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Polylepis woodland dynamics during the last 20,000 years

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Abstract

Aim: To determine the palaeoecological influences of climate change and human land use on the spatial distribution patterns of *Polylepis* woodlands in the Andes.

Location: Tropical Andes above 2,900 m between 2°S and 18°S of latitude.

Methods: Pollen and charcoal data were gathered from 13 Andean lake sediment records and were rescaled by the maximum value in each site. The rescaled pollen data were used to estimate a mean abundance and coefficient of variation to show woodland expansions/contractions and woodland fragmentation over the last 20,000 years. The rescaled charcoal was displayed as a 200-year moving median using 500-year bins to infer the influence of fire on woodland dynamics at landscape scale. Pollen and charcoal were compared with speleothem, clastic flux and archaeological data to assess the influence of moisture balance, glacial activity and human impact on the spatial distribution of *Polylepis* woodlands.

Results: Woodland expansion and fire were correlated with precipitation changes and glacier dynamics from c. 20 to 6 kcal BP (thousands of calibrated years before present). Charcoal abundances between 20 and 12 kcal BP were less common than from 12 kcal BP to modern. However, human-induced fires were unlikely to be the main cause of a woodland decline centred at 11 kcal BP, as woodlands recovered from 10.5 to 9.5 kcal BP (about twofold increase). Charcoal peaks analogous to those that induced the woodland decline at 11 kcal BP were commonplace post-9.5 kcal BP but did not trigger an equivalent woodland contraction. An increase in the coefficient of variation after c. 5.5 kcal BP suggests enhanced fragmentation and coincided with the shift from logistic to exponential growth of human populations. Over the last 1,000 years, *Polylepis* became hyper-fragmented with over half of sites losing *Polylepis* from the record and with coefficients of variation paralleling those of glacial times.

Main conclusions: *Polylepis* woodlands formed naturally patchy woodlands, rather than a continuous vegetation belt, prior to human occupation in the Andes. The main factors controlling pre-human woodland dynamics were precipitation and landscape heterogeneity. Human activity led to hyper-fragmentation during the last c. 1,000 years.

KEYWORDS

Andean forest, climate change, endemism, fossil pollen, Holocene, human impact, hyper-fragmented, interglacial, natural fires, *Polylepis* woodlands

1 | INTRODUCTION

An abrupt decline in biodiversity and endemism coincides with the transition from upper Andean forest transitions to Puna grassland (Körner, 2012; Yensen & Tarifa, 2002; Young, 1993; Young & León, 1999). The exception to this pattern is in stands of *Polylepis* woodland, which grow as islands within the grassland. The *Polylepis* woodlands support a range of endemics that are habitat specialists, and other species that only occur at such high elevations in the shelter of the woodland. Consequently, *Polylepis* is disproportionately important to local and regional biodiversity (Chesser, 2004; Fjeldså, Lambin, & Mertens, 1999; Gareca, Hermy, Fjeldså, & Honnay, 2010; Herzog et al., 2002; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Witt & Lane, 2009). The important role of *Polylepis* in providing high-elevation habitat diversity led to *Polylepis* woodland being identified as a conservation priority throughout the tropical Andes (Fjeldså, 2002a; Fjeldså & Kessler, 1996; Gareca et al., 2010; Servat Grace, Mendoza, & Ochoa, 2002; Young & León, 2007).

Polylepis is a fire-intolerant genus (Cierjacks, Salgado, Wesche, & Hensen, 2008; Kessler, 2006) that thrives in areas minimally impacted by human activities and grazing (Sylvester, Sylvester, & Kessler, 2014; Sylvester et al., 2017). *Polylepis* woodlands are present from Venezuela to northern Chile and Argentina, and can be formed by most of the 25 members of the genus (Fjeldså & Kessler, 1996; Simpson, 1979). The peak of biodiversity of other species associated with *Polylepis* woodlands occurs in Peru and Ecuador (Fjeldså, 2002b; Gareca et al., 2010; Lloyd et al., 2012). *Polylepis* can occur up to elevations of 5,200 m (Ellenberg, 1958; Fjeldså & Kessler, 1996), making them the highest growing tree in the world. Although *Polylepis* is most commonly associated with the grassland (Puna), it can also grow below the tree line within the Andean forest; with some individuals occurring as low as 2000 m a.s.l. (Kessler, 2002).

Given the breadth of potential *Polylepis* habitat, Ellenberg (1958) suggested that the modern patchy distribution of woodland could be the product of human impacts instead of a natural distribution determined by microclimate conditions (Kessler, 2002). Ellenberg's hypothesis gained acceptance based upon observations of the high degree of modern landscape modification through land use change, fires and wood extraction (Fjeldså, 2002b; Kessler, 2002). The patchy distribution of *Polylepis* was attributed to natural mechanisms such as fire and microclimate preferences that caused population disjunctions, which were later exacerbated by human activity (Fjeldså, 2002b; Gosling, Hanselman, Knox, Valencia, & Bush, 2009; Hensen, 2002; Kessler, 2002, 2006; Purcell & Brelford, 2004; Simpson, 1979).

The Last Glacial Maximum (25 to 21 thousands of calibrated radiocarbon years before present, henceforth kcal BP) was about 7–9°C cooler than today in the high Andes (Baker & Fritz, 2015; Bush, Silman, & Urrego, 2004). Andean deglaciation began c. 21 kcal BP and most glaciers had retreated to near modern limits by c. 13 kcal BP (Paduano, Bush, Baker, Fritz, & Seltzer, 2003; Seltzer et al., 2002; Smith, Mark, & Rodbell, 2008; Urrego, Niccum, La Drew, Silman, &

Bush, 2011). The deglacial warming was evident in an upslope movement of most floral elements, including *Polylepis*, between c. 20 and 13 kcal BP (Bush et al., 2004; Groot et al., 2011; van der Hammen, 1974; Valencia, Urrego, Silman, & Bush, 2010). The largest climatic event of the Holocene period (11.7 kcal BP to modern) was a sequence of droughts mostly experienced between c. 9.5 and 5 kcal BP (Bush & Gosling, 2012). Lake levels fell during this time and landscapes became fire-prone (Cross, Baker, Seltzer, Fritz, & Dunbar, 2000; Mayle & Power, 2008). Mesic conditions returned after between 5 and 4 kcal BP, and by 3 kcal BP most lakes had attained their modern levels (Bush et al., 2005; Hillyer, Valencia, Bush, Silman, & Steinitz-Kannan, 2009; Mayle & Power, 2008; Wolfe, Aravena, Abbott, Seltzer, & Gibsond, 2001).

