Quaternary Science Reviews 317 (2023) 108278

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Fire in the clouds: How changing land use shaped an Andean biodiversity hotspot

Majoi de Novaes Nascimento [a,*], Crystal N.H. McMichael [a], Zoe Kleijwegt [a,b], Christine Åkesson [c], Charlotte Gredal [a], S. Yoshi Maezumi [a,d], Mark B. Bush [c], William D. Gosling [a]

[a] Department of Ecosystem and Landscape Dynamics, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, the Netherlands
[b] Soil Geography and Landscape Group, Environmental Sciences Group, Wageningen University & Research, Wageningen, the Netherlands
[c] Institute for Global Ecology, Florida Institute of Technology, Melbourne, FL, USA
[d] Department of Archaeology, Max Planck Institute for Geoanthropology, Jena, Germany

ARTICLE INFO

Handling Editor: Claudio Latorre

Keywords:
Andes
Chachapoya
Pyrolysis temperature
Charcoal
Fire intensity
FTIR spectroscopy
Land use

ABSTRACT

Past land use, particularly fire, affects modern tropical forests. Charcoal from lake sediments is commonly used to estimate past fire parameters such as burn severity and frequency, but fire intensity also plays a major role in shaping vegetation and vegetation change. Past fire intensity has remained elusive using common paleoecological approaches. We present a new approach to reconstruct past fire (pyrolysis) temperature, a metric of fire intensity, and reveal how human fire use changed and shaped biodiverse Andean montane forests over the last 2100 years. We use spectra obtained from micro-Fourier Transformed Infrared Spectroscopy (FTIR) of individual charcoal particles recovered from the sediments of Lagua de los Condores (Peru) to characterize its chemical composition. We then compare the spectra generated from the sedimentary charcoal fragments with a modern reference dataset to infer the pyrolysis temperature at which they were formed. Reconstructed maximum pyrolysis temperature varied with changes in land use and changes in precipitation. Mid-temperature fires (500–600 °C) dominated the record, and co-occurred with maize cultivation. After 1200 CE the Chachapoya people, referred to as cloud warriors by the Incas, started to use the site for ceremonial purposes as the climate got wetter. We demonstrate a concomitant change in the complete fire regime with fires becoming less severe, less frequent and burning at a lower temperature after this transition. This change in land use resulted in the first forest recovery in 2000 years, which was mainly composed of species with low bark thickness, a trait of fire sensitivity. Our reconstruction of pyrolysis temperature demonstrates that the analysis of fire severity, frequency, and our added metric of intensity, is needed to understand the drivers of past vegetation change.

1. Introduction

The montane forests of the Andes harbor immense biodiversity and endemism and have had a long history of human alteration (White, 2013). Increased fire activity and megafaunal extinction have been attributable to humans since their arrival 14,000 years ago (White, 2013; Bush et al., 2022). Fire in the Andes was, and remains, an important means of clearing vegetation and improving pasture land (Sarmiento, 2012; Bush et al., 2022; Sales et al., 2022). On the eastern Andean flank at about 2500 m a.s.l. (meters above sea level), fire has been shown to be mostly absent for the last 30,000 years, but has increased during the last 4000 years (McMichael et al., 2021). Fire has been primarily anthropogenic in origin over the last 4000 years, a time which has been relatively wet (above 3200 mm annually) on the eastern Andean flank of Ecaudor and Peru (Van Breukelen et al., 2008; Kanner et al., 2013).

In the diverse Andean montane forests, fire can lead to lasting changes in forest structure and composition (Young and León, 2007; Oliveras et al. 2014, 2018). Three important components of the fire regime that drive vegetation responses include: (i) frequency (the number of fire events per unit of time), (ii) severity (the amount of biomass consumed), and (iii) intensity (strictly the energy released by a fire event per unit time, but often characterized as fire temperature) (Keeley, 2009). In the wet Peruvian montane forests, modern mean

* Corresponding author.
E-mail address: m.denovaesnascimento@uva.nl (M.N. Nascimento).

https://doi.org/10.1016/j.quascirev.2023.108278
Received 8 June 2023; Received in revised form 6 August 2023; Accepted 16 August 2023
Available online 28 August 2023

annual precipitation reaches 4000 mm, and fires are almost always caused by intentional human action (Sarmiento, 2002; Feeley and Silman, 2010; Zapata-Ríos et al., 2021). People use fire to clear forests and control the timber line (Feeley and Silman, 2010; Rehm and Feeley, 2015), with occational accidental fire escapes (e.g., from cooking or land cleaning fires) (Morton et al., 2013). These forests generally contain high fuel loads, and ignitions can result in high intensity (>500 °C temperature) fires (Cochrane, 2003). In these forests, high-temperature fires have the potential to fatally damage root systems and the above ground structures of all growth stages of trees (DeBano et al., 1998; Kennard and Gholz, 2001; Gould et al., 2002; Kennard et al., 2002). Conversely, lower temperatures (<500 °C) fires, such as those used to maintain open areas or in slash-and-burn cultivation (Melquiades and Thomaz, 2016; Thomaz, 2017), have limited lasting effects. Seed pods and deep roots are not destroyed and soil chemistry is not significantly altered (DeBano et al., 1998; Kennard and Gholz, 2001; Gould et al., 2002; Kennard et al., 2002; Balch et al., 2015; Brando et al., 2016).

Reconstructing the way in which people used fire in the past to manage landscapes is limited by an inability to parameterize the different aspects of past fire regimes. Charcoal recovered from sedimentary deposits allows estimations of past fire frequency and severity (Byrne et al., 1977; Winkler, 1985; Patterson et al., 1987; Clark, 1988; Whitlock and Larsen, 2002; Brown et al., 2005; Scott, 2010), but recent work based on laboratory burnings has shown that the spectral properties of charcoal fragments can also be used to estimate pyrolysis temperature (Gosling et al., 2019; Constantine IV et al., 2021; Maezumi et al., 2021). Here we apply Fourier Transformed Infrared Spectroscopy to estimate the pyrolysis temperature of sedimentary charcoal, and parameterize the three components of fire regimes in the hyperdiverse Andean montane forests. We show that all fires are not equal, and demonstrate how metrics of fire intensity (hereafter pyrolysis temperature) alongside metrics of fire severity and frequency can provide new insights into how the Chachapoya people (referred to as cloud warriors by the Inca) used fire to manipulate Andean montane forests over the last 2000 years.

