

Climate variability and human impact on the environment in South America during the last 2000 years: synthesis and perspectives

S.G.A. Flantua¹, H. Hooghiemstra¹, M. Vuille², H. Behling³, J.F. Carson⁴, W.D. Gosling^{1,5},
I. Hoyos⁶, M.P. Ledru⁷, E. Montoya⁵, F. Mayle⁸, A. Maldonado⁹, V. Rull¹⁰, M.S. Tonello¹¹,
B.S. Whitney¹², C. González-Arango¹³

[1] {Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam,
Science Park 904, 1098 XH Amsterdam, The Netherlands.}

[2] {Department of Atmospheric and Environmental Sciences, University at Albany, State
University of New York, Albany, NY, USA.}

[3] {Georg-August-University of Göttingen, Albrecht-von-Haller-Institute for Plant Sciences,
Department of Palynology and Climate Dynamics, Untere Karspüle 2, 37073, Göttingen,
Germany.}

[4] {Department of Geography and Environmental Science, University of Reading, Reading,
RG6 6AB, United Kingdom.}

[5] {Department of Environment, Earth & Ecosystems, The Open University, Walton Hall,
Milton Keynes, MK7 6AA, United Kingdom.}

[6] {Faculty of Engineering, GAIA - Institute of Physics Group Fundamentos y Enseñanza de
la Física y los Sistemas Dinámicos, Universidad de Antioquia, Medellin, Colombia.}

[7] {Institut des Sciences de l'Evolution de Montpellier (ISEM) (UM2 CNRS IRD EPHE)
Place Eugène Bataillon cc 061, 34095 Montpellier cedex, France.}

[8] {Department of Geography and Environmental Science, University of Reading, Reading,
RG6 6AB, United Kingdom.}

[9] {Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Universidad de La Serena.
Av Raúl Bitrán 1305, La Serena, Chile.}

[10] {Institute of Earth Sciences "Jaume Almera" (ICTJA-CSIC). C. Lluís Solé Sabarís s/n,
08028 Barcelona, Spain.}

[11] {Instituto de Investigaciones Marinas y Costeras CONICET – Universidad Nacional de
Mar del Plata, Mar del Plata, Argentina.}

[12] {Department of Geography, Ellison Place, Northumbria University, Newcastle-Upon-
Tyne, NE1 8ST, United Kingdom.}

[13] {Departamento de Ciencias Biológicas, Universidad los Andes, A.A. 4976 Bogotá,
Colombia.}

Correspondence to: S.G.A. Flantua (S.G.A.Flantua@uva.nl), Henry Hooghiemstra
(H.Hooghiemstra@uva.nl)

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 reconstruct regional climate modes are in the process of validating and integrating paleo-proxies. For South-America, however, the full potential of vegetation records for evaluating and improving climate models has hitherto not been sufficiently acknowledged due to its unknown spatial and temporal coverage. This paper therefore serves as a guide to high-quality pollen records that capture environmental variability during the last two millennia. We identify the pollen records with the required temporal characteristics for PAGES-2ka 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 conditions. Additionally, pollen is an excellent indicator of human impact through time. Evidence for human land use in pollen records is 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 recorded by other paleo-proxies to correctly attribute the potential causes of observed vegetation dynamics. The LOTRED-SA-2k initiative provides the ideal framework for the integration of the various paleoclimatic sub-disciplines and paleo-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

72 **Abbreviations:**

73	2k:	Last 2000 calibrated years (short writing for: 2000 cal yr BP)
74	ALLJ:	Andean low-level jet
75	AMO:	Atlantic Multidecadal Oscillation
76		
77	BP:	Before Present, present defined as AD 1950
78	C	Central
79	cal kyr:	Thousand calibrated years before present
80	Cheno/Am:	Chenopodiaceae/Amaranthaceae
81	DJF	December-January-February
82	ENSO:	El Niño – Southern Oscillation
83	GS:	Gran Sabana
84	IPO:	Interdecadal Pacific Oscillation
85	ITCZ:	Inter-Tropical Convergence Zone
86	JJA:	June-July-August
87	ka:	Thousand calibrated years before present, cal kyr BP
88	LAPD:	Latin American Pollen Database
89	LIA:	Little Ice Age
90	LOTRED-SA:	LONG-Term multi-proxy climate REconstructions and Dynamics in South
91	America	
92	masl:	meters above sea level
93	MCA:	Medieval Climate Anomaly
94	NE:	Northeast(ern)
95	NW:	Northwest(ern)
96	P/E	Precipitation/Evapotranspiration ratio
97	S:	South(ern)
98	SA:	South America
99	SACZ:	South Atlantic Convergence Zone
100	SAM:	Southern Annular Mode
101	SASM:	South American Summer Monsoon
102	SE:	Southeast(ern)
103	SPA:	Subtropical Pacific Anticyclone
104	SST:	Sea Surface Temperature
105	SI:	Supplementary Information
106	SWWB:	Southern Westerly Wind Belt
107	TNA:	Tropical North Atlantic SST
108	TSA:	Tropical South Atlantic SST
109	UFL:	Upper forest line
110	W:	West(ern)
111		

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 regions of the world with poor data coverage. 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. Stratigraphic 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 (2k) 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 this region have gained momentum by compiling multiple datasets and fine-tuning reconstruction methods (Villalba *et al.*, 2009). An adequate spatial distribution of proxy data sets is one of the key necessities identified (Villalba *et al.*, 2009; Flantua *et al.*, 2015b). Fortunately, tree rings studies have expanded their geographical coverage. These constitute a widely distributed and frequently used high-resolution climate archive (Boninsegna *et al.*, 2009; Villalba *et al.*, 2009). However, the temporal range of tree rings records is limited compared to the expanse of spatial and temporal coverage provided by pollen records. The newly updated inventory of palynological research in SA (Flantua *et al.*, 2015b) documents the extensive spatial and temporal coverage of pollen-based research available throughout the continent. Additionally, developing alternative recalibrated age models and evaluation of chronologies is another step forward in multi-proxy integration in SA (Flantua *et al.*, 2015a). 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). 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-paleoclimate reconstructions, within the framework of *Long-term multi-proxy climate REconstructions and Dynamics in South America* (LOTRED-SA, this Special Issue) and PAGES-2k. 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 South America and used as a baseline framework to identify past climatic changes from pollen records. To use pollen as a palaeoclimate proxy, the degree of human impact on the vegetation needs to be considered 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 paleoecological research in the last millennia. Records that identify significant human impact are identified and excluded from the proposed dataset for PAGES-2k, but are considered useful within the regional purposes of LOTRED-SA (this Special Issue). 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

We begin with an overview of the main climate ‘zones’ of South America to provide the climatological context for a discussion of pollen records covering the past 2000 calibrated years before present (cal kyr BP; in this paper abbreviated to “ka”). Climate zones are regions of coherent seasonality and mean climate (intra-annual climate regime), while climate ‘modes’ (discussed below) are based on ocean-atmosphere interactions with often oscillatory behaviour affecting the interannual to multidecadal climate variability in a region. Most palynological studies merely describe climate zones for their discussion of vegetation response to climate. However, interannual to multidecadal variability is equally relevant for the interpretation of spatial variability detected by pollen records. Therefore in this paper we provide a detailed exploration of the influence of these modes on South American climate. The spatial influence of climate modes is assessed by documenting their role in driving interannual precipitation and temperature variability. Following this climatic framework, we explain the procedure for selecting robust pollen records in seven regions and assess the

regional significance of climatic and human drivers of vegetation change over the last 2 ka. Records along coastlines influenced by sea level changes were not included.

Continental overview climate zones and modes

Continental SA extends from the tropics (12°N) to mid-latitudes (55°S). Three major noticeable climate zones can be distinguished; tropical South America, subtropical South America and austral South America. 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 and soil moisture (Yang 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 southern hemisphere tropics and subtropics (Garreaud et al., 2009). During the austral spring–summer (December to February, DJF) transition, 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 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 northwest (NW) to southeast (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 austral 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 austral polar low to the S. Frequent northward propagation of extratropical cold air incursions east 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 (Fig.1). Additional information is presented in Supplementary information (SI) 1.

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, Tropical North and South Atlantic Sea Surface Temperature, 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 SI-

In all correlation maps (Fig. 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 Figs. 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 SI-1 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 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). Temperature variations in western SA, and particularly along the Pacific coast, can reach $> 0.8^{\circ}\text{C}$ which is associated with a one standard deviation departure in the Niño3.4 index. 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 time 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 Pacific decadal and multidecadal variability is often described as 'ENSO-like' (e.g. Garreaud and Battisti, 1999). Its impact extends further south along the west (W) coast of SA, 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, Atlantic Multidecadal Oscillation (AMO) and Tropical North Atlantic SST (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 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 hydrologic 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 (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 ‘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 South Atlantic Convergence Zone (SACZ in Fig. 1; e.g. Doyle and Barros, 2002).

3. LAPD overview and selection of pollen records covering 2 ka

From the newly updated Latin American Pollen Database (LAPD, Flantua et al., 2015b) we selected the records that cover the last 2 ka. 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 sub-region of SA 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. Thus, 182 studies were considered suitable for paleoclimate reconstruction as outlined by the PAGES 2k criteria.

Within the working groups of PAGES, the “2k-Network” was initially established in 2008 to improve current understanding of temperature variability during the last 2 ka. Through the identification of temperature sensitive proxies, the development of climate reconstructions has advanced thanks to regional efforts (e.g. LOTRED-SA) to compile a proxy database (PAGES-2k Consortium, 2013). Both temperature and moisture records are currently being collected, requiring a set of criteria that define the suitability of individual records.

As a global initiative, a defined set of criteria guarantees the quality of the proxies used for climate reconstructions and therefore focuses on chronological accuracy and record resolution (Table 2). Within this paper we regarded criteria A (Peer-reviewed publication) and B (Minimum duration of the record of 500 yr) as the base line criteria. All criteria followed those stated by PAGES-2k except for the criterion on resolution. Implementing the criteria of a maximum resolution of 50 yr/sample, would leave only a handful of pollen records to discuss. The sparsity of samples that meet the stringent PAGES-2k resolution criterion occurs because palaeorecords with long time spans (>10,000 yrs) are typically sampled at coarser temporal resolution. Furthermore, many lowland sites have very low sedimentation rates, which preclude high-resolution sampling. Therefore we propose a more flexible temporal resolution, depending on the identified relevance of the case study. Records with a resolution of 200 to 300 yr are included in our discussion. 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 (Figs. 6A-G). The references to all records discussed are presented in Table 3. The maps of Figs. 6-14 were created using ArcGIS 10.1TM software (Esri, 2012). The hydric balance and temperature summary figures are mere qualitative representations of the climatic information that was already published. The duration, chronologies and climatic tendencies were extracted as in the original publication based solely in the available pollen information, and no further analysis or reinterpretation was made. For reference, the color scales represent climatic states assigned

by the original authors, and in most of the cases the reference (white color in the legend) is the “mean climatic state” throughout the pollen reconstruction, and not necessarily the modern climate. Therefore, the white color was assigned to intermediate states, transitional states, or intervals without clear signs of any climatic tendency. The intervals without signal or hiatuses are denoted with a cross. To unify the climatic variables, we assumed that increments in precipitation, lake level, runoff, or seasonal rainfall correspond to positive hydric balance states (and vice versa). Similarly, increments in seasonal temperatures or in the frequency of warm pulses were translated in the figure as intervals with high temperatures (and vice versa).

Climate-vegetation interaction in the Venezuelan Guayana highlands and uplands

The study area, 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, ‘tepui’). 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 SI-2.

In the GS, 22 pollen records cover the last 2ka. 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 Apakarά 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 Churí Chim-2 and Apakarά contains 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 has 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 ~2.5ka. This constancy can be extended to all the tepuian summits studied so far during the last 6 ka (except Churí). 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 a record valuable for LOTRED-SA. 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 2ka, 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. The Eruoda summit is considered unaffected by human interference (Fig. 7B). 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 dominated by broad-leaved meadows (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 centred 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 NA 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., 2015b), 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. Of this number, 21 fulfilled four of the PAGES-2k criteria, another 24 fulfilled three criteria, and the remaining records presented at least two dating control points 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 during most part of the last 2 ka, and were therefore excluded for climate reconstructions. From the remaining records, only Laguna Pallcacocha and Papallacta PA1-08 in Ecuador 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. Most of the records complying with three criteria (n=24), most of them identify human presence in the near surrounding of the record during a reasonable period of time, leaving only ECSF Refugio potentially suitable for 2k climate reconstructions.

Beginning at the far N of the region (Fig. 8B and Fig. 8), Lake Valencia is represented by three cores with varying quality in chronology and resolution. In spite of the low resolution sampling (10-14 samples for the last 2 ka), some general information can be derived from the joint interpretation of these three cores. 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 forest 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 Medieval Climate Anomaly (MCA, ~ 1.15-0.65 ka), while a period of scarce vegetation could be related to the LIA (~ 0.6-0.1 ka). 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 eastern Colombian savannas, three pollen records fulfil at least three criteria. 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; Wille et al., 2003). 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, expanding *Mauritia* palm forest during this period was observed in several records considered to reflect increased local water availability and precipitation (Fig. 8B), and/or human impact (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. Interestingly, 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. Andean records can display dissimilar timing and trends behaviours due to differences in precipitation along the eastern Andean flank and specific regional landscapes (Moscol Olivera and Hooghiemstra, 2010; Marchant et al., 2001). A different kind of index to highlight vegetation-climate interaction was used in the eastern Ecuadorian Andes at Papallacta PA1-08. Established to characterize the SASM and ENSO, the index interprets cloud transported forest pollen taxa 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 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). Cold and moist conditions are related to high abundances of Poaceae, *Isoëtes* and *Gentianella*. 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 1.4 ka and 0.8 ka respectively. Climate was considered to be drier overall before 1.2 ka.

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 eastern Andean flank, at mid-elevation (1370 masl) within the cloud forest fulfils two of the criteria, while (ii) Urpi Cocha on the Pacific coast at sea-level, ~ 1 km inland within the archaeological site of Pachacmac (near Lima), satisfies four of the criteria. Of the seven sites considered in this review during the last 2 ka: 2 records (Cerro Llamoca and Consuelo) show no human interference, 1 record (Chicha-Soras) indicates humans from 1.5 ka onwards, and the other 4 (Marcacocha, Pacucha, Nevado Coropuna, and Urpi Cocha) indicate human impact 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 Schitteck 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 (4450 masl) indicates a succession of dry and moist episodes (Fig. 9B). After 0.5 ka sediments at Cerro Llamoca 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 eastern 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 (~ 3500 masl) 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., 2013). 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 over 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 (3300 masl) successive peaks in Cyperaceae pollen have been interpreted as indicative of three periods of elevated aridity while elevated *Plantago* ~1.9 ka is suggested to indicate cooler conditions, and *Alnus* ~1-0.5 ka could indicate warmer and drier conditions (Chepstow-Lusty et al., 1996); 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 Kocho significant changes to the pollen assemblage in the last 2 ka are attributed to human activity rather than climate.

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 communities and human populations. However, two records infer significant changes in temperature related to vegetation/human occupation: (1) Marcacocha when the sudden stop in agricultural activities is attributed to colder temperatures, and (2) at Coropuna when the increase of human occupation (expansion of Inca culture) at higher elevation shows that there was no glacier and warmer temperatures. On the Altiplano variation in the SASM has been attributed as a major driver of changes in moisture balance at Llamoca, Coropuna, Pacucha through altering the summer precipitation. SASM is also thought to be responsible for precipitation variation on the eastern Andean flank (Consuelo), while on the western Andean flank (Urpi Cocha) precipitation variation is attributed to the ENSO through tsunamis and the abrupt floodings on the Pacific coast. Although the pollen records of the Altiplano are likely to be somewhat obscured by the agricultural activities and irrigation of the crops all the records point towards a dry event occurring roughly between 1.2 and 0.75 ka.

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. Only 5 records complied with all four of the criteria and 11 records met with three criteria (Table 3). Most of the remaining records span a period ≥ 0.5 ka, but do not meet with any of the other criteria. One of these records, Laguna 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.

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. However, 5 records were found to meet the criteria: Quistococha, Werth, Granja, Fazenda Cigana and French Guiana K-VIII (Table 3, Fig. 10A).

Lake Quistococha in the NE Peruvian Amazon is an infilled river channel 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. Site Werth is surrounded by humid evergreen rainforest. 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. Its location is at the margin of the modern Madeira-Tapajós rainforest ecoregion, which extends southwards from the main Amazon River to the southern margin of the Amazon Basin in Bolivia (Olson et al., 2010). The record has a maximum age of 6 ka and indicates that savanna characterised the landscape around Granja 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 derived from a palm swamp in the savanna-gallery forest mosaic landscape of N Roraima State, 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, which the authors attribute 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) infer 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 is situated in from the coastal wetland savanna of French Guiana. The 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, however, charcoal abundance increases, probably reflecting more intensive use of fire by colonial populations. This again is a record that reflects substantial anthropogenic impact on the landscape, and is therefore not suitable as an independent proxy record of climate-induced vegetation change; at least not within the last ~0.8 ka.

Climate-vegetation interaction in Southern and Southeastern Brazil

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). The Atlantic rainforest occurs in S-SE Brazil as a 100 to 200 km narrow zone in the coastal lowlands along the Atlantic Ocean, and on the coastal eastern slopes of the mountain ranges. The tropical semi-deciduous forest occurs further inland in SE Brazil. The Cerrado is found primarily in C Brazil, but also in the N part of SE Brazil. The subtropical grasslands are found in highland S Brazil and lowlands of the southernmost region of S Brazil. Additional background information is provided in SI-3.