Terracing and irrigation for several millennia before European arrival provide compelling evidence that pre-Columbian cultures transformed many Andean landscapes through agriculture (Covey, 2008; Denevan, 2001; Isbell, 2008). The earliest archaeological evidence suggesting human occupation of the Andes dates c. 13 kcal BP (Dillehay et al., 2008; Rademaker et al., 2014), although coastal areas in the Pacific showed occupation evidence at c. 18 kcal BP (Dillehay et al., 2015). These data bring into question earlier assertions that humans could not have shaped Andean landscapes until c. 10 to 9 kcal BP (Aldenderfer, 2008; Rademaker et al., 2014; Sandweiss & Richardson, 2008). Moreover, models based on archaeological data show that the exponential phase of human population growth did not occur until 6 to 5 kcal BP (Goldberg, Mychajliw, & Hadly, 2016). Whether the human colonists existed at sufficient density in the early Holocene, or during the mid-Holocene, to cause wide frequency ecological change in the Andes remains to be investigated. Palaeoecological reconstructions that pre-date the human incursion (taken to be c. 13 kcal BP) in the Andes can provide invaluable insights into the natural dynamics of *Polylepis* woodlands. Here, we synthesize data from 13 palaeoecological records from the high Andes of Ecuador, Peru and Bolivia, to address a series of research questions: (1) Did *Polylepis* woodlands form a continuous belt at any time since the Last Glacial Maximum at c. 21 kcal BP? (2) Did *Polylepis* woodlands contract due to human-induced fires immediately after human arrival (i.e. 13 kcal BP, *sensu* Rademaker 2014) in the high Andes? (3) Did *Polylepis* woodlands decline in concert with the growth of human populations?

2 | MATERIALS AND METHODS

2.1 | Study region

The region selected for study lies between 2°S and 18°S, occupies an elevation range from 2,900 to 4,150 m a.s.l., and provides a representative overview of the geographical area occupied by *Polylepis* woodlands (Figure 1 and Table 1; Fjeldså & Kessler, 1996). This area excludes sites where *Polylepis sericea* Wedd. is distributed because this species is not found above tree line (Kessler, 2002). Mean annual temperatures range from c. 6 to 15°C, with the differential between daytime maxima and night time minima exceeding 20°C.

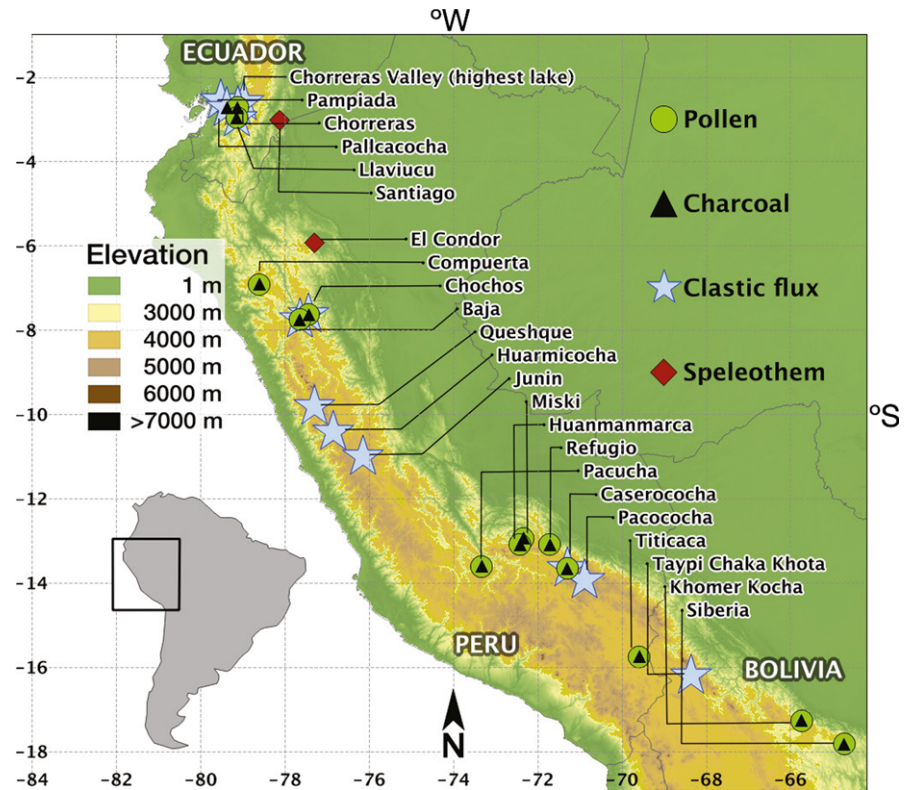


FIGURE 1 Map depicting the location of sites providing the pollen, charcoal, clastic flux and speleothem records used in this review (details in Table 1) [Colour figure can be viewed at wileyonlinelibrary.com]

Frost is most likely in the austral winter but could occur year round. Precipitation within the study region is seasonal with an austral summer wet season coinciding with the development of the South American Summer Monsoon (Marengo, Soares, Saulo, & Nicolini, 2004; Vuille & Bradley, 2000; Zhou & Lau, 1998). A gradient of modern precipitation exists with northern sites (e.g. Ecuador) receiving in excess of 1,500 mm, while those in the Bolivian Altiplano receive just 400–700 mm per year (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

2.2 | Records of past environmental change

In this synthesis, we review data from published lake sediment records of fossil pollen and charcoal sites (13 sites) above 2,900 m a.s.l from 2°S to 18°S (Table 1; Figures 1 and 2). The palaeoenvironmental records obtained from the lake sediments provide a regional climate, vegetation and fire history above the elevation of tree line (Bush et al., 2005; Hansen et al., 2003; Valencia et al., 2010, 2016; Weng et al., 2006; Williams, Gosling, Brooks, Coe, & Xu, 2011).