Laguna de Los Condores, located in the montane forests of Peru (Fig. 1), was occupied by humans for at least the least 2100 years (Åkesson et al., 2019). Agricultural activity (based on *Zea mays* pollen) and fire occurrences (based on sedimentary charcoal) were present around the lake throughout the whole period (Åkesson et al., 2019). From c. 800 years ago (1200 CE) until 1550 CE, 31 human burial sites built into high rocky cliffs around Laguna de los Condores indicated that the site was used as a mausoleum by the Chachapoya and the Incan cultures (Von Hagen and Guillén, 1998; von Hagen, 2002; Wild et al., 2007; Åkesson et al., 2019). Here we combine charcoal surface area measurements (a metric of fire severity) and the occurrence of charcoal fragments per unit time (a metric of fire frequency) (Åkesson et al., 2019) with estimates of past fire intensity derived from comparing the spectral properties of the recovered charcoal fragments with a database of spectra based on known pyrolysis temperatures (Gosling et al., 2019; Maezumi et al., 2021) to present a multi-dimensional, multi-millennial, reconstruction of fire regime changes in this Andean biodiversity and cultural diversity hotspot.

2. Methods

2.1. Site description

Laguna de los Condores (6° 51′ 03.02″ S, 77° 41’ 43.28” W) is located at 2860 m above sea level in a deep, forested valley on the eastern flank of the Peruvian Andes. The 60-m deep lake is about 2300 m long and 700 m wide and is dammed by a terminal moraine that indicated the lake was formed during deglaciation 16,000–14,000 years ago (Stansell et al., 2013). The northern shoreline of the deep black waters of lake is formed by a steep, shaded, glacial lateral moraine, while the southern (north-facing) shore is formed by sunny 100 m-high white cliffs. The lake is fed by small inlet streams draining rainwater from the valley.

The valley surrounding Laguna de los Condores contains remnant montane forests rich in Araliaceae, Ericaceae, *Hedyosmum*, Lauraceae, Melastomataceae, Rubiaceae, Urticaceae and *Weinmannia*. The area outside the lake basin, at the north facing slopes of the northern moraine, are grassy pastures (Fig. 1). Today, the valley is uninhabited and the nearest village (Leymebamba) is located c. 19 km to the northwest. The mean annual temperature ranges from 12 to 17 °C, and mean annual precipitation is 3200–4000 mm (Hijmans et al., 2005), with the peak of the wet season occurring between November and April (Garreaud et al., 2009).

A mausoleum containing more than 200 mummy bundles and archaeological artefacts from the Chachapoya and Incan periods was found in the high cliffs and ledges surrounding Laguna de los Condores

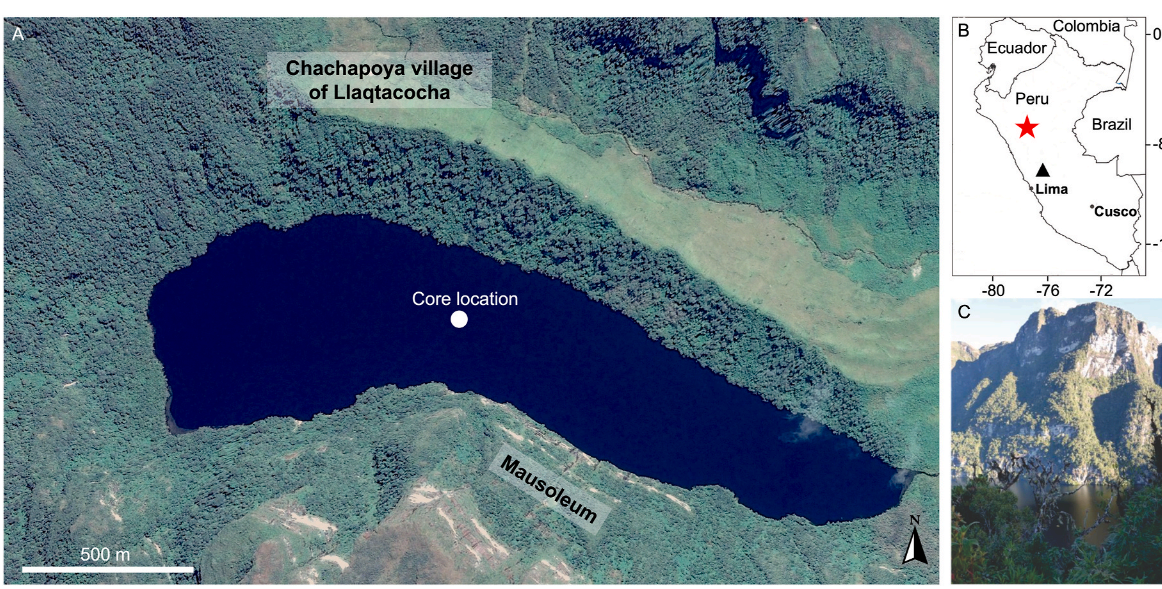

Fig. 1. A) Laguna de los Condores, which has a 2100-year history of fire, maize cultivation, forest clearing, and mausoleum construction (Von Hagen and Guillén, 1998; von Hagen, 2002; Wild et al., 2007; Åkesson et al., 2019). B) Map of Peru showing the location of Laguna de los Condores (star), and the location of a 2300-year reconstruction of precipitation at Lake Pomacochas (triangle). C) Photo of the cliffs that house the mausoleum. Photo by Mark Bush.

(Von Hagen and Guillén, 1998; von Hagen, 2002) (Fig. 1). A total of 31 radiocarbon dates showed that the occupation of the area by the Chachapoyas took place both before and during Incan conquest, ranging from 1160 –1530 CE (Guillén, 2003; Wild et al., 2007; Cherkinsky and Urton, 2014). On the north facing slopes of the moraine there were numerous circular stone structures; the remains of Llaqtacocha, a late Chachapoya village, was dated from 1200 –1550 CE (von Hagen, 2002).

Using fossil pollen, macrocharcoal (>180 μm), diatom, and sediment chemistry data, a high-resolution palaeoecological reconstruction of the vegetation around Laguna de los Condores showed the expansion of pre-Columbian maize agriculture during dry times and reforestation during wet periods over the last 2100 years (Matthews-Bird et al., 2017; Åkesson et al., 2019). About 1200 CE, land use in the valley appeared to shift from maize cultivation and regular burning of the forest to mummy interment. The burial phase coincided with forest regrowth and reduced charcoal abundances (Åkesson et al., 2019). The present study analyzed the macrocharcoal particles collected during this previous palaeoecological reconstruction (Åkesson et al., 2019) to evaluate how charcoal pyrolysis temperature related to changing land use.