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 are presented, considering the 7 records sites that fulfil some of the criteria (Table 3, Fig.11A).

Sites located in the mountains of S-SE Brazil and from the transition area between the subtropics and tropics are sensitive to both temperature and precipitation, e.g. the length of the dry season is considered to play an important role. 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 Rincão 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 in the late Holocene period under the current climatic conditions with a ~ 3-month dry seasons. In the mountains of SE Brazil (e.g. Serra dos Orgãos 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 Pampa plains

This region extends E of the Andes, between 30 and 40°S (Fig. 6F) and is characterized by dominant aeolian landforms marking the structural characteristics of the subsurface geology and climatic gradient of the landscape (Zárate and Tripaldi, 2012). The natural vegetation of the Pampa is a tree-less grassland. Potential vegetation units can be characterized as: E Pampa, inland Pampa and S Pampa, based on phytosociological characteristics, historical observations on land use, and climatic and geomorphological differences (Tonello and Prieto, 2008; SI-4). The 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.

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 (Fig. 12A; 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 or exposed plains. The multi-proxy approach allows the identification of responses to natural and/or anthropogenic forcing factors. Pollen together with non-pollen palynomorphs and plant macrofossil analysis present similar trends in the lake evolution that support climate to be a regional trigger of change (Stutz et al., 2015). From 2 to 0.5 ka an instable regional environment with drier climatic conditions than present are inferred from the region, 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 switched to Cyperaceae dominance and aquatic plants similar to modern community. 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 0.3 ka, indicated by high Cyperaceae abundances (Fig. 12B).

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 (SI-5). 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.

In this region, there are 47 pollen records that cover the last 2 ka with at least one chronological control point during this period. Of these, the 18 records that fulfil PAGES-2k criteria are mostly concentrated in the temperate forests, and only 2 records originate each from subtropical forest (sclerophyllous forest) and Patagonia (Table 3; Fig. 13A).

At the most southerly sites, 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). 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). Similarly, 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 Southern Annular Mode (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, 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.12A). 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 followed by 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), Laguna 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 6k with an important reversion 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*. Laguna 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 cold-warm phases which were associated with the MCA period, whereas cold and wet conditions 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 Laguna Aculeo record (34°S) shows dominance of Poaceae dominance 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 alternating with several dry pulses. A major dry peak at 0.4 ka may be related to climate and/or human activity.

Laguna Potrok Aike and Laguna 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 general, indicators of human activities in pollen records are decrease in forest taxa (degraded forest) and/or forest representation (deforestation), presence of crops like *Zea mays*, *Manihot esculenta*, *Phaseolus* and *Ipomoea*, crop-related herbs *Rumex*, increase of grasses/herbs like Poaceae, Cyperaceae and Asteraceae subf. Cichorioideae, increase of disturbance indicators like Chenop/Am, *Cecropia*, *Vismia*, ferns and palms (e.g. *Mauritia* and *Euterpe/Geonoma*), and presence of charcoal peaks due to anthropogenic fire (Fig.14). *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 species known as disturbance indicators (*Cecropia* and *Mauritia*) need additional proxies to derive conclusive findings. Only by looking at pollen changes in context with other evidence – e.g. charcoal, limnology, sedimentology, archaeology- can the correct origin of these changes be identified.

In any palaeo-reconstruction concerning the past 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. Similar to human indicators in pollen records, complementary paleo-proxies can support more confident interpretation. This further highlights the difficulty of inferring climate-induced vegetation changes, without reference to independent climate proxy data, such as geochemical records from speleothems.

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 high fire regimes 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 to the study area 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 (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 (van Geel and Van Der Hammen, 1973) and Pantano de Genagra (Behling et al., 1998b). In several Andean diagrams, *Rumex* marked the onset of more intense land use by Europeans since 0.4 ka (Bellwood, 2004). 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 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) are 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 eastern Andean flank (Consuelo), and low in the west (Urpi Kocha; 52 masl), nearby archaeological site).

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 (Behling et al., 1998a). 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).

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 land use 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 S Andes and Patagonia, there is not conclusive evidence of native human activities in the pollen records and native-fire disturbance has been long discussed. Charcoal records from E Andes 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).

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 (cow and horse) and crops (wheat, sunflower), but the intensive agricultural activities only began 0.05 ka (Ghersa and León, 2001). The paleoenvironmental 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.

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 (e.g. Granja, French Guiana K-VIII in the Amazon basin) 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, 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. 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 2 ka reconstruction.

Venezuelan Guayana highlands and uplands

In this region, highlands and uplands are discussed separately due to their outstanding disparities 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 paleoecological records, they have remained in this state at least since the early Holocene. Therefore, climate has been the main driver of change. Paleoecological 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 on these proposals. So far, paleoecological 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, thus avoiding circularity. 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., in prep.).

In the GS uplands, the situation is very different and the main driver of ecological change is fire. This does not mean that eventual 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 paleoclimatic trends based on the Cariaco records have been used as a reference for the GS uplands (Rull et al., 2013) but a more local paleoclimatic record for this area is still lacking and urgently needed, not only for the last 2 ka but also for the entire Holocene. For the highlands, such record should be based on multiproxy high-resolution records. In this case, lakes are abundant and finding a suitable coring site should be much easier but administrative constraints also apply. Here fieldwork permits are even more difficult to obtain as most potential coring sites fall within indigenous territories. Another limitation is that most paleoecological 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 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 (Rull *et al.*, in prep.).

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., 2011). Before that time, the GS landscape was different from the present, including larger extents of forested areas since the Lateglacial 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 area, the vegetation responses studied have been normally related to ENSO and ITCZ movements and their consequences in the ocean-atmosphere circulation patterns. These two main drivers are included in Niño 3.4, AMO, IPO and TNA modes, which are those acting in the area as shown in the Figs. 2-5 (especially regarding temperature). Previously the effect of SAM has hardly been considered and the lack of AMO in the region regarding precipitation is surprising. It is noteworthy to compare the climatic inferences made through fossil pollen records and 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 in a wide range of factors, including both temperature and precipitation. Its interpretation in the fossil record is therefore complex and sometimes ambiguous. On the other hand, climate modes have showed the potential large effect of both temperature and precipitation trends 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 previous 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 driven modes in this region have been of a lesser magnitude than those required to cross the vegetation tolerance ranges or the intrinsic characteristics of the sites studied so far inhibit detecting any change.

Northern Andes

Pristine regions have been not identified with certainty within this region, inhibiting 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 or human influence. Along the Pacific coast, general wetter conditions prevailed (Fig. 8B) but tectonic events might be unsettling clear patterns. Interpretation of the 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 strong overlapping climate signals within and between years (Figs. 2-5; Marchant et al., 2001). The Papallacta highlights the two modes of precipitation variability that interplay in this region, namely the eastern equatorial Pacific SST and the Atlantic SST, showed dominant climate forcing in the N Andes until 0.45 ka and interdecadal variability during the last 0.5 ka, respectively. 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 (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. The sites in the Andean region are much more influenced by local geographical variability, causing a more variable response mechanism.

Central Andes

The records of the Altiplano suggest an oscillation in moisture availability (precipitation) on a multi-centennial timescale during the last 2 ka (Fig. 9). These oscillations are probably due to 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 (the high elevation grassland (Puna) versus mid elevation Andean forest). The archaeological site of Cerro Llamoca provides the most robustly dated record (33 radiocarbon ages); however, the strong local human influence means that climatic interpretations of palaeological evidence should be done with caution. Records of glacial advance and retreat from the Altiplano record variations associated with the LIA, but in all records, apart from

Llamoca, any climatic impact of the LIA on vegetation is masked by the European conquest effects (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. However, modelling suggests that on an annual scale temperature (Figs. 2 and 3), rather than precipitation (Figs. 4 and 5) is more likely to have altered due to switch in climate mode; particularly in the western part of the C Andes. The increase in temperature observed at Coropuna during the Inca period, after 0.85 ka, could correspond to El Niño or IPO forcing and the decrease in temperature observed at Marcacocha between 1.85 and 0.85 ka could be related to La Niña. Similarly these modes, show a high influence on 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. Also the TSA mode shows a strong influence on the Bolivian Altiplano. 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 communities and human populations. The increase of temperature induced by Niño and IPO on the Figs. 2 and 3 show no link with the precipitation. On the Altiplano variation in the SASM has been attributed as a major driver of changes in moisture balance at Llamoca, Coropuna, Pacucha, Consuelo through altering the summer precipitation. Precipitation patterns (Figs. 4 and 5) are less pronounced as it occurs here during a short seasonal period of 2-3 months, hence the used month average weakens the correlation. Notwithstanding, ENSO has been shown to have significant influence in the region (both temperature and precipitation) in numerous studies.

Lowland Amazon basin

Figs. 2-5 reinforce the importance of the SAM in Amazonia, a pattern that has been identified and discussed extensively in the palaeoecology literature of lowland Amazonia. The SAM is recognised as a key driver of precipitation and attributed to the expansion of rainforest during the late Holocene, which is observed in the large lake records from S Amazonia (Chaplin, Bella Vista, Orícore, Carajás). However, these sites do not meet the PAGES-2k dating criteria. As for its effect on temperature, in this region vegetation records are probably not sensitive to small temperature changes (e.g. 0.5°C) that might relate to SAM

strength. The sensitivity of the records could be related to the temperature and precipitation ranges of tropical plant families (Punyasena, 2008; Punyasena et al., 2008). Figs. 2-5 also show considerable spatial complexity in climate over lowland Amazonia, in terms of the impact of different climate modes, especially ENSO. However, if modes such as ENSO do have a long term drying effect over the past 2 ka in lowland Amazonia, it does not appear to affect vegetation in a way that is visible in the pollen records that we have reviewed. Given the size of the region and the relative sparseness of sites, it is perhaps unlikely that such spatial complexity would be captured.

The better-resolved late Holocene records tend to come from small lake basins (e.g. oxbows), which have small pollen catchment areas. This means that they reflect predominantly local-scale changes and are, therefore, more susceptible to having their palaeo-record 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 records (Iriarte et al., 2012; Whitney et al., 2014; Carson et al., 2014, 2015);.

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, an 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. Including 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 Laguna 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 and Orícore, 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 eastern 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: (1) Many archives, in particular peat bogs have a very low sedimentation rates. Often 100 cm of peat deposits cover already the complete Holocene and the last 2000 years have relative small amount of deposits; (2) The upper part of peat archives actively growing roots and it is difficult to date.

However, general vegetation changes in S/SE Brazil can be explained by a change to wetter conditions, in particular due the reduction of the dry season length. This is generally reflected in SE Brazil between 6 to 4 ka, and in particular strong in S/SE Brazil during the ~ 1 ka. Several new records for S/SE Brazil are in process or to be studied in the next years. These records will most likely present improved chronology for the last 2 ka. Additional studies on this period are considered relevant for regional vegetation conservation and management plans (Behling and Pillar, 2007). The climate modes of the continent display a relatively simple pattern within this region as the degree of overlap is minimal.

Pampa plains

There are several pollen records in Pampa plains that span Holocene times, but few of them have well resolved chronologies for the last 2 ka. Just one site fulfils all PAGES-2k criteria. Conventionally, pollen analyses in the region were carried out in 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 has been focused on elucidating palaeoenvironmental changes at high temporal resolution during the last 2 ka. Furthermore, the Pampa plains has 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 higher resolution is necessary.

General climatic tendencies in the region can be inferred although the few accurate pollen records are available. While individual palaeoecological studies reveal local developments, general patterns emerge when information from several sites is combined together, such as Lonkoy and Hinojales-San Leoncio. A multiproxy approach, including pollen analyses, shows synchronic 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.*, 2015). These climatic inferences are valid for the SE region but do not extend to the entire Pampa plains. As seen in Figs. 2-5, these plains falls outside the areas influenced by strong climate modes expressions. New paleoenvironmental reconstructions based on pollen records are needed to disentangle the intrinsic ecosystem variability from climate, and to elucidate if climatic events as MCA or LIA had different expressions in the Pampa region.

Southern Andes and Patagonia

Even though a high number of pollen records are available in the region, just 18 (between 32-54°S) fulfil the PAGES-2k criteria. In Patagonia most of pollen studies have been carried out on long temporal records (in many cases until end of Last Glacial Maximum) focusing on the Pleistocene-Holocene transition or the entire Holocene vegetation and climate dynamics. Moreover, appropriate records in areas of northern S Andes and Patagonia, are scarce because of the absence of depositional sites and archives or the lack of palaeo-research.

The pollen records are considered to mainly reflect the SWWB. 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 in a latitudinal gradient. Those sites located in the Patagonia receive extreme precipitation events from east. Superimposed to SWWB and SPA dynamics are Southern Annular Mode/Antarctic Oscillation (SAM) and ENSO (Figs. 2-5). Thus, the comparison between N and S records could shed light on expansion/retraction and/or latitudinal shifts of the SWWB, or differential influence of 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. Records N of 41°S show more climatic variability. Differences in seasonality is a key feature of precipitation records between N Patagonia (summer rainfall, e.g. Lago San Pedro) and central Chile (winter rainfall, e.g. Lago Aculeo and Palo Colorado). Furthermore, southernmost Patagonia arises as a key area to study climate-vegetation variability associated to SAM (e.g. Lago Cipreces). Sites in N Patagonia and C Chile reflect synchronicity with ENSO activity (e.g. Lagos San Pedro and Aculeo) given the relationship between high precipitation/El Niño phase and low precipitation/La Niña phase (Montecinos and Aceituno, 2003). LIA and MCA chronozones are well recorded both in southern and northern Patagonia (e.g. Lagos Cipreces, Peninsula Avellaneda Bajo, San Pedro), however not in central Chile. The region cannot be explained by a single climate unit due to the presence of different climatic modes and forcing. Different patterns are distinguished (Fig. 13B), due to their geographical position, latitude and E/W side of the Andes, and intrinsic sensitivity of each record to climatic variability. For example, wet conditions are inferred in N Patagonia between ~1.5-0.3 ka whilst in S Patagonia dry conditions dominated with increased variability.

6. Synthesis and Conclusions

Although the number of pollen records suitable for a 2 ka climate reconstruction is still relatively small compared to the total potential number of records available from South America (Flantua et al., 2015b), an increasing number of records are showing potential for inclusion in PAGES-2k. From reviewing c. 180 pollen records from South America we conclude that:

- The lack of South American records that fulfil PAGES-2k criteria is an issue of short versus long records. Most of the more important records have been ruled out because they turned out to be “old” and based on the sedimentation rates of the sedimentary archives, radiocarbon samples within the last two millennia are mostly missing.
- Pollen records detect long-distance synchronicity (differences and similarities) in vegetation changes as an indication of regional precipitation and temperature variability, but they also detect the local-scale change/variability. 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. Hence pollen records can serve as integrating proxies over long distances and allow assessing changes in the large-scale atmospheric circulation. Therefore they can serve as powerful archives, which can help better understand past changes in the strength and area of influence of climate modes such as ENSO or the AMO.

- Throughout South America a number of overlapping climate modes operate, meaning that every single pollen record most likely captures the signal of various 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 best ascribed to the degree of climate mode interaction at a location.
- Depending on the geographical and altitudinal location a record may be more sensitive 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 /precipitation- driven changes to forcing from climate modes originating in either from Atlantic or Pacific.
- For human impact studies, it is important to consider a set of different proxies to make more confident interpretations in terms of climate vs human drivers of vegetation changes.
- There is a need to increase efforts in high- resolution studies with accurate chronology for the last 2 ka.
- 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 notorious known for its paucity of records with good dating (e.g. Ledru et al., 1998). Therefore the few valuable sites available should be considered for the overall purpose of understanding vegetation-climate linkages..

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-proxy dataset is hampered by the current gap between the palynological and the climate dynamics and modelling 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.*, 2013) 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 this southern SA. Providing additional climate estimates is not common feature in palynological studies and this missing link becomes more obvious when the palynology community is being engaged into 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 artefacts (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 and any climatic interpretation is aimed.

3. For the stated purposes of the current and future PAGES initiatives, researchers should be motivated to further improve chronologies for existing sites. 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 modelling, which can provide a framework for identifying patterns and trajectories of change (e.g. Gosling and Williams, 2013).
4. 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 with NE Brazil-Guianas and Brazil with SE border with Argentina.).
5. All Andean zones are quite active from tectonic and volcanic points of view, and those drivers will have had huge impacts on the vegetation and maybe in the fossil pollen records signal. However, this feature has been only included in the southern region of 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 multi-proxy approach for paleoecological integration (Flantua et al., 2015).
6. In this paper we focused less on the seasonal contrasts throughout the continent, but in southern SA the seasonal component is extremely important, as the latitudinal gradient heavily influences the rainfall pattern throughout the continent. Precipitation in this region is the limiting factor for the growth and production of pollen. 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.

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Contributions

S.F., C.G., H.H. conceived the paper and H.H. supervised the project. M.V. developed the climate modes and corresponding figures, IO supported the interpretation of the climate settings of the N and C Andes; HB the S and SE Brazil sections, JFC, FM, BSW the lowland Amazon sections, WDG, MPL the C Andes sections, SF, VR, HH the N Andes sections; AM, MST the Patagonia and S Andes sections; AM the Pampa sections, CGZ and SF provided the initial drafts of the climate summary figures and all authors discussed the results and implications; SF, CH, MV, BSW, JFC, HH structured and edited the manuscript; All authors commented on the manuscript at all stages.

