

# 2,100 years of human adaptation to climate change in the High Andes

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**Humid montane forests are challenging environments for human habitation. We used high-resolution fossil pollen, charcoal, diatom and sediment chemistry data from the iconic archaeological setting of Laguna de los Condores, Peru to reconstruct changing land uses and climates in a forested Andean valley. Forest clearance and maize cultivation were initiated during periods of drought, with periods of forest recovery occurring during wetter conditions. Between AD 800 and 1000 forest regrowth was evident, but this trend was reversed between AD 1000 and 1200 as drier conditions coincided with renewed land clearance, the establishment of a permanent village and the use of cliffs overlooking the lake as a burial site. By AD 1230 forests had regrown in the valley and maize cultivation was greatly reduced. An elevational transect investigating regional patterns showed a parallel, but earlier, history of reduced maize cultivation and forest regeneration at mid-elevation. However, a lowland site showed continuous maize agriculture until European conquest but very little subsequent change in forest cover. Divergent, climate-sensitive landscape histories do not support categorical assessments that forest regrowth and peak carbon sequestration coincided with European arrival.**

When and how much humans altered humid Andean montane forests is debated. It was long argued that these systems were virtually uninhabitable<sup>1–3</sup>, but recent archaeological<sup>4–6</sup> and palaeoecological<sup>7,8</sup> data show long-term occupation of some settings but not others<sup>9</sup>. Recently, it has been suggested that the Andean forests of today may have been treeless fields at the time of the European conquest<sup>8,10</sup>. If these arguments are true, then successional recovery following human population collapse conceals a history of past deforestation. The consequent sequestration of carbon by regrowing forests is suggested to have contributed to global cooling during the Little Ice Age<sup>11–13</sup>. Here, we present a detailed multi-proxy palaeoecological record spanning the last 2,130 years from a montane forest setting that demonstrates the importance of climate change to pre-Columbian agricultural strategies and that forest regrowth began long before the European conquest.

The montane forests on the eastern slopes of the Central Andes are one of the most biologically diverse systems on Earth but are reputedly among the most inhospitable for human occupation. Oxygen deprivation and year-round freezing night-time temperatures are conditions typical of high montane settings<sup>14,15</sup>. Steep slopes covered by unstable soils, pervasive moisture and frequent ground-level clouds make these forests particularly uncomfortable for humans and challenging for crop cultivation<sup>15</sup>. Nevertheless, a long history of occupation of these mid-elevation settings is now emerging<sup>16,17</sup>.

Palaeoclimatic reconstructions of the last two millennia from Peru and Ecuador reveal local variability, but two broad trends in precipitation. Most data indicate that the period from ca. AD 700 to 1200 was dry and prone to severe droughts but that conditions became much wetter after ca. AD 1200 (refs. 18–20).

The likelihood that past climate change in the Andes provoked societal changes, even displacement, has long been argued<sup>21,22</sup> although consensus often remains elusive<sup>23–25</sup>. Human ingenuity

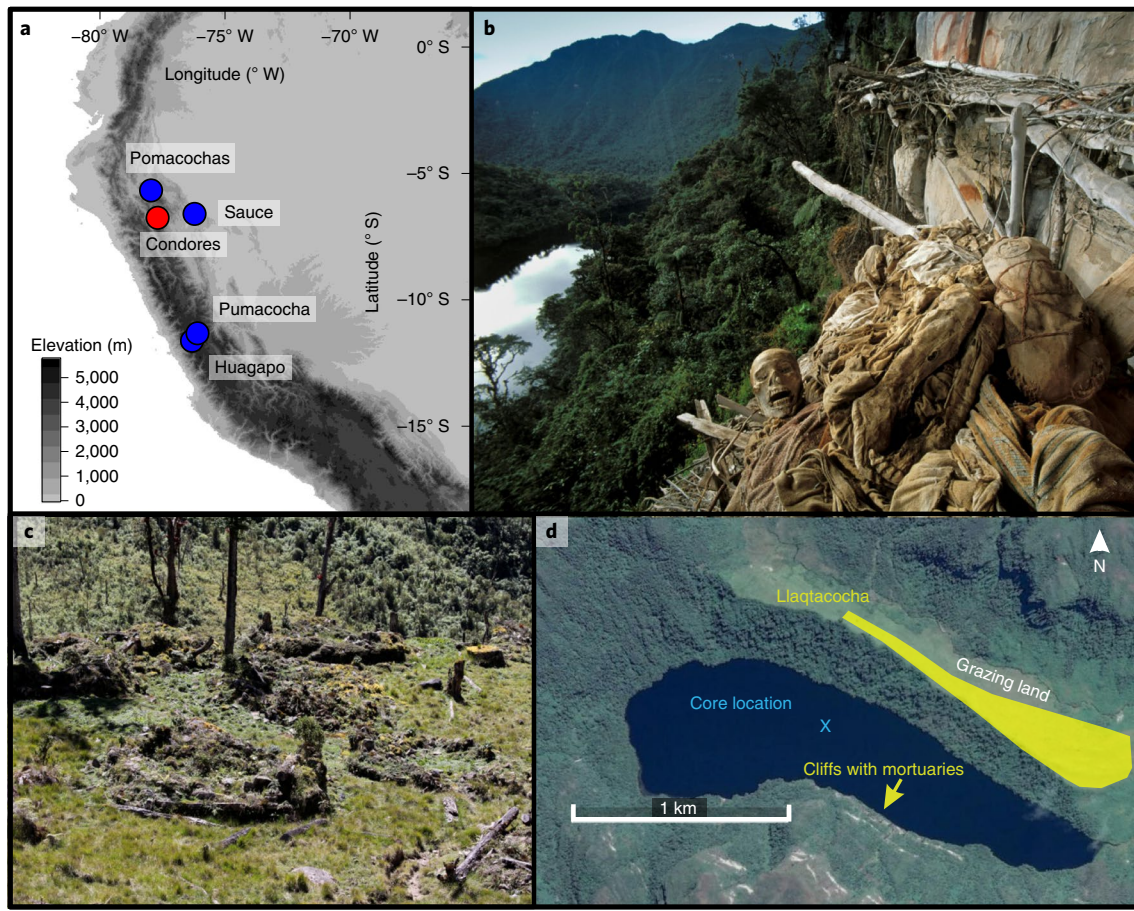
and invention are evident in offsetting problems posed by inimical environments to agriculture; for example irrigation systems<sup>26</sup>, raised field agriculture<sup>27</sup> and terracing<sup>28</sup>. Nevertheless, when conditions fall outside a given range, new problems or opportunities may produce societal change<sup>29–31</sup>. Indeed, populations living in marginal settings, that is on the cusp of hardship, are likely to be the most responsive to adverse conditions.

Laguna de los Condores (also known as Lake of the Mummies and hereafter Condores) lies at 6° 51' 03.02" S, 77° 41' 43.28" W at 2,860 metres above sea level in a deep, forested valley. A glacial-aged lateral moraine forms a steep, shaded northern shoreline and 100-m-high sunlit white cliffs form the southern shore overlooking deep, black water. Sometime after ca. AD 900, indigenous peoples, referred to as the Chachapoya, used high cliff ledges above the lake to construct scaffolded ledges and burial chambers. Radiocarbon ages (Supplementary Table 2) for this material range from AD 1160 to 1530 (refs. 32,33), confirming that most interments took place before and during the Inca conquest and occupation of the Chachapoya region (AD 1470–1532)<sup>34</sup>.

