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 The Holocene

Changes in the vegetation and water cycle of the Ecuadorian páramo during the last 5000 years

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1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25

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Abstract

We analyzed changes in the long-term vegetation cover and in fire activity over the past 5,000 years in the Ecuadorian páramo using a sediment core from Papallacta (Ecuador). The chronology is constrained by three tephra layers and 32 AMS ¹⁴C ages, and 168 samples yielded a high-resolution record of environmental changes. We estimated the upslope wind convectivity as the ratio between pollen transported from the Andean cloud forest and Poaceae pollen to distinguish changes in atmospheric moisture from changes in soil moisture. The record showed that the two sources of moisture, either from year-round adiabatic cloud dripping linked to SASM activity or to ENSO variability at decadal-scale, influenced vegetation-cover changes. Between 5000 and 2450 cal yr BP, both soil moisture and biomass burning were higher than after 2450 cal yr BP. The shift between the two states matches the zonal increase in summer insolation that drove the ITCZ to its southernmost position. Our results underline resilience to volcanic activity, the importance of the upslope convective dripping with the lowest convective index observed at ~4500 cal yr BP, the anomalous last century with the highest convective activity and the driest soil conditions recorded in the last 5000 years, the recent increase in fire activity and the link between soil moisture and the position of the ITCZ.

26 Introduction

27 Páramo (or páramos) is a widespread treeless grassland neotropical ecosystem located in the wetter
28 northern Andes (Borrelli et al., 2015) between the upper limit of the cloud forest (c. 3,000 m asl) and
29 the upper limit of plant life (c. 4,700 m asl; Luteyn 1999; Körner and Paulsen, 2004). Páramos play an
30 important ecological role in regional water storage (Buytaert et al., 2006) and in the global carbon
31 balance and host high biodiversity (Zúñiga-Escobar et al., 2013). Water drains from the wetlands into
32 the thick volcanic soils that form the “sponge” of the páramo, where the precipitation is stored.
33 Currently, tussock grassland (*Calamagrostis* sp or/and *Festuca* sp), acaulescent rosettes and cushions,
34 the dominant growth forms of the páramo (Ramsay and Oxley, 1997), are undergoing severe degradation
35 due to burning and grazing (Grub et al., 2020). Degraded areas only recover slowly due to the high
36 elevation as well as the effects of the oxygen level, high radiation and drying wind; as a result, the high
37 biodiversity of this ecosystem is under threat. An additional issue is ongoing and future climate change
38 with increasing temperatures and the associated glacier retreat and an increase in drought events and in
39 fire frequency due to enhanced precipitation seasonality (Urrutia and Vuille, 2009).

40 The long-term management of the páramo requires a detailed understanding of the role of fire
41 (Sarmiento and Frohlich, 2002). While the grasslands are highly flammable, their ability to sprout and
42 germinate after fires can be viewed as is considered as an adaptation to disturbance by fire (Borrelli et
43 al., 2015; Horn and Kapelle, 2009). Accordingly, direct observations of lightning strikes and
44 palaeoecological evidence of fires both clearly demonstrate that fires occur in neotropical páramo
45 without human intervention (Horn and Kapelle 2009). However, the extent to which the páramo can be
46 viewed as a fire-dependent ecosystem is still a matter of debate (Horn and Kappelle, 2009). Today, fire
47 frequency in the páramo is higher than before, probably due to human-set fires that are used to remove
48 the dead standing biomass of native grasses and promote the growth of young grass shoots that are easier
49 to stock (Matson and Bart 2013).

50 Long-term palaeoecological records from natural archives (lacustrine sediments, peat) make it possible
51 to document vegetation responses to climate and fire-regime changes under environmental conditions
52 that differ substantially from those that occurred during the historical period. For instance, in Colombia,
53 the upper tree line shifted in conjunction with glacier advances and retreats during the glacial-
54 interglacial cycles over the Quaternary (Hooghiemstra and Flantua, 2019). During the Holocene, at
55 millennial time scales, the South American Summer Monsoon (SASM) gradually intensified in response
56 to increasing southern hemisphere summer insolation. Thus, during the mid-Holocene (7000 to 5000 yr
57 BP), a weaker SASM system produced drier conditions in large parts of the neotropics south of the
58 equator (Prado et al., 2013; Valencia et al., 2018). Further north, near the Pacific coast of Ecuador, the
59 strengthening of the cold Humboldt current led to cooler climatic conditions between 4200 and 2850 cal
60 BP (Seillès et al., 2015) and drier conditions in the Ecuadorian Andes between 5500 and 2500 cal yr BP
61 (Rodbell et al., 1999) when the InterTropical Convergence Zone (ITCZ) was in its northernmost
62 position. Andean pollen records for the late Holocene rather centered on changes in the upper forest

63 limit, with the highest position reached around 4900 cal yr BP in conjunction with wetter climate
64 conditions and the lowermost altitude reached between ~910 and 520 cal yr BP in conjunction with drier
65 climate conditions (Bakker et al., 2008; Jansen et al., 2013). Similarly, little is known about the floristic
66 changes of the páramo.

67 Here we present new high-resolution pollen and macroscopic charcoal records spanning the past 5,000
68 years from a peat bog (Papallacta) located in the páramo of Antisana, one of the main hydrological
69 basins for Quito, the capital city of Ecuador (Buytaert et al., 2006). The pollen record from this site for
70 the last 1,000 years showed that vegetation was highly sensitive to moisture from two main sources, one
71 the annual amount of rainfall retained in the soil, and the other from the upslope cloud convection that
72 delivers moisture from the Amazon basin to the summits (Ledru et al., 2013). By extending the
73 Papallacta record further back in time, we explore the longer-term drivers of changes in hydrological
74 conditions, fire and vegetation in a high elevation ecosystem in the tropics.

75

76 **Study area**

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78 The Papallacta (or Sucus) peat bog is located on the eastern part of the Chacana volcanic complex, and
79 at 12-14 km to the north slope of the Antisana volcano at an elevation of 3,815 m asl (00°2'30" S,
80 78°11'37" W) on the Eastern Cordillera range (EC) (Fig. 1A). The Antisana (5,704 m asl) is a potentially
81 active volcano in the Ecuadorian Eastern Cordillera, whose most recent fumarolic activity was reported
82 by Humboldt at the beginning of the 19th century (Hall et al., 2017). Antisana's base diameter is ca. 14
83 km, running north-south. There, glaciers descend to approximately 4,600 m (eastern side) and 4,800 m
84 (western side), while older moraines dated to the Younger Dryas cold event indicate glaciers about 1,200
85 m lower on the eastern side (Hastenrath, 1981; Clapperton et al., 1997). Average annual temperature is
86 between 7.5 °C (at 3,500 m asl) and 5 °C (at 4,000 m asl) (Jorgensen and Leon-Yanez, 1999).

87 The climate in the equatorial Andes is influenced by complex and heterogeneous atmospheric
88 mechanisms (Segura et al., 2019). Currently, both the Eastern (EC) and the Western Cordillera (WC)
89 are under the seasonal influence of the Intertropical Convergence Zone (ITCZ), a zone of deep
90 convection that produces heavy precipitation due to the convergence of the trade winds at low latitudes
91 between February and April (Garreaud, 2009). The EC receives year-round rainfall fed by moist air
92 resulting from evapotranspiration of the trees in the Amazon basin (Bendix et al., 2006a, 2006b). Upon
93 meeting the Andes, these moist air masses ascend, cool, and lose a substantial portion of their humidity
94 (orographic rain) thereby attenuating the dry season. As a result, large parts of the EC are currently
95 characterized by the absence of a dry season (Fig. 1B). However, extreme monthly wet (dry) events are
96 associated with anomalous southward (northward) shifts of the eastern pacific ITCZ during the rainy
97 season (Segura et al., 2019).

98 Today, at the high elevation of the Papallacata bog on the north-western slope of the Antisana, two main
99 mechanisms are responsible for the year-round precipitation: regular SASM activity observed every

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3 100 year and variable El Niño activity (Vuille and Werner 2005). First, the South American Summer
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5 101 Monsoon (SASM) is paced by the southward migration of the ITCZ over the tropical Atlantic and
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7 102 Pacific Oceans during austral summer and causes precipitation during the austral summer (Fig. 1A;
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9 103 Ledru et al., 2013). Second, the interannual variability in precipitation related to ENSO (El Niño
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11 104 Southern Oscillation) with El Niño (La Niña) episodes associated with warmer (cooler) and below
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13 105 (above) average rainfall in the Amazon Basin (Marengo and Nobre, 2001; Marengo, 2009) as well as
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15 106 glacier regression (expansion) in Ecuador (Caceres et al., 2006). At millennial scale, paleoclimatic
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17 107 records reconstructed mean-state variations in ENSO-like behavior, for instance, in the lacustrine
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19 108 sediment of the Galapagos with an increase in ENSO variability in the Late Holocene (Moy et al., 2002;
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21 109 Conroy et al., 2009; Zhang et al., 2014).

22
23 110 Sucus bog, located close to the town of Papallacta, hereafter named Papallacta bog, is a wetland area
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25 111 located within the páramo. Patches of *Polylepis* forest grow on the slopes above the bog (Fig. 1C). In
26
27 112 the region of Antisana, the cloud forest (or upper montane rain forest) occurs between *ca.* 2,500 m a.s.l.
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29 113 and 3,400-3,600 m a.s.l. and is mainly dominated by *Weinmannia pinata*, *Schefflera sodiroi*,
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31 114 *Myrcianthes rhopaloides*, *Hedyosmum cumbalense*, *H. luteynii*, *Oreopanax ecuadoriensis*,
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33 115 *Hesperomeles ferruginea*, and *Weinmannia fagaroides*. Between 3,600 and 4,300 m asl, in the Páramo,
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35 116 *Gynoxys acostae*, *Escallonia myrtilloides*, *Buddleia*, *Polylepis* are observed and, high elevation, or super
36
37 117 páramo extends between 4,200 and 4,600 m on the eastern side. Shrubby vegetation dominated by
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39 118 *Loricaria antisananensis* grows on the eastern humid side at *ca.* 4,200 m (Sklenar and Jorgensen, 1999)
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41 119 (Table 1).