8. References

- Andreoli, R. V. and Kayano, M. T.: ENSO-related rainfall anomalies in South America and associated circulation features during warm and cold Pacific decadal oscillation regimes, *Int. J. Climatol.*, 25(15), 2017–2030, doi:10.1002/joc.1222, 2005.
- Behling, H. and Pillar, V. D.: Late Quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern Araucaria forest and grassland ecosystems, *Philos. Trans. R. Soc. B Biol. Sci.*, 362(1478), 243–251, doi:10.1098/rstb.2006.1984, 2007.
- Behling, H., Hooghiemstra, H. and Negret, A.: Holocene history of the Chocó rain forest from Laguna Piusbi, Southern Pacific lowlands of Colombia, *Quat. Res.*, 50, 300–308, 1998a.
- Behling, H., Negret, A. J. and Hooghiemstra, H.: Late Quaternary vegetational and climatic change in the Popayán region, southern Colombian Andes, *J. Quat. Sci.*, 13(1), 43–53, 1998b.
- Bellwood, P.: *First Farmers: The Origins of Agricultural Societies*, Wiley., 2004.

- 1410 Berrio, J. C., Hooghiemstra, H., Behling, H., Botero, P. and Van der Borg, K.: Late-
1411 Quaternary savanna history of the Colombian Llanos Orientales from Lagunas Chenevo and
1412 Mozambique: a transect synthesis, *The Holocene*, 12(1), 35–48,
1413 doi:10.1191/0959683602hl518rp, 2002.
- 1414 Berry, P. E., Huber, O. and Holst, B. K.: Floristic analysis and phytogeography, in *Flora of*
1415 *the Venezuelan Guayana*, vol. 1. Introduction, edited by P. E. Berry, B. K. Holst, and K.
1416 Yatskievych, pp. 161–191, Missouri Botanical Garden Press, St. Louis., 1995.
- 1417 Boninsegna, J. A., Argollo, J., Aravena, J. C., Barichivich, J., Christie, D., Ferrero, M. E.,
1418 Lara, A., Le Quesne, C., Luckman, B. H., Masiokas, M., Morales, M., Oliveira, J. M., Roig,
1419 F., Srur, A. and Villalba, R.: Dendroclimatological reconstructions in South America: A
1420 review, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 281(3–4), 210–228,
1421 doi:10.1016/j.palaeo.2009.07.020, 2009.
- 1422 Briceño, H., Schubert, C. and Paolini, J.: Table-mountain geology and surficial geochemistry:
1423 Chimantá Massif, Venezuelan Guayana shield, *J. South Am. Earth Sci.*, 3(4), 179–194,
1424 doi:10.1016/0895-9811(90)90002-I, 1990.
- 1425 Bush, M. B. and Rivera, R.: Reproductive ecology and pollen representation among
1426 neotropical trees, *Glob. Ecol. Biogeogr.*, 10, 359–367, 2001.
- 1427 Bush, M. B., De Oliveira, P. E., Colinvaux, P. A., Miller, M. C. and Moreno, J. E.:
1428 Amazonian paleoecological histories: one hill, three watersheds, *Palaeogeogr. Palaeoclimatol.*
1429 *Palaeoecol.*, 214(4), 359–393, doi:10.1016/j.palaeo.2004.07.031, 2004.
- 1430 Carson, J. F., Whitney, B. S., Mayle, F. E., Iriarte, J., Prümers, H., Soto, J. D. and Watling, J.:
1431 Environmental impact of geometric earthwork construction in pre-Columbian Amazonia,
1432 *Proc. Natl. Acad. Sci.*, 111(29), 10497–10502, doi:10.1073/pnas.1321770111, 2014.
- 1433 Carson, J. F., Watling, J., Mayle, F. E., Whitney, B. S., Iriarte, J., Prümers, H. and Soto, J. D.:
1434 Pre-Columbian land use in the ring-ditch region of the Bolivian Amazon, *The Holocene*,
1435 0959683615581204, doi:10.1177/0959683615581204, 2015.
- 1436 Carvalho, L. M. V., Jones, C. and Ambrizzi, T.: Opposite phases of the Antarctic Oscillation
1437 and relationships with intraseasonal to interannual activity in the tropics during the Austral
1438 Summer, *J. Clim.*, 18(5), 702–718, doi:10.1175/JCLI-3284.1, 2005.
- 1439 Cheng, H., Sinha, A., Cruz, F. W., Wang, X., Edwards, R. L., d’ Horta, F. M., Ribas, C. C.,
1440 Vuille, M., Stott, L. D. and Auler, A. S.: Climate change patterns in Amazonia and
1441 biodiversity, *Nat. Commun.*, 4, 1411, doi:10.1038/ncomms2415, 2013.
- 1442 Chepstow-Lusty, A.: Agro-pastoralism and social change in the Cuzco heartland of Peru: a
1443 brief history using environmental proxies, *Antiquity*, 85(328), 570–582,
1444 doi:10.1017/S0003598X0006796X, 2011.
- 1445 Chepstow-Lusty, A. and Jonsson, P.: Inca Agroforestry: Lessons from the Past, *AMBIO J.*
1446 *Hum. Environ.*, 29(6), 322–328, doi:10.1579/0044-7447-29.6.322, 2000.

- 1447 Chepstow-Lusty, A. J., Bennett, K. D., Switsur, V. R. and Kendall, A.: 4000 years of human
1448 impact and vegetation change in the central Peruvian Andes — with events paralleling the
1449 Maya record?, *Antiquity*, 70(270), 824–833, doi:10.1017/S0003598X0008409X, 1996.
- 1450 Cohen, M. C. L., Pessenda, L. C. R., Behling, H., de Fátima Rossetti, D., França, M. C.,
1451 Guimarães, J. T. F., Friaes, Y. and Smith, C. B.: Holocene palaeoenvironmental history of the
1452 Amazonian mangrove belt, *Quat. Sci. Rev.*, 55, 50–58, doi:10.1016/j.quascirev.2012.08.019,
1453 2012.
- 1454 Colson, A. B.: Routes of knowledge, an aspect of regional integration in the circum-Roraima
1455 area of the Guayana highlands., *Antropológica*, 63/64, 103–149, 1985.
- 1456 Curtis, S. and Hastenrath, S.: Forcing of anomalous sea surface temperature evolution in the
1457 tropical Atlantic during Pacific warm events, *J. Geophys. Res. Oceans*, 100(C8), 15835–
1458 15847, doi:10.1029/95JC01502, 1995.
- 1459 D’Apolito, C., Absy, M. L. and Latrubesse, E. M.: The Hill of Six Lakes revisited: new data
1460 and re-evaluation of a key Pleistocene Amazon site, *Quat. Sci. Rev.*, 76, 140–155,
1461 doi:10.1016/j.quascirev.2013.07.013, 2013.
- 1462 Dillehay, T. D., Eling, H. H. and Rossen, J.: Preceramic irrigation canals in the Peruvian
1463 Andes, *Proc. Natl. Acad. Sci. U. S. A.*, 102(47), 17241–17244,
1464 doi:10.1073/pnas.0508583102, 2005.
- 1465 Doyle, M. E. and Barros, V. R.: Midsummer low-level circulation and precipitation in
1466 subtropical South America and related sea surface temperature anomalies in the South
1467 Atlantic, *J. Clim.*, 15(23), 3394–3410, doi:10.1175/1520-
1468 0442(2002)015<3394:MLLCAP>2.0.CO;2, 2002.
- 1469 Enfield, D. B., Mestas-Núñez, A. M., Mayer, D. A. and Cid-Serrano, L.: How ubiquitous is
1470 the dipole relationship in tropical Atlantic sea surface temperatures?, *J. Geophys. Res.*
1471 *Oceans*, 104(C4), 7841–7848, doi:10.1029/1998JC900109, 1999.
- 1472 Enfield, D. B., Mestas-Núñez, A. M. and Trimble, P. J.: The Atlantic Multidecadal
1473 Oscillation and its relation to rainfall and river flows in the continental U.S., *Geophys. Res.*
1474 *Lett.*, 28(10), 2077–2080, doi:10.1029/2000GL012745, 2001.
- 1475 Espinoza Villar, J. C., Ronchail, J., Guyot, J. L., Cochonneau, G., Naziano, F., Lavado, W.,
1476 De Oliveira, E., Pombosa, R. and Vauchel, P.: Spatio-temporal rainfall variability in the
1477 Amazon basin countries (Brazil, Peru, Bolivia, Colombia, and Ecuador), *Int. J. Climatol.*,
1478 29(11), 1574–1594, doi:10.1002/joc.1791, 2009.
- 1479 Esri: ArcGIS, Redlands, CA., 2012.
- 1480 Fjeldsø, J. and Kessler, M.: Conserving the Biological Diversity of Polylepis Woodlands of
1481 the Highland of Peru and Bolivia. A Contribution to Sustainable Natural Resource
1482 Management in the Andes., NORDECO, Copenhagen., 1996.

- 1483 Flantua, S. G. A., Hooghiemstra, H. and Blaauw, M.: Quality assessment of chronologies in
 1484 Latin American pollen records: a contribution to centennial to millennial scale studies of
 1485 environmental change, *Clim Past Discuss*, 11(2), 1219–1262, doi:10.5194/cpd-11-1219-2015,
 1486 2015a.
- 1487 Flantua, S. G. A., Hooghiemstra, H., Grimm, E. C., Behling, H., Bush, M. B., González-
 1488 Arango, C., Gosling, W. D., Ledru, M. P., Lozano-García, S., Maldonado, A., Prieto, A. R.,
 1489 Rull, V. and Van Boxel, J. H.: Updated site compilation of the Latin American Pollen
 1490 Database: Challenging palynological research thriving, *Rev. Palaeobot. Palynol.*, In press,
 1491 2015b.
- 1492 Folland, C. K., Renwick, J. A., Salinger, M. J. and Mullan, A. B.: Relative influences of the
 1493 Interdecadal Pacific Oscillation and ENSO on the South Pacific Convergence Zone, *Geophys.*
 1494 *Res. Lett.*, 29(13), 21–1, doi:10.1029/2001GL014201, 2002.
- 1495 Garreaud, R. and Battisti, D. S.: Interannual (ENSO) and Interdecadal (ENSO-like)
 1496 Variability in the Southern Hemisphere Tropospheric Circulation*, *J. Clim.*, 12(7), 2113–
 1497 2123, doi:10.1175/1520-0442(1999)012<2113:IEAIEL>2.0.CO;2, 1999.
- 1498 Garreaud, R., Lopez, P., Minvielle, M. and Rojas, M.: Large-Scale control on the Patagonian
 1499 climate, *J. Clim.*, 26(1), 215–230, doi:10.1175/JCLI-D-12-00001.1, 2013.
- 1500 Garreaud, R. D., Vuille, M., Compagnucci, R. and Marengo, J.: Present-day South American
 1501 climate, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 281(3–4), 180–195,
 1502 doi:10.1016/j.palaeo.2007.10.032, 2009.
- 1503 Van Geel, B. and Van Der Hammen, T.: Upper Quaternary Vegetational and Climatic
 1504 Secuense of the Fuquene Area (Eastern Cordillera, Colombia)., *Palaeogeogr. Palaeoclimatol.*
 1505 *Palaeoecol.*, 14, 9–92, 1973.
- 1506 Ghera, C. M. and León, R. J. C.: Ecología del paisaje Pampeano: consideraciones para su
 1507 manejo y conservación, in *Ecología de Paisajes.*, edited by Z. Naveh and A. S. Lieberman, pp.
 1508 471–512, Editorial Facultad de Agronomía, Buenos Aires., 2001.
- 1509 Giannini, A., Chiang, J. C. H., Cane, M. A., Kushnir, Y. and Seager, R.: The ENSO
 1510 Teleconnection to the Tropical Atlantic Ocean: Contributions of the Remote and Local SSTs
 1511 to Rainfall Variability in the Tropical Americas*, *J. Clim.*, 14(24), 4530–4544,
 1512 doi:10.1175/1520-0442(2001)014<4530:TETTTT>2.0.CO;2, 2001.
- 1513 Gillett, N. P., Kell, T. D. and Jones, P. D.: Regional climate impacts of the Southern Annular
 1514 Mode, *Geophys. Res. Lett.*, 33(23), L23704, doi:10.1029/2006GL027721, 2006.
- 1515 González-Carranza, Z., Hooghiemstra, H. and Vélez, M. I.: Major altitudinal shifts in Andean
 1516 vegetation on the Amazonian flank show temporary loss of biota in the Holocene, *The*
 1517 *Holocene*, 22(11), 1227–1241, 2012.
- 1518 Gosling, W. D. and Williams, J. J.: Ecosystem service provision sets the pace for pre-
 1519 Hispanic societal development in the central Andes, *The Holocene*, 23(11), 1619–1624,
 1520 doi:10.1177/0959683613496296, 2013.

- 1521 Grimm, A. M., Barros, V. R. and Doyle, M. E.: Climate Variability in Southern South
1522 America Associated with El Niño and La Niña Events, *J. Clim.*, 13(1), 35–58,
1523 doi:10.1175/1520-0442(2000)013<0035:CVISSA>2.0.CO;2, 2000.
- 1524 Groot, M. H. M., Hooghiemstra, H., Berrio, J. C. and Giraldo, C.: North Andean
1525 environmental and climatic change at orbital to submillennial time-scales: Vegetation, water
1526 levels and sedimentary regimes from Lake Fúquene 130–27 ka, *Rev. Palaeobot. Palynol.*,
1527 197, 186–204, doi:10.1016/j.revpalbo.2013.04.005, 2013.
- 1528 Gupta, A. S. and England, M. H.: Coupled ocean–atmosphere–ice response to variations in
1529 the Southern Annular Mode, *J. Clim.*, 19(18), 4457–4486, doi:10.1175/JCLI3843.1, 2006.
- 1530 Van der Hammen, T. and Correal Urrego, G.: Prehistoric man of the Sabana de Bogotá: Data
1531 for an ecological prehistory, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 25(1–2), 179–190,
1532 doi:10.1016/0031-0182(78)90077-9, 1978.
- 1533 Hastenrath, S. and Greischar, L.: Circulation mechanisms related to northeast Brazil rainfall
1534 anomalies, *J. Geophys. Res. Atmospheres*, 98(D3), 5093–5102, doi:10.1029/92JD02646,
1535 1993.
- 1536 Hermanowski, B., da Costa, M. L. and Behling, H.: Environmental changes in southeastern
1537 Amazonia during the last 25,000 yr revealed from a paleoecological record, *Quat. Res.*, 77(1),
1538 138–148, doi:10.1016/j.yqres.2011.10.009, 2012.
- 1539 Huber, O.: Recent advances in the phytogeography of the Guayana region, South America.,
1540 *Mém. Société Biogéographique*, 3(4), 53–63, 1994.
- 1541 Huber, O.: Geographical and physical features, in *Flora of the Venezuelan Guayana*, vol. 1.
1542 Introduction, edited by P. E. Berry, B. K. Holst, and K. Yatskievych, pp. 1–62, Missouri
1543 Botanical Garden Press, St. Louis., 1995a.
- 1544 Huber, O.: Vegetation, in *Flora of the Venezuelan Guayana*, vol. 1. Introduction, edited by P.
1545 E. Berry, B. K. Holst, and K. Yatskievych, pp. 97–160, Missouri Botanical Garden Press, St.
1546 Louis., 1995b.
- 1547 Huber, O. and Febres, G.: *Guía ecológica de la Gran Sabana*, 1st ed., The Nature
1548 Conservancy, Caracas, Venezuela., 2000.
- 1549 Huber, O. and Riina, R., Eds.: *Glosario fitoecológico de las Américas: América del Sur:*
1550 *países hispanoparlantes*, Tamandúa., UNESCO; Fundación Instituto Botánico de Venezuela,
1551 Caracas, Venezuela., 1997.
- 1552 Iglesias, V. and Whitlock, C.: Fire responses to postglacial climate change and human impact
1553 in northern Patagonia (41–43°S), *Proc. Natl. Acad. Sci. U. S. A.*, 111(51), E5545–5554,
1554 doi:10.1073/pnas.1410443111, 2014.
- 1555 Iriarte, J., Power, M. J., Rostain, S., Mayle, F. E., Jones, H., Watling, J., Whitney, B. S. and
1556 McKey, D. B.: Fire-free land use in pre-1492 Amazonian savannas, *Proc. Natl. Acad. Sci.*,
1557 109(17), 6473–6478, doi:10.1073/pnas.1201461109, 2012.