On the crest of the moraine and on its north-facing slopes lie the ruins of a late pre-Hispanic Chachapoya village that archaeologists named Llaqtacocha (Fig. 1 and Supplementary Fig. 1). Test excavations were carried out in 1999. One of the 130 stone circular and rectilinear buildings has been carbon-14 (<sup>14</sup>C) dated, which suggests that the occupation encompassed the period from AD 1200 to 1550 (ref. 35).

The lake is about 2,300 m long and 700 m wide and is dammed by a terminal moraine. Based on the elevation of the moraine, the lake would have been formed during deglaciation 16,000–14,000 years ago<sup>36</sup>. Small inlet streams draining from steep valley sides and precipitation provide the water to the lake. Water is lost from the system by evaporation and via a small outlet stream through the moraine dam.

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**Fig. 1 | The location of Laguna de los Condores, Pomacochas and Sauce, Peru.** **a**, Locations of the study site Condores (red circle) and other sites mentioned in text (blue circles); Pomacochas, Sauce, Pumacocha and Huagapo. **b**, Mummified remains on a burial scaffold built onto cliffs above Condores. **c**, The remains of six of the circular dwellings of Llaqtacocha. **d**, Google Earth image of Condores, showing the forested valley, the location of the Chachapoya village of Llaqtacocha (shaded yellow) on the crest of the moraine, cliffs where more than 200 mummies were entombed, modern grazing land and the core location. Credit: **b**, Reused with permission from Ronald Wagter; **c**, photo by Mark Bush; **d**, map data: Google.

The valley in which Condores lies is small, barely double the size of the lake, and currently uninhabited and the nearest village, Leymebamba, is about 19 km away. The valley has a montane forest that is rich in Araliaceae, Ericaceae, *Hedyosmum*, Lauraceae, Melastomataceae, Rubiaceae, Urticaceae and *Weinmannia*. Over the crest of the moraine to the north, outside the lake basin, the north-facing slopes are maintained for grazing (Fig. 1d).

At Lake Condores, mean monthly temperatures range between 15.5 and 17°C with precipitation in excess of 3,200–4,000 mm (ref. 37). In the late Holocene natural variations in tropical Andean temperature were about 0.5–0.8°C (refs. 38–40). Such temperature changes would have translated to a ~100–160 m vertical change in growing conditions. As Condores lies about 700 m below the modern upper forest limit and 500 m below where maize is commonly grown, even the coldest periods would still have been potentially productive for maize cultivation. Furthermore, the act of clearing land in tropical systems leads to a local warming of about 2–4°C in mean annual temperature, with very little compensation in nighttime cooling<sup>41–43</sup>. Consequently, temperature is unlikely to have played a decisive role in determining cultivational patterns<sup>40</sup>.

Maize grows best in well-drained soils and bright sunlight. As photosynthetically active radiation falls below 1,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  maize productivity starts to decline, and when it falls below 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  this decline steepens<sup>44</sup>. High precipitation, relative humidity and low-level clouds are more likely to be important

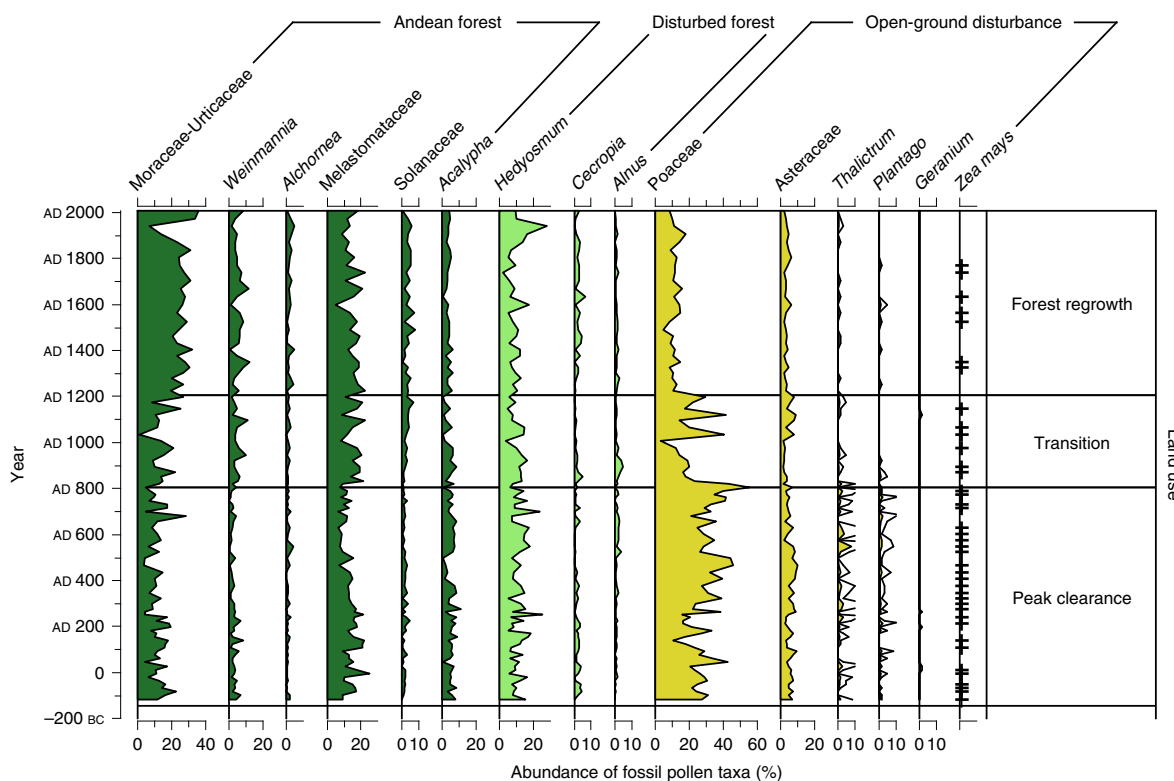
constraints on maize growth than temperature. The peak of the wet season at Condores occurs between November and April, and thus the austral summer would be the worst time to grow maize<sup>45</sup>. At 2,860 m elevation, dry season photosynthetically active radiation would be about 700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , falling to ~500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in the wet season<sup>46</sup>. Thus, at Condores any increase in cloudiness or increased cloud immersion, which reduces light availability and wets leaves, would cause reduced maize productivity<sup>47,48</sup>.

## Results and discussion

Analysis of the sediments for fossil pollen and charcoal reveal times of deforestation and forest recovery. The chronology of the record was established on 11 <sup>14</sup>C dates (Supplementary Table 1 and Extended Data 1).

The fossil pollen record comprised 110 identified types that we describe in three zones (Fig. 2). The basal zone (ca. 150 BC–AD 800) was rich in disturbance taxa, for example Poaceae, *Thalictrum*, *Geranium* and *Plantago*, and was where *Zea mays* (maize) occurred in most samples (Extended Data 2). The intermediate zone (ca. AD 800–1200) showed strong oscillations between forested and disturbed states but an overall increase in forest pollen abundance. In the upper zone (ca. AD 1200 to modern times), forest taxa were >80% of the pollen sum and *Zea* was represented sporadically (Fig. 2).