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122 **Table 1.** Description of the vegetation cover around Papallacta bog (from Ledru et al., 2013).
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Site	Family	Species	Family	Species
Paramo 3,600- 4,000 m asl	Poaceae	<i>Calamagrostis</i>	Asteraceae	<i>Diplostephium</i>
		<i>Festuca</i>		
	Rosaceae	<i>Polylepis</i>		<i>Pentacalia</i>
	Hypericaceae	<i>Hypericum</i>		
Papallacta bog 3,815 m asl	Asteraceae	<i>Loricaria toyoides</i>	Gunneraceae	<i>Gunnera magellanica</i>
		<i>Dorobaea pinpinelifolia</i>	Ranunculaceae	<i>Ranunculus sp.</i>
		<i>Monticalia vaccinioides</i>	Clusiaceae	<i>Hypericum laricifolium</i>
		<i>Hippochoeris sp.</i>		<i>Hypericum sp.</i>
		<i>Xenophyllum sp.</i>	Geraniaceae	<i>Geranium sp.</i>
		<i>Werneria sp.</i>	Polygonaceae	<i>Muehlenbeckia volcanica</i>
	Valerianaceae	<i>Valeriana microphylla</i>	Apiaceae	<i>Hydrocotyle</i>
	Lycopodiaceae	<i>Huperzia sp.</i>		<i>Azorella</i>
	Gentianaceae	<i>Gentiana sedifolia</i>	Plantaginaceae	<i>Plantago rigida</i>
		<i>Halemia weddeliana</i>	Cyperaceae	<i>Carex lechmanii</i>
	<i>Gentianella sp.</i>			
Poaceae	<i>Cortaderia sericanta</i>			

		<i>Bromus sp.</i>		
		<i>Cortaderia nitida</i>		
Cushion paramo	Apiaceae	<i>Azorella</i>	Plantaginaceae	<i>Plantago</i>
Paramo >4,000 m asl	Malvaceae	<i>Nototriche</i>	Brassicaceae	<i>Draba</i>
	Apiaceae	<i>Azorella</i>	Plantaginaceae	<i>Plantago</i>
	Asteraceae	<i>Chuquiraga</i>		
		<i>Loricaria</i>		
		<i>Werneria</i>		

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Material and methods

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Coring

The 9-m long sediment core named PA1-08 was collected from Papallacta peat bog in 2008 using a Russian-type corer (drives 1 m long, diameter 5 cm) (Fig. 1D). Sediment drives were transferred onto PVC half-tubes and sealed in a plastic sheath (Fig. 2). The sediments were then sliced into 2-cm thick slices, which were placed individually in labelled plastic bags and stored at +4 °C at the University of Montpellier.

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Chronology

A total of 34 bulk sediment samples were sent for radiocarbon Accelerator Mass Spectrometry (AMS) dating and measured at the *Laboratoire de Mesure du Carbone14* (LMC14)–UMS 2572 (CEA/DSM – CNRS–IRD–IRSN–Ministère de la Culture et de la Communication, Saclay, France), and at the BetaAnalytics laboratory (USA). In addition to radiocarbon dating, we used tephrochronology when tephra layers resulting from known volcanic eruptions were available. Tephrochronology is used to determine the age of a volcanic eruption based either on evidence from a historical archive or from prior dating of tephra in other sediment records (Turney and Lowe, 2001). The geochemical and mineralogical composition of the main of the tephra layers makes it possible to identify the origin of the uppermost ash layers (Table 3). However, our knowledge of the origin of the eruption and its corresponding ages become uncertain as one goes deeper in time (Table S1). We classified the tephra layers recognized in PA1-08 in three categories, from 0 for no uncertainty to 3 for maximum uncertainty, and only the three most recent tephra layers were usable for our age model (Table S2).

The chronology of the core was determined using rBacon v2.5.6 (Blaauw et al., 2021). It is constrained by 35 control points: 31 ¹⁴C dates, the estimated age of the sediment surface (Table 2), and the ages of the three most recent tephra layers identified (Fig. 2). Three ¹⁴C dates that were taken near sediment-drive ends were rejected as they reported much younger ages than expected based on adjacent dates. We excised sediments identified as tephra layers before age-modeling (and added them after age-modeling) as these sections are assumed to be abrupt accumulations. All ¹⁴C dates were calibrated with a mixed

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3 153 calibration curve (50% IntCal20 and 50% SHCal20) as the study site receives a mixture of northern and
4 154 southern air masses (Hogg et al., 2020).

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6 156 *Charcoal analysis*

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10 157 We took a total of 322 samples, 69 of which originated from tephra layers, from the contiguous 2-cm
11 158 thick sediment slices down to a depth of 700 cm, measured sample volumes by water displacement
12 159 (median volume = 1 cm³; range: 0.1-4 cm³), and then soaked the samples in a 7.5% hydrogen peroxide
13 160 solution for at least 24 hours (Schlachter and Horn, 2010) before gently washing them through a sieve
14 161 with a 125 µm screen. To quantify charcoal abundances, we transferred the sieving residues into a
15 162 white porcelain evaporating dish to facilitate the identification and counting of charcoal particles
16 163 against the white background (Finsinger et al., 2014) and identified charcoal particles under a Leica
17 164 M80 stereomicroscope at 7.5-60x magnifications based on the following features: dark, shiny and
18 165 geometric particles that are brittle at low less pressure (Whitlock and Larsen, 2001). As charcoal
19 166 morphology helps interpret the fuel source (Jensen et al., 2007; Feurdean, 2021), we counted charcoal
20 167 pieces of Poaceae tissues (Jensen et al., 2007; Courtney-Mustaphi and Pisaric, 2014), wood and bark
21 168 (types C and S in Enache and Cumming, 2006), and other charcoal morphologies ('undiff. charcoal')
22 169 in 178 samples (34 of which were included in tephra layers). In addition, we scanned the samples at
23 170 7.5x magnification with a CMEX-5000 camera using the winSEEDLE™ software v2009 (Regent
24 171 Instruments Canada Inc.) to measure both the total charcoal abundance and the cumulative sum of
25 172 charcoal-particle areas (i.e., total charcoal per area) (Finsinger et al., 2014). To account for varying
26 173 sediment accumulation rates, we selected the samples that were not included in tephra layers and
27 174 calculated the charcoal accumulation rates (CHAR, pieces cm⁻² yr⁻¹) based on the chronology
28 175 (Whitlock and Larsen, 2001).

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41 176 To determine the centennial-scale trends in CHAR, which was interpreted as reflecting the amount of
42 177 biomass burned over time (Marlon et al. 2008; Higuera et al. 2010), and to identify peaks, which were
43 178 interpreted as fire episodes, we analyzed the CHAR data using CharAnalysis v1.1 (Higuera et al.,
44 179 2009). The analysis involved binning the charcoal record to a constant sampling resolution (here, the
45 180 3rd quartile value of the records' sampling resolution = 23 years sample⁻¹), decomposing that record
46 181 into a background trend and a peak component using a lowess smoother robust to outliers (with a 500-
47 182 year smoothing window), and evaluating peak samples using the 99th percentile of the modeled noise
48 183 distribution obtained with a Gaussian mixture model and a peak-screening test (Higuera et al., 2009).
49 184 The suitability of the record for peak detection was assessed with the signal-to-noise index (SNI; Kelly
50 185 et al. 2011). We calculated fire return intervals (FRI) using the screened peak record.

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187 *Pollen analysis*

188 A total of 200 pollen samples were taken from the 2-cm thick sediment slices down to a depth of 700
 189 cm, 37 of which were taken from tephra layers. We measured both their wet and dry weights before
 190 processing the samples using a standard protocol (Faegri and Iversen, 1989). We mounted the residue
 191 in silicone oil on microscope slides and identified and counted a minimum of 300 terrestrial pollen
 192 grains in each sample under 630x magnification. Pollen grains and spores were identified using the
 193 ISEM reference pollen collection and pollen keys (Hooghiemstra, 1984; Ortuño, 2008; Kuentz, 2009;
 194 Herrera, 2010). Pollen taxa assignments to ecological groups (bog, Andean forest, páramo) were based
 195 on published classifications of páramo pollen records (Moscol Olivera et al., 2009; Moscol Olivera and
 196 Hooghiemstra, 2010) and on our own botanical survey (Ledru et al., 2013). To calculate percentages
 197 fern spores and aquatic or water level-related taxa were excluded from the total sum. The concentration
 198 of pollen was calculated using the method of Cour (1974). Pollen assemblage zones were determined
 199 by optimal partitioning with square-root transformed percentage values for pollen types included in the
 200 pollen sum (Birks and Gordon, 1985) and for all pollen samples, including those taken from tephra
 201 layers. Statistically significant zones were assessed by comparison with the broken-stick model,
 202 following Bennett (1996). Pollen diagrams and zonation were prepared with Psimpoll v4.26 (Bennett
 203 2008).

204 To qualitatively estimate variations in convective wind activity over time we used the log-transformed
 205 Transported pollen: Poaceae pollen ratio (Ledru et al., 2013). According to our modern pollen survey,
 206 the pollen produced by three tree taxa that occur in the upper montane cloud forest (*Alnus*, *Hedyosmum*,
 207 *Podocarpus*) is transported upslope and characterizes the convective wind activity (Bendix et al.,
 208 2006c). Poaceae pollen frequency is related to the soil moisture of the páramo as plants of this family
 209 (*Calamagrostis*, *Festuca*) grow mainly on humid organic clayey soils (Liu et al 2005).

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212 **Table 2.** Radiocarbon dates of core PA1-08. Radiocarbon ages were measured on total organic matter.

213 * = calendar age; ** = rejected 14C dates

Lab number	Depth cm	Age ¹⁴ C yr BP	Lab number	Depth cm	Age ¹⁴ C yr BP
surface	0-2	-60 ±10*			
SacA-11045	22-24	0 ±30	SacA-11050	494-496	3305±30
SacA-18852	50-52	175±30	SacA-18857	516-518	3180±40
Beta-243042	80-82	270±40	SacA-14728	524-526	3790±35
SacA-14722	114-116	530±30	SacA-11051	548-550	3690±30
SacA-14723	160-162	1005±30	SacA-18858	554-556	3790±30
SacA-11046	186-188	1000±30	SacA-14677	568-570	3950±40
SacA-11047	208-210	1105±30	SacA-11052	594-596	3570±30**
SacA-14724	254-256	1540±35	Beta-243043	602-604	3440±40**
SacA-18853	284-286	1860±30	SacA-14678	636-638	4475 ±40
SacA-18855	322-324	2225±40	SacA-18859	680-682	4330±30

SacA-11048	338-340	2470±30	SacA-14679	712-714	4600 ±50
SacA-18854	350-352	2440±30	SacA-18860	742-744	4560±40
SacA-14725	386-388	2885±35	SacA-11053	766-768	4380±30
SacA-14726	404-406	2520±35	SacA-18861	788-790	4460±35
SacA-11049	438-440	2950±30	SacA-14729	806-808	4430±40
SacA-18856	450-452	2885±30	SacA-14680	832-834	4290±40
SacA-14727	476-478	2935±35	SacA-11054	862-863	3620±30**

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Table 3 Description of the tephra layers observed in PA1-08 and reported in figure 3 together with the origin and the year of the eruption re-calculated from our age model (see also supplementary Tables 1 and 2). WC Western Cordillera, EC Eastern Cordillera.