Pollen and charcoal data were rescaled by the maximum value observed in each record to allow comparisons among sites (i.e. maximum abundance accounts for 100%, Figure 2). The underlying assumption was that the maximum value observed in each site corresponded to the maximum woodland expansion or fire event that could be reached in each record. To allow for temporal comparisons, the pollen data from each site were interpolated at a resolution of 50 years and an average abundance across all sites in each time slice was calculated (i.e. landscape scale woodland abundance). This

metric of *Polylepis* abundance across the landscape (the presence at multiple sites) is hereafter referred as *Polylepis* landscape value (PLV). It should be noted that because sites deglaciated at different times, and hence were not all available to be colonized in every time slice, the PLV was estimated using only the sites that were deglaciated within each specific time slice. Furthermore, the estimation of the PLV and frequency for *Polylepis* excluded two sites (Siberia and Pacucha) where *Polylepis* could have been out-competed by other arboreal species migrating upslope in the last 12 kcal BP (i.e. possible local natural extinction; Figure S1 in Appendix S1). Thus, the total number of sites that could have supported *Polylepis* in a given time slice varied from 4 to 13 (Figures 2 and 4a).

Charcoal data were rescaled, merged into one dataset, and were bootstrapped 1,000 times using five observations per time to estimate a 200-year running median using 500-year bins (Figures 2, 3d and Figure S2 in Appendix S1). The selection of number of observations (five) corresponded to the lowest observation number encountered in all the 500-year bins. Bins smaller than 500 years were avoided because they produced zero observations per bin while larger than 500 bins would reduce the temporal resolution. Boxplots were generated with the resampled data depicting the median (central line), interquartile range (IQR, boxes), 1.5* IQR above and below the IQR (whiskers).

A Bayesian correlation test was run using the PLV, charcoal medians, isotope and clastic data at 50-year resolution following the framework proposed by Liang, Paulo, Molina, Clyde, and Berger (2008) implemented in the R-package ‘BayesMed’ (Wetzels & Wagenmakers, 2012; Table 2; Nuijten, Wetzels, Matzke, Dolan, &

TABLE 1 List of the studied sites displayed on Figure 1 by latitude (southward) as reported in the original publications. The proxies evaluated per site were pollen (Po), charcoal (Ch), clastic deposition (Cl), oxygen isotopes ($\delta^{18}\text{O}$) and carbon isotopes ($\delta^{13}\text{C}$). Pollen and charcoal data from the marked sites (*) were transformed and analysed to produce Figures 2–4

Lake or Speleothem (s)	Age (kcal BP)	Lat.	Long.	Proxies	Elev. m a.s.l.	References
Chorreras Valley (highest lake)	c. 15.8	-2.75	-79.14	Cl	4,020	Rodbell et al. (2008)
Pampiada	c. 14.8	-2.76	-79.26	Cl	4,100	Rodbell et al. (2008)
*Chorreras	c. 17.7	-2.77	-79.16	Po, Ch, Cl	3,700	Hansen et al. (2003) and Rodbell et al. (2008)
Pallcacocha	c. 15.0	-2.77	-79.23	Cl	4,060	Hansen et al. (2003) and Rodbell et al. (2008)
*Llaviucu	c. 16.7	-2.84	-79.14	Po, Ch, Cl	3,150	Mosblech et al., 2012 and Rodbell et al. (2008)
Santiago (s)	>20.0	-3.01	-78.13	$\delta^{18}\text{O}$	980	Mosblech et al. (2012)
El Condor (s)	>20.0	-5.93	-77.30	$\delta^{18}\text{O}$	860	Cheng et al. (2013)
*Compuerta	>20.0	-6.91	-78.60	Po, Ch	3,950	Weng et al. (2006)
*Chochos	c. 15.4	-7.63	-77.47	Po, Ch, Cl	3,285	Bush et al., 2005 and Rodbell et al. (2008)
*Baja	c. 18.2	-7.69	-77.53	Po, Ch, Cl	3,575	Hansen (1995) and Rodbell et al. (2008)
Qeshque	c. 18.4	-9.81	-77.30	Cl	4,275	Rodbell et al. (2008)
Huarmicocha	c. 17.3	-10.42	-76.83	Cl	4,670	Rodbell et al. (2008)
Junin	c. 42.2	-11.00	-76.10	Cl	4,000	Rodbell et al. (2008)
*Miski	c. 12.7	-13.02	-72.37	Po, Ch	3,800	Valencia et al. (2016)
*Huamanmarca	c. 12.7	-13.03	-72.37	Po, Ch	3,900	Valencia et al. (2016)
*Refugio	c. 19.5	-13.09	-71.70	Po, Ch	3,389	Urrego et al. (2011)
*Pacucha	>20.0	-13.60	-73.32	Po, Ch	3,090	Valencia et al. (2010)
*Caserococha	c. 26.2	-13.65	-71.29	Po, Ch, Cl	3,975	Paduano (2001) and Rodbell et al. (2008)
Pacococha	c. 14.4	-13.95	-70.88	Cl	4,925	Rodbell et al. (2008)
*Titicaca	>20.0	-15.80	-69.50	Po, Ch, $\delta^{13}\text{C}$	3,810	Paduano et al. (2003)
Taypi Chaka Khota	c. 13.5	-16.20	-68.35	Cl	4,300	Rodbell et al. (2008)
*Khomeer Kocho	c. 18.1	-17.27	-65.73	Po, Ch	4,150	Williams et al. (2011)
*Siberia	>20.0	-17.83	-64.72	Po, Ch	2,920	Mourguiart and Ledru (2003)

Wagenmakers, 2015). The Bayes factor (BF) in the analysis provides support for correlation when $\text{BF} > 1$, no correlation when $\text{BF} = 1$ and support against correlation when $\text{BF} < 1$. The correlations were run for a period where data are available for all the proxies (Figure 3) excluding the period younger than 6.15 kcal BP as no data were available for the Santiago isotope record (Mosblech et al., 2012). A Spearman rank correlation test run in R plotted with the R-package 'CORRLOT' (Wei & Simko, 2016) was consistent with the Bayesian correlation (Figure S3 in Appendix S1). Note that the oxygen isotope data ($\delta^{18}\text{O}$) is a proxy that registered changes in precipitation (Cheng et al., 2013; Mosblech et al., 2012) and the carbon isotopes ($\delta^{13}\text{C}$) changes in lake level (Baker, Seltzer, et al., 2001). Both isotopes ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) became enriched during dry periods (e.g. E-HDE in Figure 3). The clastic sediment flux (Figure 3e) is a proxy that recorded glacial dynamics. The clastic sediment flux had high values during periods of enhanced glacial activity.