Across a broad range of modern tropical forest landscapes ‘undisturbed’ forest produces a pollen signature in which Poaceae



**Fig. 2 | The abundance of selected fossil pollen taxa from Laguna de los Condores, Peru, plotted against time.** Only taxa with >10% abundance and other taxa mentioned in the text are shown (Andean forest, dark green; disturbed forest, pale green; open-ground disturbed, yellow). The + symbol indicates that *Zea mays* pollen grains are present.

(grass) accounts for 2–8% of pollen despite substantial variation in precipitation<sup>49–52</sup>. Human disturbance is quickly reflected in the loss of forest taxa (see Supplementary Table 3 for pollen categorization) and increased percentages of Poaceae pollen<sup>52</sup>. The modern setting of Condores yields 8% Poaceae pollen, with forest pollen accounting for 88% of the total pollen, which is consistent with a landscape that is primarily forested but showing some disturbance (Fig. 2).

In contrast, when this record began 2,130 years ago, there were Poaceae pollen inputs of 20–30% and forest pollen was only 55–60%, with the remainder of the pollen coming from weedy herbs (Fig. 2). Titanium inputs, which are a proxy for terrigenous mineral influx, 2,130–2,000 years ago were more than double those from AD 1900 to modern times (Fig. 3). Carbonates were relatively high, suggesting the lake was not overflowing and that this was a generally drier time than at present. The lake was eutrophicated at that time, compared with the modern system, and supported a diatom flora dominated by species tolerant of turbidity, for example *Punctastriata mimetica* and *Planorhynchium frequentissimum*<sup>53,54</sup>, whereas the modern dominant diatom, *Tabellaria flocculosa*, is consistent with a stratified system with good light penetration<sup>55,56</sup> (Extended Data 3).

Maize is not native to South America. It has pollen that transports poorly<sup>57</sup> and its fossil presence is an unambiguous indicator of clearance and cultivation taking place within the valley<sup>58,59</sup>. Maize (*Z. mays*) pollen occurred in the basal sample indicating that this landscape was already occupied and used when this record began; data that contrast with an absence of crop pollen in the modern samples.

Our inferences regarding human responses to climate change are divided into those aligned to decadal-scale forcing, which primarily influenced the earlier part of the record, and those of centennial forcing, which were important after ca. AD 750.

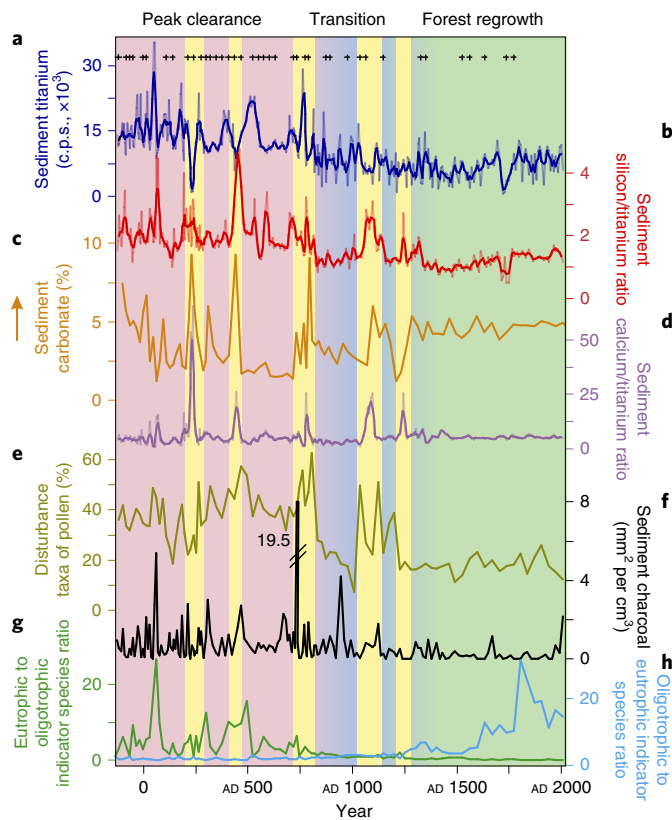
The decadal-scale events are evident in five profound droughts that caused spikes of deposition of calcium carbonate ( $\text{CaCO}_3$ ). These events were manifested in the calcium/titanium ratios of the X-ray fluorescence (XRF) data and in the separate measurement of carbonate through loss-on-ignition (Fig. 3). Carbonate deposition would have occurred when the lake stopped overflowing and evaporation increased in relative importance in the hydrological budget<sup>60,61</sup>. Decadal-scale changes were manifested as droughts during AD 220–240, 450, 780, 1070–1090 and 1250. These events were superimposed on centennial-scale climatic changes that included a wet event from ca. AD 750 to 1000, a dry period from ca. AD 1050 to 1200 and a wet event that began ca. AD 1200.

The droughts also influenced lake productivity. Local peaks in the silicon/titanium ratio, a proxy for biogenic silica, were consistent with increased pulses of nutrient availability<sup>62</sup>. Silicon/titanium peaks followed drought events and increases in taxa, which were characteristic of disturbed landscapes (Fig. 3). All but the last of the major drought events were followed by an uptick in disturbance taxa. This last drought event at AD 1230 occurred, as we shall argue, when land use in the valley was shifting towards forest regrowth. These data suggested unusually dry episodes were exploited by local people to clear the forest and increase their agricultural footprint.

Charcoal did not appear to align closely with climatic events. This is consistent with the view that fire in these wet forests was almost uniquely associated with human activity<sup>7</sup>. Fire occurred irregularly through time until AD 1100 and was much less frequent thereafter, until a spike appeared in modern times. Phases of forest recovery were suggested by forest pollen increasing to about 70–80%, at AD 200, 800 and 1200 (Fig. 4).

The drought event of AD 780 seems to mark a change in land use within the valley and also the transition to an increasingly wet system (for a broader palaeoecological context, see Supplementary





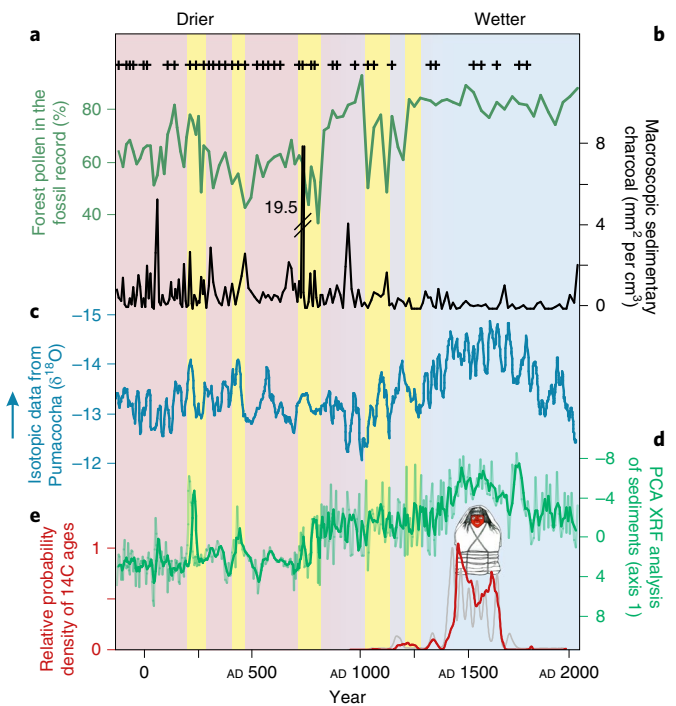
**Fig. 3 | Decadal-scale climate oscillations, human disturbance and forest impacts at Laguna de los Condores, Peru.**