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Tephra layer number	Depth cm	Cordillera	Volcano	Calibrated date of the eruption	Description of the ash layer	References
M1	110-115	WC	Guagua Pichincha	1600 AD	Fine, yellowish ash	Robin et al., 2008
M2a & b	130-148	WC	Quilotoa	1150 AD	2a white & 2b coarse grey ash with small pumice lapilli	Mothes and Hall 2008
M3	181	WC	Guagua Pichincha	975 AD	Coarse, crystal-rich ash with peat	Robin et al., 2008
M4	202-206	EC	Cotopaxi?	1165 yr BP	Yellowish ash	Hall and Mothes 2008
M5	208-226	EC	Antisana	1180 yr BP	Peat with coarse ash and disseminated lapilli	
M6	232-236	-	-	1235 yr BP	Fine, yellowish ash with peat	
M7	257-264	EC	Cotopaxi?	1460 yr BP	Coarse, crystal-rich ash with peat	
M8	318-322	-	-	2230 yr BP	Fine-medium, grey-yellow, crystal-rich ash with peat	
M9	326-332	WC	Atac	2290 yr BP	Fine, white ash	Hidalgo et al., 2008
M10	350-354	-	-	2445 yr BP	Medium ash with peat	
M11a	374-377	-	-	2560 yr BP	Fine, grey-yellowish ash	
M11b	381-386	WC	-	2585 yr BP	Fine, grey-yellowish ash with disseminated lapilli	
M12	458-464	-	-	3140 yr BP	Fine-medium, white ash, well-stratified oxidation level	Hildebrandt 1989
M13	470-473	EC	Tungurahua	3195 yr BP	Medium ash with peat	Hall et al., 1999; Le Pennec et al., 2013
M14	493-500	-	-	3500 yr BP	Fine, clay-rich, dar ash with peat	
M15	521-528	WC	Pichincha	3890 yr BP	Medium, grey-white ash with disseminated crystals	Robin et al., 2008
M16	538-542 546-562	EC	Cotopaxi	4075 y BP	Fine-medium, pseudo-stratified ash with disseminated lapilli	Hall and Mothes 2008
M17a	589-592	WC	-	4320 yr BP	Fine, white ash	
M17b	594-596	WC	-	4335 yr BP	Medium, grey-yellowish ash	
M18	658-668	EC	Atacazo-Ninahuilca	4790 yr BP	Fine, white ash	Hidalgo et al., 2008

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222 Results

223 *Lithology and chronology*

224 The core was mostly composed of brown peat intercalated with 18 tephra layers, M1 to M18,
 225 corresponding to fine-to-medium sized distal ash deposits reported in Fig 2 and Table 3. The six
 226 radiocarbon dates below a depth of 700 cm are incoherent for regular sedimentation because they report
 227 similar ages (Table 2, Fig. 2). For this reason and based on evidence of a two-meter-thick homogeneous
 228 sediment layer composed of reworked organic mud and tephra, we interpreted these 2 m-layers of

229 sediment as a fluvio-glacial deposit. While this interpretation is weakly constrained, the chronology of
230 the sediments above a depth of 700 cm is better constrained. The depth-age model shows that sediments
231 accumulated at least over the past 5,000 years with relatively high sediment deposition times (1.5-20 yr
232 cm⁻¹). Comparison of the age distributions of the tephras resulting from the depth-age model and
233 published radiocarbon dates from within the tephra and/or paleosoils located below or above the tephras
234 in the area of the volcanoes shows good coherence except when two different eruptions occurred within
235 a short time interval (Table 3, Table S1).

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237 *Vegetation dynamics and fire history*

238 The results of the pollen record are presented in a synthetic diagram along a depth scale (Fig. 3) and an
239 age scale (Fig. 4). A total of 189 taxa were identified, including 56 tree pollen taxa, 84 non-arboreal
240 pollen taxa, 27 fern taxa, 2 Algae and 22 unknown types. The Papallacta pollen diagram contains eight
241 statistically significant pollen assemblage zones (Fig. 3 and 4). The signal-to-noise index (SNI) values
242 (median SNI = 10.07, minimum SNI > 3) show that the charcoal-accumulation rate (CHAR) record is
243 suitable for peak analysis and for the detection of fire events.

244 *Pollen zone P1, (700-630 cm, 4960-4600 cal yr BP, 25 samples, resolution 14 years / sample)*

245 This zone contained one 10-cm thick tephra deposit M18 (668-658 cm) dated to 4790 cal yr BP. The
246 vegetation was dominated by Poaceae (35-72 %) with low pollen frequencies of cloud forest taxa *Alnus*
247 (0.5 – 4.5%), *Hedyosmum* (1-8%), *Podocarpus* (0-1%). Among the non-arboreal taxa, *Ambrosia* (0-
248 5%), *Gentianella* (0.2 – 1.5%) Ericaceae (0.2-5%) *Gunnera* (0.2 – 4%), *Acalypha* (0.3 – 5%),
249 Cyperaceae (7-166%) with the highest frequencies at the top of the zone between 658 and 630 cm and
250 the fern *Huperzia* (10- 95%). The quantity of burned biomass increased and two fire events were
251 detected (Fig. 5). Charcoal morphotypes indicate that fires were fed by a mixture of wood and Poaceae
252 fuel.

253 The beginning of the record, between 700 and 658 cm, was characterized by the presence of *Ambrosia*,
254 bog plant assemblages and a few Cyperaceae, an assemblage that documents sufficient soil moisture.
255 After the M18 tephra were deposited, Poaceae pollen frequency decreased while that of Cyperaceae
256 increased.

257 *Pollen Zone P2, 630-614 cm, 4600 – 4475 cal yr BP, 5 samples, resolution 25 years / sample*

258 No tephra was deposited in this zone. Pollen assemblages were characterized by low frequency of
259 Poaceae (6%), and high frequency of *Ast Senecio* (67%). *Melastomataceae* and *Polylepis* peaked
260 towards the beginning of the zone (14% and 8%, respectively), while *Apiaceae* pollen values peaked
261 towards the end of zone (20%). The upper montane cloud forest taxa (*Alnus*, *Hedyosmum*, *Podocarpus*)
262 were well represented. The decrease in bog moisture-related taxa that started at the end of P1 (*Piper*,
263 *Gunnera*, *Gentianella*, *Cyathea* and *Huperzia*) suggest drier conditions in the bog. Cyperaceae almost
264 disappeared (~8%). Less biomass was burned and the fire-return interval (FRI) was slightly higher than
265 in the previous zone.

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3 266 *Pollen Zone P3, 614-353 cm, 4475 – 2440 cal yr BP, 49 samples, resolution 41 years /sample*

4 267 Seven tephra layers (M17 to M11) were deposited on the bog during this zone (Fig. 2, Table 3). Poaceae
5 268 pollen was frequent but a sharp decrease was observed at 490 cm (3450 cal yr BP) (53% to 14%), and
6 269 remained low up to 416 cm (2800 cal yr BP). This event lasted ~650 years then increased progressively
7 270 to 68% (2575 cal yr BP) at the end of the zone, reaching 53% at 2440 cal yr BP. Poaceae (25-85%), *Ast*
8 271 *liguliflorae* (0-6%) (Apiaceae 0-8%) *Alnus* (0-5%) *Hedyosmum* (0-4.5%) were the main taxa in pollen
9 272 zone P3. While burned biomass was mostly low in this zone, distinct charcoal peaks point to the
10 273 occurrence of fire events. The lowest FRI values (50 years) occurred around 3100-3050 cal yr BP when
11 274 Poaceae pollen decreased. Charcoal morphotypes indicate that fire events around 4400-3800 and at 2600
12 275 cal BP were predominantly fuelled by Poaceae. The fire events at 4100 and 2550 cal yr BP occurred
13 276 after tephra deposition (the ~40 cm thick M16 tephra and the 8 cm thick M11 tephra, respectively).

14 277 *Pollen zone P4, 353- 280 cm, 2440-1685 cal yr BP, 24 samples, 31 years / sample*

15 278 Two 4-cm thick tephra layers (M9 and M8) were deposited in a short time interval between 2290 and
16 279 2230 cal yr BP. The zone was characterized by a sharp decrease in Poaceae (16-42%) and in cloud
17 280 forest-related tree taxa although the decrease in *Alnus* (0-3%) is masked by an increase in *Hedyosmum*
18 281 (3-11%), an increase in *Ast. Senecio* (6-25%) including a decrease during the eruptions and at the end
19 282 of the zone (0-3%). Cyperaceae disappeared progressively while *Thalictrum* (%), an herb of the paramo,
20 283 increased. *Ambrosia* began to increase at the end of the zone (0-1% to 4-12%) while *Huperzia* increased
21 284 right after the volcanic eruptions. The quantity of burned biomass remained low throughout the period
22 285 and no fire event occurred. During this 750 yr interval, the convective activity index increased (Fig. 5)
23 286 and *Polylepis* was well represented. This suggests no changes in the cloud and *Polylepis* forests but
24 287 rather in the local assemblages with drier soil conditions after the two ash fallout deposits, as indicated
25 288 by the increase in Apiaceae, which ranged from 0-1% before ash deposits and from 6-21% after the ash
26 289 deposits, by the decrease in *Ast. Senecio* (25-3%), *Gunnera* frequency which was notable (6-3%) before
27 290 the eruption and absent after the eruption (0-1%), by the increase in *Gentianella* (1-18%) which started
28 291 just before the volcanic eruption, and by a brief increase in Poaceae during the interval of the volcanic
29 292 eruption.

30 293 *Pollen Zone P5, 280-200 cm, 1685 - 1155 cal yr BP, 22 samples, resolution 24 years / sample*

31 294 Zone 5 lasted 530 years and included four tephra layers M7 (264-257 cm) and M6 (236-232 cm), M5
32 295 (226-208 cm) and M4 (206-202 cm) dated to 1460, 1235, 1180 and 1165 cal yr BP, respectively. No
33 296 major changes in the ecology of the páramo occurred during and after the ash fallout deposits.

34 297 Pollen content was characterized by *Ambrosia* (5-20%), a decrease in Apiaceae (17-1%), a progressive
35 298 decrease in *Huperzia* (62-4%), two peaks of *Gunnera* 33-36% at 248-246 cm (~1350 cal yr BP) and 11-
36 299 20% at 208-210 cm (1180 cal yr BP), the second located above the M4 tephra deposition.

37 300 The sharp decrease in convective activity that started at the beginning of P5 was accentuated by the
38 301 decrease in *Hedyosmum* (7-1%) observed at 250 cm (1375 cal yr BP). While burned biomass remained
39 302 low, FRI dropped sharply to around 150-200 years.

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3 303 *Pollen Zone P6, 200-141 cm, 1155 – 770 cal yr BP, 21 samples, resolution 18 years / sample*

4 304 Two tephra layers were deposited, M3 (181 cm) dated to 975 AD and the beginning of M2 (148-130
5 305 cm) dated to? 1150 AD. The pollen assemblages were characterized by *Ambrosia* (6-18%) and Poaceae
6 306 (12-42%) both well represented throughout the zone, a decrease in Apiaceae (4-0%) and *Gentianella*
7 307 (5-1%), a peak in Urticales (32 and 18%) before and after M3. Charcoal particles remained low with a
8 308 decrease in the middle of the P6 zone. The convective activity index first increased in zone 6 before
9 309 stabilizing. No changes occurred in the pollen assemblages of the páramo during or after the ash deposit
10 310 episodes. This zone provides evidence for high moisture and warm temperatures on the páramo.

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15 311 *Pollen Zone P7, 141-74 cm, 770 - 325 cal yr BP, 25 samples, 18 years / sample*

16 312 With two tephra layers, M2, which ended at the beginning of zone 7 (130 cm), and M1, which ended at
17 313 115-110 cm (1600 AD), zone 7 was characterized by the disappearance of *Ambrosia* (3,5-0%), an
18 314 increase in *Gentianella* (1-12%), Poaceae (17-36%) and Ast liguliflorae (from 1-7% to 15-25% at the
19 315 end of the zone). The convective activity index decreased abruptly at the beginning of the zone with the
20 316 decrease in *Alnus* and *Hedyosmum* up to 105 cm when it again started to increase. A 11-35% peak in
21 317 Urticales occurred at 122-112 cm. Charcoal particle abundance remained low with a peak at the end of
22 318 zone P7. This zone shows drier conditions than the previous zone. Burned biomass was low and no fire
23 319 events were detected.

