*, (iv) increase of grasses/herbs, e.g. Poaceae, Cyperaceae and Asteraceae subf. Cichorioideae, (v) increase of disturbance indicators, e.g. Cheno/Am, *Cecropia*, *Vismia*, ferns and palms (including *Mauritia* and *Euterpe/Geonoma*), and (vi) elevated amount of charcoal due to anthropogenic fire (Fig.14). These indicators of human activity can be split into two classes, those that directly indicate human presence, and those from which it is indirectly inferred. *Manihot esculenta* and other crops, such as *Zea mays*, are considered direct indicators of human influence and provide clear evidence of land use. Indirect indicators, such as change in forest composition (e.g. due to deforestation) or the appearance of species known as possible disturbance indicators (e.g. *Cecropia* or *Mauritia*), need further evidence from other proxies to support any inference of past human activity. Only by looking at changes in pollen spectra in context with other evidence (e.g. from charcoal, limnological, sedimentological, or archaeological data sets) can the most probable driver of any change be suggested.

In this paper, ambiguous records with fewer proxies were not immediately discarded, but considered within the context of the other records from their wider region. Based on this, an assessment could be made as to whether an anthropogenic signal may have obscured the natural vegetation change trajectory. The moisture balance and temperature summaries for

each region (Figs. 7-13) clearly indicates when human interference obscures the climate assessment and when both climate and/or human may have influenced the pollen record.

To date, major human impact in the Venezuelan Guayana uplands has been suggested for the last 2 ka and inferred from the charcoal record, without any evidence of crops. Compared to the highlands (1500-3000 masl), the situation in the uplands (500-1500 masl) differs substantially as fire is maximally responsible for vegetation change during the last 2 ka. The Urué record shows the consequence of repeated burning upon the vegetation, preventing the recovery of pre-existing forests and allowing the appearance of a 'helechal' (fern-dominated vegetation; Huber and Riina, 1997), and finally the establishment of the savanna. The occurrence of frequent fires during the last 2 ka is a common feature of mostly all the upland records analysed so far, regardless the plant association present at each location. Synchronous with this increase in fire regime, those records that nowadays are characterised by *Mauritia* palm swamps, showed parallel a sudden appearance and establishment of *Mauritia*. Human activities have been proposed as the likely cause of this high abundance of fires, and thereby of the consequences that produced upon the landscape. In this sense, the repeated use of fires would have promoted the reduction of forests and expansion of the savanna, favouring the establishment of *Mauritia* swamps after clearing. Two records are particularly relevant regarding the human influence on the Venezuelan Guayana uplands. Lake Chonita sequence (Table 3) registered among the earliest *Mauritia* establishment coeval with a significant increase in the fire regime during a likely local wet period around 2 ka. In the southernmost boundary of the Venezuelan Guayana, El Paují (Table 3) was interpreted as potentially reflecting human activities since the mid Holocene. This location is characterised today by treeless savanna surrounded by dense rainforests that established ~1.4 ka as shown by the highest abundance of algal remains (local wet conditions) and charcoal particles (fire regime). The establishment of the present-day landscape was interpreted as mainly anthropogenically driven, with the arrival of the current inhabitants. The occurrence of a previous secondary dry forest was interpreted as the result of climate-human interplay, linking land abandonment and likely drier climate as the main responsible favouring the vegetation shift. From the Colombian savannas, human occupation is attested since the mid Holocene (Berrio *et al.*, 2002). At site Loma Linda a plausible signal of human interference in the last 2 ka is shown by increased savanna, although precipitation increase during the same period

(Behling and Hooghiemstra, 1998, 1999; Marchant *et al.*, 2001, 2002) could be interfering with that signal.

The human history in the N Andean region goes back to the Lateglacial (Van der Hammen and Correal Urrego, 1978). The high plains of the Colombian Cordilleras provided suitable conditions for human settlements since the start of the Holocene. Increasing human occupation became evident in pollen records after ~3 ka, such as Fúquene-2 and Pantano de Genagra. In several Andean diagrams, *Rumex acetocella* marked the arrival of Europeans since 0.4 ka (Bellwood, 2004; Bakker *et al.*, 2008). Before these dates, indigenous populations were scarce and their practices negligible in terms of impact, especially at high elevations sites such as Piedras Blancas in Venezuela.

In the tropical lowlands along the Pacific coast, increases in the presence of palms (mainly *Euterpe/Geonoma*), are commonly interpreted as a result from more intensive forest use, e.g. Lake Piusbi. Pollen grains from crops like *Zea mays*, *Phaseolus* and *Ipomoea* are found in Piagua (Vélez *et al.*, 2001). Human disturbance to the forest is considered indicated by high percentages of abundance of *Cecropia*, ferns and palms. Decreases in human impact during the last 2 ka has been described by sites like Pitaliton, Timbio, La Genagra, Quilichao and La Teta, as grassy vegetation (Poaceae) and *Zea mays* disappeared and forest started to recover. This vegetation change could be related to the first arrival of the Spanish 'conquistadors' (González-Carranza *et al.*, 2012), or a set of different causes (Wille and Hooghiemstra, 2000).

In the C Andes a high level of human activity, spatially variable in intensity, has been shaping the landscape for the last 2 ka. Cheno/Am and *Zea mays* generally appear in all the records in the Central Andes after 4 ka, e.g. Pacucha, Marcacocha, Chicha-Soras and Urpi Kotcha. After 2 ka, *Alnus* and agroforestry practices are observed (Marcacocha, Pacucha). When irrigation started to be developed in sites without a nearby lake as for instance ~1 ka at Coropuna, *Ambrosia* may be used as a terrace consolidator. Evidence of afforestation in two sites with high human influence (Marcacocha and Pacucha) is observed. Indeed *Alnus acuminata* is a tree planted by the Inca to stabilise landscapes (Chepstow-Lusty, 2011). At lower elevation, in the Andean forest, the last 2 ka pollen data indicate little change in woodland cover which remains high on the E Andean flank (Consuelo), and low in the west (Urpi Kocha).

Of the 42 pollen records identified from the lowland Amazon basin, 15 show evidence

of pre- and post-European land use within the last millennia. Human land use is inferred from these records from cultigen pollen grains, charcoal and forest clearance (Table 3). In some cases there is also archaeological and archaeobotanical evidence for human land use. At many of the sites occupied by native Amazonians, evidence of decreased land use shows as a decline in burning by or before 0.5 ka, probably in relation to first European contact. However, some sites, such as French Guiana VII and Granja show evidence of continued post-European land use.

In SE-S Brazil, the modern vegetation is strongly affected by the logging of forests and different agricultural land-use practices. During the last few decades large-scale afforestation of grassland by *Pinus* is seen on the highlands. Similar to SE-S Brazil, the Pampa region has a relatively short farming history, since most of the area remained as native grassland until the end of the 19th and the beginning of the 20th century (Viglizzo and Frank, 2006). Today, only around 30% of the region is covered by natural or semi-natural grassland. Pampa vegetation does not show evidence of human impact prior to European settlement at 0.4 ka. Europeans introduced several tree species (e.g. *Eucalyptus*, *Pinus*), as well as cattle (*Bow taurus* and Equus) and crops (*Triticum aestivum*, *Helianthus annuus*), but the intensive agricultural activities only began 0.05 ka (Ghersa and León, 2001). The palaeoenvironmental history of shallow lakes shows a change to more productive systems (higher mass of phytoplankton and organic matter content) during the last 0.1-0.08 ka probably due to agricultural activities. On the other hand, pollen records show an increase of pollen types associated with overgrazing (*Plantago* and/or Asteraceae Asteroideae) and exotic trees during the last 0.1 ka.

In S Andes and Patagonia, anthropogenic activities during the last century have caused a range of disturbances (e.g. fire, forest clearance, grazing, agriculture) and major vegetation changes in forest and steppe areas have occurred. There is not conclusive evidence of native human activities in the pollen records and native-fire disturbance has been long discussed. Charcoal records from the E Andes flank have not revealed fire activity associated with native populations. A probable explanation for this lack of evidence is a low density of populations associated with sporadic forest impact (Iglesias and Whitlock, 2014). In general, human activities indicators are forest decrease, presence of exotic pollen types (e.g. *Rumex*) and increase of some pollen types (e.g. Asteraceae subf. Cichoroideae, Chenopodiaceae)

associated to European presence in the region. The time of colonization varied among S Andes and Patagonian sites, but ~0.1 ka can be considered the start of European activities in Patagonia. Differences in timing of the first appearance of human indicators in pollen records could reflect European settlement dynamics, with earlier presence in more northerly sites and later more isolated areas (in the south of continent). The first human indicator is recorded at Rio Rubens (52°S) with the appearance of the European weed pollen *Rumex acetosella*-type appearance in the early European era (~0.3 ka).

5. Discussion of the regional assessments

General observations for 2 ka pollen compilations

This review reveals that those records with better dating resolution in the late Holocene are often from cores that span a shorter time period, while longer temporal records have less well resolved Holocene chronologies. This likely reflects: (i) the need to spread limited numbers of radiocarbon dates in order to provide robust age models for these deeper time records, (ii) the greater interest of previous researchers in potential large-scale palaeovegetation changes, driven by glacial-interglacial climate cycles, and other significant periods of climatic change, such as the early-to-mid Holocene drought, and (iii) the low sedimentation rate during the last millennia in certain regions, e.g. lowland Amazonia. Furthermore strong anthropogenic interference during the last 2 ka complicates the interpretation of many records from a palaeoclimate perspective, but with expert knowledge climate signals can be filtered. Additional difficulties arise from the ‘one topic focus’ of many studies and authors do not often present the full range of data in their publications that are required for a comprehensive reconstruction of vegetation, climate and human impacts over the last 2 ka.

Venezuelan Guayana highlands and uplands

For the Venezuelan Guayana region here we discuss the highland and upland areas separately due to the significant differences in physiographical, climatic and ecological features, as well as in the intensity of human pressure on their respective ecosystems.

Highlands are virtually pristine and, according to the palaeoecological records, they have remained in this state at least since the early Holocene. Therefore, climate has been the

main driver of change. Palaeoecological records for the last 2 ka are scarce and generally of low resolution but a common trait is the ecological stability as expressed in the vegetation constancy. The following hypotheses have been suggested to explain these observations: (i) environmental changes were insufficient to affect the highland vegetation, (ii) the high precipitation and relative humidity of the Chimantá summits (Briceño *et al.*, 1990) have buffered climatic changes, and (iii) the study sites are unsuitable for recording significant vegetation changes because there are no vegetation ecotones nearby (Rull, 2015). Further work is needed focused test these hypothese. So far, palaeoecological fieldwork atop the tepuis has been carried out in an exploratory, non-systematic manner due to the remoteness of the tepuis, and the logistic and administrative constraints (Rull *et al.*, 2008). In the LOTRED-SA framework, the issue of vegetation constancy emerges as a priority and should be addressed properly by finding suitable coring sites to be analysed with high-resolution multiproxy tools. The use of physical-chemical proxies independent from pollen and spores is essential to record climatic shifts. Lake sediments would be excellent for this purpose but, unfortunately, lakes are absent on tepui summits, the only permanent lake known so far is Lake Gladys atop the Roraima tepui, of which age and origin remain unknown (Safont *et al.*, 2014). At present, the analysis of the Apakará PATAM9-A07 core, which meet the PAGES-2k criteria, is in progress. The preliminary study of this core showed the main Holocene vegetation trends at millennial resolution (Rull *et al.*, 2011), and the current analysis is being performed at multidecadal resolution. A new core obtained in the Uei summit (PATAM8-A07; not included in the Chimantá massif) containing a decadal record for the last 2 ka is also being currently analysed (Safont, *et al.*, submitted).

In the GS uplands, the situation is very different and the main driver of ecological change is fire caused by humans. This does not mean that climatic shifts have been absent or that they have not affected the vegetation but the action of anthropogenic fires overwhelms and obscures the action of climate (Montoya and Rull, 2011). So far, regional palaeoclimatic trends, based on independent data obtained from the Cariaco basin (~680 km to the north; González *et al.*, 2008), have been used as a reference for past climate change on the GS uplands (Rull *et al.*, 2013). Unfortunately, a more local independent palaeoclimatic record for the GS uplands is still lacking not only for the last 2 ka but also for the entire Holocene. Another limitation is that most palaeoecological records available for the GS uplands are from its southern sector, which is the lowermost part of the peneplains, and has a different climate

and vegetation regime as compared to the northern sector. Some records from the northern sector are available that fit with the chronological PAGES-2k requirements (Leal *et al.*, 2011) but only summary diagrams are provided in peer-review publications and therefore they cannot be used in this reconstruction. The decadal to multidecadal analysis of a new core obtained in Kamoirán (PATAM10-A07), in the northern GS uplands, is in progress.

It should be stressed that the last 2 ka seem to have been critical for the ecological history of the GS uplands and its detailed knowledge may be crucial to understand the origin of the present-day landscape. The reason is intimately linked to the temporal patterns of human impact using fire. The date of arrival of the current indigenous culture (Pemón) at GS is still unknown. Based mainly on historical documents, it has been postulated that this culture settled in GS ~0.6 to 0.3 ka, coming from Guyana or Brazil (Thomas, 1982; Colson, 1985, Huber, 1995a). But these could be considered minimal ages, as recent palaeoecological studies suggest that human groups with landscape management practices similar to the Pemón people would have been present in the GS since ~2 ka (Montoya and Rull, 2011; Montoya *et al.*, 2011a). Before that time, the GS landscape was different from the present, including larger extents of forested areas since the late-glacial (22-11.7 ka) and the absence of *Mauritia* palm swamps until ~2 ka. The same time period seems to have been a landmark in Neotropical history for similar reasons as Rull and Montoya (2014) showed a generalized increase of *Mauritia* pollen abundances in northern South America during the last 2 ka.