To determine the degree of site similarity among the Andean landscape, a coefficient of variation (CV; standard deviation divided by the mean*100) was calculated and used as a fragmentation indicator. The CV would take the highest values during periods where *Polylepis* is abundant in some sites and low (or locally extinct) in others (i.e. patchy landscape). On the other hand, the CV would be zero if *Polylepis* was equally abundant in all the sites within the same

time window. The CV was calculated based on the rescaled pollen data (50-year resolution). Note that the CV can take multiple values even when the PLV remains constant.

All the data were analysed and plotted against age using R (R Development Core Team, 2014).

3 | RESULTS

The rescaled abundances of *Polylepis* pollen had time transgressive peaks across each of the 13 sites during the last c. 20 kcal BP (Figure 2). Similarly, the charcoal records showed a broad tendency for increasing fire frequency between the onset of the record and the mid-Holocene, with less predictable trends in the late Holocene. The 13 sites appear to be broadly divided between those containing *Polylepis* in the deglacial period from those that had primarily Holocene peaks of occupation. Those with Pleistocene occupation peaks can be further subdivided by elevation into a high (Khomeer Khocho, Caserococha, Compuerta) and a low group (Refugio, Chochos, Llaviucu, Pacucha, Siberia) separated by about 550 m vertically (Figure 2).

Polylepis landscape values, whether amalgamated or treated as low-, mid- and high-elevation groups, were all negatively correlated

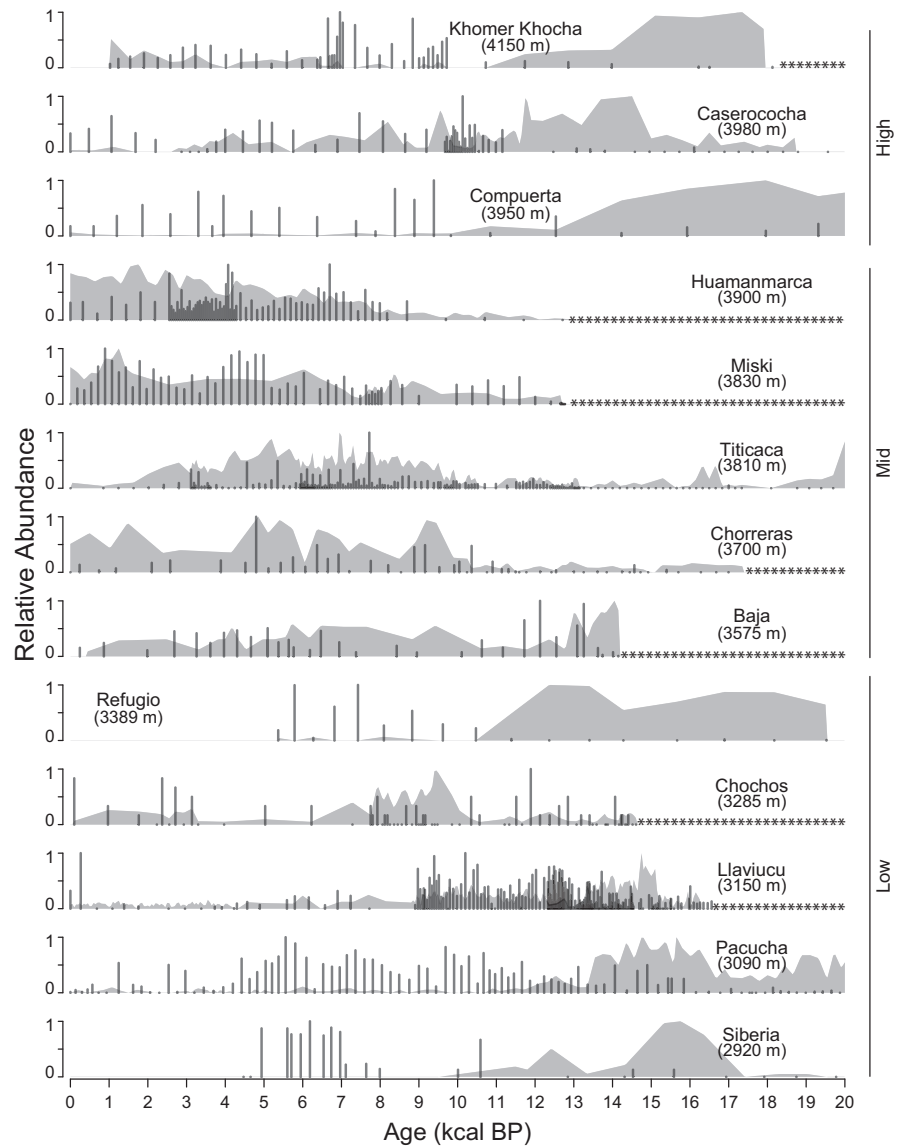


FIGURE 2 Pollen and charcoal abundances of selected Andean sites plotted from high (top) to low elevation (bottom) against time depicted in thousands of years (kcal BP). Pollen (grey silhouettes) and charcoal (black bars) abundances were rescaled by the maximum value in each site (relative abundance) observed over the last 20 kcal BP. Periods where sites were covered in ice are marked with (*). Vertical lines depict the low-, mid- and high-elevational site grouping