**a**, Sediment titanium (c.p.s., counts per second) concentration as a proxy for eroding terrigenous material washing into the lake. **b**, Sediment silicon/titanium ratio as a proxy for biogenic silica production. High values indicate drought conditions. **c**, Percentage of sedimentary carbonate. High values indicate drought conditions. **d**, Ratio of calcium/titanium as a proxy for drought. **e**, Disturbance taxa of pollen values >5–10% indicate a relatively open landscape<sup>49–52</sup>. **f**, Sedimentary charcoal >180 μm. **g**, Ratio of eutrophic to oligotrophic indicator species in the fossil diatom flora. High values suggest nutrient enrichment of the lake. **h**, Ratio of oligotrophic to eutrophic indicator species in the fossil diatom flora. High values suggest a nutrient-poor system. Not all diatoms are indicators of nutrient status, hence the two ratios are not a simple reciprocal of one another. The + symbol indicates samples where maize pollen was found. Background colours reflect hypothesized transitions in land use. Yellow bars highlight areas containing at least one sample with calcium/titanium ratio values >2 s.d. above the mean. All XRF data are expressed as 15-year running means (bold lines) overlying the raw counts (pale lines).

Material section ‘Laguna de los Condores paleoclimatology in a broader context’). There is greater volatility in the chemical records before AD 780, such that peaks and troughs for all elements are more extreme than those that follow. The landscape is still extensively deforested and human activity is manifest in the charcoal record; however, the transition from eutrophic to oligotrophic lake conditions begins at this time. Titanium and silicon/titanium inputs, both markers for soil erosion, decrease abruptly and the record of maize pollen in the sediments becomes more erratic (Fig. 3) as conditions in the valley become wetter (Fig. 4).

Centennial-scale climate change also appears to have influenced the choice of land use by humans in the Condores valley. In addition to the pulses of drought, this area was subject to a long-term climatic press of increasing precipitation.

The principle component analysis (PCA) axis 1 of the XRF data from the Condores sediments is driven by abundances of titanium,

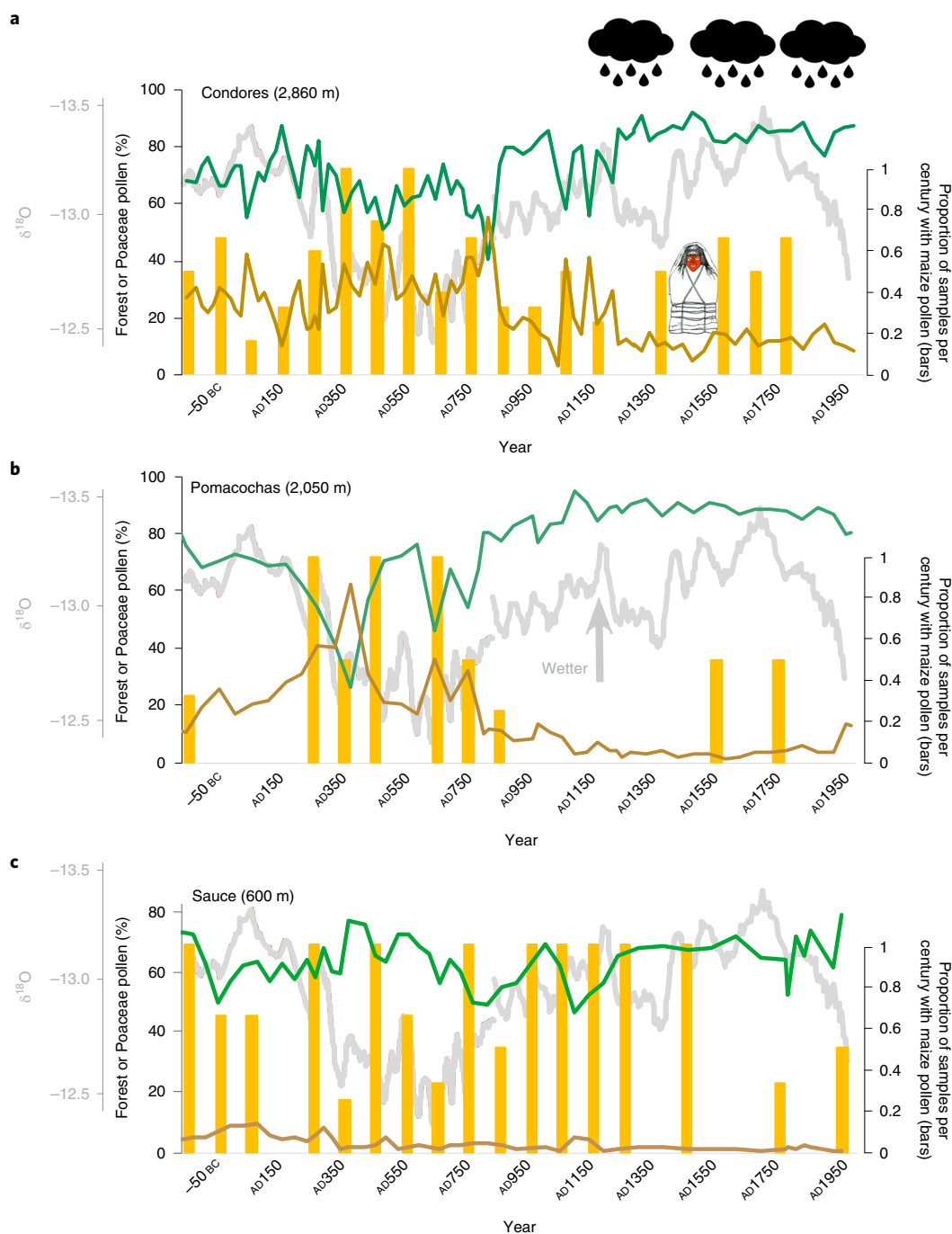


**Fig. 4 | Centennial-scale climate change and changing land use at Laguna de los Condores, Peru.**

**a**, The proportion of forest pollen in the fossil record. **b**, Macroscopic (>180 μm) sedimentary charcoal indicates fire within or close to the catchment. **c**, Isotopic data from Lake Pumacocha<sup>19</sup> indicating a transition to wetter conditions beginning ca. AD 1100. **d**, PCA axis 1 (inverted) of XRF analysis of sediments that mirrors the Lake Pumacocha<sup>19</sup> isotopic data. **e**, Probability density function of all <sup>14</sup>C ages ( $n=31$ ) from mummies and artefacts interred in the cliffs, which indicates the adoption of that practice after AD 1100. Higher values indicate wetter conditions. Yellow bars indicate drought events identified in Fig. 3. The + symbol indicates the presence of maize pollen. The PCA axis 1 of XRF data is expressed as 15-year running means (bold line) overlying the raw counts (pale line). All data are from Condores unless noted otherwise. Credit: Mummy drawing by Christiane Clados, Philipps University Marburg.

iron, aluminium, potassium, silicon and most other elements with positive scores on axis 1, with calcium at the negative extreme of the axis. This axis is interpreted to represent the component of erosion caused by rainfall, with higher values possibly reflecting stronger streamflow entering the lake (Fig. 4). When plotted through time, PCA axis 1 of the Condores XRF data produces a curve that, at a centennial-scale, is similar to that of the delta- $O-18$  ( $\delta^{18}O$ ) isotopic record from Lake Pumacocha, Peru<sup>19</sup> (Fig. 4). At a decadal scale, where the El Niño Southern Oscillation (ENSO) and other short-term events are reflected, Pumacocha shows a relatively weak connection to Lake Condores, which is to be expected given the varied responses to modern ENSO at these locations and potential mismatches in dating<sup>63</sup>.