- 1558 Kuentz, A., de Mera, A. G., Ledru, M.-P. and Thouret, J.-C.: Phytogeographical data and
1559 modern pollen rain of the puna belt in southern Peru (Nevado Coropuna, Western Cordillera),
1560 *J. Biogeogr.*, 34(10), 1762–1776, doi:10.1111/j.1365-2699.2007.01728.x, 2007.
- 1561 Leal, A., Perez, T. and Bilbao, B.: Contribution to Early Holocene vegetation and climate
1562 history of Eastern Orinoco Llanos, Venezuela, from a paleoecological record of a *Mauritia* Lf
1563 swamp, *Acta Amaz.*, 41(4), 513–520, 2011.
- 1564 Ledru, M. P., Bertraux, J. and Sifeddine, A.: Absence of Last Glacial Maximum Records,
1565 *Quat. Res.*, 49, 233–237, 1998.
- 1566 Legates, D. R. and Willmott, C. J.: Mean seasonal and spatial variability in gauge-corrected,
1567 global precipitation, *Int. J. Climatol.*, 10(2), 111–127, doi:10.1002/joc.3370100202, 1990.
- 1568 Lewis, S. L., Brando, P. M., Phillips, O. L., Van der Heijden, G. M. F. and Nepstad, D.: The
1569 2010 Amazon drought, *Science*, 331(6017), 554–554, doi:10.1126/science.1200807, 2011.
- 1570 Li, B., Nychka, D. W. and Ammann, C. M.: The value of multiproxy reconstruction of past
1571 climate, *J. Am. Stat. Assoc.*, 105(491), 883–895, 2010.
- 1572 Liebmann, B. and Marengo, J.: Interannual variability of the rainy season and rainfall in the
1573 Brazilian Amazon basin, *J. Clim.*, 14(22), 4308–4318, doi:10.1175/1520-
1574 0442(2001)014<4308:IVOTRS>2.0.CO;2, 2001.
- 1575 Li, W. and Fu, R.: Influence of cold air intrusions on the wet season onset over Amazonia, *J.*
1576 *Clim.*, 19(2), 257–275, 2006.
- 1577 Marchant, R., Behling, H., Berrio, J. C., Cleef, A., Duivenvoorden, J., Hooghiemstra, H.,
1578 Kuhry, P., Melief, B., Van Geel, B. and Van der Hammen, T.: Mid-to Late-Holocene pollen-
1579 based biome reconstructions for Colombia, *Quat. Sci. Rev.*, 20(12), 1289–1308, 2001.
- 1580 Marchant, R., Almeida, L., Behling, H., Berrio, J. C., Bush, M., Cleef, A., Duivenvoorden, J.,
1581 Kappelle, M., De Oliveira, P., Teixeira de Oliveira-Filho, A., Lozano-García, S.,
1582 Hooghiemstra, H., Ledru, M. P., Ludlow-Wiechers, B., Markgraf, V., Mancini, V., Paez, M.,
1583 Prieto, A., Rangel, O. and Salgado-Labouriau, M. L.: Distribution and ecology of parent taxa
1584 of pollen lodged within the Latin American Pollen Database, *Rev. Palaeobot. Palynol.*,
1585 121(1), 1–75, 2002.
- 1586 Marengo, J. A., Nobre, C. A., Tomasella, J., Oyama, M. D., Sampaio de Oliveira, G., de
1587 Oliveira, R., Camargo, H., Alves, L. M. and Brown, I. F.: The drought of Amazonia in 2005,
1588 *J. Clim.*, 21(3), 495–516, doi:10.1175/2007JCLI1600.1, 2008.
- 1589 Markgraf, V., Webb, R. S., Anderson, K. H. and Anderson, L.: Modern pollen/climate
1590 calibration for southern South America, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 181(4),
1591 375–397, 2002.
- 1592 Mayle, F. E. and Iriarte, J.: Integrated palaeoecology and archaeology – a powerful approach
1593 for understanding pre-Columbian Amazonia, *J. Archaeol. Sci.*, 51, 54–64,
1594 doi:10.1016/j.jas.2012.08.038, 2014.

- 1595 Mayle, F. E., Burbridge, R. and Killeen, T. J.: Millennial-Scale Dynamics of Southern
1596 Amazonian Rain Forests, *Science*, 290(5500), 2291–2294,
1597 doi:10.1126/science.290.5500.2291, 2000.
- 1598 McGlue, M. M., Silva, A., Zani, H., Corradini, F. A., Parolin, M., Abel, E. J., Cohen, A. S.,
1599 Assine, M. L., Ellis, G. S., Trees, M. A., Kuerten, S., Gradella, F. dos S. and Rasbold, G. G.:
1600 Lacustrine records of Holocene flood pulse dynamics in the Upper Paraguay River watershed
1601 (Pantanal wetlands, Brazil), *Quat. Res.*, 78(2), 285–294, doi:10.1016/j.yqres.2012.05.015,
1602 2012.
- 1603 Mendoza, V.: Evolución tetónica del Escudo de Guayana, *Bol. Geol.*, 7, 2237–2270, 1977.
- 1604 Montecinos, A. and Aceituno, P.: Seasonality of the ENSO-related rainfall variability in
1605 central Chile and associated circulation anomalies, *J. Clim.*, 16(2), 281–296,
1606 doi:10.1175/1520-0442(2003)016<0281:SOTERR>2.0.CO;2, 2003.
- 1607 Montoya, E. and Rull, V.: Gran Sabana fires (SE Venezuela): a paleoecological perspective,
1608 *Quat. Sci. Rev.*, 30(23–24), 3430–3444, doi:10.1016/j.quascirev.2011.09.005, 2011.
- 1609 Montoya, E., Rull, V., Stansell, N. D., Abbott, M. B., Nogué, S., Bird, B. W. and Díaz, W. A.:
1610 Forest–savanna–morichal dynamics in relation to fire and human occupation in the southern
1611 Gran Sabana (SE Venezuela) during the last millennia, *Quat. Res.*, 76(3), 335–344,
1612 doi:10.1016/j.yqres.2011.06.014, 2011.
- 1613 Moscol-Olivera, M. C. and Hooghiemstra, H.: Three millennia upper forest line changes in
1614 northern Ecuador: Pollen records and altitudinal vegetation distributions, *Rev. Palaeobot.*
1615 *Palynol.*, 163(1-2), 113–126, doi:10.1016/j.revpalbo.2010.10.003, 2010.
- 1616 Moscol Olivera, M. C. and Hooghiemstra, H.: Three millennia upper forest line changes in
1617 northern Ecuador: Pollen records and altitudinal vegetation distributions, *Rev. Palaeobot.*
1618 *Palynol.*, 163(1-2), 113–126, doi:10.1016/j.revpalbo.2010.10.003, 2010.
- 1619 Nobre, P. and Shukla, J.: Variations of sea surface temperature, wind stress, and rainfall over
1620 the tropical Atlantic and South America, *J. Clim.*, 9(10), 2464–2479, doi:10.1175/1520-
1621 0442(1996)009<2464:VOSSTW>2.0.CO;2, 1996.
- 1622 Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., V, G., Powell, N.,
1623 Underwood, E. C., D, J. A., Itoua, I., Strand, H. E., Morrison, J.C., Loucks, C. J., Allnutt, T.
1624 F., Ricketts, T. H., Kura, Y., Lamoreux, J.F., Wettengel, W. W., Hedao, P. and Kassem, K.
1625 R.: Terrestrial Ecoregions of the World: a new map of life on Earth, *BioScience*, 51(11), 933-
1626 938, 10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2, 2010.
- 1627 PAGES-2k Consortium: Continental-scale temperature variability during the past two
1628 millennia, *Nat. Geosci.*, 6(5), 339–346, doi:10.1038/ngeo1797, 2013.
- 1629 Polissar, P. J., Abbott, M. B., Wolfe, A. P., Bezada, M., Rull, V. and Bradley, R. S.: Solar
1630 modulation of Little Ice Age climate in the tropical Andes, *Proc. Natl. Acad. Sci.*, 103(24),
1631 8937–8942, doi:10.1073/pnas.0603118103, 2006.

- 1632 Punyasena, S. W.: Estimating Neotropical palaeotemperature and palaeoprecipitation using
1633 plant family climatic optima, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 265(3–4), 226–237,
1634 doi:10.1016/j.palaeo.2008.04.025, 2008.
- 1635 Punyasena, S. W., Eshel, G. and McElwain, J. C.: The influence of climate on the spatial
1636 patterning of Neotropical plant families, *J. Biogeogr.*, 35(1), 117–130, doi:10.1111/j.1365-
1637 2699.2007.01773.x, 2008.
- 1638 Rayner, N. A., Parker, D. E., Horton, E. B., Folland, C. K., Alexander, L. V., Rowell, D. P.,
1639 Kent, E. C. and Kaplan, A.: Global analyses of sea surface temperature, sea ice, and night
1640 marine air temperature since the late nineteenth century, *J. Geophys. Res. Atmospheres*,
1641 108(D14), 4407, doi:10.1029/2002JD002670, 2003.
- 1642 Ronchail, J., Cochonneau, G., Molinier, M., Guyot, J.-L., De Miranda Chaves, A. G.,
1643 Guimarães, V. and de Oliveira, E.: Interannual rainfall variability in the Amazon basin and
1644 sea-surface temperatures in the equatorial Pacific and the tropical Atlantic oceans, *Int. J.*
1645 *Climatol.*, 22(13), 1663–1686, doi:10.1002/joc.815, 2002.
- 1646 Rull, V.: Palaeovegetational and palaeoenvironmental trends in the summit of the
1647 Guaiquinima massif (Venezuelan Guayana) during the Holocene, *J. Quat. Sci.*, 20(2), 135–
1648 145, doi:10.1002/jqs.896, 2005a.
- 1649 Rull, V.: Vegetation and environmental constancy in the Neotropical Guayana Highlands
1650 during the last 6000 years?, *Rev. Palaeobot. Palynol.*, 135(3–4), 205–222,
1651 doi:10.1016/j.revpalbo.2005.03.008, 2005b.
- 1652 Rull, V.: Long-term vegetation stability and the concept of potential natural vegetation in the
1653 Neotropics, *J. Veg. Sci.*, n/a–n/a, doi:10.1111/jvs.12278, 2015.
- 1654 Rull, V. and Montoya, E.: *Mauritia flexuosa* palm swamp communities: natural or human-
1655 made? A palynological study of the Gran Sabana region (northern South America) within a
1656 neotropical context, *Quat. Sci. Rev.*, 99, 17–33, doi:10.1016/j.quascirev.2014.06.007, 2014.
- 1657 Rull, V. and Schubert, C.: The little ice age in the tropical Venezuelan Andes, *Acta Científica*
1658 *Venez.*, 40, 71–73, 1989.
- 1659 Rull, V., Vegas, T., Nogué, S. and Montoya, E.: Bureaucratic Obstruction of Conservation
1660 Science in the Guayana Highlands, *Conserv. Biol.*, 22(3), 508–509, doi:10.1111/j.1523-
1661 1739.2008.00960.x, 2008.
- 1662 Rull, V., Montoya, E., Nogué, S., Vegas-Vilarrúbia, T. and Safont, E.: Ecological
1663 palaeoecology in the neotropical Gran Sabana region: Long-term records of vegetation
1664 dynamics as a basis for ecological hypothesis testing, *Perspect. Plant Ecol. Evol. Syst.*, 15(6),
1665 338–359, doi:10.1016/j.ppees.2013.07.004, 2013.
- 1666 Safont, E., Rull, V., Vegas-vilarrúbia, T., Holst, B. k, Huber, O., Nozawa, S., Vivas, Y. and
1667 Silva, A.: Establishing a baseline of plant diversity and endemism on a neotropical mountain
1668 summit for future comparative studies assessing upward migration: an approach from

- 1669 biogeography and nature conservation, *Syst. Biodivers.*, 12(3), 292–314,
1670 doi:10.1080/14772000.2014.918061, 2014.
- 1671 Schäbitz, F., Wille, M., Francois, J.-P., Haberzettl, T., Quintana, F., Mayr, C., Lücke, A.,
1672 Ohlendorf, C., Mancini, V., Paez, M. M., Prieto, A. R. and Zolitschka, B.: Reconstruction of
1673 palaeoprecipitation based on pollen transfer functions – the record of the last 16 ka from
1674 Laguna Potrok Aike, southern Patagonia, *Quat. Sci. Rev.*, 71, 175–190,
1675 doi:10.1016/j.quascirev.2012.12.006, 2013.
- 1676 Schitteck, K., Forbriger, M., Mächtle, B., Schäbitz, F., Wennrich, V., Reindel, M. and Eitel,
1677 B.: Holocene environmental changes in the highlands of the southern Peruvian Andes (14° S)
1678 and their impact on pre-Columbian cultures, *Clim. Past*, 11(1), 27–44, doi:10.5194/cp-11-27-
1679 2015, 2015.
- 1680 Silverman, H.: *Andean Archaeology III: North and South*, Springer Science & Business
1681 Media., 2008.
- 1682 Silvestri, G. E. and Vera, C. S.: Antarctic Oscillation signal on precipitation anomalies over
1683 southeastern South America, *Geophys. Res. Lett.*, 30(21), 2115, doi:10.1029/2003GL018277,
1684 2003.
- 1685 Stutz, S., Tonello, M. S., Gonzalez Sagraria, M. A., Navarro, D. and Fontana, S.: Historia
1686 ambiental de los lagos someros de la llanura Pampeana desde el Holoceno medio. *Inferencias*
1687 *paleoclimáticas.*, *Lat. Am. J. Sedimentol. Basin Anal.*, In press, 2015.
- 1688 Takahashi, K.: The atmospheric circulation associated with extreme rainfall events in Piura,
1689 Peru, during the 1997–1998 and 2002 El Niño events, *Ann. Geophys.*, 22(11), 3917–3926,
1690 2004.
- 1691 Thomas, D. J.: *Order without government: the society of the Pemons indians of Venezuela*,
1692 University of Illinois Press, Illinois., 1982.
- 1693 Thompson, D. W. J. and Wallace, J. M.: Annular Modes in the Extratropical Circulation. Part
1694 I: Month-to-Month Variability*, *J. Clim.*, 13(5), 1000–1016, doi:10.1175/1520-
1695 0442(2000)013<1000:AMITEC>2.0.CO;2, 2000.
- 1696 Tonello, M. S. and Prieto, A. R.: Modern vegetation–pollen–climate relationships for the
1697 Pampa grasslands of Argentina, *J. Biogeogr.*, 35(5), 926–938, doi:10.1111/j.1365-
1698 2699.2007.01854.x, 2008.
- 1699 Tonello, M. S., Mancini, M. V. and Seppä, H.: Quantitative reconstruction of Holocene
1700 precipitation changes in southern Patagonia, *Quat. Res.*, 72(3), 410–420,
1701 doi:10.1016/j.yqres.2009.06.011, 2009.
- 1702 Tonello, M. S., Mancini, M. V., de Porras, M. E., Bamonte, F. P. and Sottile, G.: Pollen and
1703 climate dataset at southern Patagonia: evaluating weaknesses and strengths for quantitative
1704 palaeoclimatic reconstructions, Valdivia, Chile., 2010.

- 1705 Vélez, M. I., Wille, M., Hooghiemstra, H., Metcalfe, S., Vandenberghe, J. and Van der Borg,
1706 K.: Late Holocene environmental history of southern Chocó region, Pacific Colombia;
1707 sediment, diatom and pollen analysis of core El Caimito, *Palaeogeogr. Palaeoclimatol.*
1708 *Palaeoecol.*, 173(3), 197–214, 2001.
- 1709 Viglizzo, E. F. and Frank, F. C.: Ecological interactions, feedbacks, thresholds and collapses
1710 in the Argentine Pampas in response to climate and farming during the last century, *Quat. Int.*,
1711 158(1), 122–126, doi:10.1016/j.quaint.2006.05.022, 2006.
- 1712 Villalba, R., Grosjean, M. and Kiefer, T.: Long-term multi-proxy climate reconstructions and
1713 dynamics in South America (LOTRED-SA): State of the art and perspectives, *Palaeogeogr.*
1714 *Palaeoclimatol. Palaeoecol.*, 281(3–4), 175–179, doi:10.1016/j.palaeo.2009.08.007, 2009.
- 1715 Vuille, M. and Garreaud, R. D.: Ocean-atmosphere interactions on interannual to decadal
1716 timescales, in *Handbook of Environmental Change*, vol. 1, edited by J. A. Matthews, P. J.
1717 Bartlein, K. R. Briffa, A. Dawson, A. de Vernal, T. Denham, S. C. Fritz, and F. Oldfield,
1718 Sage Publications, London, Los Angeles, New Delhi, Singapore., 2012.
- 1719 Vuille, M., Bradley, R. S. and Keimig, F.: Interannual climate variability in the Central Andes
1720 and its relation to tropical Pacific and Atlantic forcing, *J. Geophys. Res. Atmospheres*,
1721 105(D10), 12447–12460, doi:10.1029/2000JD900134, 2000.
- 1722 Vuille, M., Burns, S. J., Taylor, B. L., Cruz, F. W., Bird, B. W., Abbott, M. B., Kanner, L. C.,
1723 Cheng, H. and Novello, V. F.: A review of the South American monsoon history as recorded
1724 in stable isotopic proxies over the past two millennia, *Clim Past*, 8(4), 1309–1321,
1725 doi:10.5194/cp-8-1309-2012, 2012.
- 1726 Wang, H. and Fu, R.: Cross-equatorial flow and seasonal cycle of precipitation over South
1727 America, *J. Clim.*, 15(13), 1591–1608, 2002.
- 1728 Whitney, B. S., Mayle, F. E., Punyasena, S., Fitzpatrick, K., Burn, M., Guillen, R., Chavez,
1729 E., Mann, D., Pennington, R. T. and Metcalfe, S.: A 45kyr palaeoclimate record from the
1730 lowland interior of tropical South America, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 307(1-
1731 4), 177–192, doi:10.1016/j.palaeo.2011.05.012, 2011.
- 1732 Whitney, B. S., Dickau, R., Mayle, F. E., Walker, J. H., Soto, J. D. and Iriarte, J.: Pre-
1733 Columbian raised-field agriculture and land-use in the Bolivian Amazon, *The Holocene*,
1734 24(2), 231–241, 2014.
- 1735 Wille, M. and Hooghiemstra, H.: Paleoenviromental history of the Popayán area since 27
1736 000 yr BP at Timbio, Southern Colombia, *Rev. Palaeobot. Palynol.*, 109(1), 45–63, 2000.
- 1737 Wille, M., Hooghiemstra, H., van Geel, B., Behling, H., de Jong, A. and van der Borg, K.:
1738 Submillennium-scale migrations of the rainforest–savanna boundary in Colombia: 14C
1739 wiggle-matching and pollen analysis of core Las Margaritas, *Palaeogeogr. Palaeoclimatol.*
1740 *Palaeoecol.*, 193(2), 201–223, doi:10.1016/S0031-0182(03)00226-8, 2003.
- 1741 Zárate, M. A. and Tripaldi, A.: The aeolian system of central Argentina, *Aeolian Res.*, 3(4),
1742 401–417, doi:10.1016/j.aeolia.2011.08.002, 2012.