Given the northern position of the Venezuelan Guyana, the vegetation responses studied have been normally related to ENSO and ITCZ movements. These two main drivers are represented by the Niño 3.4, AMO, IPO and TNA modes, which are indeed the exerting the main influence in the area as shown in Figs. 2-5 (especially with respect to temperature). The lack of a significant influence of AMO on precipitation in the region is surprising. It is worthwhile to compare the climatic inferences made through fossil pollen records with the climate modes' effect on the area. Fossil pollen records have suggested available moisture (or precipitation/evapotranspiration ratio: P/E) as the main climatic driver to take into account for vegetation responses. However, these inferences are based on very local spatial scale proxies (e.g. algal remains) and P/E is a complex process that relies on a wide range of factors, including both temperature and precipitation (Van Boxel *et al.*, 2013). Its interpretation in the fossil record is therefore complex and sometimes ambiguous. On the other hand, both Pacific and Atlantic climate modes appear to have a potentially large effect on both temperature and

precipitation in the region. Such findings suggest that the variations of P/E inferred from the fossil record could be caused by either of these two factors, or by both. Additional higher resolution multi-proxy analyses should shed a light on previously undetected modes in the region as well as disentangling the combined effect of several forcing factors. Nevertheless, upland records have been interpreted as primarily human-driven vegetation responses, so for the last 2 ka the climatic conclusions are constrained. Highland records have been described as an example of constancy, even insensitive to temperature change during the last 2 ka, which could confirm that the temperature variability related to climate modes in this region has been of a lesser magnitude than those required to cross the vegetation tolerance ranges. Alternatively the intrinsic characteristics of the sites studied so far, has inhibited detecting any change.

Northern Andes

Study sites without human presence have been not identified with certainty within the northern Andean region, inhibiting detection of a clear signal of climate tendencies in the last 2 ka. Drier conditions prevailed in Colombian savanna lowlands, although the increased presence of *Mauritia* suggests either increased humidity and/or human influence. Along the Pacific coast, generally wetter conditions prevailed (Fig. 8B), but tectonic events might be masking clear patterns. Interpretation of some records should be made with care due to the noisiness of the data. Furthermore, due to the geomorphological complexity of the landscape and its latitudinal characteristics, this region is prone to a combination of strongly overlapping climate signals within and between years (Figs. 2-5; Marchant *et al.*, 2001).

For the northern Andes the position of the ITCZ and the ENSO phenomenon are most important in driving changes in precipitation as clearly illustrated in the La Cocha record Figs. 4 and 5). The altitudinal gradient in temperature is most importantly modulated by ENSO and the TNA. This is shown by the increased temperature variability around 5 ka when the ENSO signal starts (Figs. 2 and 3). The Papallacacta record highlights the two modes, which affect precipitation variability in this region, namely the E equatorial Pacific and the tropical Atlantic. SST anomalies in both basins have been related to climate variability in the N Andes until 0.45 ka, with inter-decadal variability dominating during the last 0.5 ka. Also Pallcacocha in S Ecuador shows a close match with ENSO, recording its strength during the

last 15 ka. Similarly associated with ENSO are the changes in the plant assemblages detected in the high-resolution record of El Junco on the Galápagos Islands.

Comparing vegetation-climate signals between the Colombian lowlands and E Venezuela and NE Brazil has shown opposite climate conditions. Dry conditions identified in the Colombian savannas (suggesting an ENSO - La Niña), concur with similar conditions in the Bolivian pollen records. During an El Niño setting, when Bolivian savannas indicated wet conditions, the signal from Lake Valencia in Venezuela reflected dry conditions (Martin *et al.*, 1997; Wille *et al.*, 2003). Lowland sites generally show similar patterns of climate change during the last 2 ka and apparent synchronous events are observed over a larger spatial scale. This climate-sensitive transition zone is thought to reflect precession-forced changes in seasonality, latitudinal migration of the ITCZ, and changes in the ENSO (Figs. 3 and 4). The sites in the Andean region on the other hand are much more influenced by local geographical variability, causing a more variable response mechanism.

Central Andes

The records from the Central Andean Altiplano suggest an oscillation in moisture availability (precipitation) on a multi-centennial timescale during the last 2 ka (Fig. 9B). These oscillations are probably due to differences in the strength of the summer precipitation. The timing of wet and dry events is not uniform between sites, probably due to local micro-climates and differences in vegetation sensitivity to climate change; i.e. the high elevation grassland (puna) versus mid-elevation Andean forest. The high elevation peatland site of Cerro Llamoca is the only Altiplano site with no discernible local human impact and is the most robustly dated record used in this study; 33 radiocarbon ages in the last 2000 years. The Cerro Llamoca record therefore likely represents the clearest palaeoclimate signal for the C Andean region. For example, records of glacial advance and retreat, and associated vegetation changes, from the Altiplano associated with the LIA are not discernible in any record, apart from Cerro Llamoca, because they are masked by changes associated with the arrival of Europeans; i.e. abandonment of the sites, and/or changes in agricultural practices.

Interpretation of the climate signal from the C Andes fossil pollen records suggests that during the last 2 ka precipitation, rather than temperature, was the key natural driver of

vegetation change. Nonetheless, the increase in temperature observed at Nevado Coropuna during the Inca period, after 0.85 ka, could correspond to El Niño or IPO forcing. Furthermore, the decrease in temperature observed at Marcacocha between 1.85 and 0.85 ka could be related to La Niña. The Pacific modes (Figs. 2 and 3) show a strong influence along the coast, which is in agreement with the results of the coastal pollen record (Urpi Cocha), where ENSO is considered responsible for extreme flooding events.

The greater sensitivity to precipitation seen in the pollen records is probably because moisture availability is in most areas the limiting factor for both vegetation and human settlement. On the Altiplano variations in the SASM have been attributed as a major driver of changes in moisture balance at Cerro Llamoca, Nevado Coropuna, and Pacucha, through altering the summer precipitation. The SASM is also responsible for precipitation variations along the E Andean flank, as seen at Consuelo. As noted earlier, the highly seasonal precipitation in the C Andean region leads to rather weak correlations with ENSO and the IPO on an annual scale (Figs. 4 and 5). Notwithstanding this ENSO has been shown to have a significant influence in the C Andean region (both for temperature and precipitation) in numerous studies. It should also be noted that ENSO and IPO influence the intensity of the SASM (Garreaud *et al.*, 2003; Vuille and Werner, 2005) thereby affecting moisture delivery to the Altiplano region, but because both ENSO and monsoon rainfall tend to peak during a fairly short time window between November and February, this connection is not clearly expressed in Figs. 4 and 5.

Lowland Amazon basin

The lowland Amazon basin shows a high spatial complexity to the expression of the various modeled climate modes (Figs. 2–5). ENSO and IPO, for example, both indicate strong negative relationships with precipitation in the NE quarter of Amazonia, where they induce drying over this region during their positive phase. Conversely, TSA shows a positive relationship with precipitation over the NE Amazon. Precipitation in the NE Amazon region is clearly strongly linked to tropical sea-surface temperatures and ENSO variability. There are two pollen records in this region (Les Nouragues and French Guiana VII), both of which display a more local-scale forest dynamics with additional human interference. Therefore these records are not considered suitable to investigate the effect of these modes on vegetation

over the last millennia. New pollen-based reconstructions should be prioritized in this region to uncover the long-term drying effect of dominant ENSO/IPO or TSA modes on tropical lowland vegetation in the NE. The most significant late Holocene vegetation changes are observed in records from the ecotonal areas of the S Amazon (Chaplin, Bella Vista, Orícore, Carajás), where rainforest vegetation is located near the edge of its climatic range therefore, vegetation response to precipitation change is most likely to be observed. This rainforest expansion during the mid-to-late Holocene resulted from increasing insolation over the S Tropics and strengthening/migration of the SASM; a complex component of the climate system that is influenced by several dominant modes. Figures 4-5 show a weak negative precipitation anomaly across the lowland Amazon associated with the TNA mode. It is thought that higher sea surface temperatures in the tropical North Atlantic cause a reduction in Atlantic moisture reaching the Amazon during austral winter, thus extending the length/severity of the dry season; especially in S and SW Amazonia (Lewis *et al.* 2011). The influence of the TNA mode may therefore be important to consider in Amazonian pollen records given the known sensitivity of vegetation in these ecotonal areas to seasonal rainfall.

Most modes in Figures 2-3 show high correlation and regression coefficients with temperature anomalies over the lowland Amazon. Temperature anomalies can play a role, but rainforest vegetation is unlikely to have shown sensitivity to temperature changes of <1˚C (Punyasena, 2008; Punyasena *et al.* 2008), but would show greater sensitivity to reductions in minimum annual temperature (i.e. frost).

Better-resolved late Holocene records originate from small lake basins (e.g. oxbows like Maxus-1, Laguna El Cerrito and Laguna Frontera), which have small pollen catchment areas. This means that they reflect predominantly local-scale changes and are, therefore, more susceptible to having their record of past environmental change dominated by signals of ancient human land use and local hydrology (e.g. savanna gallery forest), rather than regional climate. Many of these smaller records were specifically selected in the original study to investigate local-scale human impacts around known occupation sites (Iriarte *et al.*, 2012; Whitney *et al.*, 2014; Carson *et al.*, 2014, 2015). Examples of continuous anthropogenic signals during the last 2 ka are Laguna El Cerrito, Laguna Frontera and Laguna San José (Fig.10).

In order to address these complicating factors of pollen catchment area and the anthropogenic signal, any future effort to obtain better-resolved Holocene pollen records in

the lowland Amazon should make careful consideration of the sampling methodology employed. Carson *et al.* (2014) demonstrated that sampling a combination of small and large lake basins from within the same catchment allows a distinction to be made between local-scale, anthropogenic impact and regional-scale, climate-induced vegetation changes. In regions such as the C Amazon, where lakes are predominantly limited to small oxbows, a sampling approach might be to analyse cores from multiple records within the same locality, and to compare those records, in order to identify any regionally significant pattern of palaeovegetation change (Cohen *et al.*, 2012; Whitney *et al.*, 2014). Oxbow lakes are dynamic features, and so require careful interpretation. However, their higher sedimentation rate means that they have the potential to provide the high temporal resolution palaeovegetation records of the late Holocene, which currently are largely absent from the Amazon lowlands.

Considering the large area of the Amazon basin, the number of pollen records is very small, and by applying the PAGES-2k criteria, those numbers are further reduced. Furthermore, the records which are excluded from the analysis by these criteria include some of the most important records of climate-driven vegetation change in the Amazon basin, e.g. Lakes Orícore (Carson *et al.*, 2014), Carajás (Hermanowski *et al.*, 2012), and lakes Bella Vista and Chaplin (Mayle *et al.*, 2000).

In order to avoid a "black hole" situation over the Amazon lowlands in any regional synthesis, one approach may be to apply a lower threshold of dating criteria. If the selection criteria are relaxed to allow for those records that are >500 years old and have at least two chronological control points within the last 2000 years, a further 14 records are added to the list of qualifying records. Also, if the criteria are stretched further to allow records with a lower date which is older than, but close to 2 ka, the Lake Chaplin and Gentry records would also be included. Considering these records would provide coverage from the central Amazon River region, the N Brazilian Amazon, the E and NE coastal Amazon and the SE and SW basin. However, even with these relaxed criteria, a number of key records would still be excluded, e.g. Pata (Bush *et al.*, 2004; D'Apolito *et al.*, 2013), La Gaiba (Whitney *et al.*, 2011) and Bella Vista (Mayle *et al.*, 2000).

Any future investigation of late-Holocene climate-vegetation interaction may require new dating efforts to improve the age models of these key records. A Holocene aged record from lake La Gaiba produced by McGlue *et al.* (2012) has produced a better-resolved age model than the longer record from Whitney *et al.* (2011), which would meet the PAGES-2k

criteria. However, McGlue *et al.* (2012) analysed the geochemical properties of sediments from a new core taken after the Whitney *et al.*, (2011) study, and did not include any pollen data. No attempt has been made subsequently to correlate the chronologies of the two records.

Although the dating resolution in the late Holocene is poor in many lowland Amazonian pollen records, it should be noted that the majority also show little variation in vegetation over the past ~1 or 2 ka. Whether this reflects genuine ecosystem (and climate) stability over the late Holocene, or is a product of low sampling resolution within these long records is unclear. Most of these deep temporal pollen records, as they are published now, likely have sub-sample intervals of insufficient resolution to be able to discern high-frequency events, such as vegetation changes associated with ENSO variability. However, in some cases, such as Bella Vista (Burbridge *et al.*, 2004) and Orícore (Carson *et al.*, 2014), the potential for such fine temporal reconstructions may be limited by the low sedimentation rate of the basins. Often these records come from short sediment cores, in which the Holocene time interval is contained within a short depth range (i.e. <1 m). A number of shorter records, spanning Holocene time periods, exist in the E coastal Amazon, and could potentially provide high temporal-resolution reconstruction over the last 2k. However, most do not currently meet the PAGES-2k dating criteria.

Southern and Southeastern Brazil

The limited number of pollen records from S/SE Brazil for LOTRED-SA-2k has several reasons besides the insufficiently dated cores: (i) many archives, in particular peat bogs, have very low sedimentation rates, i.e. often 100 cm of peat deposits encompass the complete Holocene (last 11.7 ka), and (ii) the upper part of peat archives contains actively growing roots and is therefore difficult to date.

Despite the limited number of study site available general vegetation changes in S/SE Brazil can be established (Fig. 11). Pollen assemblage shifts suggest a change toward wetter conditions over the last 2 ka, in particular due the reduction of the dry season length. The increased moisture availability is generally thought to commence in SE Brazil between 6 and 4 ka, but is particularly pronounced in S/SE Brazil during the last ~ 1 ka. Sites located in the highlands of S/SE Brazil along the transition zone between the subtropics and tropics are sensitive to both temperature and precipitation, but in the lower elevations the length of the

dry season plays a more important role than temperature. This dry season length is modulated by the interplay between SASM and SACZ, which bring abundant rainfall to SE Brazil during the summer months (October-March) and the South Atlantic Anticyclone, a semi-permanent high-pressure system located over the subtropical South Atlantic. The main pacemaker for rainfall on inter-annual time scales is ENSO, as El Niño events tend to bring copious rainfall to the region (Figs. 4 and 5).