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25 320 *Pollen Zone P8, 74-0 cm, 325 -0 cal yr BP, 29 samples, resolution 3 years / sample*

26 321 No tephra deposition occurred in the sediment in the last 340 years. Zone 8 was characterized by an
27 322 increase in Apiaceae and *Ambrosia* (2-11%), the highest convective index of the record (0.25), the
28 323 absence of charcoal particles except for a peak in the last decade, high *Huperzia* frequency (19-405%),
29 324 a sharp decrease in Poaceae (from 30 to 8%), a 10-22% increase followed by a 22-1% decrease in
30 325 Apiaceae throughout the zone. High convective activity and low soil moisture characterized the
31 326 hydrological pattern of this zone. Burned biomass was low and only one fire event was detected.

32 327 For a detailed description of the last 700 years, i.e. 1300 AD to 2008 AD, see Ledru et al. (2013).
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44 329 **Interpretation and Discussion**

45 330 To analyze how the forcing factors, climate, fire and tephra deposition, alternately influenced the
46 331 landscape of the páramo, we compared the convective activity index with published palaeoclimate
47 332 records that are representative of ENSO variability and SASM activity (Figs. 1A, 6). ENSO variability
48 333 refers to the changes in equatorial Pacific Sea Surface Temperature (SST) that impacted high elevation
49 334 rainfall variability at interdecadal scales (Morales et al., 2012; Garreaud et al., 2009; Ledru et al., 2013).
50 335 To characterize El Niño activity, we used the record of El Junco in the Galapagos where blooms of the
51 336 algae *Botryococcus* that are associated with high rainfall recorded weak El Niño activity until 3500 cal
52 337 yr BP (Fig. 6) (Zhang et al., 2014). Further south, at Guayaquil, Uk'37-based SST changes were
53 338 reconstructed from a marine core and revealed several fluctuations in SST during the early and mid-
54 339 Holocene until 2500 yr BP when the ITCZ reached the latitude of Guayaquil (Mollier-Vogel et al., 2013;

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3 340 Seillès et al., 2015). SASM activity at pluridecadal scale was characterized by changes in the oxygen
4 341 isotope ratio measured in speleothems located in the Eastern Cordillera. Both Shatuca (1960 m asl) and
5 342 Huagapo (further south at 3850 m asl) records show a synchronous decrease in moisture along the EC
6 343 until 2500 yr BP (Bustamante et al., 2013; Kanner et al., 2013). After this date, an out-of-phase evolution
7 344 can be observed between the records (Fig. 6), suggesting that the increase in ENSO activity is well
8 345 detected at high elevations while at Shatuca, the SASM forcing became dominant after 2500 yr BP.

9 346 At Papallacta, two main increases in the convective index reflecting higher monsoon activity occurred
10 347 at ~2500 BP and at 400 BP while the lowest values of the index occurred at 2600, 1200 and 600 cal yr
11 348 BP (Fig. 6). *Polylepis* pollen is permanently present in the area of Papallacta, with some peaks in the
12 349 bottom of the core followed by full expansion from 3500 cal yr BP until today (Fig. 4).

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14 351 *Fires and tephra deposition*

15 352 Although the páramo has been present at the elevation of Papallacta for the last 5,000 years (Di Pasquale
16 353 et al., 2008), some changes in its floristic assemblages, e.g., shifts from Poaceae dominant páramo to
17 354 Asteraceae dominant páramo, suggest high sensitivity either to climate or other disturbances such as fire
18 355 or tephra deposition. Today in the páramo, frequent burning can be either natural, or linked to volcanic
19 356 or human activities (Horn and Kapelle, 2009). Fires do not appear to have been a common disturbance
20 357 at Papallacta in the last 5,000 years as only four major episodes can be distinguished. Charcoal peaks
21 358 may appear at Papallacta due to the long-distance transport of charcoal particles from volcanic eruptions
22 359 and the associated increase in dry and highly flammable fuels due to tephra-induced plant mortality
23 360 (Horn and Kapelle, 2009). Thus, when charcoal abundances increased shortly after a tephra deposition,
24 361 we infer a potentially tephra-induced fire event occurred. Soil moisture is characterized by the frequency
25 362 of Poaceae pollen (Ledru et al., 2013) and changes can be caused either by climate or tephra deposition
26 363 (Horn and Kapelle, 2009). Three abrupt changes in soil moisture content evidenced by drops in Poaceae
27 364 pollen percentages can be seen in Figs. 3 and 4. The first drop (from 53% to 6%) at ~4700 cal BP follows
28 365 the 10-cm-thick M18 tephra deposition and is associated with higher quantities of burned biomass and
29 366 low FRI values (Fig. 5). Thus, in a scenario where tephra deposition enhances soil and fuel drought, the
30 367 Poaceae drop could have been triggered by fires. This event lasted for 260 years and the vegetation took
31 368 60 years to fully recover. Due to the relatively long duration of this drier event (260 years), we infer
32 369 that, during this interval, a volcanic effect on the soil was coupled with dry climate conditions. Although
33 370 of less amplitude than the ones described above, another fire event at 4100 cal yr BP associated with a
34 371 drop in Poaceae could result from the effect of the M16 tephra deposition.

35 372 The second drop in the frequency of Poaceae pollen occurred between 3450 and 2900 cal yr BP. No
36 373 tephra deposition was observed during this event but the FRI was low (50 yr at ~3100 yr BP). When
37 374 FRI increased again, the recovery of the vegetation lasted less than 50 years and was characterized by
38 375 the expansion of two taxa, which, according to our modern survey, are indicators of drier and cooler
39 376 climate conditions, Apiaceae and Asteraceae liguliflorae (Ledru et al, 2013). The third drop in Poaceae

377 pollen frequency occurred between 2600 and 2400 cal yr BP right after the M11 tephra deposition and
378 at the same time as a fire fueled by Poaceae observed at the beginning of this episode (Fig. 5).

379 Between 1800 and 770 cal yr BP, the synchronous increase in the concentration of charcoal particles,
380 *Ambrosia* pollen, cloud forest tree taxa and bog taxa *Huperzia* (Fig. 4, 5) suggests high moisture and
381 warm conditions and characterizes the warmest interval of the pollen record. Under such moist and
382 warm climate conditions, the low FRI is probably related to increased human activity, which reached
383 higher elevations during this interval with minor fluctuations recorded at 1750, 1550 and around 900
384 cal yr BP. The same conclusion was inferred at Lake La Cocha (González-Carranza et al., 2012).

385 Between 770 and 325 cal yr BP, the simultaneous disappearance of *Ambrosia*, Apiaceae pollen and
386 cloud forest tree taxa, and the expansion of Ast. *Senecio* suggests drier soil and atmospheric conditions
387 than in the previous interval. This is the driest interval of the pollen record which, due to its long
388 duration, could result from both tephra deposition (M2 layer) and climate conditions (Ledru et al., 2013).
389 During the last century, between 250 and 150 cal yr, the expansion of the Apiaceae pollen percentages,
390 the re-expansion of *Ambrosia* and cloud forest tree taxa and the high *Huperzia* frequency suggest high
391 moisture rates on the paramo.

392 Out of seven changes in the landscape, we attribute two to tephra deposition (4100 and 2550 cal yr
393 BP), two of longer duration are associated with the superimposed effect of tephra deposition and
394 climate change (respectively 4600-4440 cal yr BP and 770-325 cal yr BP), two events are exclusively
395 attributed to climate change (3450-2900 cal yr BP and 250-150 cal yr BP) and one to human activity
396 between 1800 and 770 cal yr BP. In the following section, we discuss the climate patterns.

398 *Climate forcings, SASM versus El Niño activity*

399 The bog at the base of core PA1-08 was not fully expanded, probably due to vegetation recovery after
400 the deposit of two meters of organic mud and reworked tephra. However, high Poaceae and cloud forest
401 tree taxa frequencies suggest a high moisture level at Papallacta at the beginning of the record.

402 The pollen record of the last 1,000 years showed statistically significant vegetation changes (pollen
403 zones P-6 to P-8; Fig. 4), including fluctuations of transported tree pollen, *Ambrosia*, and Apiaceae
404 frequencies, that were broadly synchronous with Sea Surface Temperature changes during the Medieval
405 Climate Anomaly (MCA) and the Little Ice Age (LIA) (Ledru et al., 2013). An intermediate dry period,
406 characterized by low tree frequencies and the regression of *Ambrosia* between the MCA and the LIA
407 (zone P-7), also identified by Apaéstegui et al. (2018), highlights the response of páramo biodiversity
408 under both low ENSO variability and low convective activity. Thus, the pollen record spanning the last
409 1000 years shows how the two sources of moisture, namely the year-round adiabatic cloud dripping
410 linked to SASM activity and the ENSO variability at decadal scale, influenced the vegetation cover
411 around Papallacta. Here our aim was to understand how these moisture sources behaved during the late
412 Holocene with an additional driver represented by summer insolation and including the regional
413 volcanic activity with 18 tephtras deposited over the course of the last 5,000 years.

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3 414 At millennial scale, the progressive increase in convective moisture mirrors the long-term trend toward
4 415 more intense SASM driven by higher austral summer insolation in agreement with other records (e.g.,
5 416 Seillès et al., 2015). The increase in insolation drove a progressive increase in adiabatic moisture to
6 417 higher elevation that today represents its highest index in the last 5,000 years (Fig. 6).

9 418 The first interval, between 5000 and 2450 cal yr BP, was characterized by high soil moisture, low
10 419 adiabatic moisture and four increases in the number of charcoal particles associated with fire events
11 420 (Fig. 4 and 5). The abrupt changes in environmental conditions that occurred between 4600 and 4475
12 421 cal yr BP (corresponding to pollen zone 2) lasted 150 years and were associated with less adiabatic
13 422 moisture along the eastern cordillera and low rainfall on the páramo, in agreement with the weakening
14 423 of the SASM in the Amazon basin and the low frequency of El Niño on the Pacific side (Bustamante et
15 424 al., 2013; Zhang et al., 2014). The northernmost position of the ITCZ and the weaker SASM activity
16 425 (Maksic et al., 2019) also resulted in drier climate conditions further east, in northeastern Brazil
17 426 (Montade et al., 2014; Utida et al., 2020), thus confirming similar responses to climate changes by the
18 427 high tropical Andes and Northeastern Brazil and possible links between the two regions (Vuille et al.,
19 428 1999; Mollier-Vogel et al., 2013; Sulca et al., 2016). Another simulation showed that during this
20 429 interval, northern Ecuador was under the influence of the northern hemisphere cooling but does not
21 430 exclude the possibility of cooling caused by a huge volcanic eruption (Ning et al., 2019).

30 431 Between 3450 and 2900 cal yr BP, the dry soil conditions, the increase in adiabatic moisture and the
31 432 cooler temperature are consistent with the lacustrine record of Pallacocha in Peru (4200 m asl) (Moy
32 433 et al., 2002) as well as with the speleothem records, Tigre Perdido (1000 m asl), Shatuca (1960 m asl)
33 434 and Huagapo (3850 m asl) (Fig. 6). This period of increased humidity in the Amazon basin was
34 435 interpreted as changing SST gradients in the tropical Atlantic (Bustamante et al., 2016; van Beukelen et
35 436 al., 2008; Kanner et al., 2013). At the same time, ~3500 to 2600 cal yr BP, El Niño became both more
36 437 frequent and more intense (Fig. 6) and, near the Ecuadorian coast area, the interval between 4200 and
37 438 2850 cal yr BP was marked by the coolest and driest climate conditions of the Holocene, due to the
38 439 weak influence of the ITCZ and strengthening of the Humboldt Current in the Pacific Ocean (Fig. 1A)
39 440 (Seillès et al., 2015). Thus, our results show that the increase in El Niño frequency was superimposed
40 441 on the strengthening of the Humboldt Current able to maintain drier conditions on the paramó, thus
41 442 hampering the high monsoon activity recorded in the Amazon basin.