Our evidence for agricultural activities dating to 1300 BC constitutes valley occupation during the millennium prior to construction of Llaqtacocha and the tombs. Habitation sites left by these earlier groups have not yet been identified archaeologically. We hypothesize that as conditions became wetter the suitability of the site for maize cultivation declined. There was not an immediate end to maize cultivation in the valley; rather the period between AD 750 and 1200 appears to have been transitional with a period of forest regrowth between AD 750 and 1000, followed by a resurgence of cultivation and land clearance that lasted until ca. AD 1200. It should be noted that the Wari Empire expanded out of southern Peru and

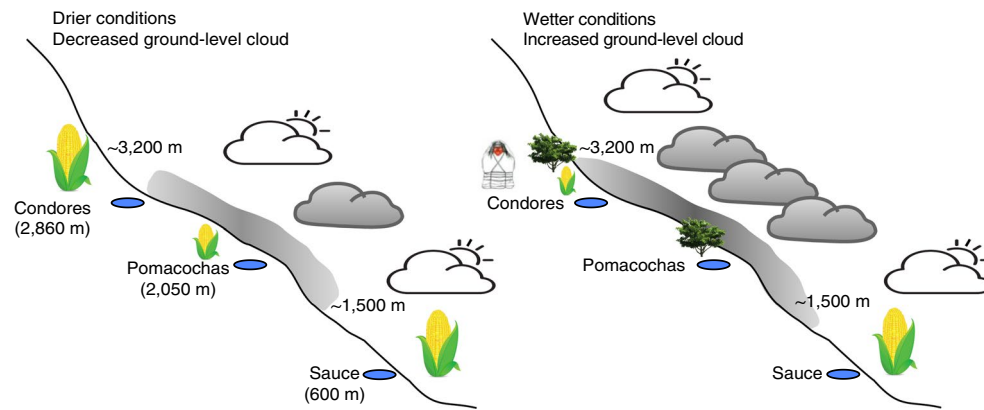


**Fig. 5 | Pollen representation across an elevational gradient through Chachapoya, Peru. a–c,** Forest (green) and Poaceae (brown) pollen abundance relative to the presence of maize pollen at Condores (**a**), Pomacochas (**b**) and Sauce (**c**). Yellow bars are the proportion of samples from each century that contained maize pollen. The grey line is a 15-year running mean of the  $\delta^{18}\text{O}$  isotopic record from Huagapo Cave, Peru<sup>18</sup> to show precipitation trends through time. Rain clouds indicate a transition to wetter conditions beginning ca. AD 1100. Credit: Mummy drawing by Christiane Clados, Philipps University Marburg.

probably introduced new farming techniques and crop varieties to northern Peru by AD 750 (refs. <sup>64,65</sup>). A Wari enclave has been identified ~28 km southeast of Condores, but further investigation is required to determine whether this arrival relates to observed forest recovery at Condores between AD 780 and 1000.

The forest recovery was interrupted by a dry period that began in ca. AD 1050 and developed into the drought of ca. AD 1070–1090. This drying coincides with increased cultivational activity, but it was not sustained after AD 1200. By AD 1230, and thereafter, forest types accounted for >80% of the pollen sum.

The south-facing, heavily shaded, steep moraine slopes may have been, at best, marginal lands for agriculture, and the wetter conditions may have favoured land use on the sunnier, north-facing slopes outside the lake basin adjacent to where the village of Llaqtacocha was established. Consistent with the adjoining region<sup>66</sup> archaeologists have identified agricultural terraces just below the eastern end of the settlement, but these are outside the catchment of the lake and are unlikely to have influenced the sedimentary signal. The use of the valley as a burial site and the decision to allow forest to regrow was therefore probably a



**Fig. 6 | The elevational gradient showing hypothesized changes in ground-level cloud immersion at Sauce, Pomacochas and Condorez.** Maize production, reversion to forest and interment of mummies are represented by corn cobs, trees and mummies, respectively. Credits: Corn: Can Stock Photo Inc/emaria; Tree: Can Stock Photo Inc/nikifiva; Mummy drawing by Christiane Clados, Philipps University Marburg.

pragmatic one, as well as possibly being a cultural/religious response to climate change.

The earliest date for a bone recovered from the cliff was AD 1250 and dates from mummy bundles entombed in the cliffs most often fell between AD 1450 and 1540 (refs. <sup>33,67</sup>). European arrival and regional population collapse led to the virtual abandonment of the site and there were few burials after AD 1580. Substantial overlap between the radiocarbon dates from Llaqtacocha and the cliff tombs suggests that by ca. AD 1250 the local population that had built the village also created the mortuaries and interred their dead in the cliffs above the lake. The archaeologists who conducted the research at the tombs and at Llaqtacocha argue that the lake itself would have been considered a *pacarina*, or sacred place from which the local community emerged in primordial time<sup>68</sup>.

The data from Condorez highlight that people responded to changing climate in the Andes opportunistically, colonizing areas when conditions were suitable and redirecting their efforts to more favourable locations or aspects when conditions deteriorated. Use of the spectacular setting for mausolea and ancestor-worship can be considered part of a larger adaptive response to changing conditions. To allow the regrowth of forest in the valley was a form of land management and contributed to the mosaic of ecosystem services within a human-dominated landscape.

A key question is: how do the data from Condorez fit into a framework of human history in the Andes<sup>69</sup>? The full length of occupation at Condorez is not known, but the fact that its occupation had become more permanent by AD 1250 fits with an exponential increase in the density of archaeological sites in Amazonia and the Andes that took place over the last 2,000 years (refs. <sup>70,71</sup>). Most palaeoecological records from the Andes show signatures of cultivation; however, in many cases the recovery of forest was not at the time of European arrival but around AD 1200 (refs. <sup>7,72</sup>).

To gain a regional perspective we compared Condorez with two other previously published sites: Lakes Pomacochas and Sauce, which lie 115 and 163 km from Lake Condorez, respectively. Pomacochas is a cool, frequently cloud-covered lake at 2,050 m elevation in a major valley system that connects the highlands to the lowlands. At the foot of this elevational transect is Lake Sauce at 600 m elevation. Although receiving more rain than Pomacochas, Sauce has much higher evaporation rates, making this a functionally drier environment.

Lakes Sauce<sup>72,73</sup> and Pomacochas<sup>7</sup> have long histories of maize cultivation. Palaeoecological data provide compelling evidence that the two montane forest sites, Condorez and Pomacochas, shared a common environmental history in which human disturbance of the

landscape and maize agriculture were favoured during dry conditions as the extent of forest clearance indicated by Poaceae pollen abundance rose and fell with precipitation (Fig. 5). In both settings forest clearance was substantial prior to AD 800, but they regained maximal forest cover between AD 1200 and 1300.