According to the pollen records the intra-annual variability plays an important role in SE and S Brazil. The generally long annual dry period during the early and mid-Holocene limited the expansion of different forest ecosystems, while a much shorter annual dry period during the late Holocene allowed a strong expansion of forests, in particular of the *Araucaria* forest in southern Brazil. Inter-annual variability, influenced by the ENSO frequency, which increased during the late Holocene, may also have a certain effect on the vegetation in the region. El Niño events cause high rainfall rates in S/SE Brazil (Garreaud *et al.*, 2009). This is consistent with results in Fig. 4, which show a positive correlation between precipitation in the region and Nino3.4 and the IPO, and to a lesser extent also the TSA. The effect of the slightly increasing precipitation in southern Brazil may be rather small, however, as rainfall is already relatively high inferred from the records of past environmental change from S Brazil.

According to Fig. 2, the correlation of annual mean temperature over SA with the climate modes Nino3.4, IPO, AMO and TNA suggest a slight warming associated with the positive phase of these modes (Fig. 3). Increasing temperatures sustained over a long period may cause a slight shift of tropical plant populations to higher elevations on the mountains in SE Brazil and a slight expansion of tropical plants on the southern highlands.

Pampean plain

There are several pollen records in the Pampean plain that span Holocene times, but few of them have well resolved chronologies for the last 2 ka. Just one site fulfills all PAGES-2k criteria. Previously, pollen analyses in the Pampean plain region has been carried out on alluvial sequences, or archaeological sites, which usually contain sedimentological discontinuities that impede a good chronological control. These pollen records show regional vegetation changes and climate inferences related to precipitation changes (humid/dry/arid

conditions) or sea level fluctuations, mainly at millennial or centennial scale. Until today, few studies have focused on elucidating palaeoenvironmental changes at high temporal resolution during the last 2 ka. Furthermore, the Pampean plain have a high number of potential sites; shallow lakes characterized by a continuous sedimentation that would provide robust age models and high quality pollen records. Conversely, the current pollen records do not have the necessary resolution to identify vegetation-human interaction during the last 0.3 ka and therefore improved chronological control and higher resolution is necessary.

General climatic tendencies in the region can be inferred although few accurately dated pollen records are available. While individual palaeoecological studies reveal local developments, general patterns emerge when information from several sites is combined, such as Lonkoy and Hinojales-San Leoncio (Fig. 12B). A multi-proxy approach, including pollen analyses, shows synchronous changes in these shallow lakes from SE Pampa that are mainly a response to precipitation variations. Thus, between 2 and 0.5 ka drier conditions than present are inferred, then a transition phase towards more humid conditions is observed, which stabilizes between ~0.3 and 0.1 ka, with values close to modern (Stutz *et al.,* 2014). These climatic inferences are valid for the SE region but do not extend to the entire Pampean plain. At S Pampean plain, multi-proxy interpretation at Sauce Grande (Fontana, 2005) shows a similar change to more humid conditions at 0.66 ka, and similar conditions to present day after 0.27 ka, but pollen composition shows low responsiveness to change (Fig. 12A). New palaeoenvironmental reconstructions based on pollen records are needed to disentangle the intrinsic ecosystem variability from climate, and to elucidate if climatic events such as the MCA or LIA had different expressions in the Pampean plain.

As seen in Figures 2-5, these plains fall outside the areas that are strongly influenced by the investigated climate modes. Nonetheless, Figures 2 and 3 indicate that the positive phase of the TSA (a warm tropical South Atlantic) leads to a cooling over the region, while a slight warming is associated with the positive phase of the IPO. In Figure 5, a weak positive correlation between rainfall in the region and the Niño 3.4 and IPO modes is observed, which was previously also discussed by Barros *et al.* (2006). The SAM on the other hand is negatively correlated with precipitation in the region (Fig. 4), consistent with results by Silvestri and Vera (2003), although this relationship has not yet been explored in pollen records as a possible influence in the region. Hitherto studies from the Pampean plain only discuss dry or humid conditions associated with reduced or increased precipitation, but no

attempt to link these observations to large-scale climate variability is made. The situation in this region is further complicated by the fact that the moisture supply to the region stems from two distinct sources, the South Atlantic (Labraga *et al.*, 2002) during austral winter and the SA monsoon system (Vera *et al.*, 2006) during the austral summer. Hence pollen-based precipitation reconstructions also need to consider changes in seasonality of precipitation and not just climate variability associated with external influences from ENSO or the SAM. Seasonally stratified analyses of the influence of ENSO or the SAM could therefore provide additional insights into the climate-vegetation interpretation as focusing on annual mean values may mask strong seasonal signals in the same way as discussed above for the C Andes.

Southern Andes and Patagonia

Even though a large number of pollen records are available in the southern Andes and Patagonia region, just 19 (between 32-54°S) fulfil the PAGES-2k criteria. In Patagonia most pollen studies have been carried out with a focus on vegetation and climate change over different or longer timescales, i.e. the Pleistocene-Holocene transition (c. 11.7 ka), or the entire Holocene (last 11.7 ka). The pollen records are considered to mainly reflect changes in the SWWB and hence indicative of the polarity of the SAM. Southern records receive precipitation related to the SWWB, whereas those located to the north (40-32°S) are also influenced by the Subtropical Pacific Anticyclone (SPA) that blocks winter precipitation along a latitudinal gradient (decreasing precipitation during JJA in the S part to scarce precipitation during DJF in the N part). Furthermore the Andean ridge provides for a fundamental climatic divide with stronger westerlies leading to enhanced precipitation to the W of the divide, while sites located in Patagonia E of the Andean divide receive enhanced precipitation associated with winds from the E (Garreaud *et al.*, 2013). In addition to this E-W asymmetry, the comparison between N and S records could also shed light on the expansion/retraction and/or latitudinal shifts of the SWWB, or a differential influence of the SPA. For example, records S of 46°S show relatively dry conditions between ~1-0.5 ka whereas drought occurs between 2-1.5 ka at sites N of this latitude (Fig. 13B). Differences in seasonality are another key feature distinguishing precipitation records in N Patagonia (summer rainfall, e.g. Lago San Pedro) from records further north in central Chile (winter

rainfall, e.g. lake Aculeo and Palo Colorado). Due to the regional complexity of the climate, the region cannot easily be characterized by a single climate mode. Different patterns are distinguished (Fig. 13B), due to their geographical position, latitude and E/W side of the Andes, and the intrinsic sensitivity of each record to climatic variability.

Superimposed on the seasonally changing SWWB and SPA dynamics are the interannual influences of the SAM/Antarctic Oscillation and ENSO (Figs. 2-5). The positive phase of the latter (El Niño) is associated with humid winters in subtropical Chile and with dry summers in NW Patagonia (Montecinos and Aceituno, 2003). Sites in N Patagonia and C Chile therefore might be suitable to study this asynchronous behaviour with regard to ENSO activity (e.g. Lagos San Pedro and Aculeo).

The strongest influence in the region on interannual time scales, however, is exerted by the SAM. Figures 2-5 showcase a highly inverse correlation with precipitation and a positive correlation with temperature over the southern tip of South America (especially south of 40°S). The strong influence of the SAM on Patagonian climate, with drier and warmer than average conditions associated with its positive phase, is well known and consistent with previous analyses by Gillet *et al.* (2006) and Garreaud *et al.* (2009). Southernmost Patagonia therefore appears as a key area to study climate-vegetation variability associated with the SAM (e.g. Lago Cipreces). LIA and MCA chronozones are well recorded both in southern and northern Patagonia (e.g. Lago Cipreses, Peninsula Avellaneda Bajo, San Pedro), however not in central Chile.

6. Synthesis and Conclusions

Through this review and analysis c. 180 fossil pollen records that fulfill at least two of the PAGES-2k criteria for robust climate reconstruction were identified for SA. Although this is still relatively small number, compared to the total number of fossil pollen records available from SA (c. 1400; Flantua *et al.*, 2015a), we expect that the number of high quality sites for reconstruction of climate over the last 2 ka is likely to increase rapidly as new work is produced. To conduct a review on this scale it was necessary to break SA down into 7 sub-regions. Firstly, we summarize the finding from each region, and then draw broad conclusions regarding the patterns across the whole of SA.

The Venezuelan Guyana highlands and uplands (7 study sites reviewed, Fig. 7):

- Moisture balance and temperature: Records show a higher sensitivity to moisture than to temperature. Two drought intervals were detected coeval to the Little Ice Age (LIA) in the Venezuelan Andes. Wet conditions prevailed on the tepuian summits during the last 1 ka.

- Humans: Impact has been inferred from the charcoal record, without any evidence of crops (4 of 7 records). Use of fires can promote the reduction of forests and expansion of the savanna, favoring the establishment of *Mauritia* swamps after clearing. Earliest *Mauritia* establishment was observed around 2 ka, but humans might have been present since the mid-Holocene leaving their signature on the present-day landscape.

- Climate modes (Table 1): Both Pacific and Atlantic climate modes (Niño 3.4, AMO, IPO and TNA modes) are predicted to have a large effect on Venezuelan Guyana, especially with regard to temperature. However, the fossil pollen records from the highland show no responses to temperature variability suggesting that tolerance ranges were not surpassed to produce vegetation shifts. The precipitation/ evapotranspiration ratio may play an additional important role not yet studied.

Northern Andes region (21 study sites reviewed; Fig. 8):

- Moisture balance and temperature: Fossil pollen records are both moisture balance and temperature sensitive, with tropical lowlands more sensitive to moisture and Andean areas more sensitive to temperature. Overall wetter conditions with warm and cold episodes are seen during the last 2 ka. These shifting temperatures are displayed asynchronous in the records, and changes in ENSO frequency have been detected in multiple records.

- Humans: Andean records without human impact are rare (just 4 of the 21 records) and a wide range of indicators for human activity is found, these include deforestation (loss of tree taxa) and the appearance of introduced taxa, e.g. palms, crops and disturbance taxa. The high level of evidence of humans in this region is not surprising given that the history of the human occupation of the Andes goes back to the Lateglacial (c. 10 ka; Van der Hammen and Correal Urrego, 1978).

- Climate modes: The altitudinal gradient in temperature is most importantly modulated by Pacific modes (Niño3.4) and the TNA. Records show a close match with precipitation variability trigged by ENSO that displays a highly diverse spatial pattern throughout the region (Fig. 4).

The Central Andes (7 study sites reviewed; Fig. 9):

- Moisture balance and temperature: Fossil pollen records are more sensitive to changes in moisture balance than temperature. The records on the E Andean flank (Amazon flank) suggest overall moist conditions during the last 2 ka, while the W Andean flank (valleys and Pacific flank) shows a succession of dry and moist episodes. Generally drier conductions occurred in the C Andes between 1.2 and 0.7 ka when compared with the rest of the last 2 ka.

- Humans: Only two of the seven records reviewed were found not to contain any evidence of human activity. Human presence and land-use provides hints on changes in temperature, i.e. the climate became more favorable for human populations. However, arid conditions during 1.5-0.5 ka may have forced humans to abandon the Andean valleys, as there is evidence of afforestation in two sites with high human influence. Human indicators are mostly from the occurrence of crop pollen, e.g. *Zea mays*.

- Climate modes: Pacific modes show a strong influence along the coast in the C Andean region. The SASM is responsible for precipitation variations along the E Andean flank leading to weak correlation of ENSO and the IPO on an annual scale. Nevertheless, ENSO and IPO influence the intensity of the SASM and have shown to influence significantly both temperature and precipitation.

Lowland Amazon Basin (19 study sites reviewed; Fig. 10)

- Moisture balance and temperature: Fossil pollen records from the lowland Amazon basin are moisture sensitive and indicate continuously wet climate throughout the last 2 ka; however, centennial-scale shifts are observed in terms of forest composition attributed to hydrological change.

- Humans: Human activity has been detected in most records (15 of 19 sites), evidenced by fire (charcoal abundances), forest clearance, and crops, e.g. *Zea mays* and *Manihot esculenta*. After European contact, land use decreases as shown by a decline in burning around 0.5 ka.
- Climate modes: Precipitation in the NE Amazon region is strongly linked to tropical sea-surface temperatures and ENSO variability. ENSO and IPO induce drying in the NE Amazonia during their positive phase, while TSA induces precipitation. Both Pacific as Atlantic modes show high correlation and regression coefficients with temperature anomalies over the lowland Amazon.

Southern and Southeastern Brazil (7 study site reviewed; Fig. 11):

- Moisture balance and temperature: Records are moisture sensitive and indicate continuously wet climate throughout the last 2 ka. Changes in forest composition suggest a relative humid and warm phase during the LIA, in contrast to other regions.
- Humans: Most human impact occurred during the last 0.4 ka as indicated by increased use of fire. Furthermore, in the southern part of Brazil, human modification of ecosystems is indicated by the appearance of introduced taxa such as *Pinus* and *Eucalyptus*.
- Climate modes: Nino3.4, IPO, AMO and TNA suggest a slight warming associated with the positive phase of these modes. There is a positive correlation between precipitation in the region and Nino3.4 and the IPO, and to a lesser extent also the TSA. The ENSO frequency influences the inter-annual variability of precipitation and may affect the vegetation in the region where the duration of the dry season is more important than temperature.

Pampean plain (3 study sites reviewed; Fig. 12):

- Moisture balance and temperature: Fossil pollen records are moisture sensitive and do not detect temperature shifts. From 2 to 0.7-0.4 ka drier climatic conditions than present are inferred while after 0.3 ka a noticeable increase of precipitation occurred (more positive moisture balance).