1743 Zhou, J. and Lau, K.-M.: Principal modes of interannual and decadal variability of summer
1744 rainfall over South America, *Int. J. Climatol.*, 21(13), 1623–1644, doi:10.1002/joc.700, 2001.

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Abbreviation	Mode	Methods	Description	Reference
Niño 3.4	Niño3.4 index	SST averaged over 5N-5S, 170W-120W calculated from Hadisst data	Describes interannual (2-7 yr) variability of tropical Pacific SST	Rayner et al., 2003
AMO	Atlantic Multidecadal 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 multidecadal (50-70 yr) time scales	Enfield et al., 2001
IPO	Interdecadal Pacific Oscillation	Multidecadal Pacific-wide mode of SST variability, calculated as the 2 nd EOF of low-frequency filtered HadSST data	Describes joint variations of Pacific SST in both hemispheres on multidecadal (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 5.5N-23.5N, 15W-57.5W and calculated from HadISST and NOAA OI 1x1 datasets	Describes interannual variability of SST variations in the tropical North Atlantic	Enfield et al. (1999)
TSA	Tropical South Atlantic SST	Defined as SST averaged over -20S, 10E-30W (TSA), calculated from HadISST and NOAA OI 1x1 datasets	Describes interannual 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 abbreviation
A	Described in peer-reviewed publication	Described in peer-reviewed publication	
B	Minimum duration of record ≥ 500 yr	Minimum duration of record ≥ 500 yr	
1	Not specified	More than 2 chronological tie-points within the last 2 ka	CONTROL2
2	Resolution ≤ 50 yr	<i>Resolution ≤ 200 yr*</i>	RES200
3	Tie points near the end part of the records and one near the oldest part	Tie points near the end part of the records and one near the oldest part	TOP-END
4	Records longer than 1 ka must include min. 1 additional age midway between the other two.	Records longer than 1 ka must include min. 1 additional age midway between the other two.	1000-MID

1756

1757 Table 2. Comparison of PAGES 2k criteria with criteria implemented in this study. * flexible
 1758 criteria of 200-300 years

1759

1760 Table 3. List of pollen records used and metadata

1761 (See Appendix 1)

1762

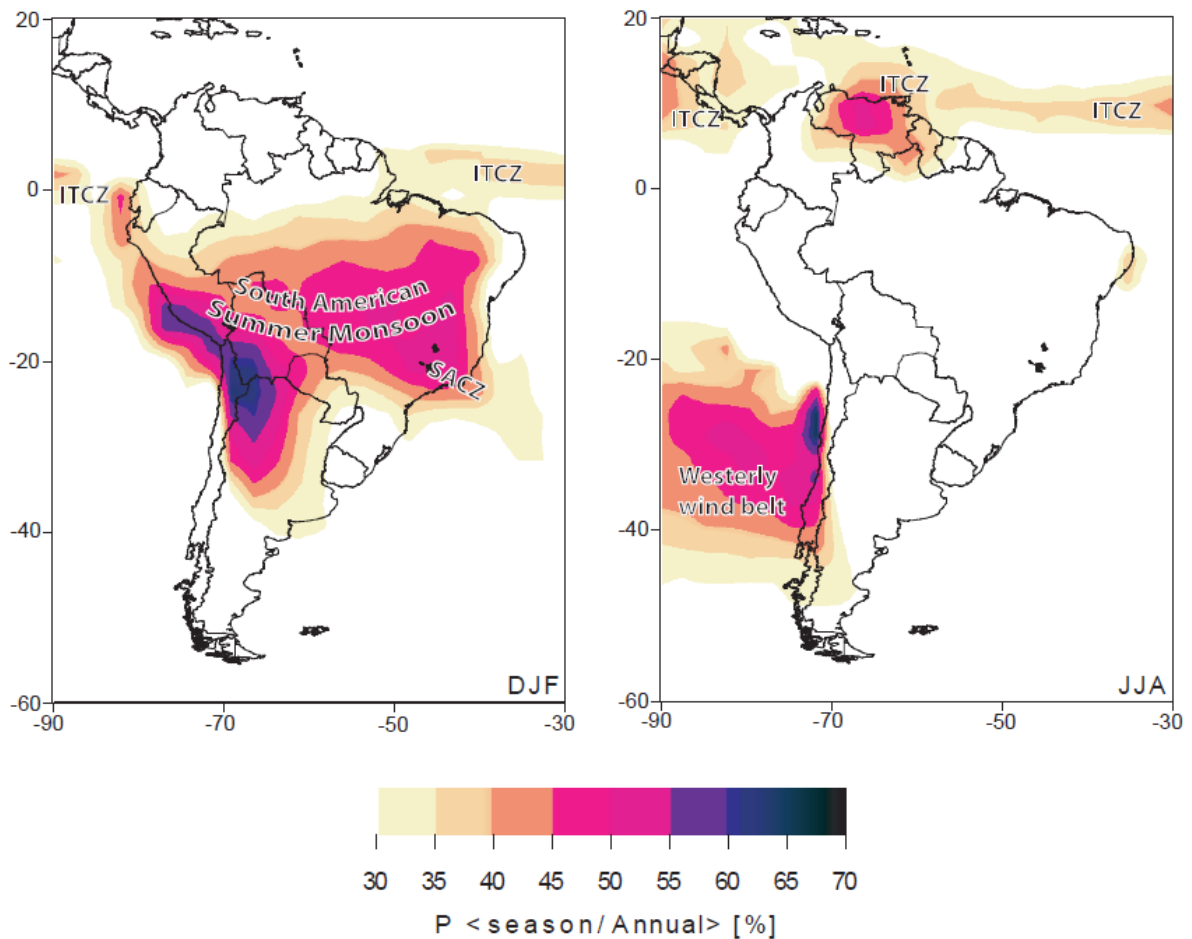


Figure 1. Map showing the relative precipitation amount over South America during the key seasons DJF (austral summer and mature monsoon phase) and JJA (dry season over much of tropical South America), highlighting the Intertropical Convergence Zone (ITCZ), South American Summer Monsoon (SASM), South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

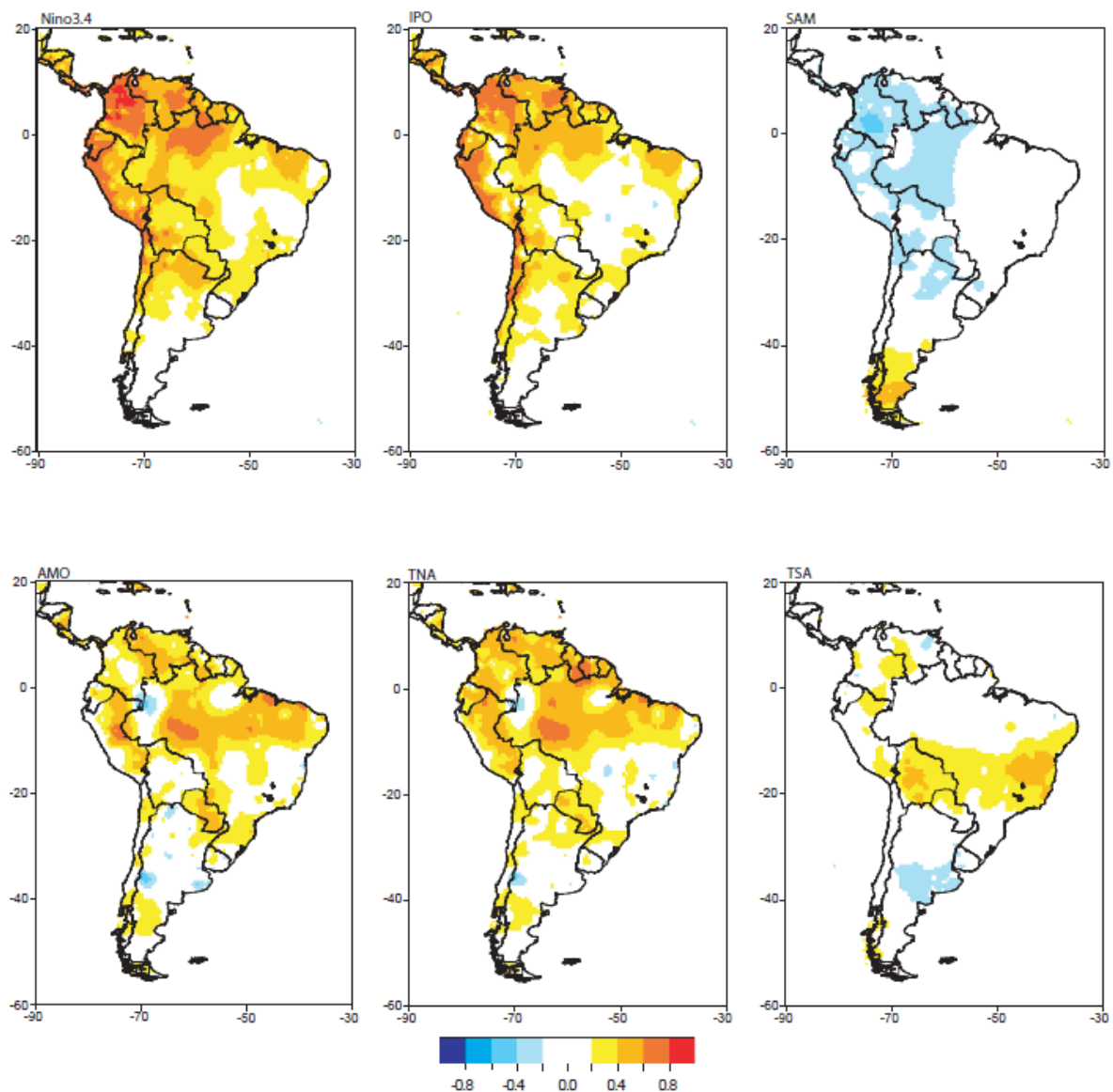


Figure 2. Correlation of annual mean temperature over South America with climate modes Niño3.4, IPO (Interdecadal Pacific Oscillation), SAM (Southern Annular Mode), AMO (Atlantic Multidecadal Oscillation), TNA (Tropical North Atlantic SST) and TSA (Tropical South Atlantic SST). High positive values of 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).

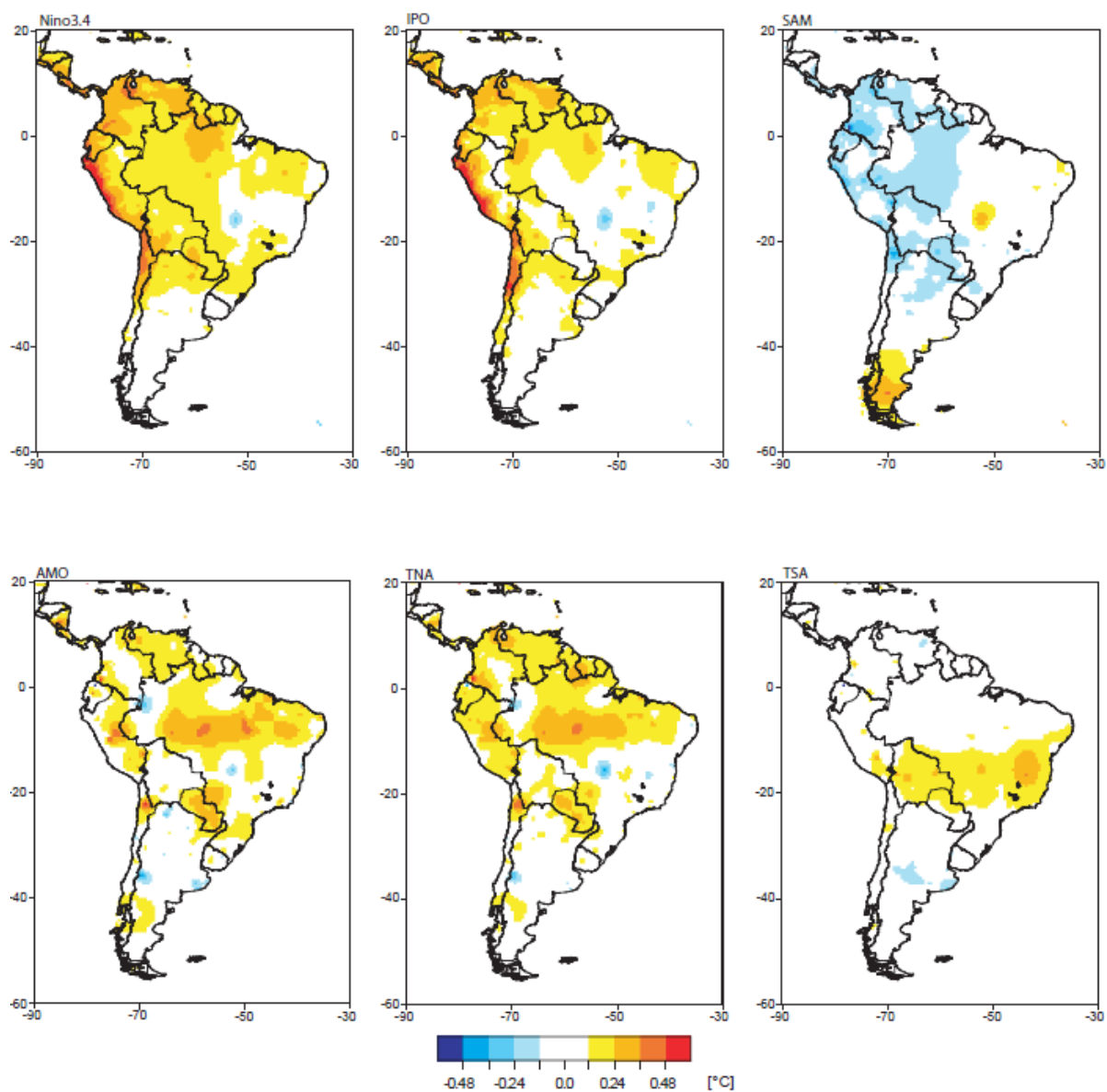


Figure 3. Annual mean temperature regressed upon regression with modes Niño3.4, IPO (Interdecadal Pacific Oscillation), SAM (Southern Annular Mode), AMO (Atlantic Multidecadal Oscillation), TNA (Tropical North Atlantic SST), TSA (Tropical South Atlantic SST). High positive values of the regression coefficient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

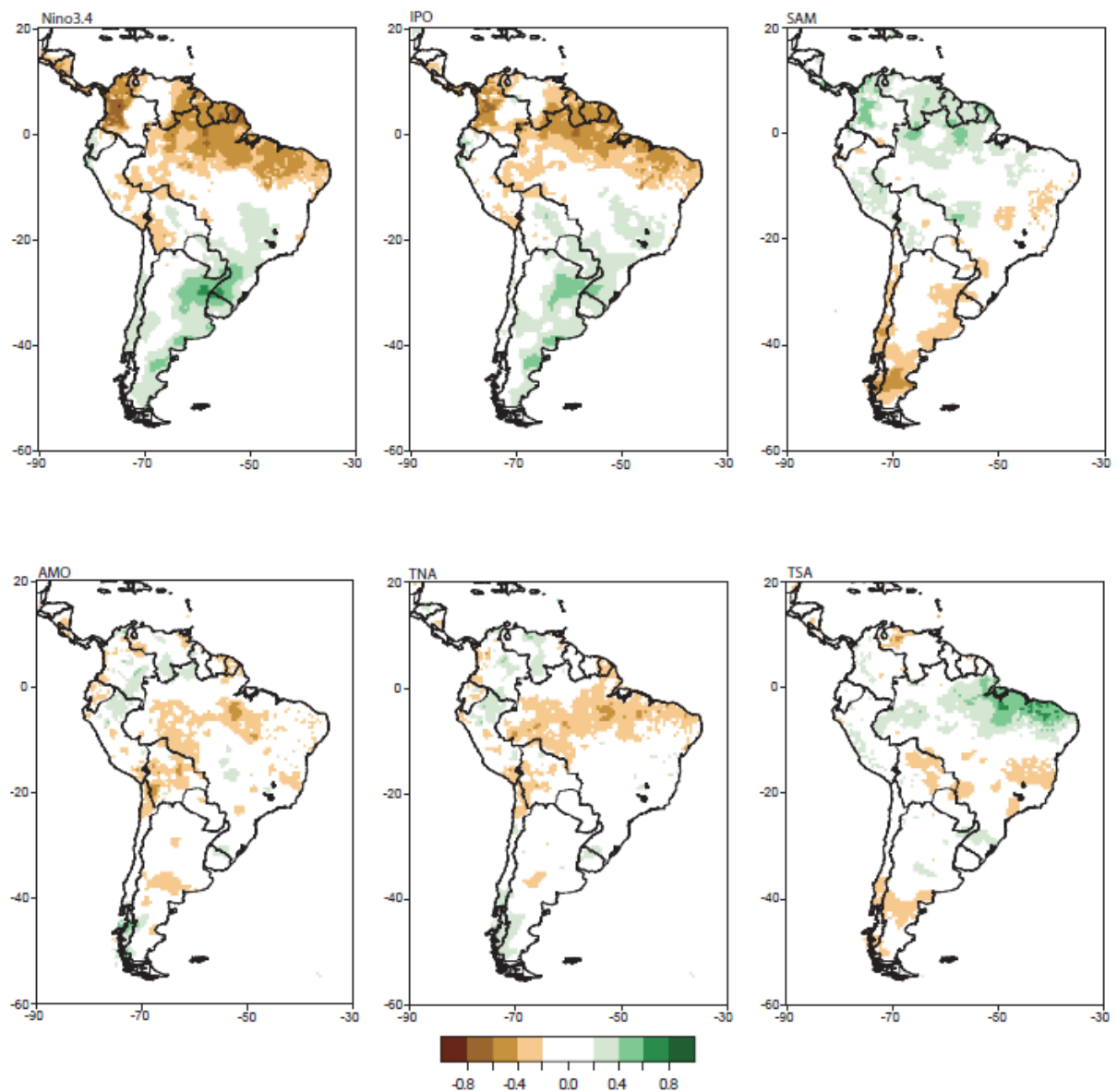


Figure 4. Precipitation correlation with modes Niño3.4, IPO (Interdecadal Pacific Oscillation), SAM (Southern Annular Mode), AMO (Atlantic Multidecadal Oscillation), TNA (Tropical North Atlantic SST), TSA (Tropical South Atlantic SST). High positive values of the correlation coefficient indicate both 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.