Maize pollen follows the pattern of Poaceae abundance, which provides evidence that humans clearing the forest are responsible for the pattern of Poaceae pollen. The linkage between drier conditions and maize cultivation is evident in these data. We suggest that the earlier abandonment of maize cultivation at Pomacochas compared to Condorez is because Pomacochas is the most marginal setting for maize production. Low-hanging cloud limits evaporation and light availability and increases humidity, which are unfavourable conditions for growing maize (Fig. 6). Under drier conditions we hypothesize that ground-level cloud would have been rare or less dense at the margins of its occurrence. As conditions became progressively wetter, Pomacochas would have become unsuitable for maize cultivation before Condorez. On the other hand, in the brighter, warmer lowland setting of Lake Sauce, Poaceae representation and maize pollen are not closely linked. In this record, maize cultivation does not seem to be linked to precipitation (Fig. 5), and its cessation coincides with the timing of European arrival. These data support the hypothesis that the areas most impacted by ground-level cloud were most strongly affected by climatic change (Fig. 6). Climate was a potent force that structured the human response in these mid-elevational systems, but probably to a lesser degree at low elevations.

The 10% Poaceae pollen representation for the peak clearance in the last 2,000 years from Lake Sauce is considerably less than from either Pomacochas or Condorez. The use of Sauce, although stretching back >6,000 years, did not result in large-scale clearance of the forest. In the last 2,000 years, the maximal extent of small-scale clearings in which maize was cultivated was at AD 0–300 at Lake Sauce, AD 300–800 at Pomacochas and AD 100–800 at Condorez. A commonality of all these settings is that the population collapse caused by European contact occurred long after forest regrowth was initiated. In no case was there a significant increase in forest cover in the 1500s, contra the expectations of the ‘Great Dying’<sup>13</sup>.

Although heavily trafficked valleys, such as the Quijos Valley of Ecuador, showed active use until the time of conquest<sup>8</sup>, the Peruvian forests described here had been recovering for as much as a millennium before European contact. Our data are consistent with northern Peruvian high-valley settings that supported substantial human populations at European contact<sup>5</sup>, but that did not exhibit deforested landscapes<sup>74</sup>. Other settings on the eastern

flank of the Peruvian Andes show no history of human occupation<sup>9</sup>. A key message arising from this study is that although the Andean flank supported human populations who modified landscapes, their densities changed through time and they did not follow a simple upward trajectory of intensifying maize agriculture, and ecological and climatic processes contributed to these patterns. Oversimplification of patterns of forest regrowth, and an unrealistic expectation that they coincide with European arrival, leads to misconceptions regarding carbon sequestration and climate impacts. Just as studies in lowland Amazonia revealed a heterogeneous occupational history<sup>75,76</sup>, generalizations about the history of Andean forests should be avoided.

## Conclusions

Long histories of maize agriculture in the Chachapoyas region of Peru did not follow the trajectory of overall population growth but showed retrenchment associated with climate change. Drought promoted penetration and use of the wetter cloud forests, but during wet intervals people would have moved elsewhere or relocated their cultivation activities away from these settings. When permanent villages became common throughout the region, responses lacked mobility, but land use decisions that balanced food production and societal needs were apparent. Andean forests had heterogeneous histories of occupation and successional recovery following changed land use. In all cases explored here, that recovery took place long before European arrival. The Andean forests of this region are not all post-Columbian regrowth systems, should not be assumed to be young or even aged and do not conform to expectations of suddenly becoming a carbon sink in the mid-1500s.

## Methods

In June 2010, our limnological survey revealed that dissolved oxygen fell to trace amounts 15 m below the surface and that Laguna de los Condores had a Secchi depth of about 2 m. A 1.84-m finely laminated sediment core was raised from Condores using a universal piston sampler deployed from a floating platform. The core was collected from the deepest point of the lake at about 60 m of water deep. Bedrock was not reached and the retrieved core only represents the most recent history of Condores. The core chronology was established using <sup>14</sup>C accelerator mass spectrometry dates on ten bulk sediment samples and one wood macrofossil. The age–depth model was generated using the package ‘bacon’<sup>77</sup> in R v.3.5.2 (ref. <sup>78</sup>) using the IntCal13 calibration curve<sup>79</sup> (Supplementary Table 1 and Extended Data 1). Radiocarbon dates ( $n = 31$ ) of all archaeological samples associated with the Condores burials (Supplementary Table 2) were amalgamated using the package BChron<sup>80</sup> in R v.3.5.2 (ref. <sup>78</sup>) and the IntCal13 calibration curve. A total probability density function was created from the ages<sup>81</sup>.

The core chemistry was analyzed using an Avaatech XRF core scanner at 0.5-cm (about 5-year) resolution to provide elemental data<sup>82</sup>. Measurements of elements aluminium, bismuth, bromine, calcium, chlorine, chromium, cobalt, copper, gallium, iron, lead, manganese, molybdenum, nickel, niobium, phosphorus, potassium, rhenium, rubidium, silicon, strontium, sulphur, titanium, vanadium, yttrium, zinc and zirconium were made using a slit size of  $1 \times 1 \text{ cm}^2$  at 10 kV and 30 kV over a 20-s counting period<sup>83</sup>. XRF data were transformed to obtain  $z$ -scores prior to PCA. PCA was conducted in R v.3.5.2 (ref. <sup>78</sup>) using the package vegan v.2.0–10 (ref. <sup>84</sup>). Loss-on-ignition analysis was performed according to standard methods<sup>85</sup> at a 2-cm (about 20-year) resolution ( $n = 93$ ).

The core was subsampled for fossil diatoms ( $n = 91$ )<sup>86</sup> and pollen ( $n = 92$ ) at a 2-cm (about 20-year) resolution for the entire 1.84-m sequence. Diatoms were extracted using standard methods described by Battarbee<sup>87</sup> using 10% hydrochloric acid and 30% hydrogen peroxide. The samples were mounted in Naphrax. Identifications were made using standard texts for the region<sup>88,89</sup> and online resources for example [www.algaebase.org](http://www.algaebase.org).

Exotic *Lycopodium* spores<sup>90</sup> were added to allow calculation of pollen concentrations. Standard methods were used to extract pollen<sup>91</sup>. The samples were mounted in glycerol. The Neotropical Pollen Database<sup>92</sup> (<https://research.fit.edu/paleolab/pollen-database/>) and standard texts for the region<sup>93</sup> were used for identifications. After initial counts were made, all pollen extracts were filtered using a 60- $\mu\text{m}$  mesh. The retained material was mounted in glycerol and reanalyzed to search for *Zea* (maize) grains. Maize pollen grains were only found in the original counts to 300 grains in two samples from AD 520–550, all other maize grains were found in the extended analysis of filtered samples. A CONISS-constrained clustering analysis was performed to aid with the zonation<sup>94</sup>. Tilia<sup>94</sup> and C2 (ref. <sup>95</sup>) software packages were used to construct fossil percentage diagrams.

Charcoal was sampled continuously along the core in 1-cm (about 10-year) increments ( $n = 184$ ) and 0.5-cm<sup>3</sup> of subsample were filtered using a 180- $\mu\text{m}$  mesh and the residue inspected for charcoal. The surface area of charcoal particles was quantified using ImageJ software<sup>96</sup>.

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## Data availability

The datasets generated from this study are available through NEOTOMA Paleocology Database (<https://neotomadb.org/>), which include pollen, charcoal, diatom, loss-on-ignition (carbonate) and XRF (Ti, Si and Ca) data visualized in Figs. 2–4.