- Humans: All records have human impact but this widespread impact only occurs during the last 0.1 ka, and is a consequence of the introduction of exotic tree species such as *Eucalyptus* and *Pinus*.
- Climate modes: Models suggest that the climate modes explored here exert only weak influences over the Pampean region. Precipitation seasonality probably plays a more important role as moisture supply stems from distinct sources during the year.

Southern Andes and Patagonia (23 study sites reviewed; Fig. 13):

- Moisture balance and temperature: Fossil pollen records are both moisture and temperature sensitive, showing a highly diverse pattern of alternating phases during the last 2 ka. One record displays major ENSO frequency between 1.8-1.3 ka and 0.7-0.3 ka.
- Humans: Impact is present in most records (17 out of 23). Only the last centuries show clear human intervention associated to European arrival through the occurrence of *Plantago* (indicator of overgrazing), increased grasses, introduced taxa (*Pinus*) and crop-related herbs (*Rumex).* European colonization followed a clear north to south migration pattern while evidence for the presence of earlier human populations in the region is not conclusive from palaeoecological records.
- Climate modes: The strongest influence in the region is exerted by the SAM for both temperature as precipitation. The pollen records are considered to mainly reflect changes in the Southern Westerly Wind Belt and hence indicative of the SAM. ENSO influences mostly precipitation.

On the basis of the region-by-region assessments from SA we conclude more generally that:

- The low number of SA records that fulfill all the PAGES-2k criteria (only 44) is a consequence of the age and quantity of the sediments recovered (which place fundamental limits on the duration and resolution of any study), and the focus of the original research. Many SA records have been excluded because their long time span (>10 ka) coupled with a relatively slow sedimentation allows only low temporal resolution of sampling; furthermore, slow sedimentation rates mean that many records do not have radiocarbon ages from within the last 2 ka.

- Pollen records in SA can detect long-distance (between sites) synchronicity (differences and similarities) in vegetation changes as an indication of regional precipitation and temperature variability; however, they can also detect the local-scale change/variability, which needs to be understood to determine if a long-distance signal is present. This interaction between long-distance and local-scale signal has long been a problem for palynologists (e.g. Jacobson & Bradshaw, 1981), but interestingly in SA it seems that the degree of variation in signal varies between regions, i.e. in lowland regions there seems to be less between site variability (consistent long-distance signal) compared with Andean sites (high local site specific variability). This variation between lowland and Andean sites is probably a function of topographic complexity and hence lowland pollen records provide a relatively cleaner long-distance signal from which large-scale atmospheric circulation (climate) change can be assessed. However, we show that fossil pollen records from all regions of SA can be compared to help better understand past changes in the intensity and area of influence of different climate modes, such as ENSO or the AMO.
- Throughout SA a number of overlapping climate modes operate. We assess the correlation and regression coefficients of the six most relevant climate modes to identify the modes with the most significant influence on interannual temperature and precipitation variability. Every single pollen record most likely captures the signal of various climate modes (Figs. 2-5), although they do not all operate in the same frequency bands and modes interact with one another through constructive interference. The causes of ambiguous climate-vegetation responses observed in pollen records can therefor probably be ascribed to the degree of climate mode interaction at a location.
- The geographical location (latitude, longitude, and altitude) of a record naturally affects the sensitivity of a study site to temperature- or precipitation- related forcing (Figs. 7-13). The baseline for understanding climate-driven changes in vegetation is related to either of these variables, but interpreting pollen records in terms of a response to large-scale climatic forcing may yield further insights as it allows for an attribution of temperature- and/or precipitation- driven changes to forcing from climate modes originating in either the Atlantic or Pacific Ocean.

7. Recommendations

Below we list a few specific recommendations for future engagements between climate- and pollen-related studies:

1. Quantitative translation from pollen metrics to climate variables: Assembling a meaningful multi-site and multi-proxy dataset is hampered by the current gap between the palynological and the climate dynamics and modeling community, both in terms of interpretation and quantitative translation of pollen data into climate indicators. This gap can be narrowed when pollen studies provide, if the data is suitable for that purpose, their own temperature or precipitation approximations. There are only a few pollen studies that provide a quantitative interpretation of their pollen data in terms of a climate variable. In the Andes, La Cocha-1 (González *et al.*, 2012) and Papallacta PA1-08 (Ledru *et al.*, 2013a) provide such estimates of climatological changes. In both cases the percentage of arboreal pollen was used as a measurement of moisture or temperature changes. Similarly Punyasena *et al.* (2008) and Whitney *et al.* (2011) present innovative methodologies for climate reconstructions in the lowland tropics, and Markgraf *et al.* (2002), Tonello and Prieto, (2008) Tonello *et al.* (2009, 2010) and Schäbitz *et al.* (2013) in the southern SA. Providing additional climate estimates is not a common feature in palynological studies and this missing link becomes more obvious when the palynology community is being engaged in a multi-disciplinary effort such as LOTRED-SA and PAGES-2k.

2. Multi-proxy based research should become a mandatory goal for all further investigations. Caution should be exercised when interpreting apparently contradictory records provided by different groups for the same region; the interpretation of climatic and anthropogenic signals in each record may be based on very different (indirect) proxies. Hence the apparent asynchronies or contradictory interpretations could simply occur as a result of methodological artifacts (e.g. by not including charcoal records, non-pollen palynomorphs, geochemical analyses, etc.). On the other hand, this is especially relevant for those areas where human impact has been found for the last 2 ka, yet a climatic interpretation is the aim of the study. Developing proxies suitable for generating independent climate reconstructions from lake sediments in SA include

Chironomids (Matthews-Bird et al., 2015; Williams et al., 2012), while indications of humans can come from non-pollen palynomorphs, such as the dung fungus *Sporomiella* (Williams et al., 2011).

3. For the stated purposes of the current and future PAGES initiatives, researchers should be motivated to further improve chronologies for existing sites. There is a need to increase efforts in high- resolution studies with accurate chronology for the last 2 ka. At the same time, the PAGES-2k criteria should be adjusted for pollen records, especially by applying a lower threshold of dating criteria. A region such as the lowland Amazon is notoriously known for its paucity of records with good dating (e.g. Ledru *et al.*, 1998). Therefore additional valuable sites available should be considered for the overall purpose of studying vegetation-climate linkages.
4. Further advances in understanding climate-human relationships are also likely to be made by the integration of palaeoecological and archaeological data (e.g. Mayle and Iriarte, 2014) through conceptual modeling, which can provide a framework for identifying patterns and trajectories of change (e.g. Gosling and Williams, 2013).
5. Multi-proxy studies should compare data between different regions and records (but comparable in terms of chronology and resolution) as it may yield insight into anti-phased climate variability resulting from certain dominant climate modes (e.g. a comparison between the coast of Colombia and NE Brazil-Guianas versus Brazil and E Argentina).
6. All Andean zones are quite active from tectonic and volcanic points of view, and those drivers will have had significant impacts on the vegetation and maybe in the fossil pollen records as well. However, this aspect was only discussed for the southern region of the Andes. A chronology database focused on tephra control points could support current chronology constraints and improve comparison between records. The recent geochronological database of the LAPD can support such a multi-proxy approach for palaeoecological integration (Flantua *et al.*, 2015b).
7. In this paper we focused less on the seasonal contrasts throughout the continent, but in southern SA the seasonal component is extremely important, as precipitation shifts latitudinally over the course of the year. Precipitation in this region is the limiting factor for vegetation growth and pollen production. Key questions that need further study include a) a better understanding of the relationship between winter and summer

rainfall, b) if this relationship has remained stationary over the last 2 ka, c) if changes in the intensity or location (latitudinal shift) of rainfall have occurred.

8. High-resolution time series should be explored with frequency analysis to find support for operating climate modes.
9. Optimal exploration of the presence of climate modes in pollen records requires a specific research design. Temporal resolution should be increased to below decadal scale, chronological control of the sediments optimized, main frequencies in the time series analysed and compared with a frequency spectrum to be developed that shows characteristics of the climate modes.

The Supplementary Information related to this article is available online.

Author contributions. S. G. A. Flantua, C. González-Arango, H. Hooghiemstra conceived the paper and H. Hooghiemstra supervised the project. M. Vuille developed the climate modes and corresponding figures, supported the climate interpretations at a regional level and edited the English writing throughout the paper. Hoyos supported the interpretation of the climate settings of the N and C Andes; V. Rull and E. Montoya the palaeoecological and climate interpretation of the Venezuelan Guayana; S. G. A. Flantua, V. Rull, H. Hooghiemstra the N Andes sections; W. D. Gosling, M. P. Ledru the C Andes sections; H. Behling the S and SE Brazil sections; J. F. Carson, F. Mayle, B. S. Whitney the lowland Amazon sections; A. Maldonado and M. S. Tonello the Patagonia and S Andes sections; M. S. Tonello the Pampa sections; C. González-Arango and S. G. A. Flantua provided the initial drafts of the climate summary figures and all authors discussed the results and implications; S. G. A. Flantua, C. González-Arango, M. Vuille, B. S. Whitney, J. F. Carson, W. D. Gosling and H. Hooghiemstra structured and edited the manuscript during all phases.

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Abbre-viation	Mode	Methods	Description	Reference
Niño 3.4	Niño3.4 index	SST averaged over 5°N-5°S, 170°W-120°W calculated from Hadisst data	Describes inter-annual (2-7 yr) variability of tropical Pacific SST	Rayner *et al.*, 2003
AMO	Atlantic Multi-decadal Oscillation	Defined as the area-averaged SST in the Atlantic north of the equator, calculated from Kaplan SST V2	Describes coherent variations in North Atlantic SST on multi-decadal (50-70 yr) time scales	Enfield *et al.*, 2001
IPO	Inter-decadal Pacific Oscillation	Multi-decadal Pacific-wide mode of SST variability, calculated as the 2nd EOF of low-frequency filtered HadSST data	Describes joint variations of Pacific SST in both hemispheres on multi-decadal (20- 30 yr) time scale	Folland *et al.*, 2002
SAM	Southern Annular Mode or Antarctic Oscillation	Calculated as leading principal component (PC) of 850 hPa geopotential height anomalies south of 20S	Determines strength and location of circumpolar vortex (location of the extratropical westerly storm tracks)	Thompson and Wallace, 2000
TNA	Tropical North Atlantic SST	Defined as SST averaged over 5.5°N-23.5°N, 15°W-57.5°W and calculated from HadISST and NOAA OI 1x1 datasets	Describes inter-annual variability of SST variations in the tropical North Atlantic	Enfield *et al.* (1999)
TSA	Tropical South Atlantic SST	Defined as SST averaged over 0-20°S, 10°E-30°W (TSA), calculated from HadISST and NOAA OI 1x1 datasets	Describes inter-annual variability of SST variations in the tropical South Atlantic	Enfield *et al.* (1999)

Table 1. Climate modes used relevant for South America

Criteria	PAGES 2k	This paper	Criteria abbreviations for Table 3
A	Described in peer-reviewed publication	Described in peer-reviewed publication	
B	Resolution ≤ 50 yr	Resolution ≤ 300 yr	(not specified)
1	Minimum duration of record ≥ 500 yr	Minimum duration of record ≥ 500 yr	DUR500
2	Not specified	More than two chronological tie-points within the last 2 ka	CONTROL2
3	Tie points near the end part (most recent) of the records and one near the oldest part	Tie points near the end part (most recent) of the records and one near the oldest part	TOP_END
4	Records longer than 1 ka must include a minimum of one additional age midway between the other two.	Records longer than 1 ka must include minimum of one additional age midway between the other two.	1000-MID3

Table 2. Comparison of PAGES 2k criteria with criteria implemented in this study.

Table 3. List of pollen records used and metadata. For each record it is indicated which criteria has been fulfilled (Table 2), the human indicators observed during the last 2ka, and if the pollen record is considered sensitive to precipitation (humidity) and/or temperature.