2.2. Laboratory analysis

The published chronology of the 184 cm sediment record was based 11 radiocarbon (^{14}C) dates and is shown in Supplementary Data 01, Table 3 (Matthews-Bird et al., 2017; Åkesson et al., 2019). The age-depth model (Fig. S1) was constructed in (R Core Team, 2023) with the Bacon function of the 'rbacon' package (Blaauw and Christen, 2011), using the IntCal13 calibration curve (Hogg et al., 2013). According to this chronology, each 1 cm sample represented c. 6–18 years of sediment deposition.

Of the 184 samples studied, 151 contained at least three charcoal fragments larger than 0.2 mm. Those 151 fragments were analyzed using Fourier Transform Infrared Spectroscopy (FTIR) to estimate the likely pyrolysis temperature (Gosling et al., 2019). For each of the 151 samples, 3 to 12 individual charcoal fragments were analyzed (depending on the amount available for the sample), totaling 805 wavelength measurements (Supplementary Data 1). The measured wavelengths (spectra) of each charcoal fragment were compared with a database of reference charcoal spectra (e.g. FTIR measurements derived from known plant species that were burned at known temperatures in the laboratory, Supplementary Data 2). In the reference database, each plant fragment was burned at known temperatures in 100 °C intervals ranging from 200°C to 700 °C (Gosling et al., 2019; Maezumi et al., 2021). In total, all the charcoal fragments analyzed from Laguna de los Condores (N = 805) were compared with a reference database containing 1262 samples.

2.3. Data analysis

Modern analog matching (Simpson, 2012) was used to estimate the likely pyrolysis temperature for each charcoal fragment analyzed using FTIR methods. Analog matching uses Euclidean distances to assign 'analogs' from the reference database to each fragment analyzed from Laguna de los Condores. We used a 10% dissimilarity threshold to identify analogs for each sample, and the number of fragments with analogs per sample ranged from 0 to 6 fragments. An estimated temperature for each charcoal fragment was assigned based on the most frequent (modal) value of known temperatures from the set of identified analogs. For visual display of estimated likely pyrolysis temperatures, we grouped the estimates into high-temperatures (600–700 °C), mid-temperatures (400–500 °C), and low-temperatures (200–300 °C). We showed the proportion of fragments identified as such for each depth interval and relative to the surface area of charcoal fragments. Thus, the FTIR spectra for each depth interval was expressed as the proportion of fragments representing each of these ranges (high, mid, and low temperatures).

To evaluate the vegetation response to changes in fire regime, the pyrolysis temperature proportions were compared with the summed percentages of pollen from forest and open ground environments (Åkesson et al., 2019) and with measures pollen diversity (species richness and Hill N_1, Hill (1973)). We also assessed shifts in bark thickness (a proxy for fire sensitivity) in relation to changing fire regimes. The pollen assemblages were divided into taxa with maximum bark thickness below 5 mm, representing fire sensitive species, and above 5 mm, representing fire resistant species (Pausas, 2015; Archibald et al., 2018). Information on bark thickness was extracted from the TRY Plant Trait Database (Kattge et al., 2011; Fraser, 2020), and specialized studies (Silva-Matos et al., 2005; Lawes et al., 2013; Poorter et al., 2014; Kitzberger et al., 2016; Potts et al., 2022). Only trait data derived from humid tropical South American forests were used (Supplementary Data 1, Tables 4 and 5). To estimate the correlation between fire severity (charcoal area) and fire intensity (pyrolysis temperature), we used a Spearman Rank correlation test.

3. Results

Of the 151 sedimentary samples from which charcoal was recovered, 145 samples (95%) had at least one fragment with a matching analog in the reference database, and 146 samples (96%) had at least one fragment that could not be confidently matched to the reference spectra (hereafter called non-analog fragments). Out of the 145 samples with analogs, 62 samples contained 87 fragments that could be confidently matched (within 10% dissimilarity threshold) to reference spectra obtained from charcoal pyrolysed at low temperatures (200–300 °C), while 110 samples contained 186 fragments that matched with mid-temperature pyrolysis temperatures (400–500 °C), and 59 samples contained 81 fragments matched to high temperature pyrolysis temperatures (>600 °C) (Supplementary Data 1, Table 2, Fig. S2). The remaining 451 fragments had at least one measurement defined as non-analog.

Most samples with identified temperature analogs contained a mix of charcoals pyrolysed at low-, mid-, and high-temperatures (Fig. 2). Thirteen samples, however, contained all low temperature analogs, 41 samples contained entirely mid temperature analogs, and nine samples contained entirely high temperature analogs (Supplementary Data 1, Table 2). The relative proportions of charcoal pyrolysis temperatures changed from primarily mid- and high-temperature charcoals in sediments prior to 1200 CE, to primarily low- and mid-temperature charcoals after 1200 CE (Fig. 2). Charcoal abundance (surface areas) and frequency (number of samples with charcoal per 100 years) was also higher in the period before 1200 CE (Åkesson et al., 2019) (Fig. 2). In 13 out of the 153 samples (8%), none of the fragments analyzed could be confidently matched to a reference spectrum. The number of fragments that could not confidently be matched to any of the reference spectra (non-analogs) per sample were not significantly correlated with charcoal abundance (Fig. S4). There was also no correlation between charcoal abundance and the proportion of low-, mid-, or high-temperature charcoals within samples(Fig. S3).

From the onset of the record until 1200 CE, the fossil pollen assemblages contained higher abundances of open ground taxa (15–55%) and increased maize frequency compared with more recent sections of the record (Fig. 2). After 1200 CE, forest pollen taxa increased in abundance, reaching >80% of the pollen sum, and maize frequency decreased. Average pollen richness was 29 morpotypes per sample prior to 1200 CE, at which point the average increased to 31 morphotypes per sample. The Hill N_1 values were also lower prior to 1200 CE and increased afterwards (11.4 and 12.9, respectively). Bark thickness traits also shifted around 1200 CE. Samples prior to 1200 CE contained higher abundances of taxa with thicker bark (>5 mm). The increase in forest taxa after 1200 CE included increases in taxa with bark thickness below 5 mm (mostly Moraceae and *Weinmannia*, see Supplementary Data 1, Tables 4 and 5).