with charcoal and positively correlated with clastic flux, which can be taken as a proxy for glacial outflow (Figures S4 and S5 in Appendix S1). As our primary question addresses patch occupancy where *Polylepis* occurs at any given time in the past, we use the amalgamated PLV value, as its calculation is elevation-independent. Values for PLV ranged from 13% to 60% during the last c. 20 kcal BP (Figure 3a). PLV was consistently higher than 25% from c. 20 to 12 kcal BP, dipped to c. < 20% at 12 to 10 kcal BP, but was predominantly above 20% the last c. 10 kcal BP (c. 26% on average). Between c. 20 and 6.2 kcal BP the Bayes factor was consistently >100 and provided very strong evidence for correlation between *Polylepis* abundances (PLV) with isotopic, clastic flux and charcoal data (*sensu* Nuijten, Ruud, Matzke, Dolan, & Wagenmakers, 2015; Nuijten, Wetzels, Matzke, Dolan, & Wagenmakers, 2015; Figure 3; Table 2). The PLV is lowest (<20%) between 12 and 10 kcal BP when enriched $\delta^{18}\text{O}$ (<-5‰) in nearby speleothems, and high charcoal abundances (>33%) in lake sediments, indicate an early Holocene Dry Event (E-HDE) (Figure 3). Pollen abundances (PLV) remained > 20% after 9.5 kcal BP and did not decline during the mid-HDE phase

9.5–5 kcal BP indicated by charcoal values >45%. The charcoal abundances indicated an additional period of outstanding fire activity (values >50%) during the last c. 2 kcal BP. The mid-HDE also saw a halving of the number of sites where *Polylepis* was documented and the onset of major civilizations in the high Andes. The CV (dimensionless), a proxy for fragmentation, increased after c. 5.5 kcal BP but the trend was steeper during the last two millennia increasing from 1.2 to 1.8 units. The magnitude of fragmentation recorded over the last millennia was analogous to that of the early deglacial time, that is from c. 20 to 17 kcal BP, when CV was >1.2 units (Figure 4).

4 | DISCUSSION

4.1 | *Polylepis* woodland cover prior to human occupation

For over half a century, it has been debated whether the modern patchy distribution of *Polylepis* woodlands was natural, or the result of anthropogenic activities that fragmented what once was a larger-

TABLE 2 Correlation of climate proxies with *Polylepis* PLV from sites shown in Table 1. There is a strong evidence for correlation between all the variables (i.e. Bayes factor was >100 for all the comparisons). Note that the negative correlation coefficient between PLV and the isotopic data ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) implies a positive correlation of PLV with inferred precipitation (e.g. Figure 3a–c and f). The datasets used are proxies for enhanced glacial activity (clastic flux), fire activity (charcoal), precipitation ($\delta^{18}\text{O}$ from Condor to Santiago speleothems) and lake level ($\delta^{13}\text{C}$ from Lake Titicaca)

	Clastic flux	Charcoal	Condor ($\delta^{18}\text{O}$ vs. BPDB)	Santiago ($\delta^{18}\text{O}$ vs. BPDB)	Titicaca ($\delta^{13}\text{C}$ vs. PDB)
Charcoal	-0.9149				
Condor	-0.8295	0.8507			
Santiago	-0.7485	0.6680	0.7184		
Titicaca	-0.7388	0.7904	0.6571	0.3960	
PLV	0.8078	-0.8109	-0.7664	-0.8212	-0.6589

than-present and continuous woodland belt along the Andes (Ellenberg, 1958; Lauer, 1981). Furthermore, it was suggested that following human arrival (c. 12.8 kcal BP), *Polylepis* woodlands could have been easily eradicated by frequent fires (Cierjacks et al., 2008; Renison, Cingolani, & Schinner, 2002). Like modern humans who use fire for land management, small groups of early hunter-gatherers may have transformed large areas of forest using fire (Kessler, 2002; Veblen & Lorenz, 1987). Such a downturn in woodland cover soon after human arrival has not been tested in the light of evidence for a late Pleistocene human presence in the Andes (Rademaker et al., 2014).

Our analysis revealed that landscape scale *Polylepis* abundance, as indicated by PLVs, was positively correlated with inferred precipitation from speleothems between c. 20 and 6.2 kcal BP (Figure 3, Table 2). This relationship suggests that the woodland dynamics were influenced by precipitation changes over $>13,000$ years. Clastic fluxes (Rodbell, Seltzer, Mark, Smith, & Abbott, 2008) were also in phase with the PLVs and isotopic data suggesting that either temperature and precipitation were negatively correlated or that precipitation played a major role controlling glacial extent in the Andes (Rodbell et al., 2008; Shakun et al., 2015; Thackray, Lundeen, & Borgert, 2004).

Following an early deglaciation onset in the Andes, the period between c. 20 and 17 kcal BP (Figures 3 and 4) was still characterized by glaciated landscapes and no human influence (Seltzer et al., 2002). The PLVs ($<50\%$) and CVs (1.5–2) showed that *Polylepis* woodlands were very patchy, and charcoal abundances indicate fire events were rare. After 17 kcal BP, *Polylepis* woodlands expanded reaching a maximum cover from c. 17 to 14 kcal BP (c. 42%–60%, Figure 3a) and CVs were lower (1–1.1). Although mesic conditions characterized the period between c. 20 and 14 kcal BP, the time interval between c. 18 and 14 kcal BP was wetter than between c. 20 and 18 kcal BP as indicated by the $\delta^{18}\text{O}$ and clastic flux data (Baker, Seltzer, et al., 2001; Cheng et al., 2013; Mosblech et al., 2012; Rodbell et al., 2008). These observations were consistent with the formation of palaeolakes in the Altiplano inferred from natural gamma radiation and isotopic analysis on carbonate deposits and coincided with the maximum woodland expansion (Baker, Rigsby, et al., 2001; Blard et al., 2011). Given the limitations of current temperature reconstructions for the Neotropics (Baker & Fritz, 2015;