49 443 The progressive uplift in adiabatic moisture and in the upper forest limit started after 2450 cal yr BP and
50 444 was characterized by an abrupt change in Poaceae and fire activity on the paramo (Fig. 4, 5). On the
51 445 Pacific side, the date of ~2500 cal yr BP marks the time when the ITCZ reached the latitude of Papallacta
52 446 and the beginning of the bimodal precipitation regime observed today along the coast (Mollier-Vogel et
53 447 al., 2013). At higher elevations, this bimodal regime is hampered by permanent moisture originating
54 448 from the Amazon basin, also related to the southern shift of the ITCZ and SASM activity, which is
55 449 superimposed on moisture linked to the Pacific-SST. Within these two intervals separated by 2450 cal
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3 450 yr BP and superimposed on the long-term influence of insolation on the Andean records, centennial- or
4 451 multidecadal-scale environmental changes occurred at Papallacta and are described below (Fig. 6).

6 452 During the second interval of the record, between 2450 and 0 cal yr BP, lower Poaceae frequencies
7 453 (~30%), there was no - or only weak - fire activity (Fig. 4, 5). In addition, the progressive increase in
9 454 the convective index (Fig. 5) suggests upslope expansion of the upper forest limit synchronous with a
11 455 southward shift of the the ITCZ (Seillès et al., 2015) and enhanced SASM on the Amazon side, as also
13 456 reported at Lake La Cocha (2,780 m asl) near Papallacta (González-Carranza et al., 2012; van Boxel et
14 457 al., 2014). From 2300 to 1900 cal yr BP, drier soil conditions and colder temperatures were followed by
16 458 a warmer episode that lasted until 1550 cal yr BP, synchronous with an increase in ENSO activity
18 459 between 2000 and 1500 cal yr BP (Rein et al., 2005; Zhang et al., 2014). Changes in the convective
20 460 index point to two drier episodes at 2550 and 1300 cal yr BP (Fig 6). At about 500 km south of Papallacta
22 461 and at 3,800 m asl, two drier episodes, between 2700 and 2000 cal yr BP and between 1700 and 1000 cal
24 462 yr BP, were also observed in the lacustrine record of Tres Lagunas (Frederick et al., 2018) and can be
26 463 attributed to abrupt changes in SASM activity at centennial scale.

28 464 Modern-day El Niño conditions are characterized by a weaker monsoon and reduced transport of
30 465 moisture and warmer temperatures on the páramo with the reverse situation under La Niña conditions
32 466 (Garreaud, 2009). The wet climate episodes observed at Papallacta before 2450 cal yr BP and in the last
34 467 500 years were both characterized by low El Niño frequency while the dry episode with low soil
36 468 moisture between 2450 and 1300 cal yr BP was characterized by high El Niño frequency between 2400
38 469 and 2000 cal yr BP and low El Niño frequency after 2000 cal yr BP (Zhang et al., 2014) (Fig. 6). Between
40 470 1500 and 1000 cal yr BP, the low El Niño frequency (Fig. 6) probably impacted the SASM activity as
42 471 a marked decrease in adiabatic moisture was observed at Papallacta during this interval (Vuille et al
44 472 2000). High SASM activity (high convective index) was observed up to the elevation of Papallacta at
46 473 4600 cal yr BP, 4400 cal yr BP, between 2400 and 1500 cal yr BP and during the last 500 years, while
48 474 low SASM activity (low convective index) was observed at ~4550, 2550, 1200 and 700 cal yr BP (Fig.
50 475 6).

52 476 Thus, our results show that the influences of the long-term insolation (precession-scale) forcing and of
54 477 the multi-century fluctuations in SASM activity on precipitation over the high summits of the Andes are
56 478 stronger than the influence of ENSO variability at multi-centennial to multi-decadal scales. Differences
58 479 in the intensity and/or amplitude of the signal are also observed between the Andean records
60 480 emphasizing the considerable spatial variability associated with SASM activity. For instance, at Shatuca
and Tigre Perdido, the long dry period that lasted ~200 years at about 2300 cal yr BP (Bustamante et
al., 2016; van Breukelen et al., 2008) does not correspond to the driest period at Papallacta. The multi-
decadal changes observed in the speleothem records, for instance, the increase in moisture between 3500
and 2900 cal yr BP, are not observed at Papallacta or in the lacustrine record of Tres Lagunas (Frederick
et al., 2018), suggesting that the vegetation was not impacted and/or that the amplitude of the event was
smaller at higher elevations. The influence of the intensity of the SASM on precipitation variability over

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3 487 the high summits of the Andes after 2500 yr BP is also visible in the Ti/Ca sediment record of Mollier-
4 488 Vogel et al. (2013) from the Gulf of Guayaquil (4°S) (Fig. 6). However, during the late Holocene, at
5 489 both low and high elevations, the influence of the precession cycle on the gradual increase in moisture
6 490 was punctuated by centennial-scale deviations, indicating other influences triggered the considerable
7 491 spatial variability associated with the SASM (Kanner et al.2013; Vuille and Werner, 2005).

11 492

12 493 **Conclusion**

14 494 Our results show that the páramo is a very sensitive ecosystem to long-term insolation and to the series
15 495 of multi-centennial to multi-decadal-scale events in the late Holocene. We found two types of responses
16 496 of the vegetation cover depending on the origin of the moisture: soil with the expansion/regression of
17 497 Poaceae / Ast. *Senecio*, and atmospheric moisture with cloud dripping enhanced by the adiabatic upslope
18 498 between the Amazon basin and the high summits of the Eastern Cordillera. During the last 5,000 years,
19 499 the Andean forest upper limit never reached the elevation of the Sucus bog at Papallacta and the 18
20 500 regional tephra fallout deposits had almost no impact on the biodiversity of the páramo, only on the
21 501 local drainage of the bog. However, in the long term, at precession scale, and superimposed on the short
22 502 term, multi-centennial to multi-decadal climate events strongly modified the floristic composition of the
23 503 páramo with frequent fires before 2450 cal yr BP. The driest event in the last 5,000 years characterized
24 504 by the lowest convective index occurred at ~4500 cal yr BP, when both mean annual precipitation
25 505 decreased and convective moisture abruptly stopped reaching the elevation of Papallacta. In the last
26 506 century, the adiabatic moisture upslope reached its strongest amplitude. By comparing our results with
27 507 marine, speleothem, lake or bog records, we also emphasize how in the Tropics, a single climate event
28 508 may be manifest in a wide range of effects depending on the elevation and location of the site,
29 509 confirming the influence of the SASM on precipitation variability over the high summits of the Andes.

39 510

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3 827 **List of tables**

4 828

6 829 **Table 1** Description of the vegetation cover around Papallacta bog (from Ledru et al., 2013).

8 830

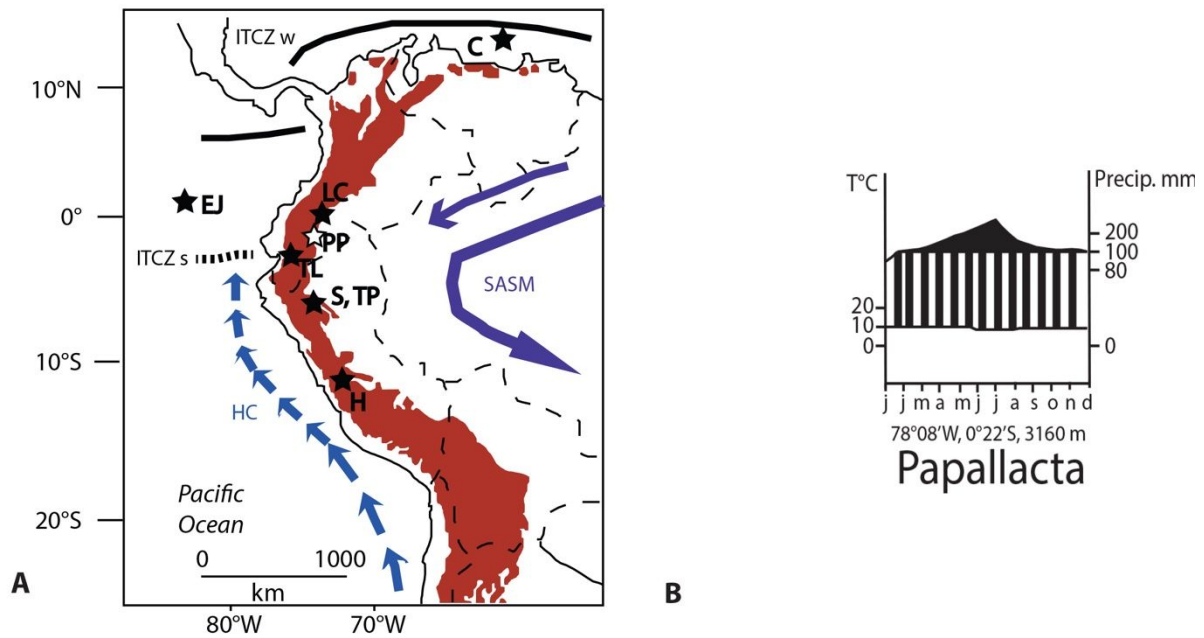
9 831 **Table 2** Chronology of core PA1-08. Radiocarbon ages measured on total organic matter from
11 832 sediments in the PA1-08 core.

12 833

14 834 **Table 3** Description of the tephra layers in PA1-08 shown in Fig. 3 with the origin and the year of the
15 835 eruption re-calculated from our age model (see also supplementary Tables S1 and S2). WC Western
17 836 Cordillera, EC Eastern Cordillera.