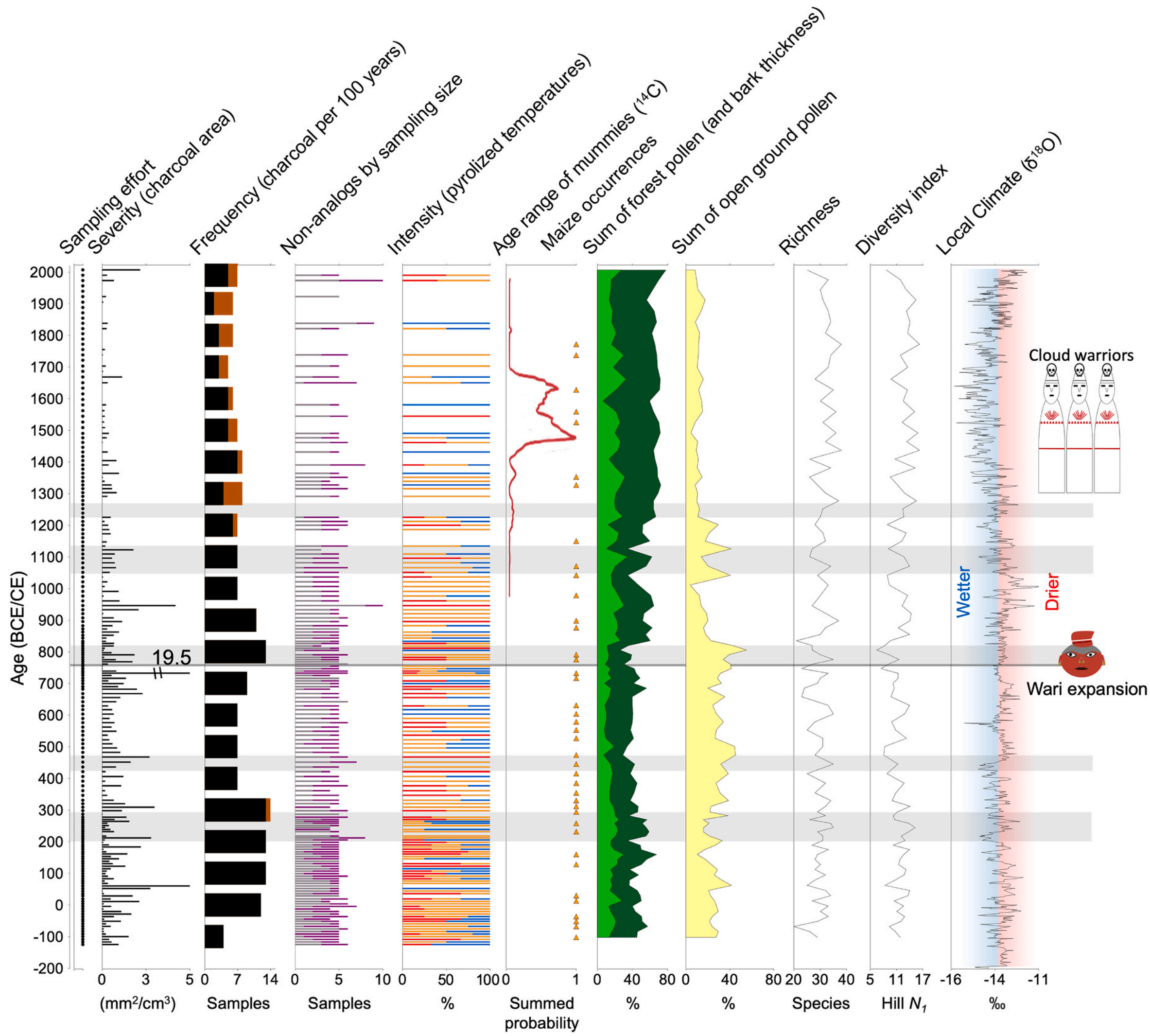

Fig. 2. Reconstruction of past fire regime at Laguna de los Condores (Peru) over the last 2100 years. Fire severity is estimated by charcoal abundance (surface area: mm^2/cm^3) (Åkesson et al., 2019). Fire frequency is the number of samples containing (black) and lacking (brown) charcoal in a 100-year interval. The number of non-analog particles (grey) is shown in relation to number of charcoal fragments analyzed per sample (purple). Fire intensity is the proportion of charcoal particles pyrolysed at low- (blue), mid- (orange) and high- (red) temperatures per sample. The probable age range of dated mummies is shown with a red line and maize occurrence as orange triangles (Åkesson et al., 2019). Vegetation change is represented by total proportion of forest pollen taxa (green) and open ground pollen taxa (yellow) documented by pollen analysis of the sediments (Åkesson et al., 2019). The sum of forest pollen is divided between species with maximum bark thickness below 5 mm (dark green), representing taxa sensitive to fire, and above 5 mm (light green), representing taxa resistant to fire. Local climate, based on isotopic data from Lake Pumacocha (Bird et al., 2011), indicates the transition from dry (pink) to wet (blue) conditions. Grey bars highlight drought events identified by high ratios of calcium/titanium within the Laguna de Condores record (Åkesson et al., 2019). Dark grey line shows the approximated period in which Wari expansion began. Drawings by Majoi N. Nascimento based on photos of mummies and artefacts.

4. Discussion

Our FTIR analysis of charcoal fragments at Laguna de los Condores yielded significant insights into how the synergy of pyrolysis temperatures (fire intensity), fire severity, and fire frequency affect vegetation and shape various ecological responses to land use and climate (Fig. 2, Supplementary Data 1, Table 2.). Many of the charcoal fragments that we analyzed, however, had no analogs, (i.e., were unable to be assigned to a pyrolysis temperature based on the 10% similarity threshold). The non-analogs could be a product of four potential confounding factors: (i) Limitations with the reference dataset in terms of temperature range. Crown fires are known to exceed 1300 °C (Butler et al., 2004; Silvani and Morandini, 2009; Morandini and Silvani, 2010; Cruz et al., 2011; Mueller et al., 2018), with charcoal formation occurring up to c. 900 °C (Scott and Glasspool, 2005). Because ashing occurred above 800 °C when generating reference material, no spectra could be generated for these higher temperatures (Gosling et al., 2019; Maezumi et al., 2021). Consequently, it is not currently possible to estimate these higher pyrolysis temperatures. (ii) Limitations with the reference dataset in terms of species composition. Only nine plant species are included in our reference database (Gosling et al., 2019), and though these plant species share the physical (structural) and physiological (e.g. lignin content and configuration) characteristics of Andean plants, they do not comprise the wide range of possible plant traits found within the forest. (iii) potential post-formation alteration of charcoal. Charcoal can also undergo diagenic processes, resulting in changes to its physicochemical properties (Sigmund et al., 2018) and consequently its wavelength spectra. Although charcoal fragments obtained from lake sediments are deposited into anoxic conditions that would hinder the degradation process, reworked charcoal could go through physicochemical changes prior to sedimentary deposition. And (iv) possibility of charcoal misidentification. In sedimentary records, charcoal is identified based on its color (lustrous black), its fracture type (splintery or powdery), and on the preservation of characteristics of plant anatomy (Scott, 2010). Some of these attributes can be difficult to identify on small particles smaller than 0.05 mm. Further research is needed to explore these possibilities.