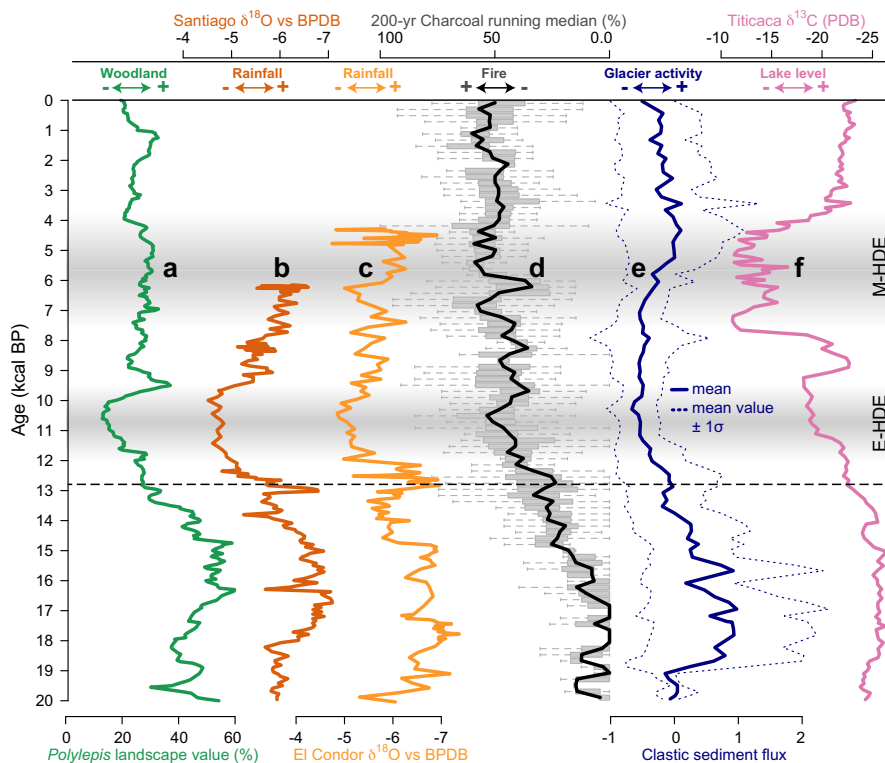


FIGURE 3 A comparison of *Polylepis* representation with proxies for climate change. (a) *Polylepis* landscape value (PLV) depicts the average across sites of the proportion of maximum cover of woodland at each individual site (Table 1). (b) Isotopic $\delta^{18}\text{O}$ from Santiago (Mosblech et al., 2012) and (c) El Condor records (Cheng et al., 2013). (d) Charcoal 200-year running median using 500-year bins (Table 1). (e) Glacial dynamics for the Andes inferred from detrital clastic material (Rodbell et al., 2008). (f) Isotopic $\delta^{13}\text{C}$ of sedimentary organic content from Lake Titicaca. Labels and arrows on top of each diagram show the inferred estimate for each proxy. The early Holocene Dry Event (E-HDE) and mid-Holocene dry event (M-HDE) were depicted by horizontal grey bands. The horizontal dashed line shows the earliest known archaeological evidence for the high Andes (Goldberg et al., 2016; Rademaker et al., 2014) [Colour figure can be viewed at wileyonlinelibrary.com]

Shakun et al., 2015), the role of temperature modulating PLVs could not be evaluated in detail. The PLV maxima from c. 17 to 14 kcal BP could have being favoured by an upslope *Polylepis* migration as temperature rose.

The distribution of sites containing *Polylepis* in the deglacial period appears to support an initial split representation, with one set of sites at high elevation, that is 3,950–4,200 m, and another set of sites further downslope at c. 2,800–3,400 m. The intermediate elevation set of sites gain *Polylepis* representation in the Holocene, though it needs to be noted that only two of them have Pleistocene-aged sequences. Tentatively, we infer that the high- and low-elevation groups may represent two different niches, one being close to the ice front, and the other in a puna or super-puna landscape. The modern ecology of *Polylepis* includes species that occupy such habitats, such as the high-elevation specialist *Polylepis tarapacana*, which today is found in very dry settings in Bolivia. That *P. tarapacana* can survive at 5,200 m elevation in modern climates (Rada et al., 2001) shows that this genus is adapted to extreme cold, but we consider it unlikely that it was this species represented in these wetter Peruvian settings (Baker, Seltzer, et al., 2001; Hillyer et al., 2009). A species of *Polylepis*

that lived close to the ice margin was apparently lost from these records with Holocene warming. The *Polylepis* representation of the lower slopes also wanes as representation in the mid-elevation sites increases, potentially indicating an upslope migration due to warming. The loss of *Polylepis* from the lower edge of its Pleistocene range would be expected as Andean forest moved upslope, probably out-competing *Polylepis* below tree line. Again, we caveat this observation and note that *Polylepis* would undoubtedly have been responding to warming, but other factors such as the interaction between fire and topography (Valencia et al., 2016), the loss of megafauna (Rozas-Dávila, Valencia, & Bush, 2016) and changes in precipitation (Gosling et al., 2009) could have contributed to the observed pattern.

The strong evidence for correlation between isotopic data, clastic flux, PLV (woodlands) and charcoal depicted in Table 2 suggested that fires and human activity were unlikely to have constrained *Polylepis* abundance prior to 6.2 kcal BP. Although a correlation does not imply causation, it was more likely that climate (isotopic and clastic data as proxies for precipitation and temperature) modulated fire and woodland cover than the other way around (i.e. fire or woodland cover modulating precipitation and temperature).