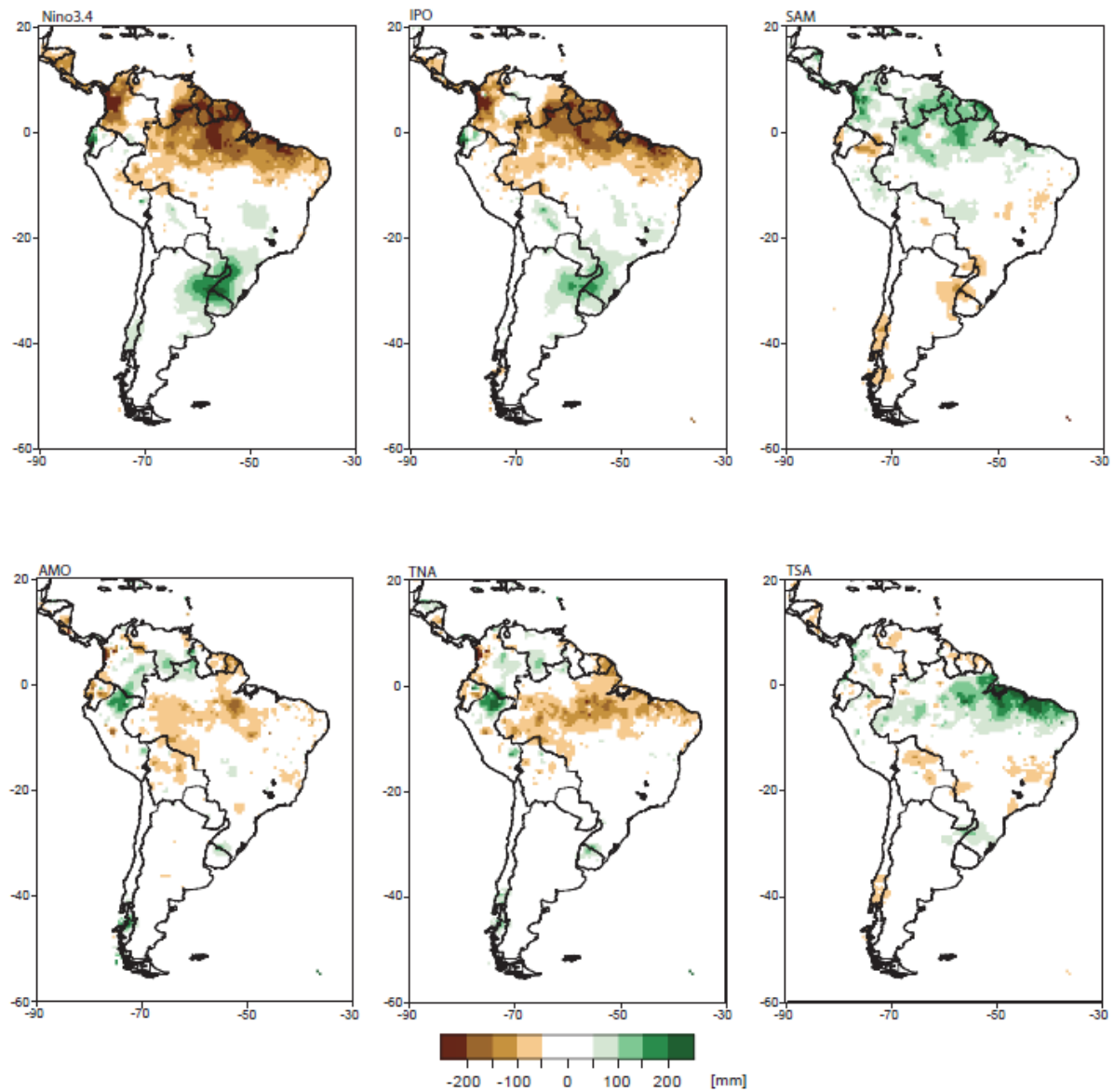
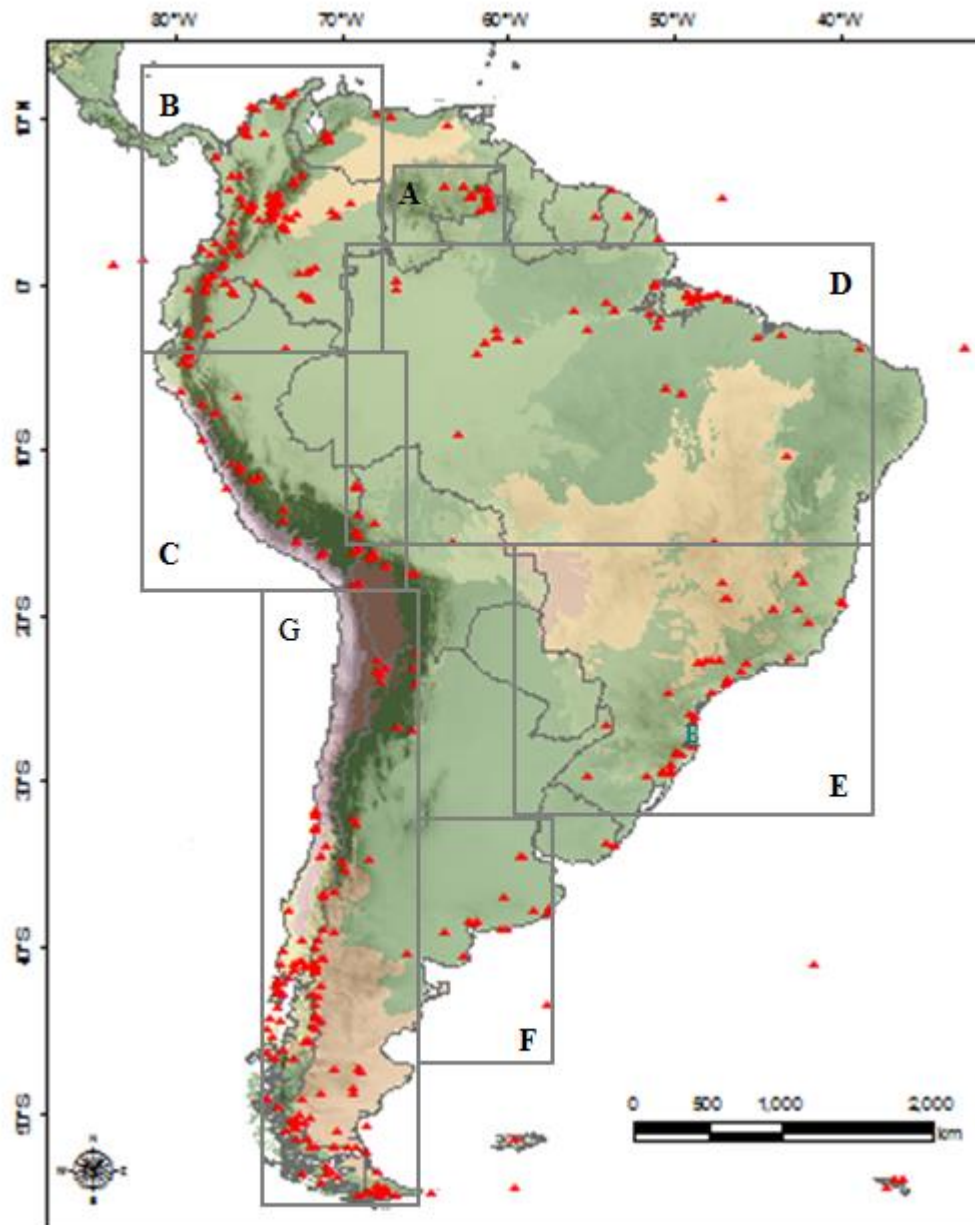


Figure 5. Precipitation regression with modes Niño3.4, IPO (Interdecadal Pacific Oscillation), SAM (Southern Annular Mode), AMO (Atlantic Multidecadal Oscillation), TNA (Tropical North Atlantic SST), TSA (Tropical South Atlantic SST). High positive values of the regression coefficient indicate high anomalies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



1809

1810 Figure 6. Map showing the location of LAPD pollen records that cover the last 2 ka (after

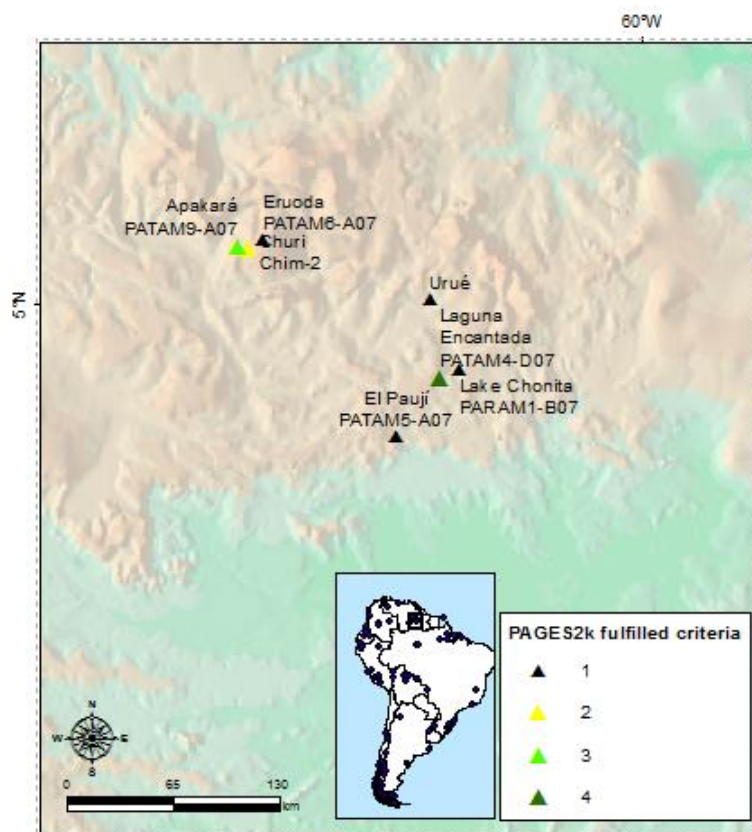
1811 Flantua *et al.*, 2015). General regional delimitations as discussed in this paper are shown; A:

1812 Venezuelan Guyana highlands and uplands; B: Northern Andes; C: Central Andes; D:

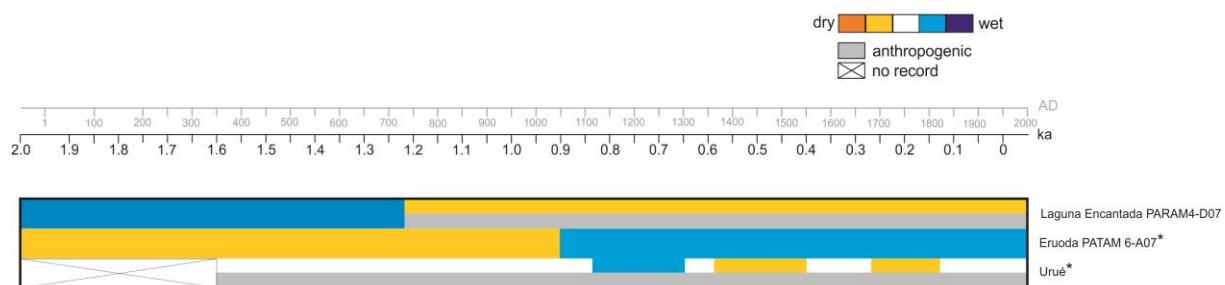
1813 Amazon basin; E: Southeastern and southeastern Brazil; F: Pampa plains; G: Southern Andes

1814 and Patagonia;

1815



Hydric balance summary- Gran Sabana



Temperature summary- Gran Sabana

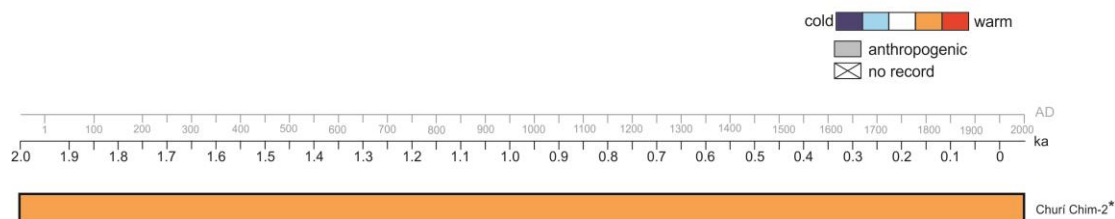


Figure 7A: Map showing the discussed pollen records in the Venezuelan Guayana highlands and uplands; B: Summary of hydric balance and temperature including human interference for the pollen records discussed.

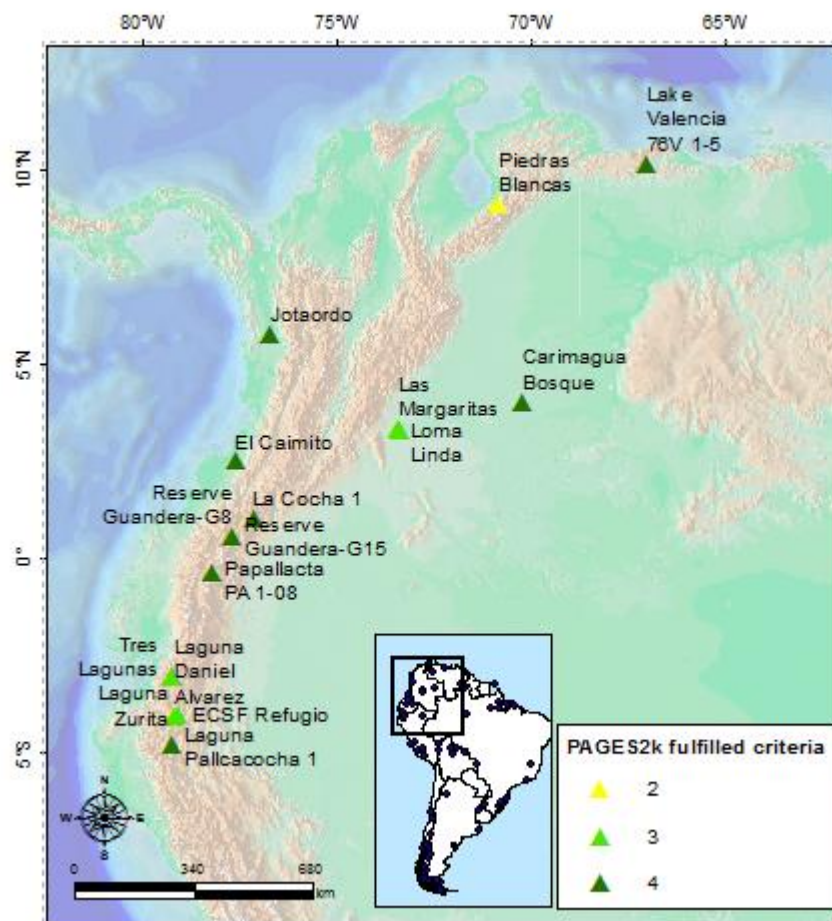
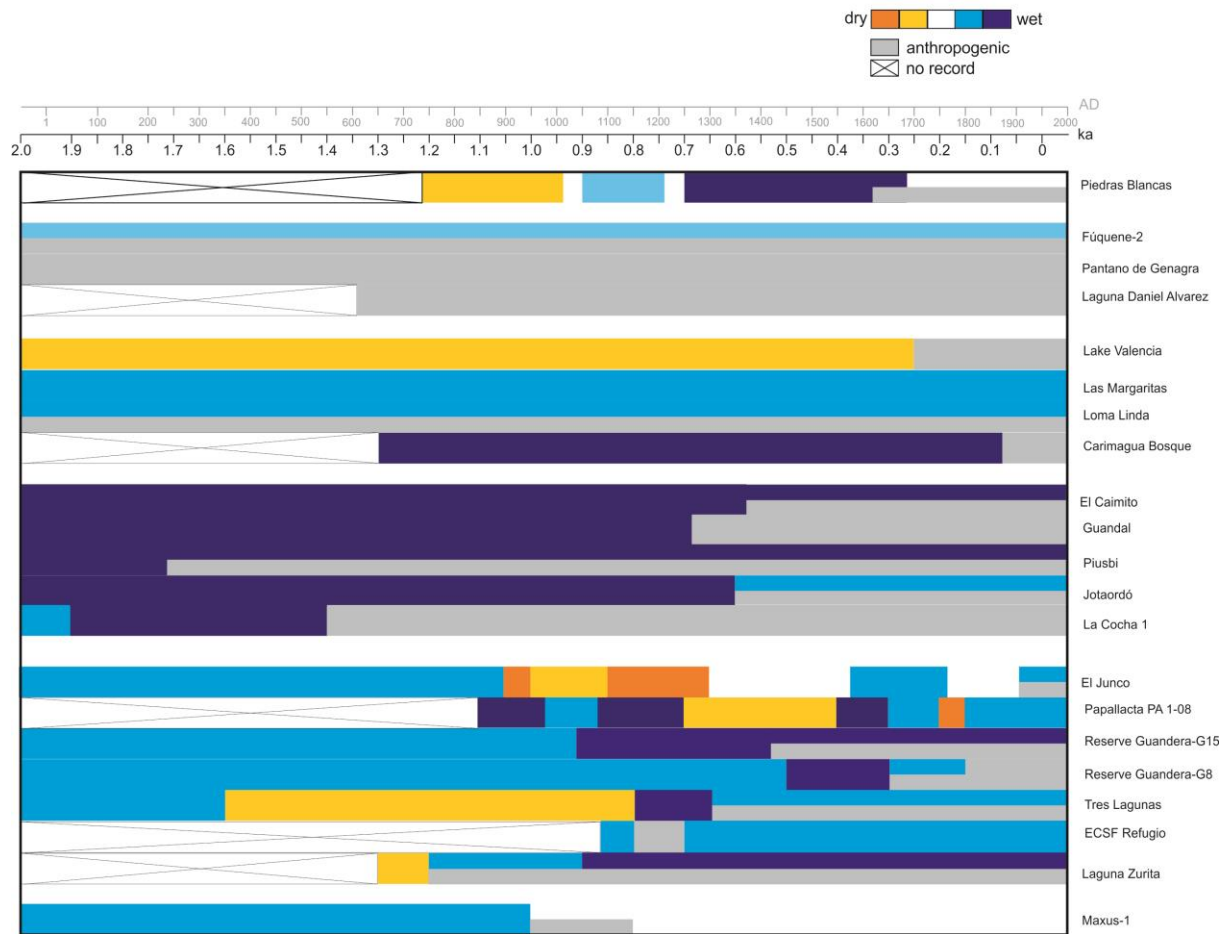