Regardless of the cause of charcoal fragments lacking analogs in our reference database, we have shown that the FTIR methodology of estimating pyrolysis temperature is robust and corresponds with other independently observed changes in land use and climate around Laguna de los Condores (Fig. 2). The area around Condores has been cultivated for maize (and potentially other crops) during the last 2100 years, though at changing magnitudes and frequencies over this period (Åkesson et al., 2019). Slash-and-burn cultivation was (and still is) commonly practiced in the region (Carneiro, 1961; Arroyo-Kalin, 2012), and includes land clearance combined with a short-term release of nutrients that promotes crop growth (Carneiro, 1960; Gafur et al., 2000; Bender Koch et al., 2005). Often, the cleared land is used for 2–5 years and then left uncultivated for periods ranging from 3 to 20 years (Brady, 1996; Borggaard et al., 2003). Slash-and-burn fires are known to occur at temperatures averaging 455–484 °C (Melquiades and Thomaz, 2016; Thomaz, 2017). The dominance of mid-temperature fires (400–500 °C) and co-occurrence of maize pollen throughout the record shows that our FTIR analysis can likely detect mid-temperature slash-and-burn types of fire (Fig. 2). When combined with other proxies, it is also possible that the dominance of mid-temperature fires can indicate cultivation of crops not detectable with pollen or phytoliths (i.e., potatoes).

Maize cultivation (based on pollen evidence) was more frequent from the onset of the record until 1200 CE, coinciding with higher amounts and frequencies of macrocharcoal, and alongside higher pyrolysis temperatures (Fig. 2). These data suggest that both deforestation and cultivation were occurring for a 900-year period, as high temperature fires (>600 °C) are typically a result of intentional forest clearing. Increased forest clearing during this time is also supported by the higher amounts of disturbance and open ground taxa and lower amounts of overall forest taxa found in the pollen record (Fig. 2) (Åkesson et al., 2019). The multi-proxy data suggest that human populations around the lake continued to grow and thus land use expanded or intensified from -100 to 800 CE. This strengthened period of land use was also occurring during a period when regional climate was drier (Åkesson et al., 2019). From 800 to 1200 CE, a transitional period was marked by the decrease in maize cultivation, fire intensity and forest clearance (Fig. 2).

Pyrolysis temperature is a component of fire intensity, which is regulated by fuel and moisture availability (Pompe and Vines, 1966; Sikkink and Keane, 2012). At Laguna de los Condores, some of the high-intensity fires aligned with or preceded strong drought events previously identified by peaks of Ca/Ti and carbonate deposition (pink bars in Fig. 2) (Åkesson et al., 2019). Increases in Ca/Ti ratio and carbonate deposition would have occurred as the hydrological balance of the lake became dominated by evaporation (Haberzettl et al., 2007; Kylander et al., 2013), indicating a lowered lake level. Although this alignment is absent for some samples, it is possible that in some cases dry events started exerting their effects on terrestrial environments and facilitating fire decades earlier than prolonged droughts affected lake level. One of these peaks in high-intensity fires (from c. 650 CE to 820 CE) also coincided with the expansion of the Wari Empire (Schreiber, 2001; Tung, 2007; Watanabe et al., 2016). Laguna de los Condores is located at about 28 km north of a Wari territory, but the lack of dated Wari material does not permit direct causality of these high pyrolysis temperature events. Regardless of the source, this peak in high-intensity fires resulted in the highest amount of forest clearance and increase in open ground vegetation documented in the last 2100 years (Fig. 2).

At Laguna de los Condores, the increase in precipitation that occurred after c. 1200 CE was accompanied by a change in land use. Fire severity, frequency and intensity (pyrolysis temperatures) decreased alongside the transition to a wetter climate (Fig. 2). Low temperature fires (<500 °C) have typically been associated with the clearing of forest understories or maintenance of open ground (Kennard, 2002). These low intensity fires combined with decreased levels of slash-and-burn cultivation (mid-temperature pyrolysis), continued around the site from 1200 CE until the late 1950s (Fig. 2). During this period, many forests that were previously opened began to recover and biodiversity (based on pollen morphotypes) increased. Regrowing forests contained higher abundances of species with low bark thickness (below 5 mm), a trait that indicates sensitivity to fire (Poorter et al., 2014; Pausas, 2015; Archibald et al., 2018). Around 1450 CE, the Chachapoya (Cloud Wariors) changed their use of Laguna de los Condores by building a mausoleum in the cliff and using the site for ceremonial purposes (Guillén, 2003; Wild et al., 2007; Cherkinsky and Urton, 2014). The maize cultivated during this period may have been for ceremonial rather than everyday use, similarly to what has been documented at Machu Picchu, c. 900 km away (Burger and Salazar, 2004; Reinhard, 2007).

Though we expected fire severity to be correlated with pyrolysis temperature, our results show that both low temperature and high temperature pyrolysis can produce high (or low) amounts of charcoal (Fig. S1). We likely missed the original high-temperature fires associated with the start of forest clearance, as the record already shows high levels of burning and forest opening at its onset c. 2100 years ago. Thus, the higher charcoal amounts documented before 1200 CE may not be the most intense in the duration of human occupation around the lake. Alternatively, it is possible that, due to the high local precipitation levels, the region was too wet to produce a strong signal of the onset of deforestation, even during periods of drier climate (Bird et al., 2011; Åkesson et al., 2019).