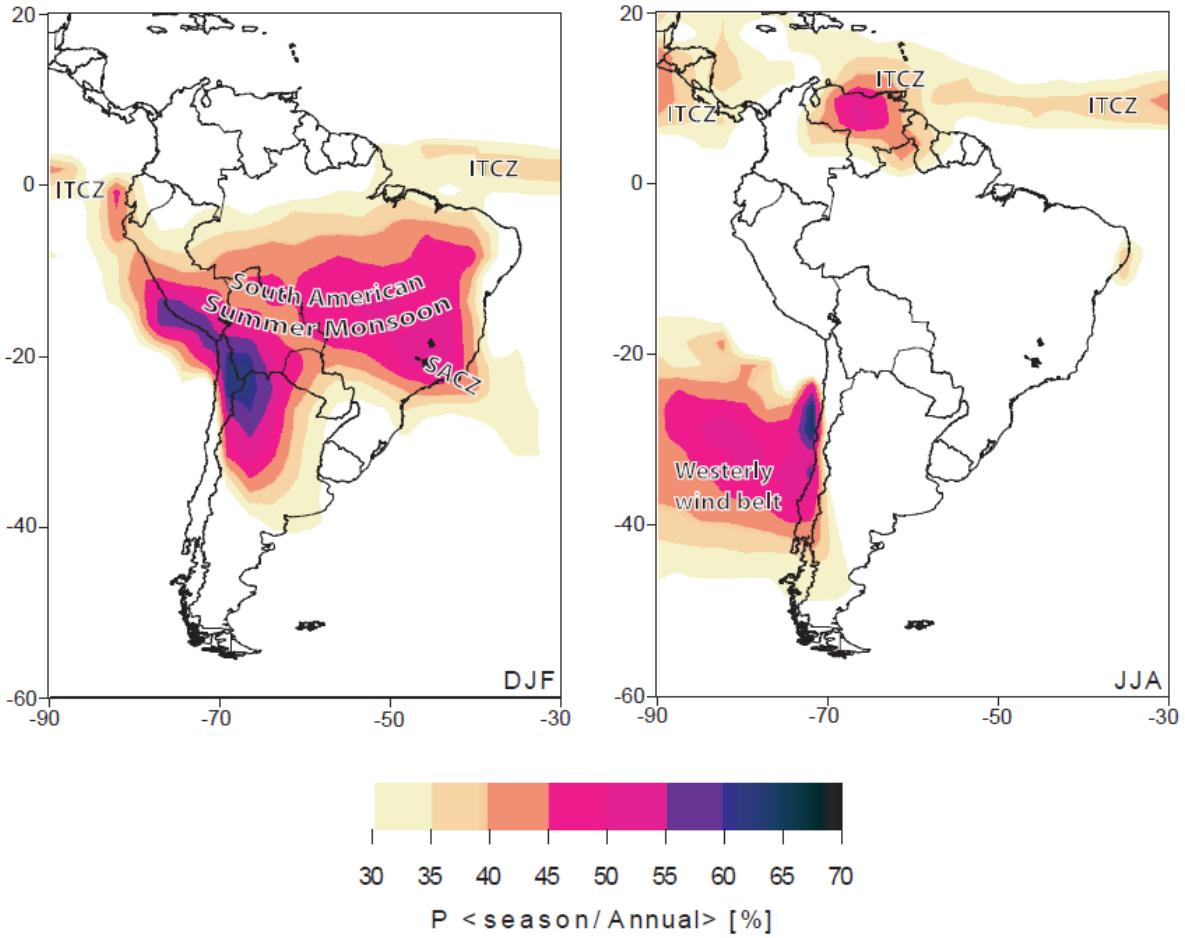

Figure 1. Map showing the relative precipitation amount over South America during the key seasons DJF (austral summer and mature monsoon phase) and JJA (dry season over much of tropical South America), highlighting the Intertropical Convergence Zone (ITCZ), South American Summer Monsoon (SASM), South Atlantic Convergence Zone (SACZ) and extratropical westerlies. Figure based on CMAP precipitation data. Adapted after Vuille *et al.* (2012).

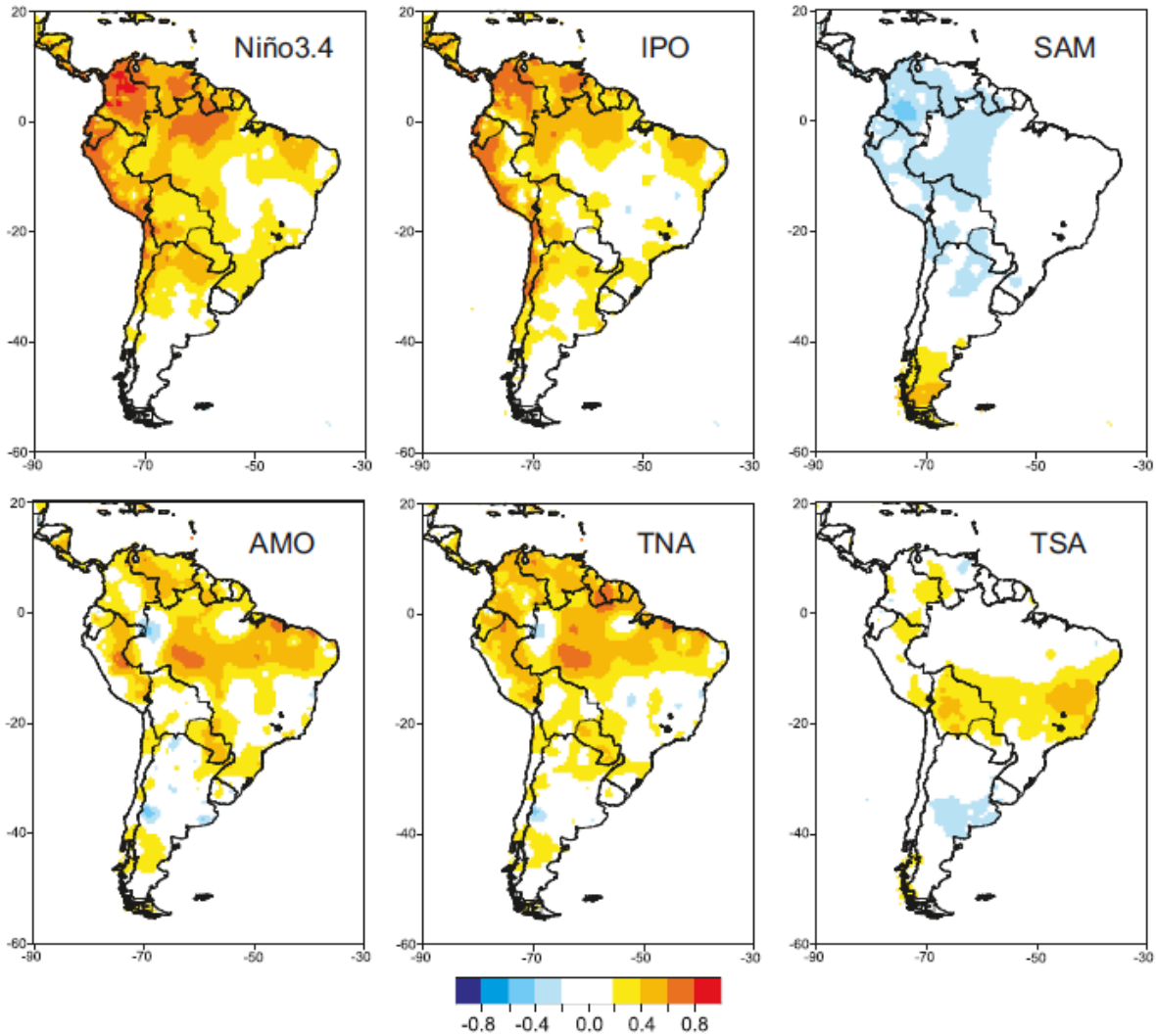

Figure 2. Correlation of annual mean temperature over South America with climate modes Niño3.4, IPO (Interdecadal Pacific Oscillation), SAM (Southern Annular Mode), AMO (Atlantic Multidecadal Oscillation), TNA (Tropical North Atlantic SST) and TSA (Tropical South Atlantic SST). High positive values of the correlation coefficient indicate both increasing/decreasing values of the mode in question and the local temperature at each grid cell. High negative values indicate that the increasing (decreasing) mode in question cause a significant decrease (increase) in temperature at the grid cell. Gridded temperature fields are from University of Delaware (1958–2008). Only correlations in excess of ±0.2 are shown (roughly the threshold of the 95% significance level).

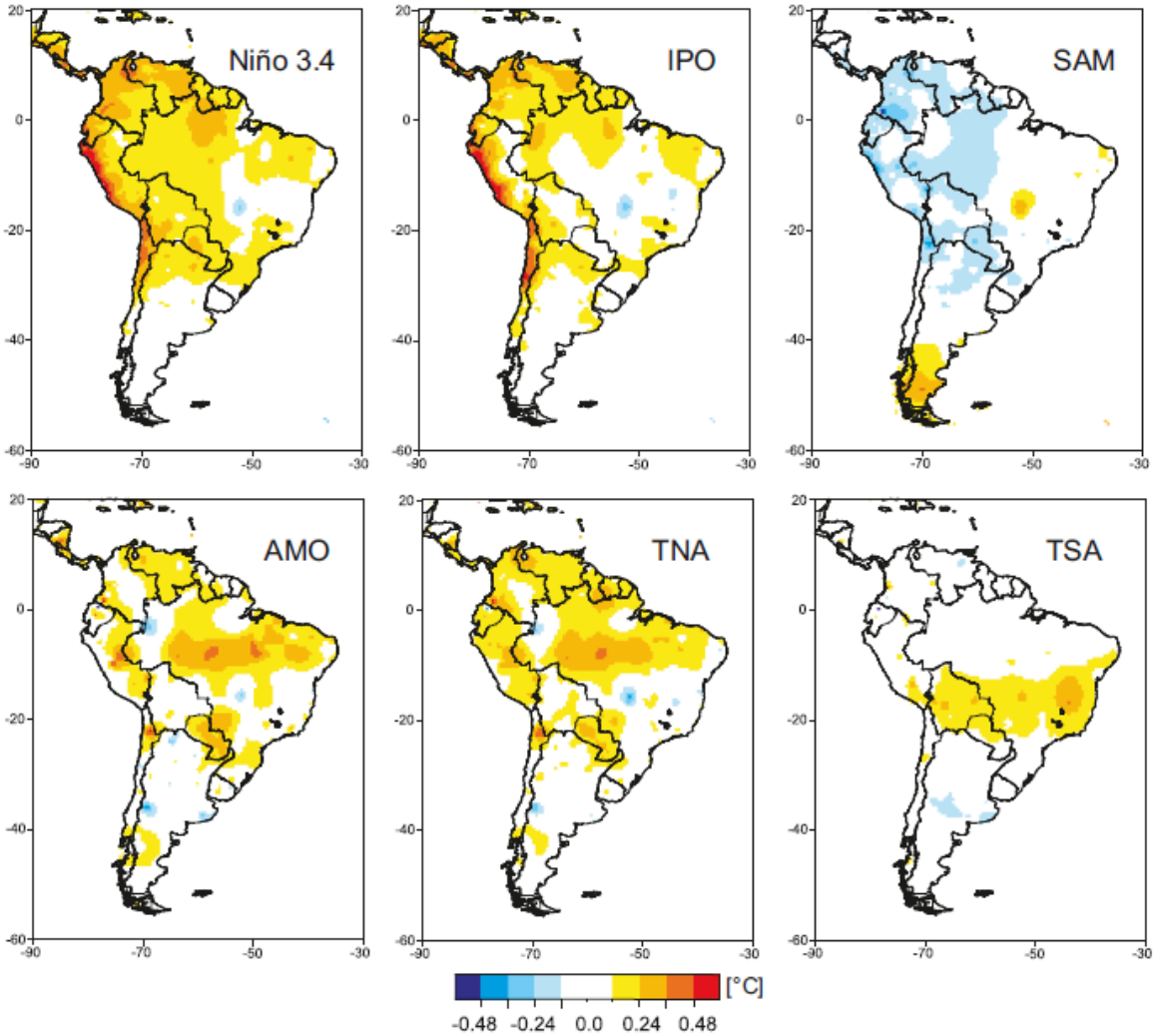

Figure 3. Annual mean temperature regressed upon Niño3.4, IPO (Interdecadal Pacific Oscillation), SAM (Southern Annular Mode), AMO (Atlantic Multidecadal Oscillation), TNA (Tropical North Atlantic SST), TSA (Tropical South Atlantic SST). High positive values of the regression coefficient indicate that positive (negative) temperature anomalies occur during the positive (negative) phase of the mode in question. High negative values indicate that the positive (negative) phase of a mode leads to a decrease (increase) in temperature at the grid cell. Gridded temperature fields are from University of Delaware (1958–2008).

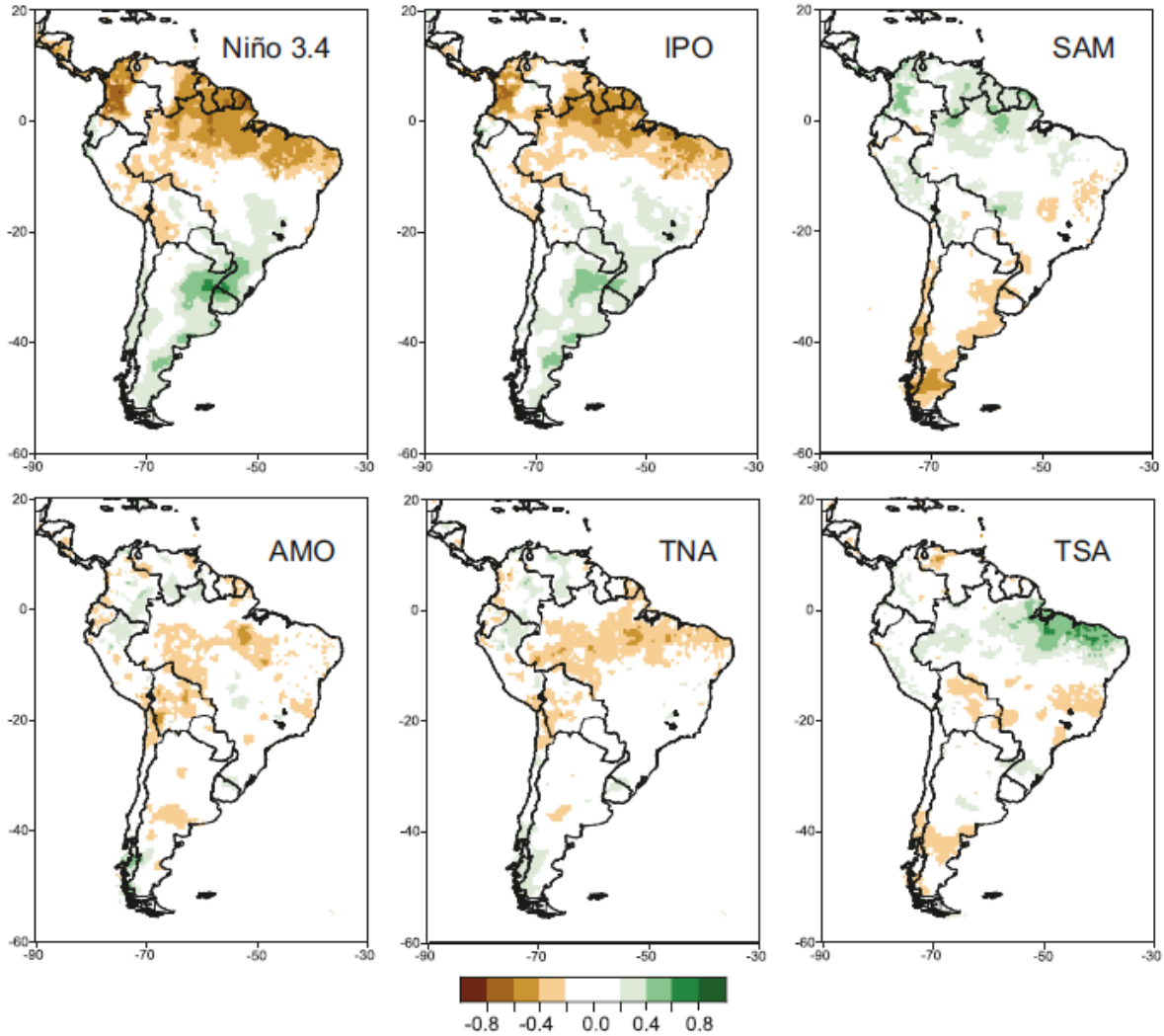

Figure 4. Precipitation correlation with modes Niño3.4, IPO (Interdecadal Pacific Oscillation), SAM (Southern Annular Mode), AMO (Atlantic Multidecadal Oscillation), TNA (Tropical North Atlantic SST), TSA (Tropical South Atlantic SST). High positive values of the correlation coefficient indicate both increasing/decreasing values of the mode in question and the local precipitation at each grid cell. High negative values indicate that the increasing (decreasing) mode in question cause a significant decrease (increase) in precipitation at the grid cell.