Figure 8A: Map showing the discussed pollen records in the Northern Andes.

Hydric balance summary - Northern Andes



Temperature summary - Northern Andes

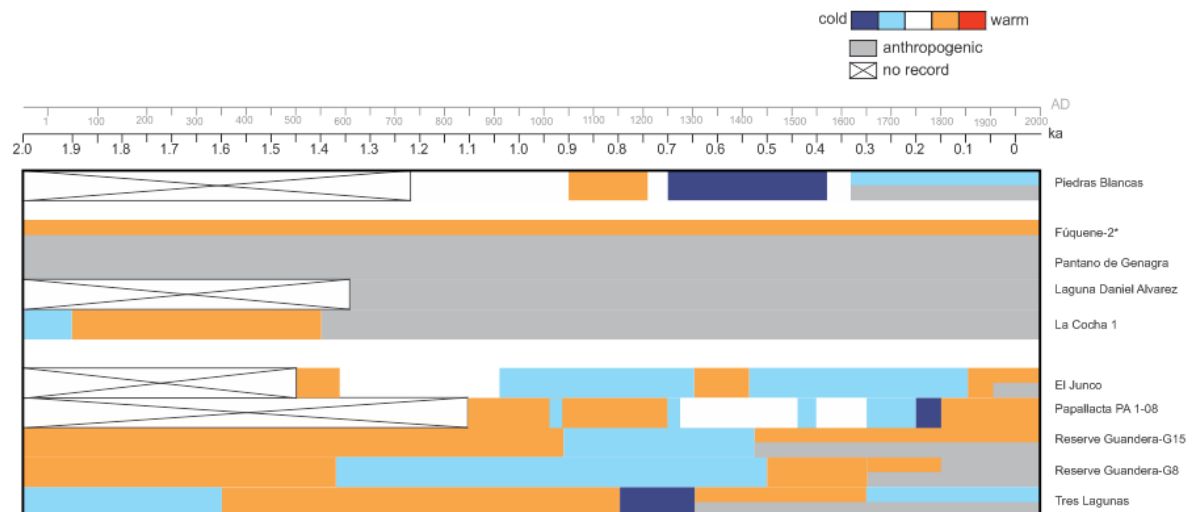
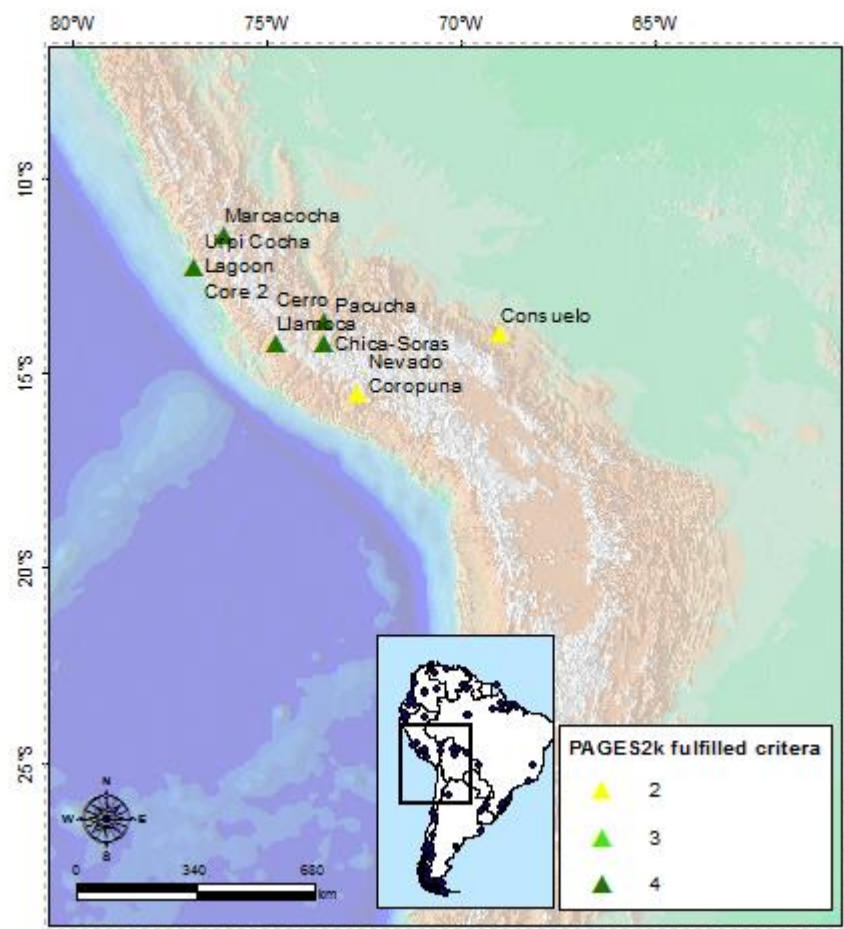


Figure 8B: Summary of hydric balance and temperature including human interference for the pollen records discussed.

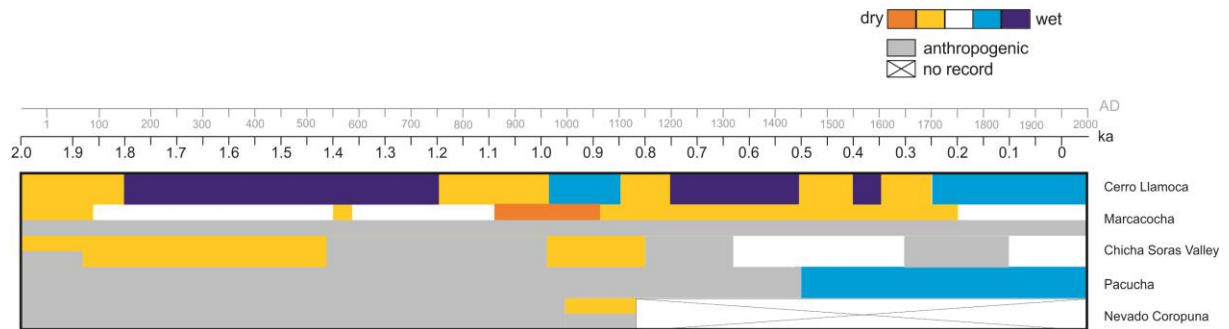
1829



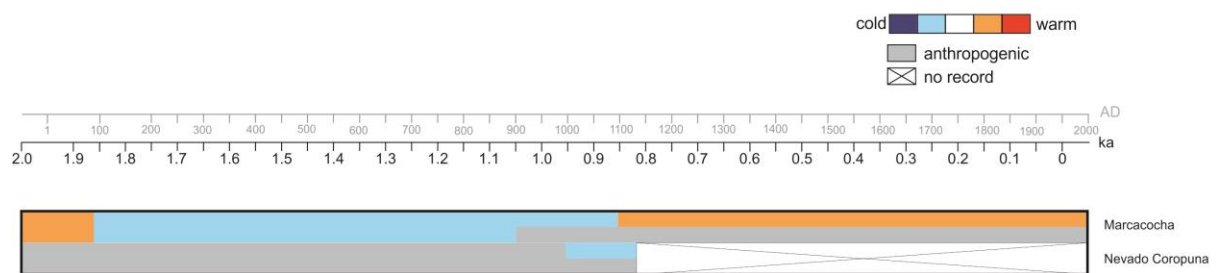
1830

1831 Figure 9A: Map showing the discussed pollen records in the Central Andes.

Hydric balance summary - Central Andes



Temperature summary - Central Andes

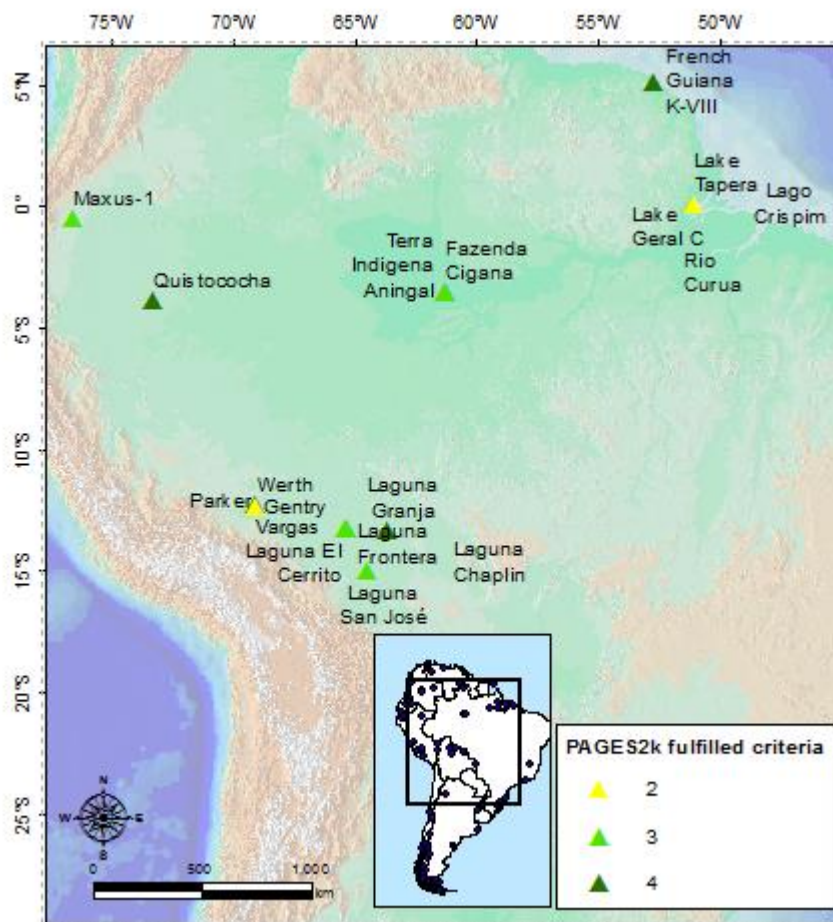


1832

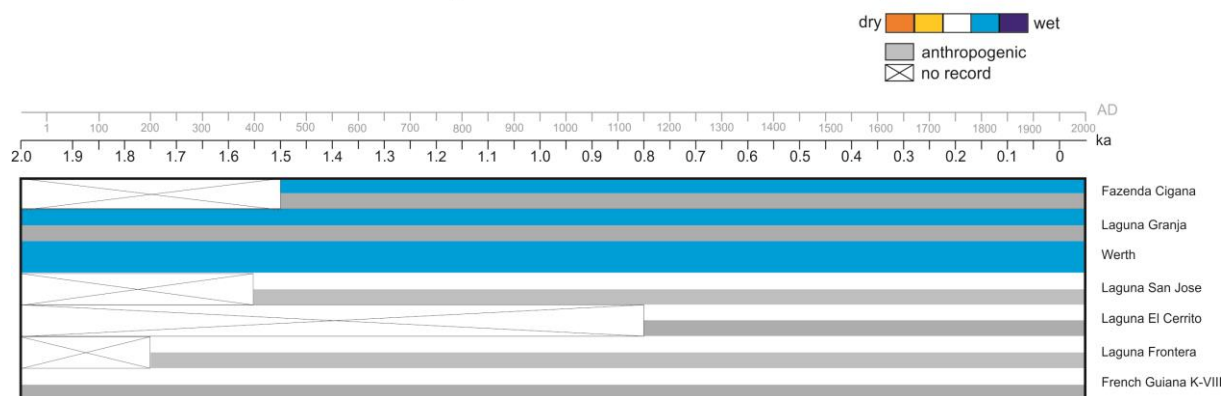
1833

1834 Figure 9B: Summary of hydric balance and temperature including human interference for the
 1835 pollen records discussed.

1836



Hydric balance summary -Amazon



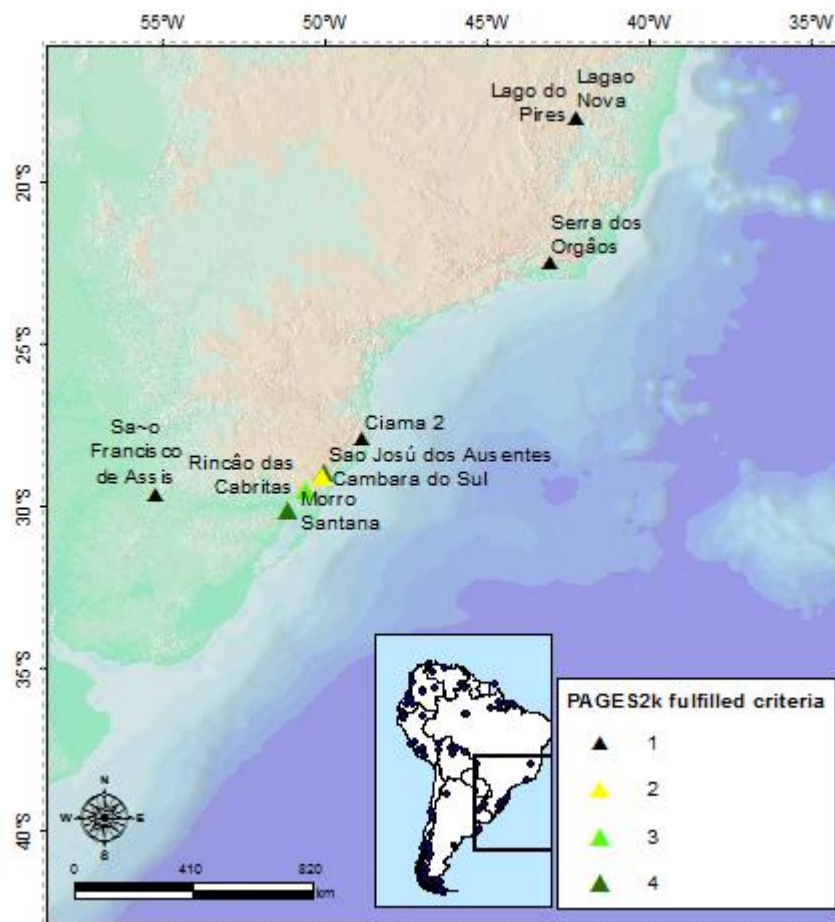
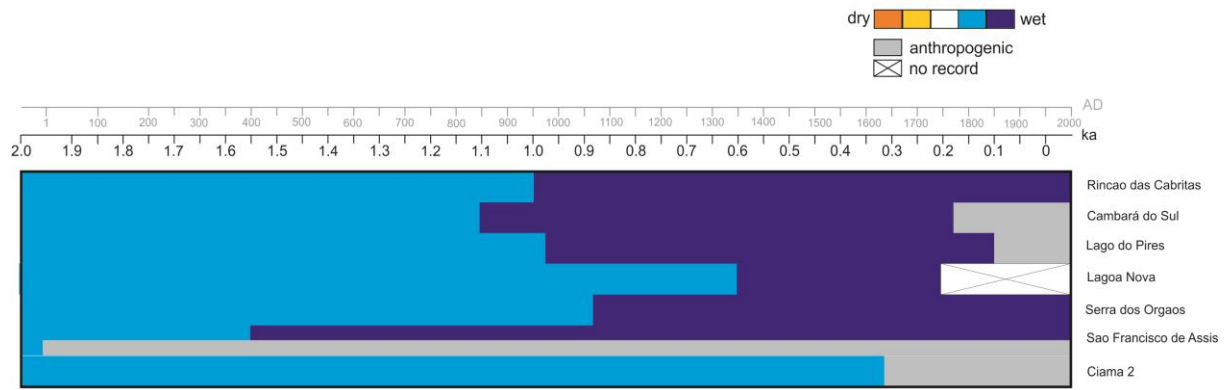


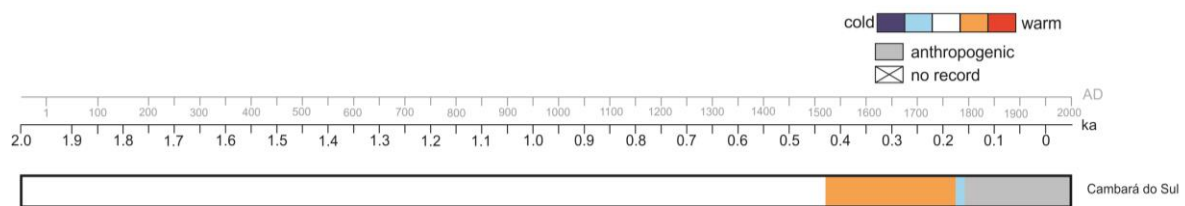
Figure 11A: Map showing the discussed pollen records in the Southern and Southeastern Brazil.