Received: 10 April 2019; Accepted: 6 November 2019;

Published online: 09 December 2019

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## Acknowledgements

We are grateful to the community of Leymebamba for allowing us access to Lake Condores, and to archaeologists S. Guillén and A. von Hagen who have provided the foundational work on the mortuaries and Llaqtaocha. 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) and National Geographic Society (grant no. 8763-10) to M.B.B.

## Author contributions

C.M.Á., F.M.-B., M.B., C.-J.F., L.C.P. and W.B.C. performed research. C.M.Á., F.M.-B., L.C.P. and M.B.B. analysed data. C.M.Á., F.M.-B., L.C.P., W.B.C., B.G.V. and M.B.B. wrote the paper. M.B.B. designed the research project. M.B.B. and B.G.V. conducted the field project.

## Competing interests

The authors declare no competing interests.

## Additional information

**Extended data** is available for this paper at <https://doi.org/10.1038/s41559-019-1056-2>.

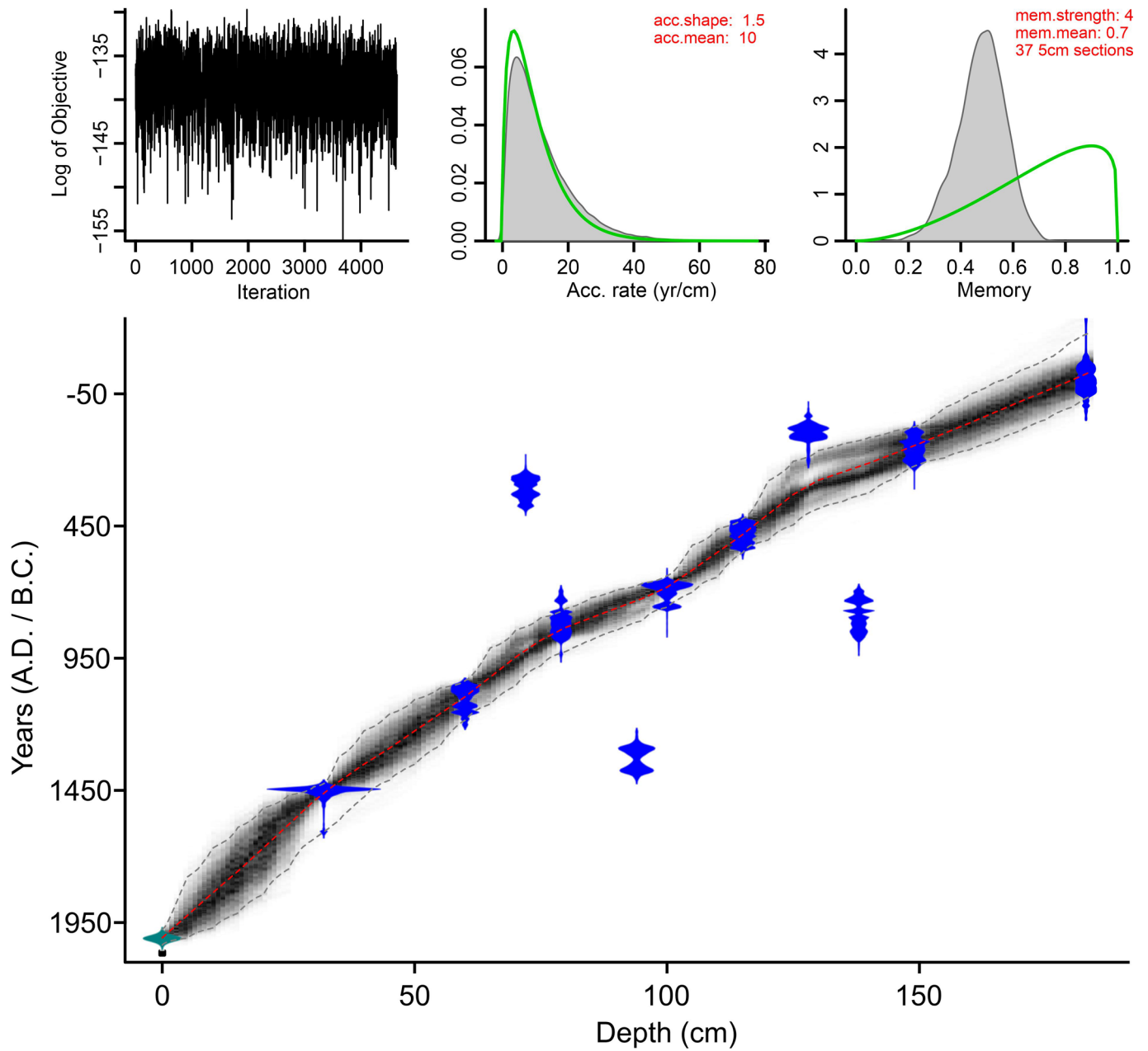
**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41559-019-1056-2>.