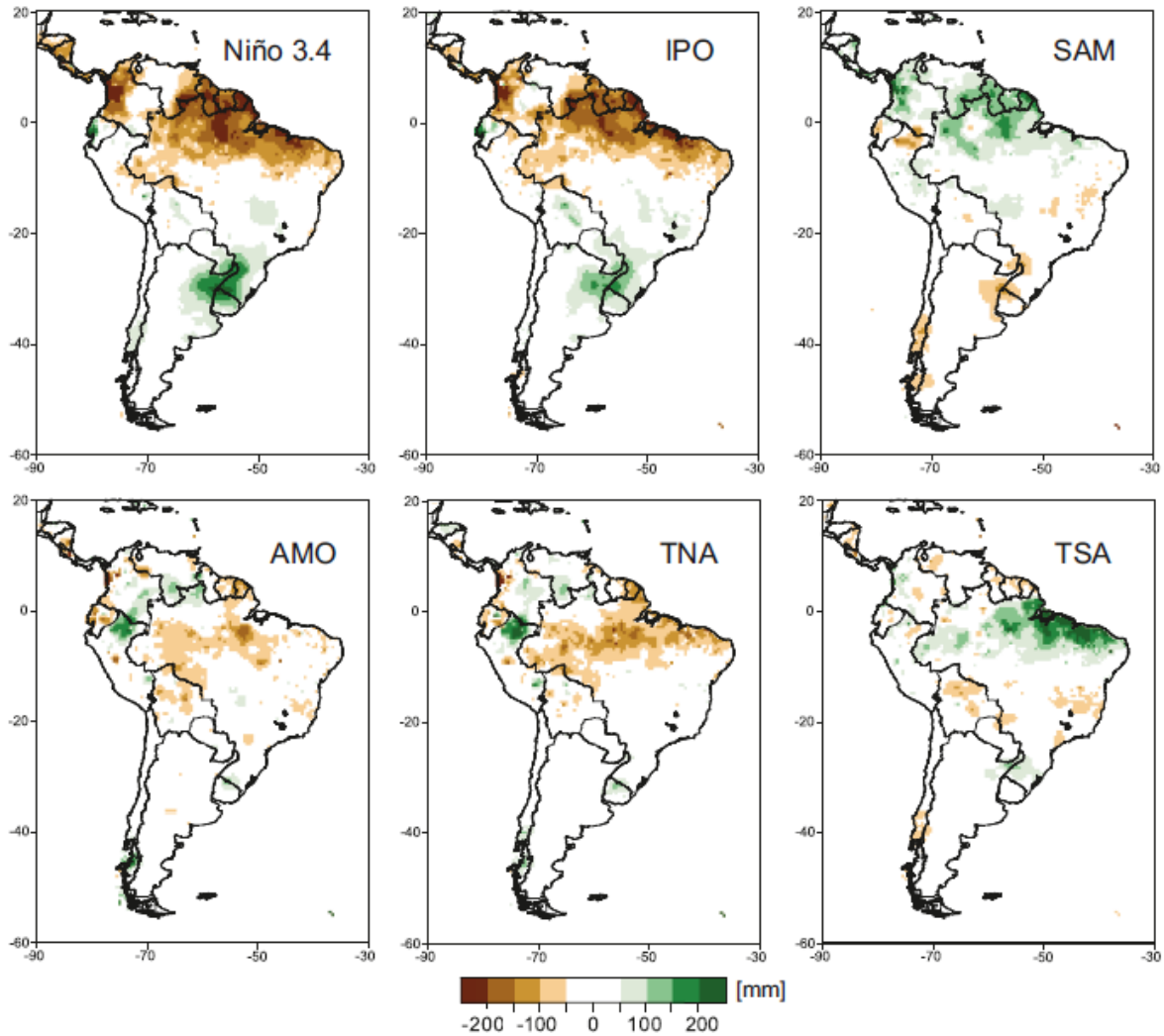

Figure 5. Precipitation regression with modes Niño3.4, IPO (Interdecadal Pacific Oscillation), SAM (Southern Annular Mode), AMO (Atlantic Multidecadal Oscillation), TNA (Tropical North Atlantic SST), TSA (Tropical South Atlantic SST). High positive values of the regression coefficient indicate that positive (negative) precipitation anomalies occur during the positive (negative) phase of the mode in question. High negative values indicate that the positive (negative) phase of a mode leads to a decrease (increase) in precipitation at the grid cell

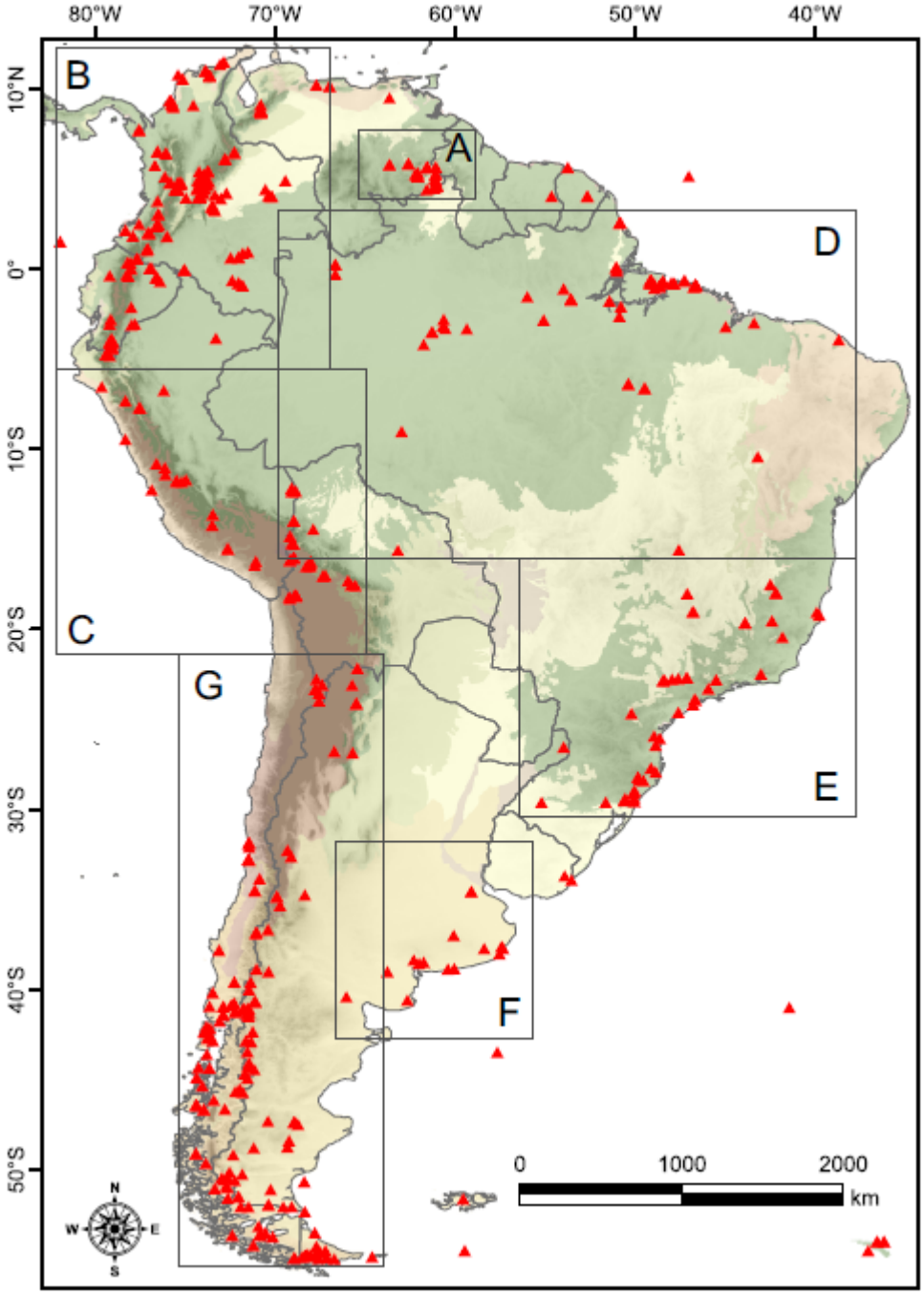

Figure 6. Map showing the location of LAPD pollen records that cover the last 2 ka (after Flantua *et al.*, 2015a). General regional delimitations as discussed in this paper are shown; A: Venezuelan Guyana highlands and uplands; B: Northern Andes; C: Central Andes; D: Lowland Amazon; E: Southern and southeastern Brazil; F: Pampean plain; G: Southern Andes and Patagonia.

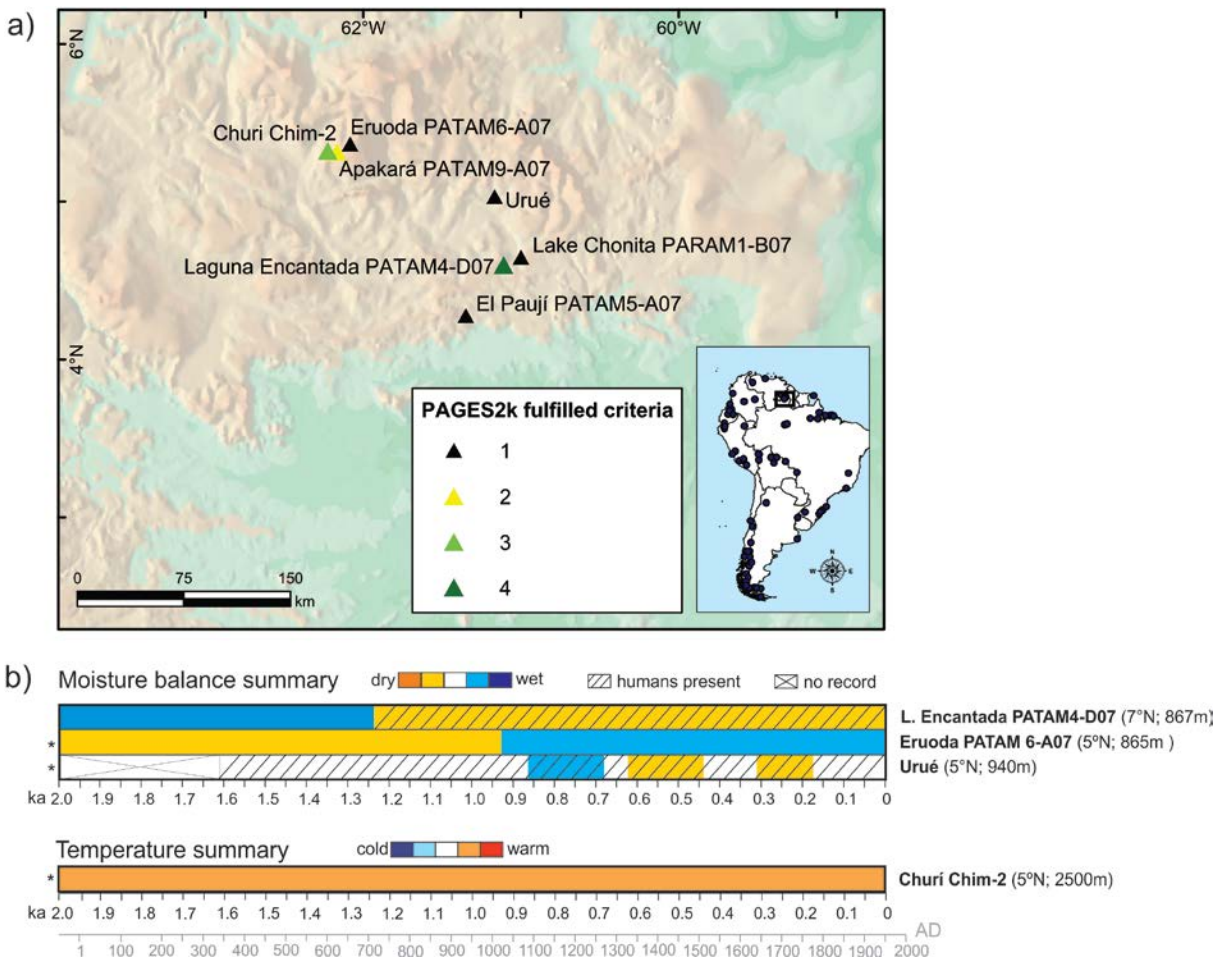

Figure 7A: Map showing the discussed pollen records in the Venezuelan Guayana highlands and uplands and the number of PAGES2k criteria these records fulfill. B: Summary of moisture balance and temperature including human interference for the pollen records discussed. Not all records are suitable to derive both moisture and temperature signal. Climate and human presence is shown overlapping when the pollen record is not conclusive on the derived signal. Bars are totally greyed out when the climate signal is totally obscured by human interference. * Records fulfilling 1 or 2 criteria indicated by star.