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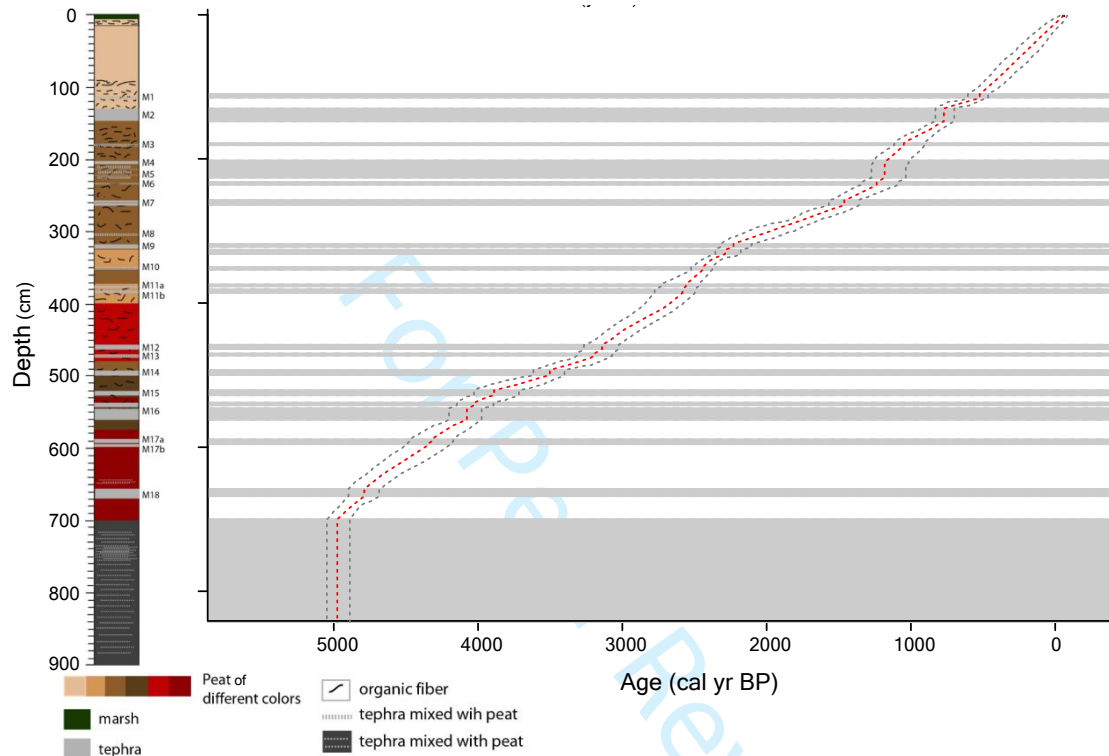
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839 **Figures with Figure captions**

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843 **Figure 1:** A) Map of western South America showing the tropical Andes (in red), the location of
844 Papallacta bog (white star), the location of some of the records cited in the text (C Cariaco (Haug et al.,
845 2001), LC Lake La Cocha (González-Carranza et al., 2012), TL Tres Laguna (Frederick et al., 2018), S
846 Shatuca (Bustamante et al., 2016), TP Tigre Perdido (van Breukelen et al., 2008), H Huagapo (Kanner
847 et al., 2013)) and the main climatic features discussed in the text (ITCZw is the position of the
848 InterTropical Convergence Zone in winter, ITCZs in summer, HC the Humboldt Current, SASM South
849 American Summer Monsoon). B) Climate information represented on a Walter diagram (Luteyn, 1999).
850 Temperature is shown by the bottom curve, precipitation by the upper curve. C) The bog at Papallacta
851 with patches of *Polylepis* forest on the background slopes. D) View of the M2 tephra in core PA1-08
852 (©MP Ledru)

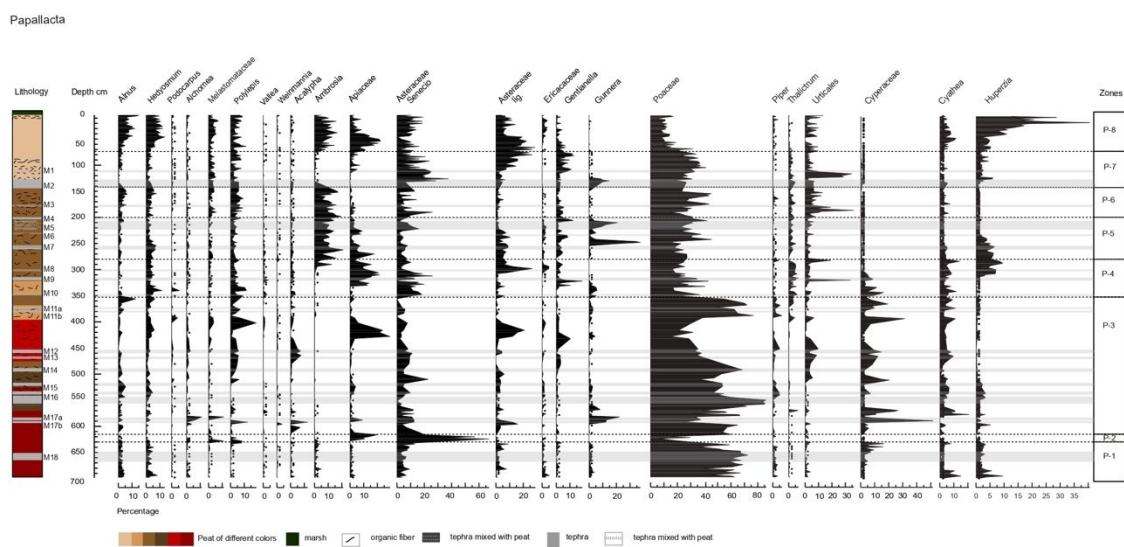
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 856 **Figure 2:** Lithology of the PA1-08 core of Papallacta showing the location of tephra layers M1 to M18
 857 (see Table 3). Grey rectangles along the depth scale indicate the thickness of the tephra layers. Bacon
 858 age/depth model of core PA1-08 (red dashed line) overlaying the calibrated distributions of the
 859 individual radiocarbon dates (blue) (see Table 2) and the age of the tephra deposits (in green) reported
 860 in Table 3. Dark grey areas show the 95% confidence intervals of the models (Blaauw and Christen,
 861 2011).
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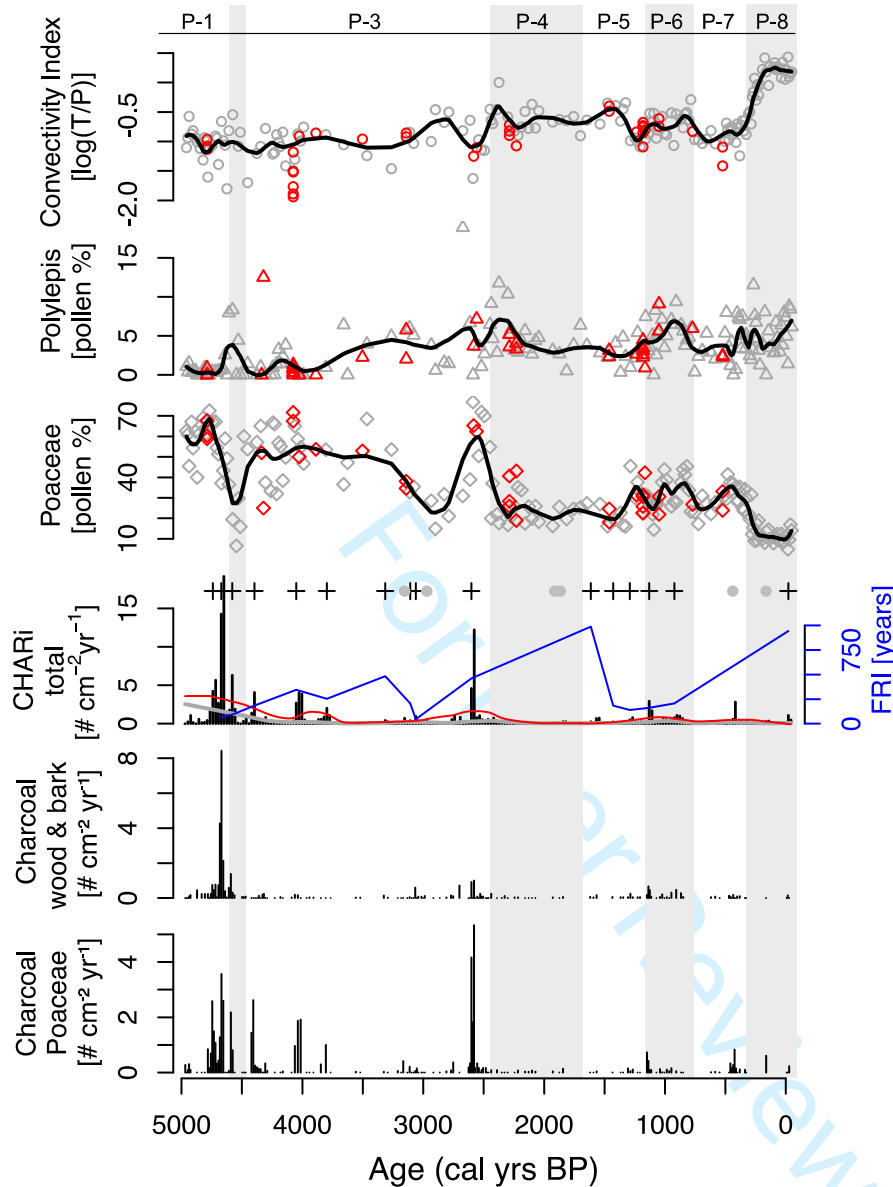
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Figure 3: Percentages of 23 selected pollen and non-pollen taxa sampled in core PA1-08 plotted along a depth scale. Grey shaded areas indicate tephras; dashed horizontal lines: statistically significant pollen assemblage zone boundaries.

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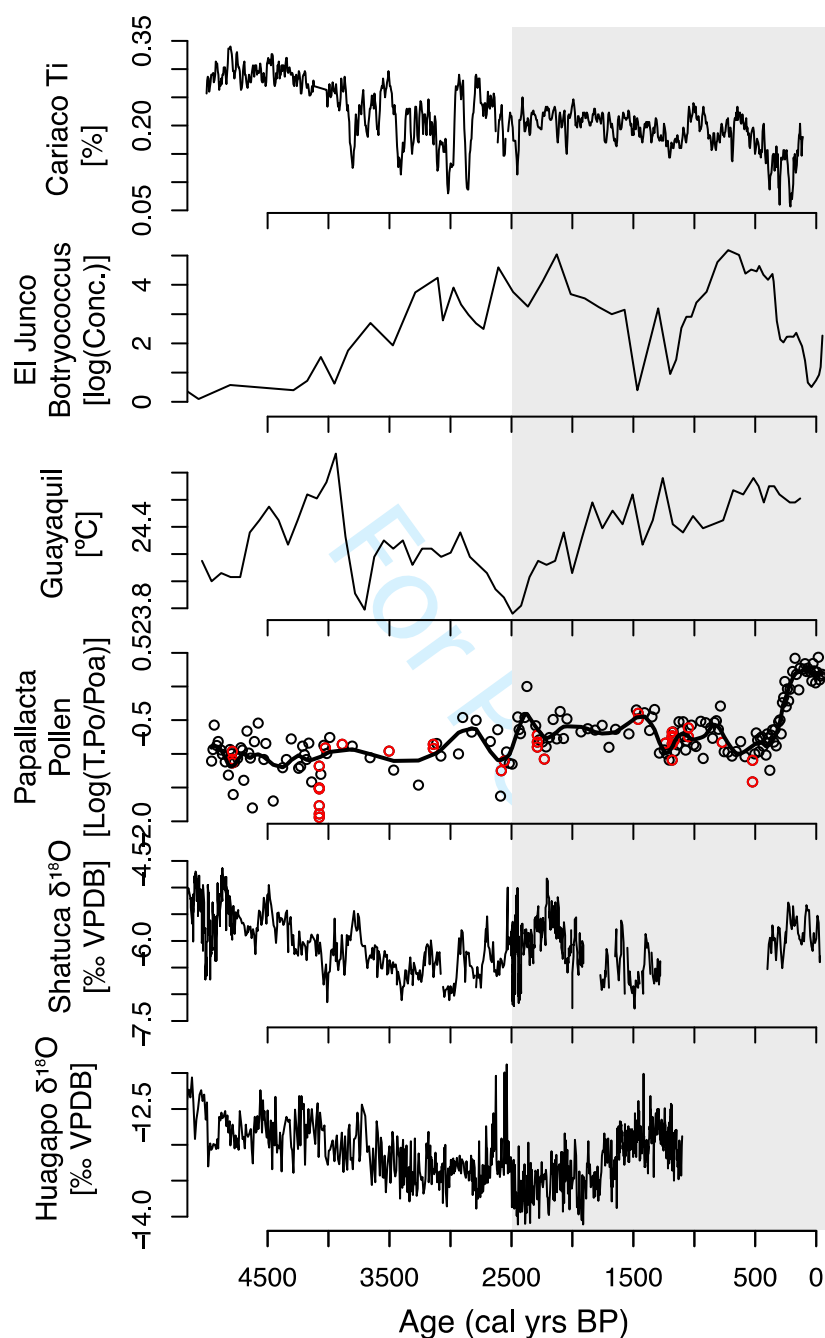
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Figure 5: Results of core PA1-08. Comparison between vegetation dynamics and fire history in Papallacta bog. From top to bottom: the convective wind activity (convectivity index) inferred from the log-transformed Transported pollen:Poaceae pollen ratio ($\log(T/P)$), *Polyepis* and Poaceae pollen percentages, and fire history based on the abundance of all particles of charcoal, wood and bark charcoal, and Poaceae charcoal. Red empty symbols: samples from tephra layers; black thick lines: loess smoothed records; histograms: charcoal accumulation rate; thick grey line: burned biomass; thin red line: threshold; crosses: fire events; gray circles: insignificant charcoal peaks; blue line: fire return interval (FRI).