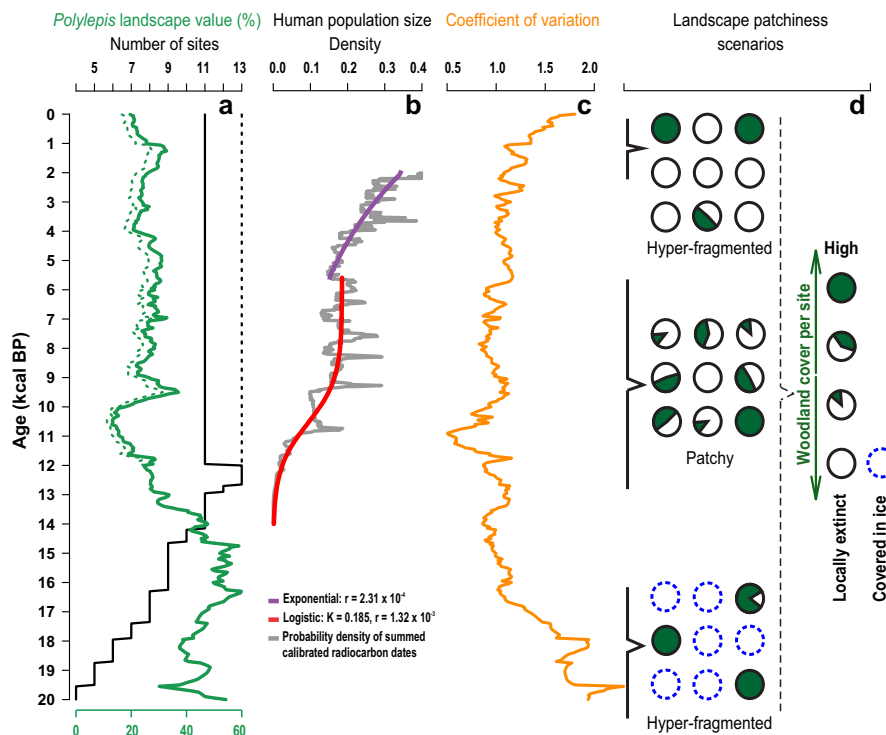


FIGURE 4 A comparison of *Polylepis* woodland representation with human population size estimation and spatial woodland cover patterns. (a) Depicts the *Polylepis* average abundance (PLV, solid green line) weighted by the number of available sites (solid black line). The PLV (solid green line) and site number (solid black line) excluded the lowest sites Siberia and Pacucha over the last 12 kcal BP as *Polylepis* could have been naturally out-competed by other arboreal taxa. The dashed green line (PLV) and the dashed black line (number of sites) represent the PLV and number of sites when Siberia and Pacucha are not excluded in the analysis over the last 12 kcal BP. (b) Logistic (red) and exponential (blue) best-fit growth models for human populations in the Andes (Goldberg et al., 2016). The models were based on probability density of summed calibrated radiocarbon dates. (c) Coefficient of variation for *Polylepis* pollen abundances. (d) Conceptual model for landscape patchiness. Note that green solid circles depict the maximum cover that can be attained at each site and empty dashed circles sites that were covered in ice [Colour figure can be viewed at wileyonlinelibrary.com]

4.2 | Did *Polylepis* woodlands form a continuous belt at any time since the last glacial maximum (c. 21 kcal BP)?

Polylepis woodlands covered larger areas prior to human incursion than any time after c. 12.8 kcal BP. The PLV (Figure 3a) showed that the *Polylepis* woodland cover was consistently higher from 20 to 12.8 kcal BP (30%–60%) than any time after 12.8 kcal BP (usually <30% and c. 25% on average). During the period between c. 17 and 14 kcal BP, *Polylepis* was twice as abundant (c. 50% on average) as the post c. 12.8 kcal BP average. Given the average abundance (c. 50%) and that all nine available records contained *Polylepis*, we infer that the genus attained its maximum abundance of the last 20,000 years between c. 17 and 14 kcal BP. Despite this abundance between c. 17 and 14 kcal BP, it is unlikely that a continuous woodland belt ever formed. The PLV (woodland cover) did not exceed c. 60%, suggesting that regardless of the *Polylepis* abundance; the local woodland cover was still patchy. The patterning of *Polylepis* distribution within each catchment, however, has yet to be resolved.

Landscape heterogeneity probably played an important role in controlling local woodland distribution (Valencia et al., 2016) interacting with the constant flux of climate that promoted local vegetation instability and therefore constrained the potential dominance of any given species (Garreaud, 2009; Hutchinson, 1957; Killeen et al., 2007; Phillips, Anderson, & Schapire, 2006; Valencia et al., 2016). Our pollen-based evidence that *Polylepis* woodlands did not form a continuous cover is consistent with genetic studies on *P. tarapacana*, which suggested the presence of larger, but disjunct, populations of this species during the Pleistocene than in the Holocene (Peng et al., 2015). Consequently, our inference of discontinuous *Polylepis* woodlands along the Andes during the terminal Pleistocene does not support the hypothesis that *Polylepis* formed a continuous woodland belt in the Late Pleistocene or Holocene *sensu* Ellenberg (1958).

4.3 | Did *Polylepis* woodlands contract due to human-induced fires immediately after human arrival in the high Andes?

Humans are now known to have inhabited the high Andes by c. 12.8 kcal BP (Rademaker et al., 2014). The PLV showed that woodland cover declined from c. 13 to 10.5 kcal BP. A threshold of increased charcoal abundance is found at many sites during this time period. Increased fire frequency and human arrival were closely related in Africa, Australia and potentially in the Andes (Berna et al., 2012; Roebroeks & Villa, 2011). Occasional fire was clearly present in the Andes long before human presence (Hanselman et al., 2011), but the regular occurrence of fire may be taken as a much stronger indication of human activity. Although unsupported by archaeological data, we suggest that the regular occurrence of fire at c. 15 kcal BP (Figure 3d) may have been caused by human activity. The increase in fire activity and the synchronous woodland decline was more intricate than a straight cause–effect interaction. Although humans became the most probable ignition agent when they arrived in the

Andes, fires were most likely to be recorded during dry times when fire intensity, frequency and spread would be larger compared with those observed during wet periods (Bush, Silman, McMichael, & Saatchi, 2008; Cochrane & Ryan, 2009).