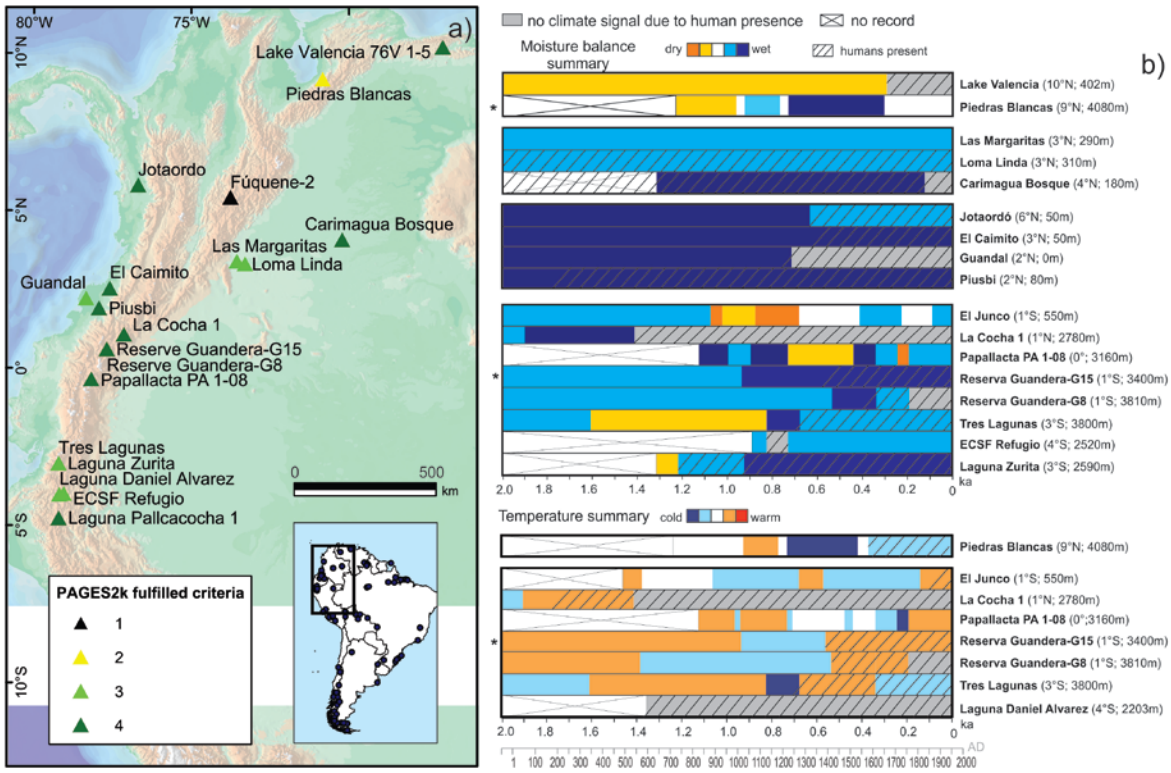

Figure 8A: Map showing the discussed pollen records in the Northern Andes and the number of PAGES2k criteria these records fulfill. B: Summary of moisture balance and temperature including human interference for the pollen records discussed. Not all records are suitable to derive both moisture and temperature signal. Climate and human presence is shown overlapping when the pollen record is not conclusive on the derived signal. Bars are greyed out when the climate signal is obscured by human interference. * Records fulfilling 1 or 2 criteria indicated by star. Galapagos Islands not shown.

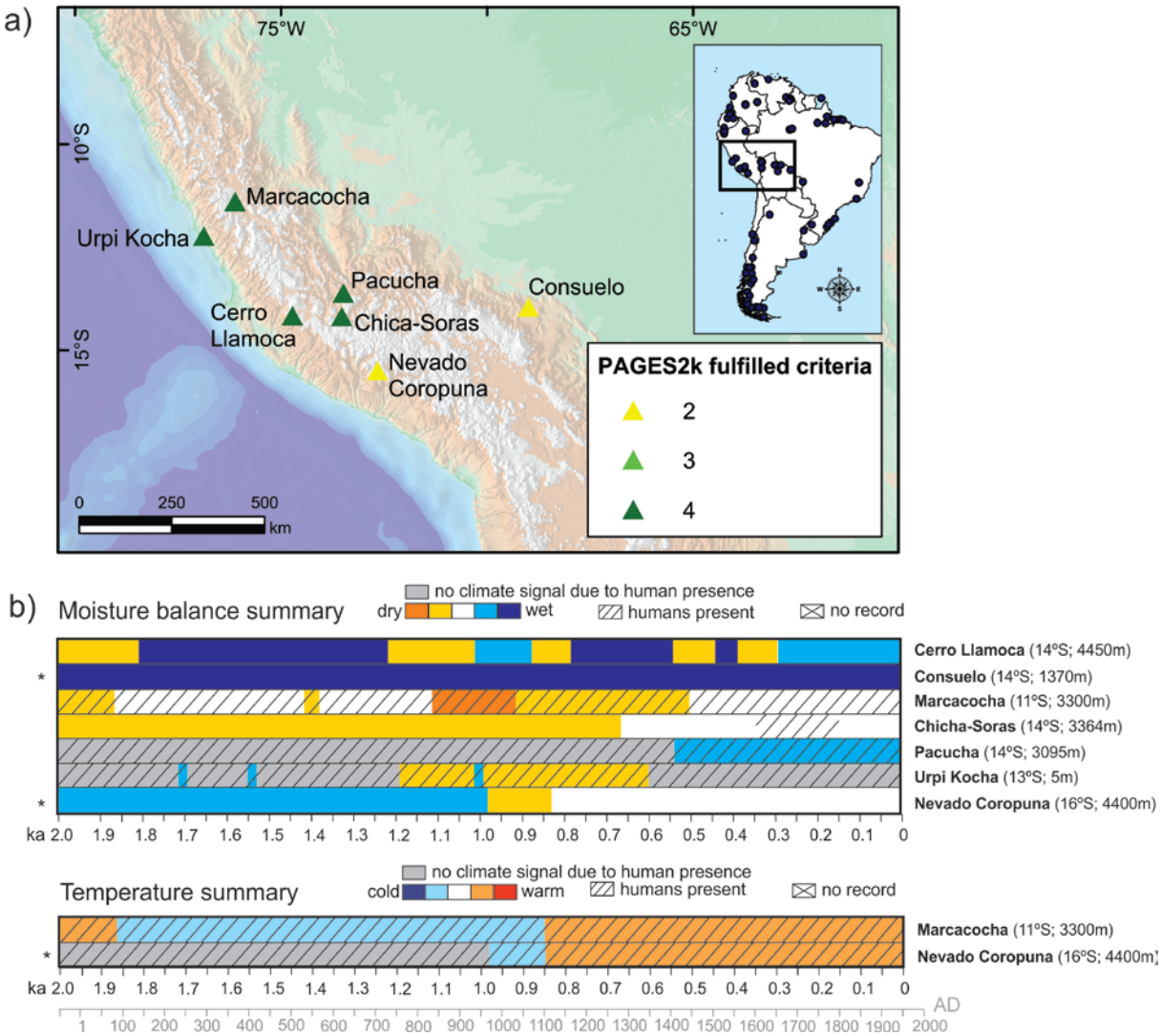

Figure 9A: Map showing the discussed pollen records in the Central Andes and the number of PAGES2k criteria these records fulfill. B: Summary of moisture balance and temperature including human interference for the pollen records discussed. Not all records are suitable to derive both moisture and temperature signal. Climate and human presence is shown overlapping when the pollen record is not conclusive on the derived signal. Bars are greyed out when the climate signal is obscured by human interference. * Records fulfilling 1 or 2 criteria indicated by star.

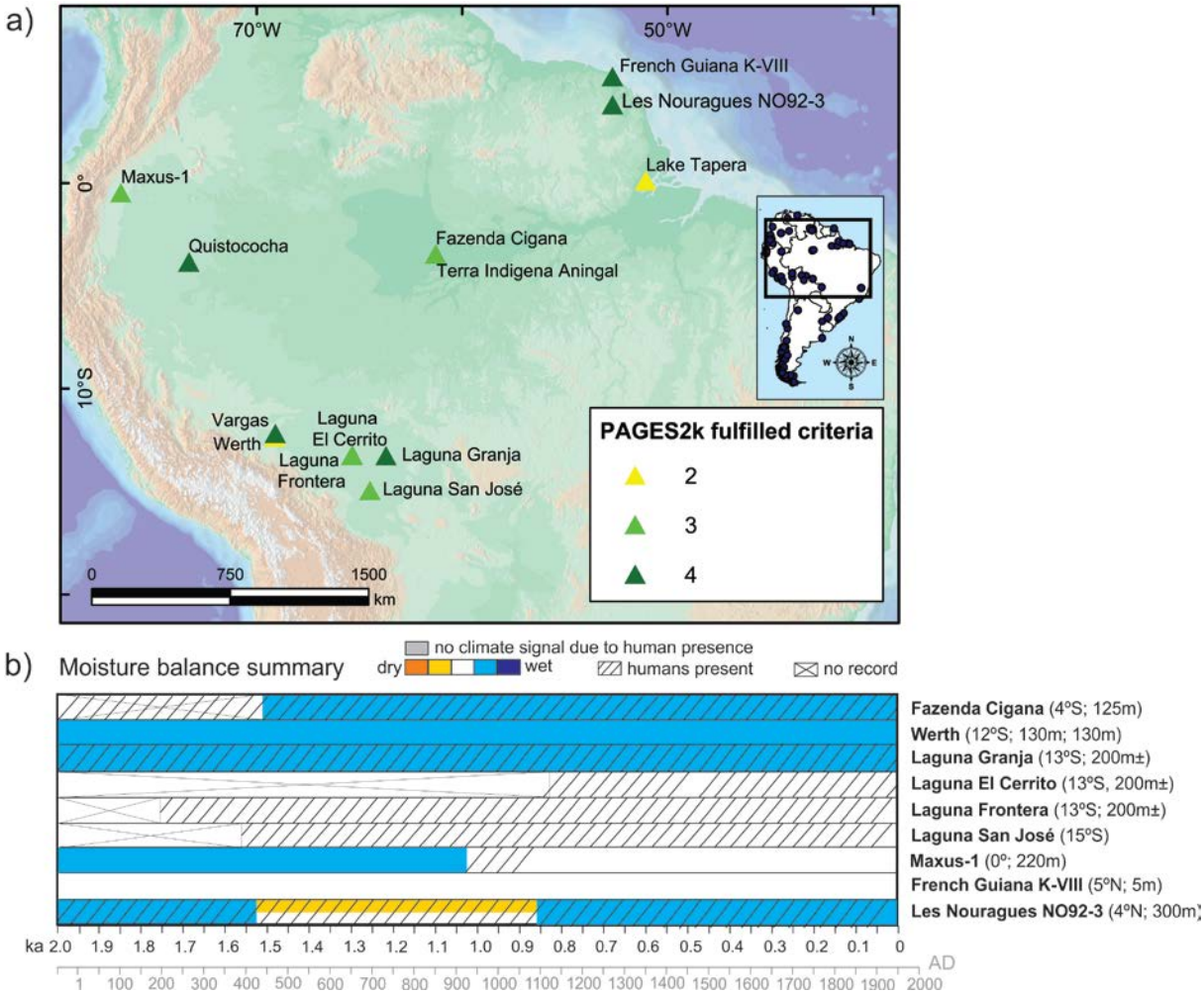

Figure 10A: Map showing the discussed pollen records in the lowland Amazon Basin and the number of PAGES2k criteria these records fulfill. B: Summary of moisture balance and temperature including human interference for the pollen records discussed. Not all records are suitable to derive both moisture and temperature signal. Climate and human presence is shown overlapping when the pollen record is not conclusive on the derived signal. Bars are greyed out when the climate signal is obscured by human interference. * Records fulfilling 1 or 2 criteria indicated by star. m± : masl based on coordinates.