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890 **Figure 6:** Records documenting past changes in precipitation in western tropical South America for
 891 the past 5,000 years. From north to south (A) the changes in Ti% associated with shifts in ITCZ at
 892 Cariaco (10°N) (Haug et al., 2001) (B) changes in *Botryococcus* frequencies at El Junco (Galapagos),
 893 a record of El Niño frequency (Zhang et al., 2014) (C) SST in the Bay of Guayaquil (Ecuador;
 894 Mollier-Vogel et al., 2013) (D) the Papallacta T/P index of upslope convective activity calculated
 895 from the PA1-08 pollen record; (E) changes in $\delta^{18}\text{O}$ at Shatuca (Peru): a record of SASM intensity
 896 (Bustamante et al., 2016); (F) changes in $\delta^{18}\text{O}$ at Huagapo (Peru): a record of SASM intensity (Kanner
 897 et al., 2013).

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5 899 **Supplementary Table**
6 900 **Table S1** Radiocarbon ages of the eruptions dated *in situ* taken from volcanologic studies, including
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8 901 the location of the dated material inside (I), under (U) or above (O) the tephra, the link with the tephra
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10 902 layers observed at Papallacta and the associated references.
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13 904
14 905 **Sample number Lab number Material Position Age 14C Reference**
15 906
16 907
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Tephra M1: 1560-1660 AD

Sample number	Lab number	Material	Position	Age 14C	Reference
PICH-98C	GrN25522	charcoal	I	240 ± 20	Robin et al .,2008
PICH-98B1	GrN25521	charcoal	I	290 ± 20	
PICH-90A	GrN25517	charcoal	I	320 ± 20	
PICH-33B	GrA32951	charcoal	I	330 ± 30	
PICH-128B	GrA32953	charcoal	I	330 ± 30	
PICH-30G	GrN25508	charcoal	I	335 ± 20	

Tephra M2: Quilotoa

Beta analytic	charcoal	I	840 ± 50	Mothes and Hall, 2008
USGS-M	charcoal	I	900 ± 150	
USGS-M	charcoal	I	1150 ± 300	
Teledyne isotopic	paleosoil	U	820 ± 80	
Beta analytic	charcoal	I	770 ± 40	
Beta analytic	charcoal	I	780 ± 40	

Tephra M3: 10th century eruption of the Guagua Pichincha

PICH-36C	GrN30187	paleosoil	U	930 ± 60	Robin et al., 2008
PICH-127C	GrN30189	charcoal	I	1020 ± 25	
PICH-85	GrN25513	paleosoil	U	1100 ± 40	
PICH-87	GrN25515	charcoal	I	1100 ± 90	
PICH-38E	GrN24776	charcoal	I	1120 ± 30	
PICH-127B	GrN25809	charcoal	I	1180 ± 30	
PICH-127A	GrN26206	charcoal	I	1260 ± 70	

Tephra M4 (?): Cotopaxi "X" eruption

paleosoil	U	1180 ± 80	Hall and Mothes, 2008
paleosoil	U	1210 ± 80	

Tephra M9-10: N6 eruption of the Atacazo-Ninahuilca

SA-22E4	GrN28724	charcoal	I	2320 ± 30	Hidalgo et al., 2008
SA-22A	GrN28723	paleosoil	U	2300 ± 30	

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SA-45B	GrN28730	charcoal	I	2260 ± 30	
SA-38C1	GrN28728	paleosoil	U	2250 ± 30	
SA-52B	GrN28731	charcoal	I	2230 ± 40	
SA-42D	GrN28729	charcoal	I	2220 ± 40	

Tephra M12 (?): Cuicocha eruption**Tephra M13 (?): Tungurahua 3000 BP eruption**

		wood	I	2995 ± 90	Hall et al., 1999; Le Pennec et al. 2013
	GrN27847	charcoal	I	2640 ± 45	
	GrA34159	charcoal	I	2845 ± 40	
	GrA23911	charcoal	I	2915 ± 40	
	GrA30884	charcoal	I	2960 ± 30	
	GrA33878	charcoal	I	3045 ± 45	
	GrA24128	charcoal	U	3195 ± 45	

Tephra M14-15 (?): Guagua Pichincha

PICH-29B	GrN25507	charcoal	I	3540 ± 30	Robin et al., 2008
PICH-72	GrN25512	paleosoil	U	3700 ± 30	

Tephra M16: Cotopaxi rhyolites (F or Colorado canyon)

		paleosoil	O	4420 ± 80	Hall and Mothes, 2008
		paleosoil	O	4670 ± 70	
		charcoal	I	4460 ± 140	
		paleosoil	O	4170 ± 110	
		paleosoil	O	3950 ± 70	

Tephra M18 (?): N5 eruption of the Atacazo-Ninahuilca

SA-24C	GrN28725	charcoal	I	4360 ± 50	Hidalgo et al., 2008
SA-24I	GrN28726	charcoal	I	4440 ± 50	
SA-38A	GrN28727	paleosoil	U	4600 ± 40	

Tephra M18 (?): Chachimbiro eruption

		peat overlying tephra dep	O	4615 ± 40	Bernard et al., 2014
CHA-BB-016	SacA19708				
CHA-BB-009	GrN32372	charcoal	I	4790 ± 65	
CHA-BB-021	GrN32373	charcoal	I	4766 ± 50	
CHA-BB-022	SacA19694	charcoal	I	4760 ± 40	

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911 **Table S2** Age of the tephra layers calculated from the age model based on the identification
 912 of the origin of the ash deposit reported in Table S1. Only three tephras showed no or little
 913 identification uncertainty and were included in the final age model (Fig. 2).
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Papallaca PA1-08					Ages of the tephras based on documentary evidence and 14C dates			
Tephra ID	TopDepth	BotDepth	Depth	Thickness	Cal BP	¹⁴ C BP	error	Uncertainty 0 no; 3 max
M1	110	115	112.5	5	430		20	1
M2ab	130	148	139	18	793		24	0
M3	178	181	181	3	1096		15	1
M4	202	206	204	4		1210	200	2
M4	202	206	204	4		1230	30	2
M5	208	226	217	18		#N/A	#N/A	3
M6	232	236	234	4		#N/A	#N/A	3
M7	257	264	260.5	7		#N/A	#N/A	3
M8	318	322	320	4		#N/A	#N/A	3
M9	326	332	329	6		2320	30	3
M9	326	332	329	6		2300	30	3
M9	326	332	329	6		2260	30	3
M9	326	332	329	6		2250	30	3
M9	326	332	329	6		2230	40	3
M9	326	332	329	6		2220	40	3
M10	350	354	352	4		2320	30	3
M10	350	354	352	4		2300	30	3
M10	350	354	352	4		2260	30	3
M10	350	354	352	4		2250	30	3
M10	350	354	352	4		2230	40	3
M10	350	354	352	4		2220	40	3
M11a	374	377	375.5	3		2450	30	3
M11b	381	386	383.5	5		2520	30	3
M12	458	464	461	6		In progress		
M13	470	473	471.5	3		2995	90	3
M13	470	473	471.5	3		2640	45	3
M13	470	473	471.5	3		2845	40	3
M13	470	473	471.5	3		2915	40	3
M13	470	473	471.5	3		2960	30	3
M13	470	473	471.5	3		3045	45	3
M13	470	473	471.5	3		3195	45	3
M14	493	500	496.5	7		3540	30	3
M14	493	500	496.5	7		3700	30	3
M15	521	528	524.5	7		3540	30	3
M15	521	528	524.5	7		3700	30	3
M16a	538	542	540	4		4420	80	3
M16b	546	562	554	16		4670	70	3

M16b	546	562	554	16		4460	140	3
M16b	546	562	554	16		4170	110	3
M16b	546	562	554	16		3950	70	3
M17a	589	592	590.5	3		#N/A	#N/A	
M17b	594	596	595	2		#N/A	#N/A	
M18	658	668	663	10		4615	40	
M18	658	668	663	10		4790	65	
M18	658	668	663	10		4766	50	
M18	658	668	663	10		4760	40	
M18	658	668	663	10		4360	50	
M18	658	668	663	10		4440	50	
M18	658	668	663	10		4600	40	

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Table 1. Description of the vegetation cover around Papallacta bog (from Ledru et al., 2013).

Site	Family	Species	Family	Species	
Paramo 3,600- 4,000 m asl	Poaceae	<i>Calamagrostis sp.</i> <i>Festuca sp.</i>	Asteraceae	<i>Diplostephium sp.</i>	
	Rosaceae	<i>Polylepis sp.</i>		<i>Pentacalia sp.</i>	
	Hypericaceae	<i>Hypericum sp.</i>			
Papallacta bog 3,815 m asl	Asteraceae	<i>Loricaria toyoides</i> <i>Dorobaea pinpinelifolia</i> <i>Monticalia vaccinioides</i>	Gunneraceae Ranunculaceae Clusiaceae	<i>Gunnera magellanica</i> <i>Ranunculus sp.</i> <i>Hypericum laricifolium</i>	
		<i>Hippochoeris sp.</i>		<i>Hypericum sp.</i>	
		<i>Xenophyllum sp.</i>	Geraniaceae	<i>Geranium sp.</i>	
		<i>Werneria sp.</i>	Polygonaceae	<i>Muehlenbeckia volcanica</i>	
	Valerianaceae	<i>Valeriana microphylla</i>	Apiaceae	<i>Hydrocotyle sp.</i>	
	Lycopodiaceae	<i>Huperzia sp.</i>		<i>Azorella sp.</i>	
	Gentianaceae	<i>Gentiana sedifolia</i> <i>Halemia weddeliana</i> <i>Gentianella sp.</i>	Plantaginaceae Cyperaceae	<i>Plantago rigida</i> <i>Carex lechmanii</i>	
	Poaceae	<i>Cortaderia sericanta</i> <i>Bromus sp.</i> <i>Cortaderia nitida</i>			
	Cushion paramo	Apiaceae	<i>Azorella sp.</i>	Plantaginaceae	<i>Plantago sp.</i>
	Paramo >4,000 m asl	Malvaceae	<i>Nototriche sp.</i>	Brassicaceae	<i>Draba sp.</i>
		Apiaceae	<i>Azorella sp.</i>	Plantaginaceae	<i>Plantago sp.</i>
Asteraceae		<i>Chuquiraga sp.</i> <i>Loricaria sp.</i> <i>Werneria sp.</i>			