It has often been assumed that higher amounts of charcoal (fire severity) result in a greater ecological or vegetation response. A lack of correlation between charcoal amounts and ecological responses, as seen in pollen data (Millspaugh et al., 2000; Gavin, 2001) can thus be at least partially explained by the lack of data on fire intensity (pyrolysis temperature). Here we have provided a comprehensive assessment of the past fire regime at Laguna de los Condores and show that the corresponding ecological response is dependent on all parameters of fire, including fire severity, frequency and intensity. Our work can be used as a template for future paleoecological studies in any geographic region. The FTIR-based methodology of estimating pyrolysis temperatures has the potential to help paleoecological studies to differentiate between past fires caused by humans practicing slash-and-burn cultivation (burned <500 °C), and non-human ignited fires, especially in dry regions where fire is a natural component of the landscape.

Our reconstruction of fire pyrolysis temperatures at Laguna de los Condores demonstrates that while charcoal area measurements provide insight into past frequency and amount of biomass consumed, additional measurements of pyrolysis temperature (fire intensity) are needed to understand the way people managed past landscapes and the way landscapes changed through time.

Author contributions

C.N.H.M., Z.K., C.M.Å., C.G., M.B.B., W.D.G. collected the data. M.N. N., C.N.H.M., Z.K., S.Y.M., M.B.B., W.D.G. analyzed the data. C.N.H.M. and W.D.G. conceived the ideas and designed the methodology. M.N.N. and C.N.H.M. led the writing of the manuscript with review and editing from M.B.B. and W.D.G. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

All our data will be openly published, and we (all coauthors) have no competing interests to declare.

Data availability

Data used is available on the online data repository Zenodo, and in the supplementary data. Other datasets used here available through

NEOTOMA Paleoecology Database.

Acknowledgements

We would like to aknowledge the community of Leymebamba for allowing access to Lake Condores. This work was funded by grants from the National Aeronautics and Space Administration (grant no. NNX14AD31G), the National Science Foundation (grant no. EAR1338694 and 1624207), National Geographic Society (grant no. 8763–10), the Netherlands Organisation for Scientific Research (NWO - award ALWOP.322), and the European Research Council Starting Grant (StG 853394).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2023.108278.