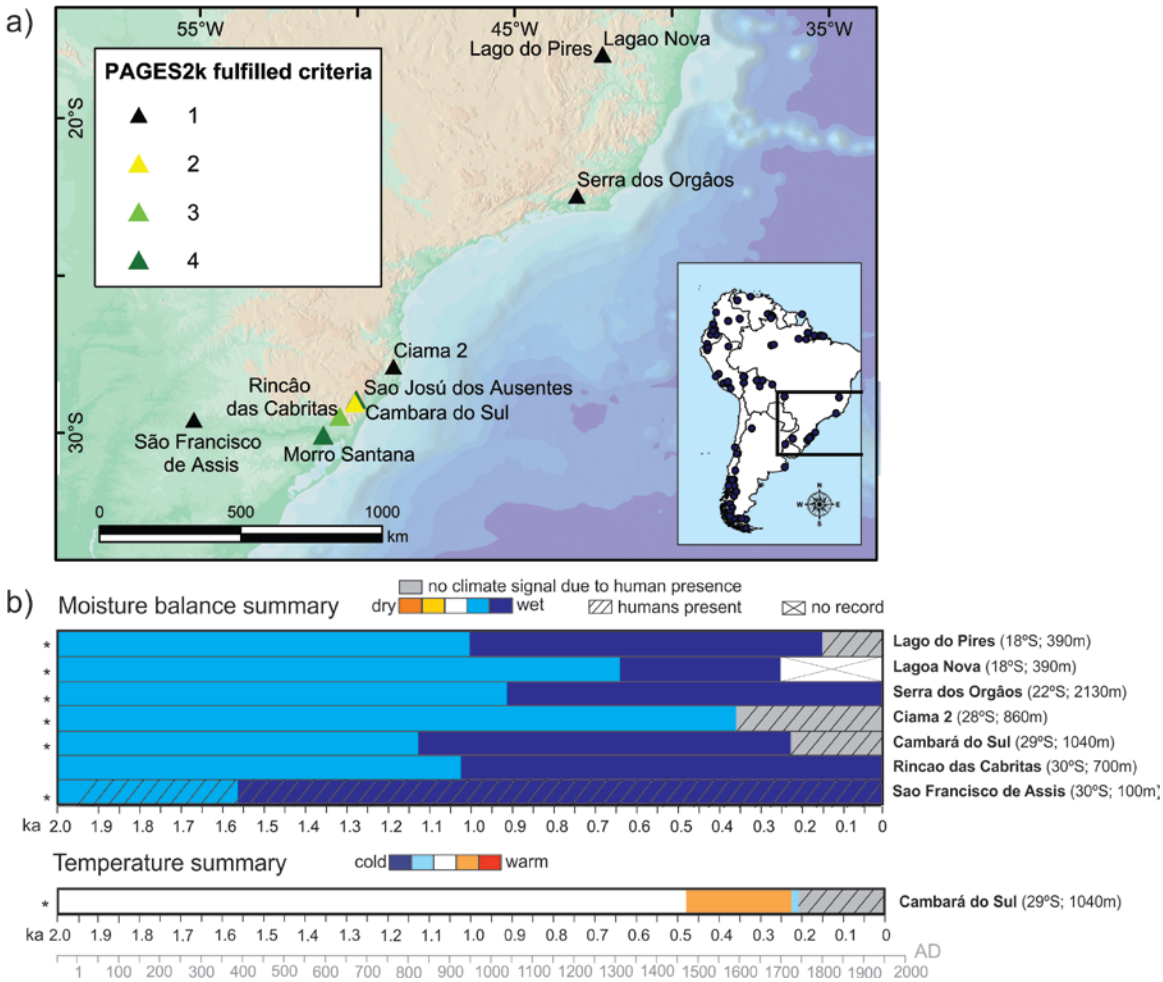

Figure 11A: Map showing the discussed pollen records in the Southern and Southeastern Brazil and the number of PAGES2k criteria these records fulfill. B: Summary of moisture balance and temperature including human interference for the pollen records discussed. Not all records are suitable to derive both moisture and temperature signal. Climate and human presence is shown overlapping when the pollen record is not conclusive on the derived signal. Bars are greyed out when the climate signal is obscured by human interference. * Records fulfilling 1 or 2 criteria indicated by star.

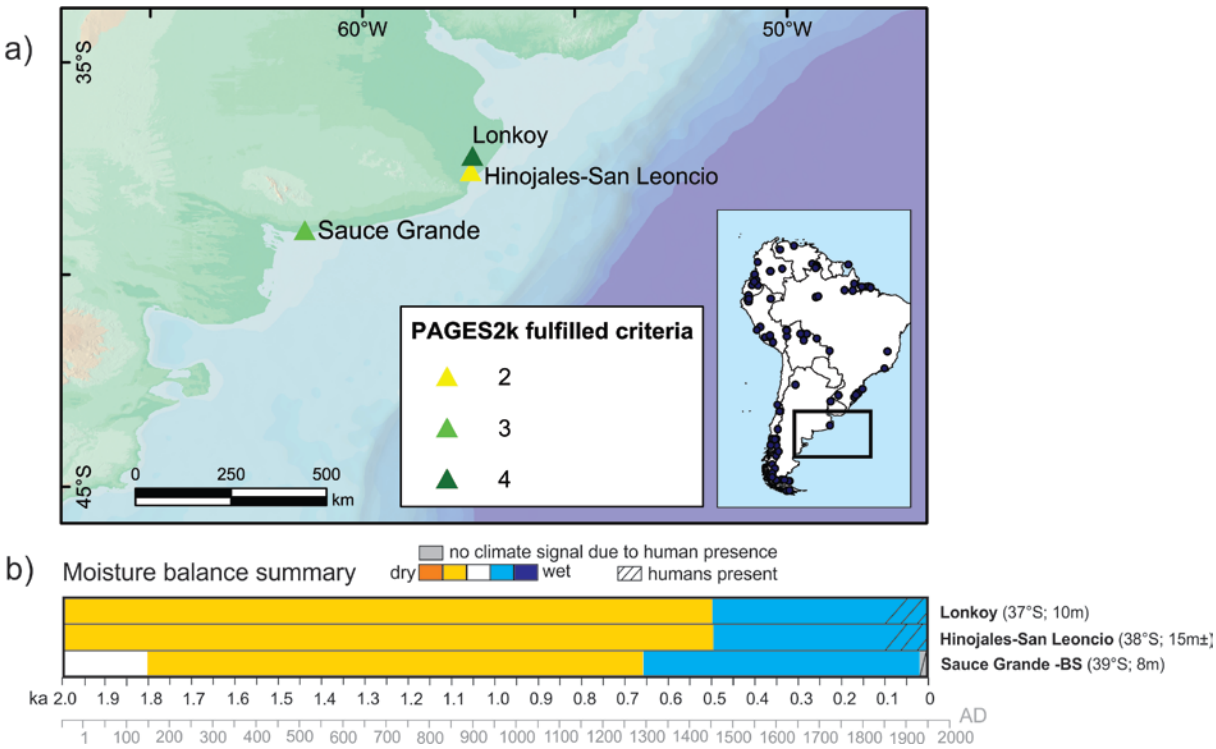

Figure 12A: Map showing the discussed pollen records in the Pampean plain and the number of PAGES2k criteria these records fulfill. B: Summary of moisture balance and temperature including human interference for the pollen records discussed. Not all records are suitable to derive both moisture and temperature signal. Climate and human presence is shown overlapping when the pollen record is not conclusive on the derived signal. Bars are greyed out when the climate signal is obscured by human interference. m± : masl based on coordinates.

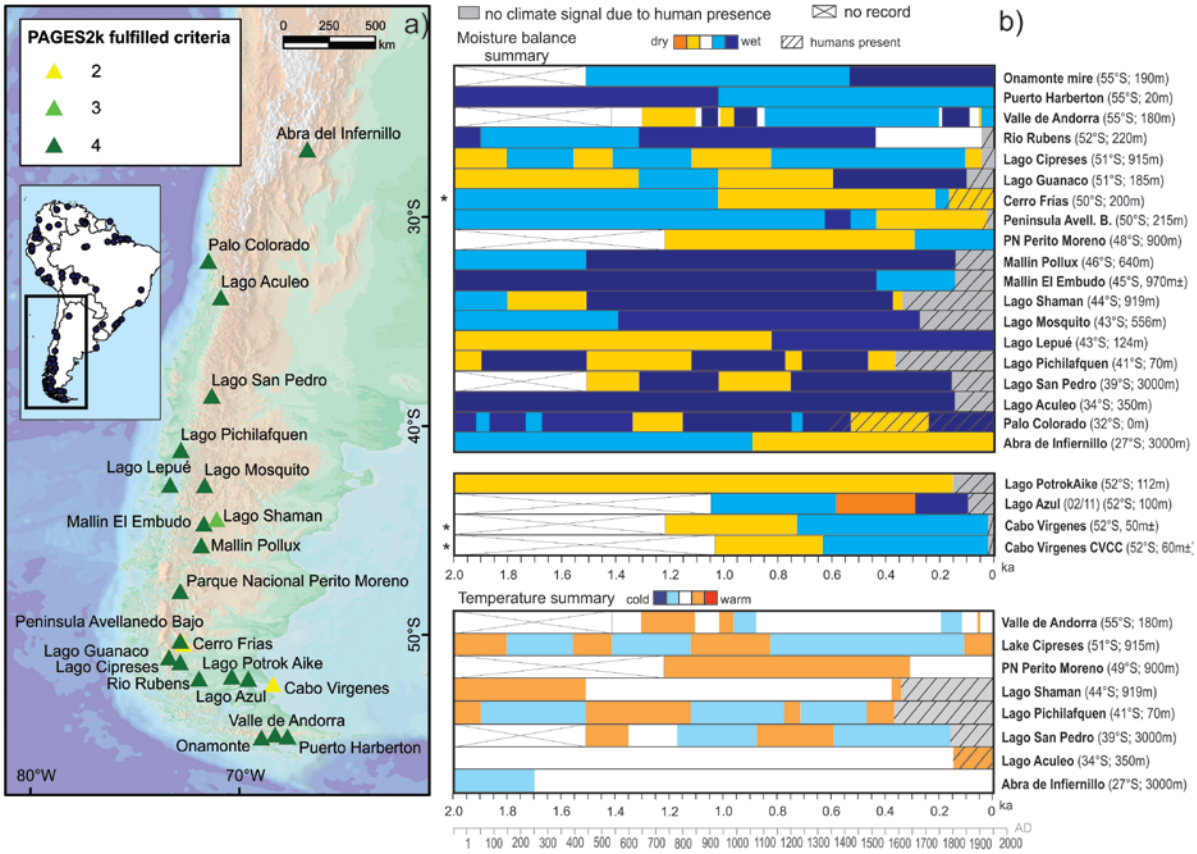

Figure 13A. Map showing the discussed pollen records in the Southern Andes and Patagonia and the number of PAGES2k criteria these records fulfill. B: Summary of moisture balance and temperature including human interference for the pollen records discussed. Not all records are suitable to derive both moisture and temperature signal. Climate and human presence is shown overlapping when the pollen record is not conclusive on the derived signal. Bars are greyed out when the climate signal is obscured by human interference. * Records fulfilling 1 or 2 criteria indicated by star. m± : masl based on coordinates.

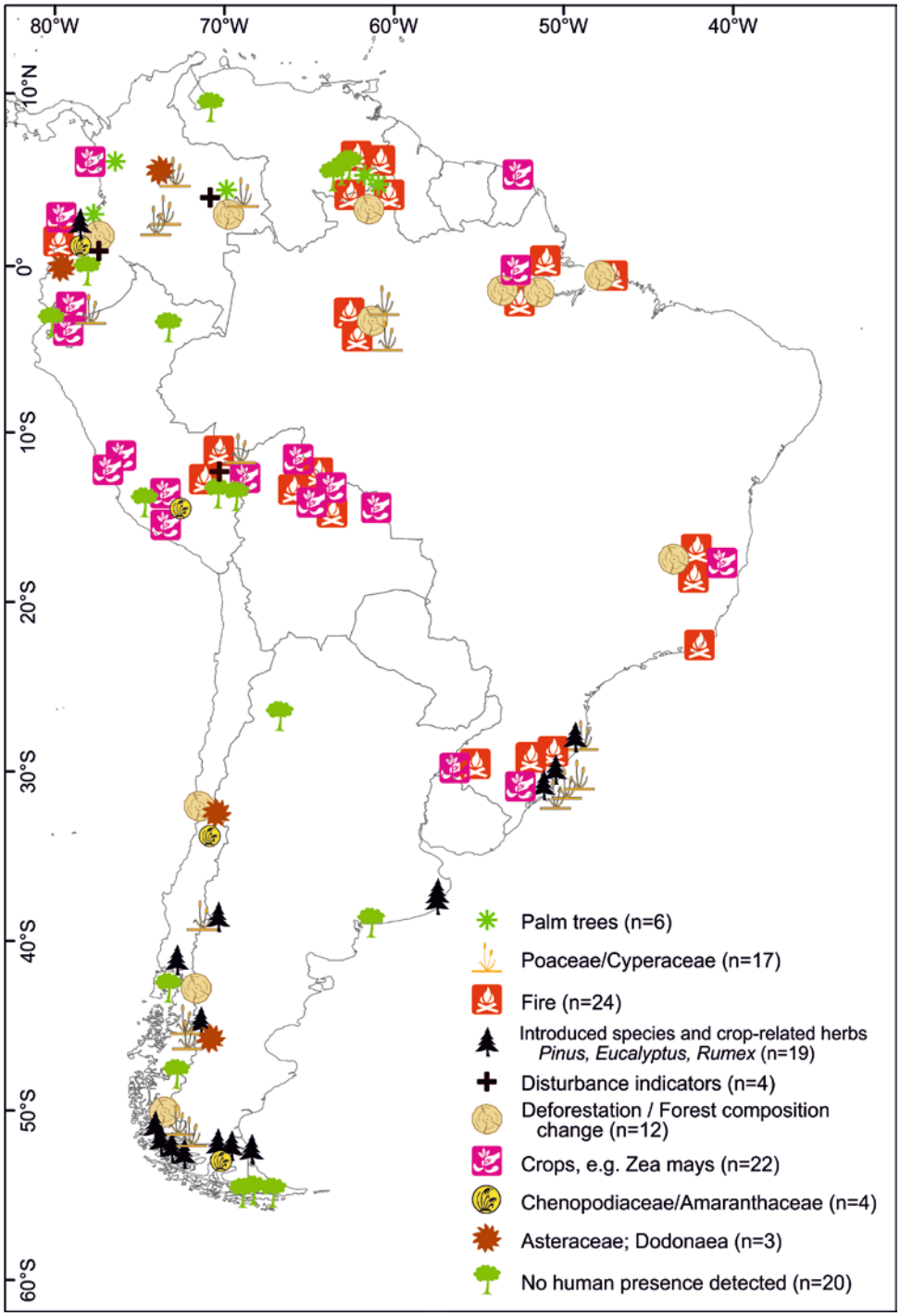

Figure 14. Map showing human indicators observed in the discussed pollen records (n = 68). The number of pollen records for each human indicator is shown in the figure legend. A pollen record can have different human indicators and therefor the symbols may be show an offset relative to their exact location to avoid overlapping point symbols. Details are found in Table 3.