Table 2. Radiocarbon dates of core PA1-08. Radiocarbon ages were measured on total organic matter.
 * = calendar age; ** = rejected ^{14}C dates

Lab number	Depth cm	Age ^{14}C yr BP	Lab number	Depth cm	Age ^{14}C yr BP
surface	0-2	-60 \pm 10*			
SacA-11045	22-24	0 \pm 30	SacA-11050	494-496	3305 \pm 30
SacA-18852	50-52	175 \pm 30	SacA-18857	516-518	3180 \pm 40
Beta-243042	80-82	270 \pm 40	SacA-14728	524-526	3790 \pm 35
SacA-14722	114-116	530 \pm 30	SacA-11051	548-550	3690 \pm 30
SacA-14723	160-162	1005 \pm 30	SacA-18858	554-556	3790 \pm 30
SacA-11046	186-188	1000 \pm 30	SacA-14677	568-570	3950 \pm 40
SacA-11047	208-210	1105 \pm 30	SacA-11052	594-596	3570 \pm 30**
SacA-14724	254-256	1540 \pm 35	Beta-243043	602-604	3440 \pm 40**
SacA-18853	284-286	1860 \pm 30	SacA-14678	636-638	4475 \pm 40
SacA-18855	322-324	2225 \pm 40	SacA-18859	680-682	4330 \pm 30
SacA-11048	338-340	2470 \pm 30	SacA-14679	712-714	4600 \pm 50
SacA-18854	350-352	2440 \pm 30	SacA-18860	742-744	4560 \pm 40
SacA-14725	386-388	2885 \pm 35	SacA-11053	766-768	4380 \pm 30
SacA-14726	404-406	2520 \pm 35	SacA-18861	788-790	4460 \pm 35
SacA-11049	438-440	2950 \pm 30	SacA-14729	806-808	4430 \pm 40
SacA-18856	450-452	2885 \pm 30	SacA-14680	832-834	4290 \pm 40
SacA-14727	476-478	2935 \pm 35	SacA-11054	862-863	3620 \pm 30**

Tephra layer number	Depth cm	Cordillera	Volcano	Calibrated date of the eruption	Description of the ash layer	References
M1	110-115	WC	Guagua Pichincha	1600 AD	Fine, yellowish ash	Robin et al., 2008
M2a & b	130-148	WC	Quilotoa	1150 AD	2a white & 2b coarse grey ash with small pumice lapilli	Mothes and Hall 2008
M3	181	WC	Guagua Pichincha	975 AD	Coarse, crystal-rich ash with peat	Robin et al., 2008
M4	202-206	EC	Cotopaxi?	1165 yr BP	Yellowish ash	Hall and Mothes 2008
M5	208-226	EC	Antisana	1180 yr BP	Peat with coarse ash and disseminated lapilli	
M6	232-236	-	-	1235 yr BP	Fine, yellowish ash with peat	
M7	257-264	EC	Cotopaxi?	1460 yr BP	Coarse, crystal-rich ash with peat	
M8	318-322	-	-	2230 yr BP	Fine-medium, grey-yellow, crystal-rich ash with peat	
M9	326-332	WC	Atac	2290 yr BP	Fine, white ash	Hidalgo et al., 2008
M10	350-354	-	-	2445 yr BP	Medium ash with peat	
M11a	374-377	-	-	2560 yr BP	Fine, grey-yellowish ash	
M11b	381-386	WC	-	2585 yr BP	Fine, grey-yellowish ash with disseminated lapilli	
M12	458-464	-	-	3140 yr BP	Fine-medium, white ash, well-stratified oxidation level	Hildebrandt 1989
M13	470-473	EC	Tungurahua	3195 yr BP	Medium ash with peat	Hall et al., 1999; Le Pennec et al., 2013
M14	493-500	-	-	3500 yr BP	Fine, clay-rich, dar ash with peat	
M15	521-528	WC	Pichincha	3890 yr BP	Medium, grey-white ash with disseminated crystals	Robin et al., 2008
M16	538-542	EC	Cotopaxi	4075 y BP	Fine-medium, pseudo-stratified ash with disseminated lapilli	Hall and Mothes 2008
M17a	546-562	WC	-	4320 yr BP	Fine, white ash	
M17b	589-592	WC	-	4335 yr BP	Medium, grey-yellowish ash	
M18	594-596	EC	Atacazo-Ninahuilca	4790 yr BP	Fine, white ash	Hidalgo et al., 2008
	658-668					

Supplementary table Radiocarbon ages of the eruptions dated in situ by the volcanologists with the location of the dated material I inside U under the tephra O above the tephra, the link with the tephra layers observed at Papallacta and the associated references.

Sample number	Lab number	Material	Position	Age ^{14}C	Reference
Tephra M1: 1560-1660 AD					
PICH-98C	GrN25522	charcoal	I	240 ± 20	Robin et al., 2008
PICH-98B1	GrN25521	charcoal	I	290 ± 20	
PICH-90A	GrN25517	charcoal	I	320 ± 20	
PICH-33B	GrA32951	charcoal	I	330 ± 30	
PICH-128B	GrA32953	charcoal	I	330 ± 30	
PICH-30G	GrN25508	charcoal	I	335 ± 20	
Tephra M2: Quilotoa					
	Beta analytic	charcoal	I	840 ± 50	Mothes and Hall, 2008
	USGS-M	charcoal	I	900 ± 150	
	USGS-M	charcoal	I	1150 ± 300	
	Teledyne isotopic	paleosoil	U	820 ± 80	
	Beta analytic	charcoal	I	770 ± 40	
	Beta analytic	charcoal	I	780 ± 40	
Tephra M3: 10th century eruption of the Guagua Pichincha					
PICH-36C	GrN30187	paleosoil	U	930 ± 60	Robin et al., 2008
PICH-127C	GrN30189	charcoal	I	1020 ± 25	
PICH-85	GrN25513	paleosoil	U	1100 ± 40	

PICH-87	GrN25515	charcoal	I	1100 ± 90	
PICH-38E	GrN24776	charcoal	I	1120 ± 30	
PICH-127B	GrN25809	charcoal	I	1180 ± 30	
PICH-127A	GrN26206	charcoal	I	1260 ± 70	
Tephra M4 (?): Cotopaxi "X" eruption					
		paleosoil	U	1180 ± 80	Hall and Mothes, 2008
		paleosoil	U	1210 ± 80	
Tephra M9-10: N6 eruption of the Atacazo-Ninahuilca					
SA-22E4	GrN28724	charcoal	I	2320 ± 30	Hidalgo et al., 2008
SA-22A	GrN28723	paleosoil	U	2300 ± 30	
SA-45B	GrN28730	charcoal	I	2260 ± 30	
SA-38C1	GrN28728	paleosoil	U	2250 ± 30	
SA-52B	GrN28731	charcoal	I	2230 ± 40	
SA-42D	GrN28729	charcoal	I	2220 ± 40	
Tephra M12 (?): Cuicocha eruption					
Tephra M13 (?): Tungurahua 3000 BP eruption					
		wood	I	2995 ± 90	Hall et al., 1999; Le Pennec et al., 2013
	GrN27847	charcoal	I	2640 ± 45	
	GrA34159	charcoal	I	2845 ± 40	
	GrA23911	charcoal	I	2915 ± 40	
	GrA30884	charcoal	I	2960 ± 30	
	GrA33878	charcoal	I	3045 ± 45	
	GrA24128	charcoal	U	3195 ± 45	
Tephra M14-15 (?): Guagua Pichincha					

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3	PICH-29B	GrN25507	charcoal	I	3540 ± 30	Robin et al., 2008
4	PICH-72	GrN25512	paleosoil	U	3700 ± 30	
5						
6						
7	Tephra M16: Cotopaxi rhyolites (F or Colorado canyon)					
8			paleosoil	O	4420 ± 80	Hall and Mothes, 2008
9			paleosoil	O	4670 ± 70	
10			charcoal	I	4460 ± 140	
11			paleosoil	O	4170 ± 110	
12			paleosoil	O	3950 ± 70	
13						
14						
15						
16	Tephra M18 (?): N5 eruption of the Atacazo-Ninahuilca					
17	SA-24C	GrN28725	charcoal	I	4360 ± 50	Hidalgo et al., 2008
18	SA-24I	GrN28726	charcoal	I	4440 ± 50	
19	SA-38A	GrN28727	paleosoil	U	4600 ± 40	
20						
21						
22	Tephra M18 (?): Chachimbiro eruption					
23			peat			
24			overlying			
25	CHA-BB-016	SacA19708	tephra dep	O	4615 ± 40	Bernard et al., 2014
26	CHA-BB-009	GrN32372	charcoal	I	4790 ± 65	
27	CHA-BB-021	GrN32373	charcoal	I	4766 ± 50	
28	CHA-BB-022	SacA19694	charcoal	I	4760 ± 40	
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32	References					
33						
34	Bernard B, Hidalgo S, Robin C <i>et al.</i> (2014) The 3640–3510 BC rhyodacite eruption of Chachimbiro compound volcano, Ecuador: a violent directed blast					
35	produced by a satellite dome. <i>Bull Volcanol</i> 76: 849.					
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Table S2 Age of the tephra layers calculated from the age model based on the identification of the origin of the ash deposit reported in Table S1. Only three tephras showed no or little identification uncertainty and were included in the final age model (Fig. 2).

Papallaca PA1-08					Ages of the tephras based on documentary evidence and 14C dates			
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M3	178	181	181	3	1096		15	1
M4	202	206	204	4		1210	200	2
M4	202	206	204	4		1230	30	2
M5	208	226	217	18		#N/A	#N/A	3
M6	232	236	234	4		#N/A	#N/A	3
M7	257	264	260.5	7		#N/A	#N/A	3
M8	318	322	320	4		#N/A	#N/A	3
M9	326	332	329	6		2320	30	3
M9	326	332	329	6		2300	30	3
M9	326	332	329	6		2260	30	3
M9	326	332	329	6		2250	30	3
M9	326	332	329	6		2230	40	3
M9	326	332	329	6		2220	40	3
M10	350	354	352	4		2320	30	3
M10	350	354	352	4		2300	30	3
M10	350	354	352	4		2260	30	3
M10	350	354	352	4		2250	30	3
M10	350	354	352	4		2230	40	3
M10	350	354	352	4		2220	40	3
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M13	470	473	471.5	3		2640	45	3
M13	470	473	471.5	3		2845	40	3
M13	470	473	471.5	3		2915	40	3
M13	470	473	471.5	3		2960	30	3
M13	470	473	471.5	3		3045	45	3
M13	470	473	471.5	3		3195	45	3
M14	493	500	496.5	7		3540	30	3
M14	493	500	496.5	7		3700	30	3
M15	521	528	524.5	7		3540	30	3
M15	521	528	524.5	7		3700	30	3
M16a	538	542	540	4		4420	80	3
M16b	546	562	554	16		4670	70	3

M16b	546	562	554	16		4460	140	3
M16b	546	562	554	16		4170	110	3
M16b	546	562	554	16		3950	70	3
M17a	589	592	590.5	3		#N/A	#N/A	
M17b	594	596	595	2		#N/A	#N/A	
M18	658	668	663	10		4615	40	
M18	658	668	663	10		4790	65	
M18	658	668	663	10		4766	50	
M18	658	668	663	10		4760	40	
M18	658	668	663	10		4360	50	
M18	658	668	663	10		4440	50	
M18	658	668	663	10		4600	40	

For Peer Review