References

Åkesson, C.M., Matthews-Bird, F., Bitting, M., Fennell, C.-J., Church, W.B., Peterson, L. C., Valencia, B.G., Bush, M.B., 2019. 2,100 years of human adaptation to climate change in the High Andes. Nature Ecology & Evolution 1–9.
Archibald, S., Lehmann, C.E., Belcher, C.M., Bond, W.J., Bradstock, R.A., Daniau, A.-L., Dexter, K.G., Forrestel, E.J., Greve, M., He, T., 2018. Biological and geophysical feedbacks with fire in the Earth system. Environ. Res. Lett. 13, 033003.
Arroyo-Kalin, M., 2012. Slash-burn-and-churn: landscape history and crop cultivation in pre-Columbian Amazonia. Quat. Int. 249, 4–18.
Balch, J.K., Brando, P.M., Nepstad, D.C., Coe, M.T., Silvério, D., Massad, T.J., Davidson, E.A., Lefebvre, P., Oliveira-Santos, C., Rocha, W., 2015. The susceptibility of southeastern amazon forests to fire: insights from a large-scale burn experiment. Bioscience 65, 893–905.
Bender Koch, C., Borggaard, O., Gafur, A., 2005. Formation of iron oxides in soils developed under natural fires and slash-and-burn based agriculture in a monsoonal climate (Chittagong Hill Tracts, Bangladesh). Hyperfine Interact. 166, 579–584.
Bird, B.W., Abbott, M.B., Vuille, M., Rodbell, D.T., Stansell, N.D., Rosenmeier, M.F., 2011. A 2,300-year-long annually resolved record of the South American summer monsoon from the Peruvian Andes. Proc. Natl. Acad. Sci. USA 108, 8583–8588.
Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Analysis 6, 457–474.
Borggaard, O.K., Gafur, A., Petersen, L., 2003. Sustainability appraisal of shifting cultivation in the chittagong Hill tracts of Bangladesh. AMBIO A J. Hum. Environ. 32, 118–123.
Brady, N.C., 1996. Alternatives to slash-and-burn: a global imperative. Agric. Ecosyst. Environ. 58, 3–11.
Brando, P.M., Oliveria-Santos, C., Rocha, W., Cury, R., Coe, M.T., 2016. Effects of experimental fuel additions on fire intensity and severity: unexpected carbon resilience of a neotropical forest. Global Change Biol. 22, 2516–2525.
Brown, K., Clark, J., Grimm, E., Donovan, J., Mueller, P., Hansen, B., Stefanova, I., 2005. Fire cycles in North American interior grasslands and their relation to prairie drought. Proc. Natl. Acad. Sci. USA 102, 8865–8870.
Burger, R.L., Salazar, L.C., 2004. Machu Picchu: Unveiling the Mystery of the Incas. Yale University Press.
Bush, M.B., Rozas-Davila, A., Raczka, M., Nascimento, M., Valencia, B., Sales, R.K., McMichael, C.N.H., Gosling, W.D., 2022. A palaeoecological perspective on the transformation of the tropical Andes by early human activity. Phil. Trans. Biol. Sci. 377, 20200497.
Butler, B., Cohen, J., Latham, D., Schuette, R., Sopko, P., Shannon, K., Jimenez, D., Bradshaw, L., 2004. Measurements of radiant emissive power and temperatures in crown fires. Can. J. For. Res. 34, 1577–1587.
Byrne, R., Michaelsen, J., Soutar, A., 1977. Fossil charcoal as a measure of wildfire frequency in southern California: a preliminary analysis. In: Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. Forest Service/US Department of Agriculture (USDA), Washington DC/ Palo Alto, CA, pp. 361–367. General Technical Report WO-3.
Carneiro, R.L., 1960. Slash-and-burn Agriculture: a Closer Look at its Implications for Settlement Patterns. Bobbs-Merrill.
Carneiro, R.L., 1961. Slash-and-burn cultivation among the Kuikuru and its implications for cultural development in the Amazon Basin. In: Wilbert, J. (Ed.), The Evolution of Horticultural Systems in Native South America, Causes and Consequences. Editorial Sucre, Caracas, Venezuela, pp. 122–132.
Cherkinsky, A., Urton, G., 2014. Radiocarbon chronology of Andean khipus. Open J. Archaeometry 2.
Clark, J.S., 1988. Particle motion and the theory of charcoal analysis: source area, transport, deposition, and sampling. Quat. Res. 30, 67–80.
Cochrane, M.A., 2003. Fire science for rainforests. Nature 421, 913–919.
Constantine IV, M., Mooney, S., Hibbert, B., Marjo, C., Bird, M., Cohen, T., Forbes, M., McBeath, A., Rich, A., Stride, J., 2021. Using charcoal, ATR FTIR and chemometrics to model the intensity of pyrolysis: exploratory steps towards characterising fire events. Sci. Total Environ. 783, 147052.
Cruz, M.G., Butler, B.W., Viegas, D.X., Palheiro, P., 2011. Characterization of flame radiosity in shrubland fires. Combust. Flame 158, 1970–1976.
DeBano, L.F., Neary, D.G., Ffolliott, P.F., 1998. Fire Effects on Ecosystems. John Wiley & Sons.
Feeley, K.J., Silman, M.R., 2010. Land-use and climate change effects on population size and extinction risk of Andean plants. Global Change Biol. 16, 3215–3222.
Fraser, L.H., 2020. TRY—a plant trait database of databases. Global Change Biol. 26, 189–190.
Gafur, A., Borggaard, O.K., Jensen, J.R., Petersen, L., 2000. Changes in soil nutrient content under shifting cultivation in the Chittagong Hill Tracts of Bangladesh. Geografisk Tidsskrift-Danish Journal of Geography 100, 37–46.
Garreaud, R., Vuille, M., Compagnucci, R., Marengo, J., 2009. Present-day South American climate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 281, 180–195.
Gavin, D.G., 2001. Estimation of inbuilt age in radiocarbon ages of soil charcoal for fire history studies. Radiocarbon 43, 27–44.
Gosling, W.D., Cornelissen, H.L., McMichael, C.N.H., 2019. Reconstructing past fire temperatures from ancient charcoal material. Palaeogeogr. Palaeoclimatol. Palaeoecol. 520, 128–137.
Gould, K., Fredericksen, T., Morales, F., Kennard, D., Putz, F., Mostacedo, B., Toledo, M., 2002. Post-fire tree regeneration in lowland Bolivia: implications for fire management. For. Ecol. Manag. 165, 225–234.
Guillén, S.E., 2003. De Chinchorro a Chiribaya: los ancestros de los mallquis Chachapoya-Inca. Boletín de Arqueología PUCP, pp. 287–303.
Haberzettl, T., Corbella, H., Fey, M., Janssen, S., Lücke, A., Mayr, C., Ohlendorf, C., Schäbitz, F., Schleser, G.H., Wille, M., 2007. Lateglacial and Holocene wet—dry cycles in southern Patagonia: chronology, sedimentology and geochemistry of a lacustrine record from Laguna Potrok Aike, Argentina. Holocene 17, 297–310.
Hijmans, R.J., Cameron, S.E., Parra, J.L., PG, J., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.
Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432.
Hogg, A.G., Hua, Q., Blackwell, P.G., Niu, M., Buck, C.E., Guilderson, T.P., Heaton, T.J., Palmer, J.G., Reimer, P.J., Reimer, R.W., 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 years cal BP. Radiocarbon 55, 1889–1903.
Kanner, L.C., Burns, S.J., Cheng, H., Edwards, R.L., Vuille, M., 2013. High-resolution variability of the South American summer monsoon over the last seven millennia: insights from a speleothem record from the central Peruvian Andes. Quat. Sci. Rev. 75, 1–10.
Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., 2011. TRY–a global database of plant traits. Global Change Biol. 17, 2905–2935.
Keeley, J.E., 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. Int. J. Wildland Fire 18, 116–126.
Kennard, D., Gould, K., Putz, F., Fredericksen, T., Morales, F., 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. For. Ecol. Manag. 162, 197–208.
Kennard, D.K., 2002. Secondary forest sucession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. J. Trop. Ecol. 18, 53–66.
Kennard, D.K., Gholz, H., 2001. Effects of high-and low-intensity fires on soil properties and plant growth in a Bolivian dry forest. Plant Soil 234, 119–129.
Kitzberger, T., Perry, G., Paritsis, J., Gowda, J., Tepley, A., Holz, A., Veblen, T., 2016. Fire–vegetation feedbacks and alternative states: common mechanisms of temperate forest vulnerability to fire in southern South America and New Zealand. N. Z. J. Bot. 54, 247–272.
Kylander, M.E., Klaminder, J., Wohlfarth, B., Löwemark, L., 2013. Geochemical responses to paleoclimatic changes in southern Sweden since the late glacial: the Hässeldala Port lake sediment record. J. Paleolimnol. 50, 57–70.
Lawes, M.J., Midgley, J.J., Clarke, P.J., 2013. Costs and benefits of relative bark thickness in relation to fire damage: a savanna/forest contrast. J. Ecol. 101, 517–524.
Maezumi, S.Y., Gosling, W.D., Kirschner, J., Chevalier, M., Cornelissen, H.L., Heinecke, T., McMichael, C.N., 2021. A modern analogue matching approach to characterize fire temperatures and plant species from charcoal. Palaeogeogr. Palaeoclimatol. Palaeoecol., 110580
Matthews-Bird, F., Valencia, B.G., Church, W., Peterson, L.C., Bush, M., 2017. A 2000-year history of disturbance and recovery at a sacred site in Peru's northeastern cloud forest. Holocene, 0959683617702232.
McMichael, C., Witteveen, N., Scholz, S., Zwier, M., Prins, M., Lougheed, B.C., Mothes, P., Gosling, W.D., 2021. 30,000 years of landscape and vegetation dynamics in a mid-elevation Andean valley. Quat. Sci. Rev. 258, 106866.
Melquiades, F.L., Thomaz, E.L., 2016. X-ray fluorescence to estimate the maximum temperature reached at soil surface during experimental slash-and-burn fires. J. Environ. Qual. 45, 1104–1109.
Millspaugh, S.H., Whitlock, C., Bartlein, P.J., 2000. Variations in fire frequency and climate over the past 17 000 yr in central Yellowstone National Park. Geology 28, 211–214.
Morandini, F., Silvani, X., 2010. Experimental investigation of the physical mechanisms governing the spread of wildfires. Int. J. Wildland Fire 19, 570–582.
Morton, D., Le Page, Y., DeFries, R., Collatz, G., Hurtt, G., 2013. Understorey Fire Frequency and the Fate of Burned Forests in in Southern Amazonia.
Mueller, E.V., Skowronski, N., Thomas, J.C., Clark, K., Gallagher, M.R., Hadden, R., Mell, W., Simeoni, A., 2018. Local measurements of wildland fire dynamics in a field-scale experiment. Combust. Flame 194, 452–463.
Oliveras, I., Malhi, Y., Salinas, N., Huaman, V., Urquiaga-Flores, E., Kala-Mamani, J., Quintano-Loaiza, J.A., Cuba-Torres, I., Lizarraga-Morales, N., Román-Cuesta, R.-M.,