Simple explanations of increased human activity generating fires that caused the *Polylepis* decline (c. 12 to 10 kcal BP) run into difficulties in the early Holocene. Between c. 10.5 and 9.5 kcal BP, while fires were still frequent, the *Polylepis* woodland coverage expanded by a factor of 2.5. This woodland recovery also took place when it was estimated that the human population experienced its steepest pulse of logistic growth (Figure 4b). Human population size in the Andes at this time is not known, but is assumed to have been at relatively low densities (Goldberg et al., 2016). This understanding suggests that the influence of humans was unlikely to have been large enough to have caused the *Polylepis* woodland contraction prior to c. 5–6 kcal BP. Given that modern *Polylepis* pollen counts are higher today than at 10 kcal BP in many lakes, attributing the *Polylepis* decline to humans would also imply that the impact of the early hunter-gatherers was larger than that of modern land use. The most parsimonious explanation of variations in *Polylepis* woodland cover prior to c. 5–6 kcal BP is that Andean systems changed at the onset of the Holocene, becoming fire-prone as in previous interglacials (Hanselman et al., 2011). We infer that most of the early Holocene woodland contraction was influenced by declining precipitation (Figure 3b,c) that induced the PLV decline after c. 15 kcal BP (Figure 3a). Although the fire trend was exacerbated by human arrival, the similarity of the PLV and precipitation curves until c. 5 kcal BP suggests that human activity only exceeded climatic controls after this point.

4.4 | Did *Polylepis* woodland decline in concert with the growth of human populations?

The turning point of the mid-Holocene dry event in the Peruvian Andes that led towards wetter conditions at c. 5.5 kcal BP, coincided with the estimated onset of exponential human population growth (Goldberg et al., 2016). Previously, although human populations had been growing they were not transforming landscapes to the point where local *Polylepis* extinction occurred (e.g. Figure 2, Siberia). A lack of extinction does not imply that humans produced no effect. We hypothesize that fires and land use would have affected *Polylepis* populations, but that landscape heterogeneity and rescue effects (*sensu* Brown & Kodric-Brown, 1977) allowed metapopulations to come and go, but led to overall woodland persistence particularly in inaccessible areas (Levins, 1969; Sylvester et al., 2014, 2017; Valencia et al., 2016).

The transition from logistic to exponential growth in human population between 6 and 5 kcal BP (Goldberg et al., 2016) was reflected in increased reliance on agriculture, and settlements becoming permanent. The continuous pressure exerted by humans on a landscape prevented woodland re-colonization and led to a decline in *Polylepis* occurrence across sites. Consequently, readily accessible sites for human occupation exhibited an earlier loss of *Polylepis* than those



that were inaccessible. For example, the loss of *Polylepis* around Lake Pacucha occurred c. 10 kcal BP, whereas rugged and inaccessible sites at a similar elevation, such as Lake Chochos, retained its *Polylepis* until c. 6–7 kcal BP (Valencia et al., 2016). This contrasting pattern of human-induced exploitation (locally extinct or near absent in some sites and abundant in inaccessible places) led to the formation of hyper-fragmented woodlands depicted by the increasing coefficients of variation (Figure 4c), that is fragmentation of populations that already had a patchy distribution. Because *Polylepis* woodlands were able to thrive in the early Holocene, a period characterized by droughts, a woodland expansion in the last 4,000 years would be expected. At the largely unimpacted sites of Miski and Humanmarca (Figure 2), *Polylepis* has indeed become more abundant in the late Holocene. This pattern, however, is not registered at sites with strong human influence. The increasing coefficient of variation over the last c. 4 kcal BP, strongly suggests increasingly heterogeneous landscapes consistent with a gradual hyper-fragmentation of *Polylepis* woodlands (i.e. fragmentation of populations that already had a patchy distribution). Moreover, the largest *Polylepis* woodland contraction started between c. 2 and 1 kcal BP (Figure 3a) coinciding with the onset or development of high-Andean civilizations such as Wari, Tiwanaku and Inca (Isbell, 2008). Over this period, the hyper-fragmentation of *Polylepis* woodlands became enhanced. The loss of woodland cover and resulting vegetation mosaics reduced *Polylepis* abundance to levels not seen since the early deglacial period (e.g. prior to c. 17 kcal BP; Figure 4a,c and d). Our data strongly suggest that human activities significantly reduced *Polylepis* woodland cover and abundance during the last 1,000 years. Pre-Columbian civilizations were known to have enforced agroforestry and the protection of Andean woodlands (Chepstow-Lusty & Winfield, 2000), driven by woodland shortage in their occupied landscapes. Although these practices may have been successful preventing the local forest clearance, the *Polylepis* woodland decline showed that deforestation at landscape scale was commonplace.

5 | CONCLUSIONS

The spatial distribution of *Polylepis* derived from 13 palaeoecological reconstructions was estimated for the last 20 kcal BP. *Polylepis*-rich systems showed an upslope migration response at the end of the last ice age. *Polylepis* woodlands reached their maximum expansion between c. 17 and 14 kcal BP prior to human arrival in the Andes. However, these woodlands were always patchy (i.e. maximum PLV of 60%) and did not form a continuous woodland belt over the last 20 kcal BP. The most important factors controlling the *Polylepis* woodland dynamics prior to c. 6.2 kcal BP were precipitation and landscape heterogeneity. A combination of high precipitation, low temperatures, limited flammability, low biomass (fuel load) and rare ignitions led to fire being relatively rare before c. 13 kcal BP compared with the following period. As landscapes became warmer, drier and humans more abundant, fire became a more regular component of Andean systems. Fire sensitive taxa, such as *Polylepis*, were

negatively affected by these changes. Of all these drivers, precipitation appears to have exerted such a strong influence that it could offset other trends in the early Holocene. This capacity, however, was lost as human populations grew in the late Holocene.

Our study suggests that although *Polylepis* has a naturally patchy distribution this pattern has been exacerbated over the last few millennia by human activities, a process that we identify as hyper-fragmentation. Reduced gene flow under modern hyper-fragmentation is potentially so limited that it may further compromise the long-term persistence of this genus under the ongoing effects of climate change.

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BIOSKETCH

Bryan G. Valencia is a palaeoecologist that earned his PhD at the Open University where ideas for this manuscript were drafted. He is working as a postdoctoral researcher at the Florida Institute of Technology. He is investigating plant community responses to past climate change in South American high-Andean ecosystems. His research is focused on disentangling the human–climate influences on Neotropical plant communities using a multiproxy approach.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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