Hydric balance summary -S and SE Brazil



1851

Temperature summary -S and SE Brazil

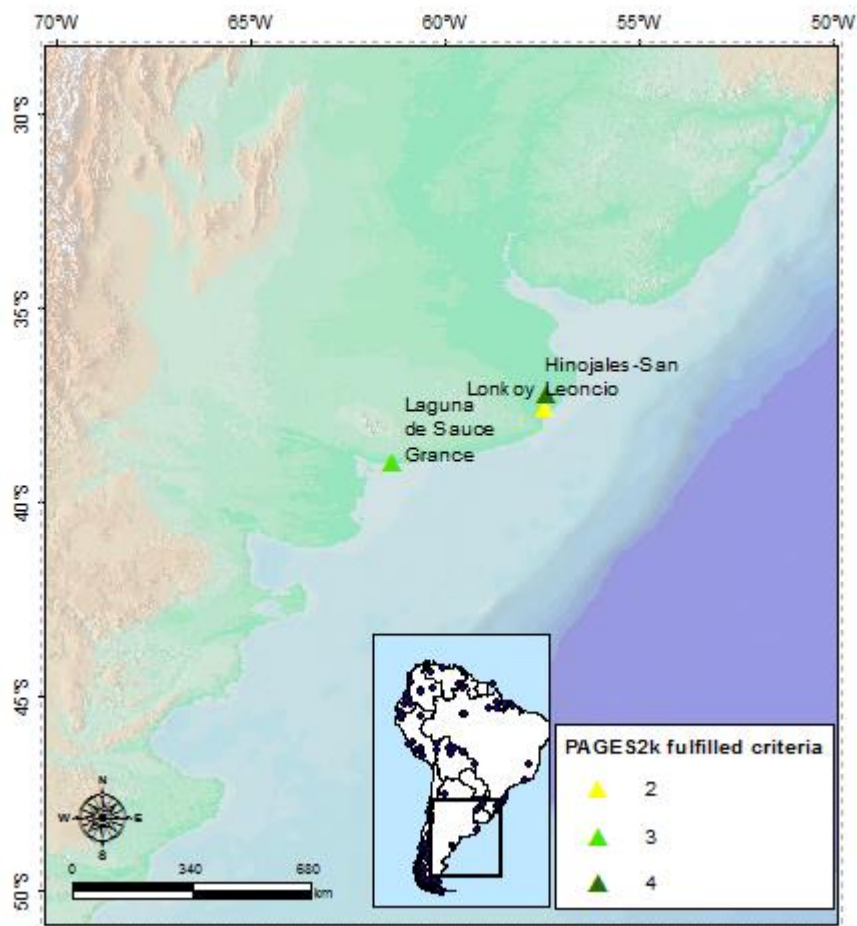


1852

1853

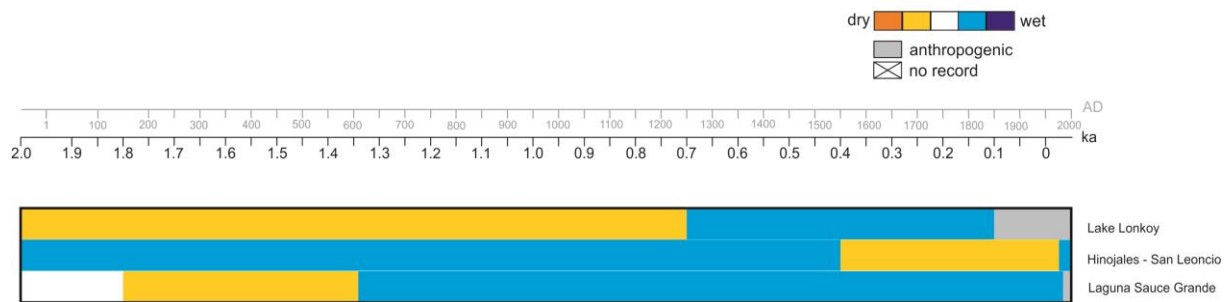
1854 Figure 11B: Summary of hydric balance and temperature including human interference for the
1855 pollen records discussed.

1856



1857

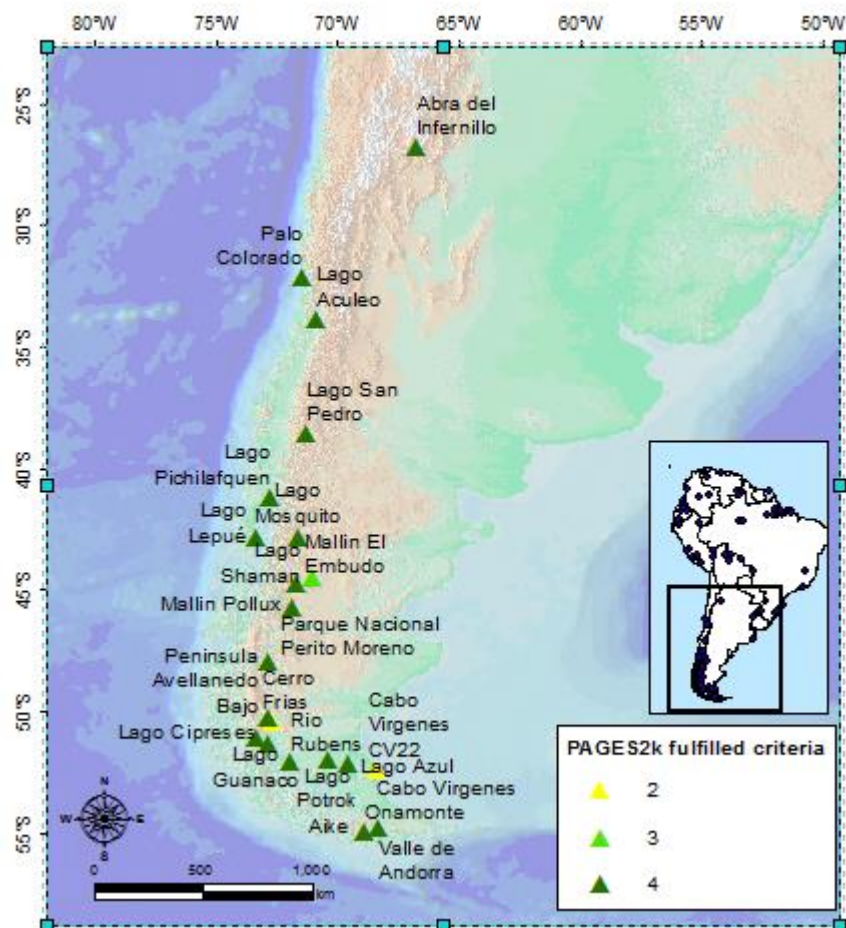
Hydric balance summary- Pampa



1858

1859 Figure 12. A: Map showing the discussed pollen records in the Pampa plains; B: Summary of
1860 hydric balance including human interference for the pollen records discussed (temperature
1861 summary could not be inferred).

1862

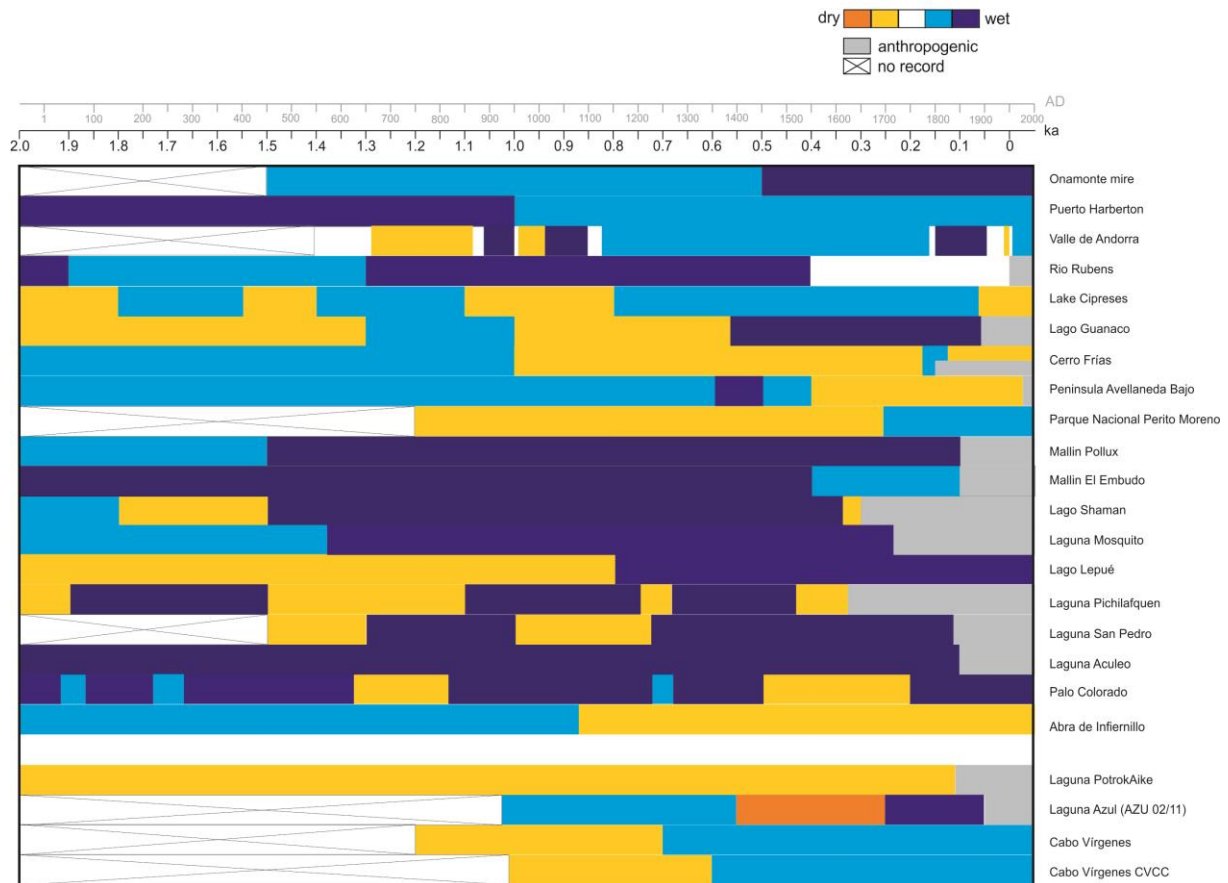


1863

1864

Figure 13A: Map showing the discussed pollen records in the Southern Andes and Patagonia.

Hydric balance summary- Southern Andes & Patagonia



Temperature summary- Southern Andes & Patagonia

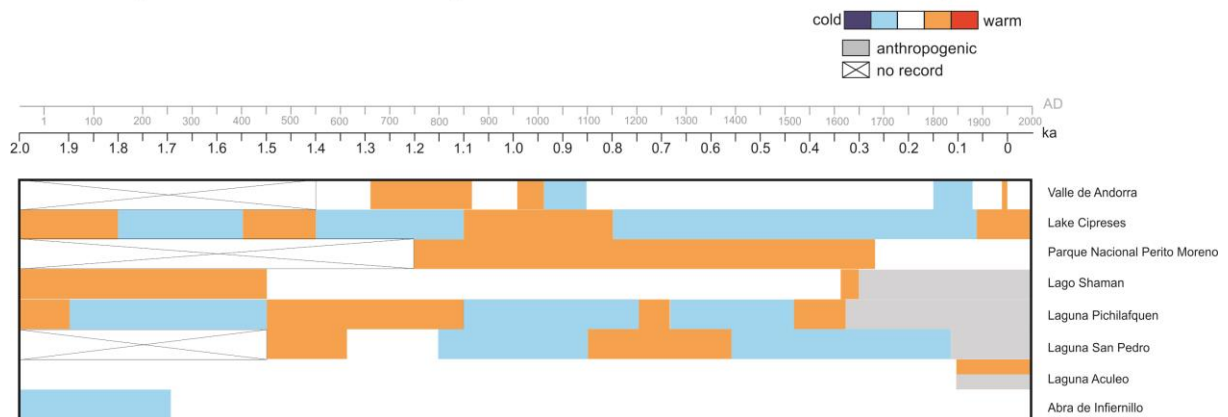


Figure 13B: Summary of hydric balance and temperature including human interference for the pollen records discussed.

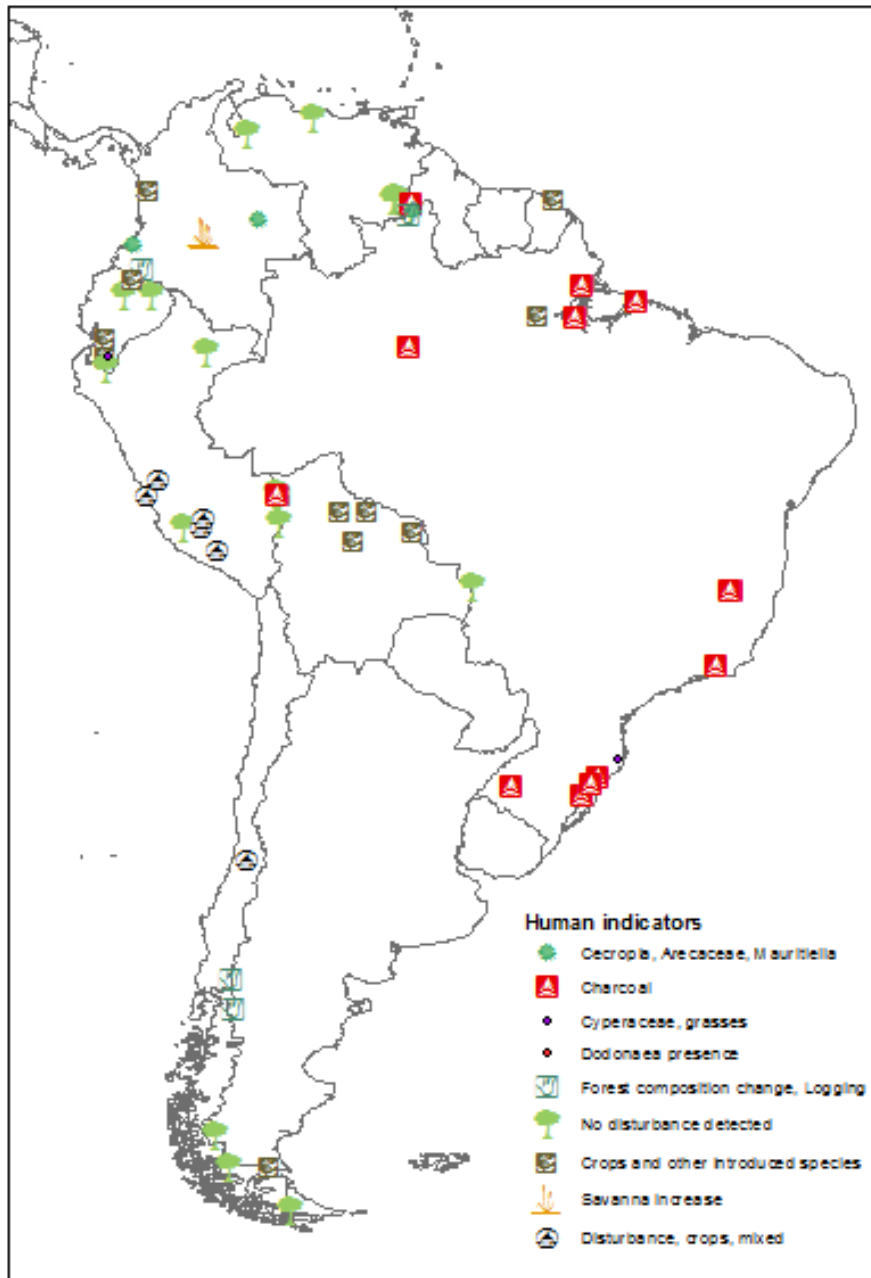


Figure 14. Map showing human indicators observed in the discussed pollen records. Additional details are found in Table 3.