2014. Changes in forest structure and composition after fire in tropical montane cloud forests near the Andean treeline. Plant Ecol. Divers. 7, 329–340.
Oliveras, I., Román-Cuesta, R.M., Urquiaga-Flores, E., Quintano Loayza, J.A., Kala, J., Huamán, V., Lizárraga, N., Sans, G., Quispe, K., Lopez, E., 2018. Fire effects and ecological recovery pathways of tropical montane cloud forests along a time chronosequence. Global Change Biol. 24, 758–772.
Patterson, W.A., Edwards, K.J., Maguire, D.J., 1987. Microscopic charcoal as a fossil indicator of fire. Quat. Sci. Rev. 6, 3–23.
Pausas, J.G., 2015. Bark thickness and fire regime. Funct. Ecol. 29, 315–327.
Pompe, A., Vines, R., 1966. The influence of moisture on the combustion of leaves. Aust. For. 30, 231–241.
Poorter, L., McNeil, A., Hurtado, V.H., Prins, H.H., Putz, F.E., 2014. Bark traits and life-history strategies of tropical dry-and moist forest trees. Funct. Ecol. 28, 232–242.
Potts, E., Tng, D., Apgaua, D., Curran, T.J., Engert, J., Laurance, S.G., 2022. Growth form and functional traits influence the shoot flammability of tropical rainforest species. For. Ecol. Manag. 522, 120485.
R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Rehm, E.M., Feeley, K.J., 2015. The inability of tropical cloud forest species to invade grasslands above treeline during climate change: potential explanations and consequences. Ecography 38, 1167–1175.
Reinhard, J., 2007. Machu Picchu: Exploring an Ancient Sacred Center. ISD LLC.
Sales, R.K., McMichael, C.N., Flantua, S.G., Hagemans, K., Zondervan, J.R., González-Arango, C., Church, W.B., Bush, M.B., 2022. Potential distributions of pre-Columbian people in Tropical Andean landscapes. Philosophical Transactions of the Royal Society B 377, 20200502.
Sarmiento, F.O., 2002. Anthropogenic change in the landscapes of highland Ecuador. Geogr. Rev. 92, 213–234.
Sarmiento, F.O., 2012. Contesting Páramo: Critical Biogeography of the Northern Andean Highlands. Kona Pub. and Media Group.
Schreiber, K., 2001. The Wari empire of Middle Horizon Peru: the epistemological challenge of documenting an empire without. Empires: Perspectives from archaeology and history 122, 70.
Scott, A.C., 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 291, 11–39.
Scott, A.C., Glasspool, I.J., 2005. Charcoal reflectance as a proxy for the emplacement temperature of pyroclastic flow deposits. Geology 33, 589–592.
Sigmund, G., Jiang, C., Hofmann, T., Chen, W., 2018. Environmental transformation of natural and engineered carbon nanoparticles and implications for the fate of organic contaminants. Environ. Sci.: Nano 5, 2500–2518.
Sikkink, P.G., Keane, R.E., 2012. Predicting fire severity using surface fuels and moisture. In: Res. Pap. RMRS-RP-96, vol. 37. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, p. 96.
Silva-Matos, D.M., Fonseca, G.D., Silva-Lima, L., 2005. Differences on post-fire regeneration of the pioneer trees Cecropia glazioui and Trema micrantha in a lowland Brazilian Atlantic Forest. Rev. Biol. Trop. 53, 01-04.
Silvani, X., Morandini, F., 2009. Fire spread experiments in the field: temperature and heat fluxes measurements. Fire Saf. J. 44, 279–285.
Simpson, G.L., 2012. Analogue methods in palaeolimnology. In: Tracking Environmental Change Using Lake Sediments. Springer, pp. 495–522.
Stansell, N.D., Rodbell, D.T., Abbott, M.B., Mark, B.G., 2013. Proglacial lake sediment records of Holocene climate change in the western Cordillera of Peru. Quat. Sci. Rev. 70, 1–14.
Thomaz, E.L., 2017. High fire temperature changes soil aggregate stability in slash-and-burn agricultural systems. Sci. Agric. 74, 157–162.
Tung, T.A., 2007. Trauma and violence in the Wari empire of the Peruvian Andes: warfare, raids, and ritual fights. In: American Journal of Physical Anthropology, vol. 133. The Official Publication of the American Association of Physical Anthropologists.
Van Breukelen, M., Vonhof, H., Hellstrom, J., Wester, W., Kroon, D., 2008. Fossil dripwater in stalagmites reveals Holocene temperature and rainfall variation in Amazonia. Earth Planet Sci. Lett. 275, 54–60.
von Hagen, A., 2002. Chachapoya iconography and society at Laguna de los Cóndores, Peru. Kluwer, New York.
Von Hagen, A., Guillén, S., 1998. Tombs with a View.
Watanabe, S., Giersz, M., Makowski, K., 2016. Cronología y dinámica social durante el período Wari: nuevos descubrimientos en el sitio arqueológico El Palacio, sierra norte del Perú, vol. 9. Andes: Boletín del Centro Estudios Precolombinos de la Universidad de Varsovia, pp. 263–286.
White, S., 2013. Grass páramo as hunter-gatherer landscape. Holocene 23, 898–915.
Whitlock, C., Larsen, C., 2002. Charcoal as a fire proxy. Tracking Environmental Ehange Using Lake Sediments 75–97.
Wild, E.M., Guillen, S., Kutschera, W., Seidler, H., Steier, P., 2007. Radiocarbon dating of the Peruvian Chachapoya/Inca site at the Laguna de los Condores. Nucl. Instrum. Methods Phys. Res. Sect. B Beam Interact. Mater. Atoms 259, 378–383.
Winkler, M.G., 1985. Charcoal analysis for paleoenvironmental interpretation: a chemical assay. Quat. Res. 23, 313–326.
Young, K.R., León, B., 2007. Tree-line changes along the Andes: implications of spatial patterns and dynamics. Philosophical Transactions of the Royal Society B 362, 263–272.
Zapata-Ríos, X., Lopez-Fabara, C., Navarrete, A., Torres-Paguay, S., Flores, M., 2021. Spatiotemporal patterns of burned areas, fire drivers, and fire probability across the equatorial Andes. J. Mt. Sci. 18, 952–972.