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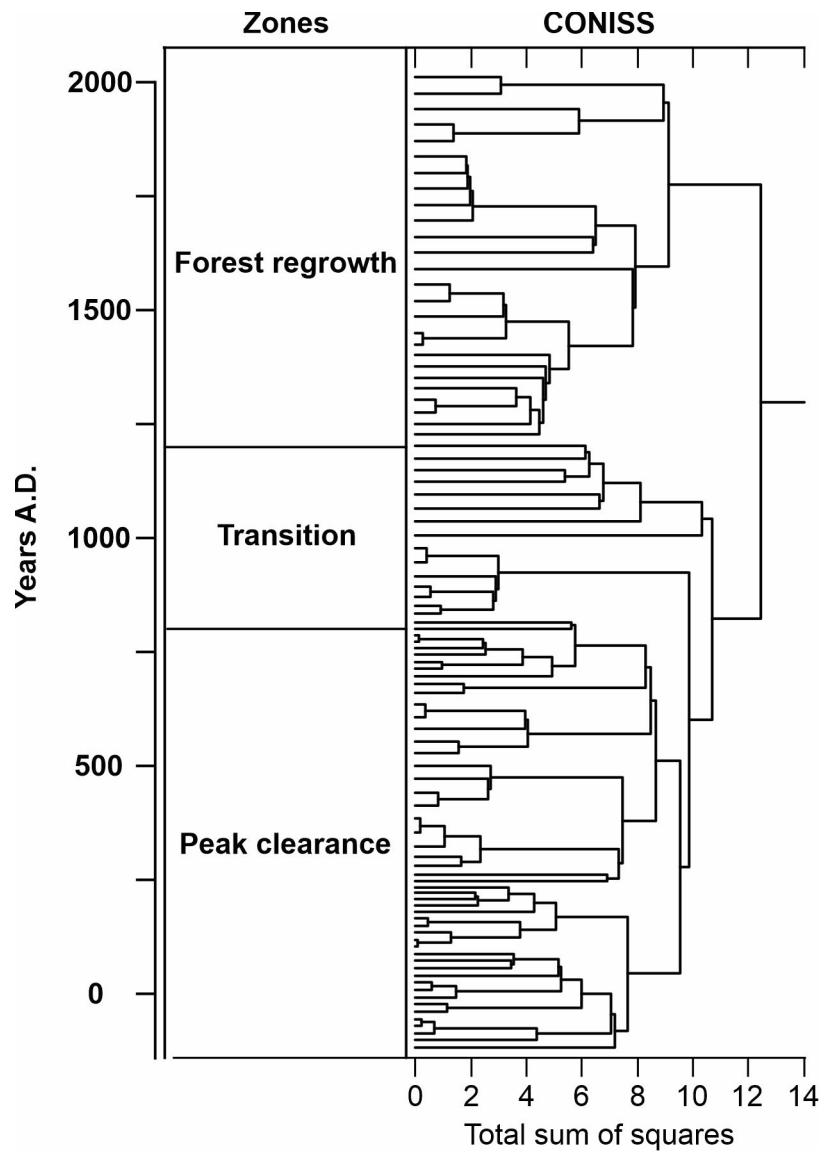
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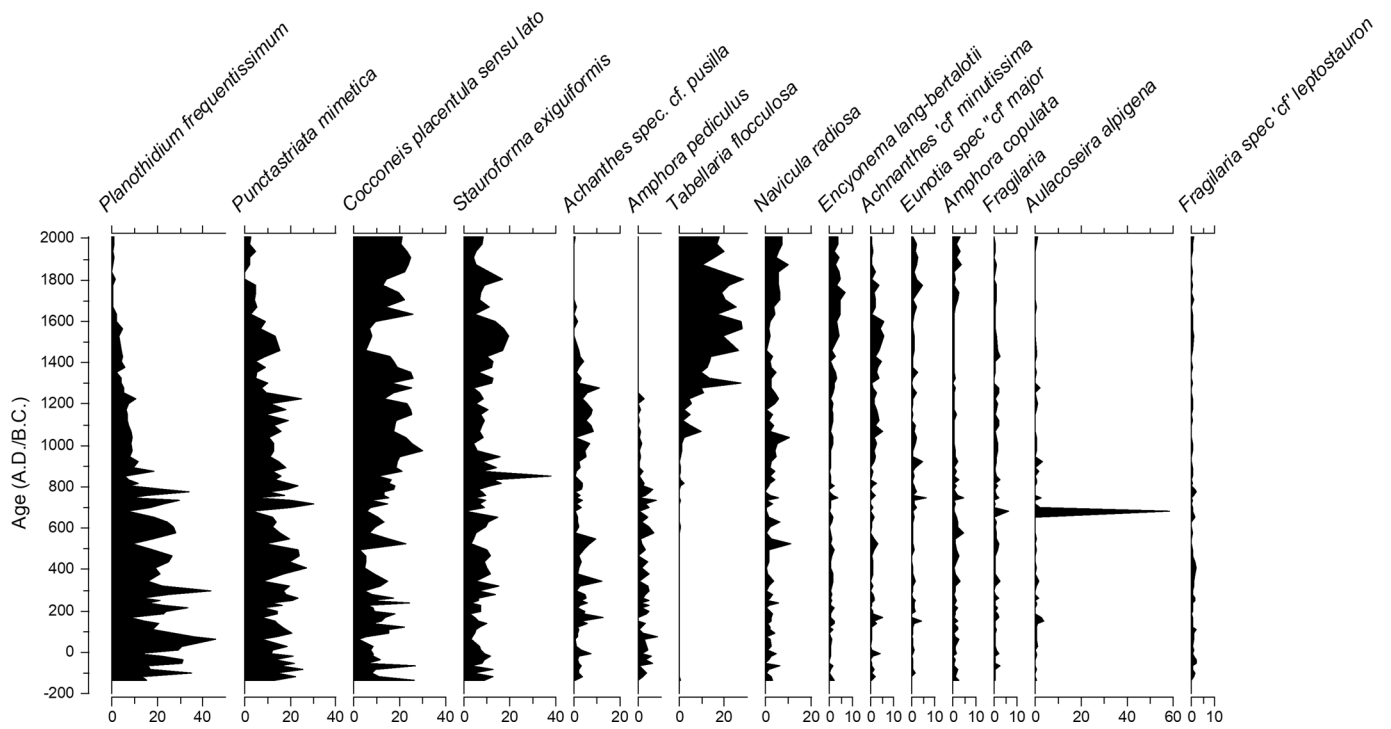


**Extended Data Fig. 1 | Age-depth model of sediments from Laguna de los Condores, Peru.** Age-depth model of sediments from Laguna de los Condores, Peru. The age-depth model was calibrated using  $^{14}\text{C}$  dates (Supplementary Table 1), Bacon<sup>77</sup>, and the IntCal13 calibration curve<sup>79</sup>.



**Extended Data Fig. 2 | CONISS zonation of the fossil pollen data from Laguna de los Condores contrasted with major use characterization of the site.**  
 CONISS zonation of the fossil pollen data from Laguna de los Condores contrasted with major use characterization of the site.





**Extended Data Fig. 3 | Fossil diatom abundances (%) of Laguna de los Condores, Peru.** Fossil diatom abundances (%) of Laguna de los Condores, Peru<sup>86</sup>. Only taxa with a >5% total abundance are shown.

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Data collection	No software was used.
Data analysis	<p>The program 'R' (3.5.2) and its packages 'bacon', 'BChron', and 'vegan' were used for the age-depth model, summed probability density function, and Principal Component Analysis, respectively. The program ImageJ was used to quantify the surface area of charcoal particles. The program Tilia was used to perform a CONISS constrained clustering analysis.</p> <ul style="list-style-type: none"> <li>- R Development Core Team. R. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <a href="http://www.R-project.org">http://www.R-project.org</a> (2018).</li> <li>- Blaauw, M. &amp; Christen, J. A. Flexible paleoclimate age-depth models using an autoregressive gamma process. <i>Bayesian Analysis</i> 6, 457-474 (2011).</li> <li>- Haslett, J. &amp; Parnell, A. A simple monotone process with application to radiocarbon-dated depth chronologies. <i>Journal of the Royal Statistical Society: Series C (Applied Statistics)</i> 57, 399-418 (2008).</li> <li>- Oksanen, J. et al. Package 'vegan'. Community ecology package, version 2, 1-295 (2013).</li> <li>- Rasband, W. S. Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, <a href="http://imagej.nih.gov/ij/">http://imagej.nih.gov/ij/</a>. (1997-2016).</li> <li>- Grimm, E. Tilia software v. 1.7. 16. Illinois State Museum, Springfield (2011).</li> </ul>

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## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	High-resolution fossil pollen, charcoal, loss-on-ignition, diatom, and sediment chemistry data were used to reconstruct changes in landuse and climate from the iconic archaeological setting of Laguna de los Condores, Peru. The study site was situated in a montane-forest setting on the eastern slopes of the Central Andes.
Research sample	Multiple samples at varying depths were analyzed from a lake sediment core retrieved from Laguna de los Condores, Peru. Fossil pollen was used as a proxy for changing vegetation, landuse, deforestation, and forest recovery. Fossil charcoal was used as a proxy for fires. Fossil diatoms provided proxy measures for nutrient inputs to the lake. X-ray fluorescence (XRF) data provide indices of chemical erosion, weathering, and lake productivity. Loss-on-ignition provided measurements of CO <sub>3</sub> . Pollen and diatoms were identified to the highest taxonomic level possible.
Sampling strategy	The sediment chemistry was analyzed in 0.5-cm increments. Charcoal was analyzed continuously in 1-cm increments. Pollen, diatoms, and loss-on-ignition were analyzed in 2-cm increments. Exotic Lycopodium spores were added to allow calculation of pollen concentrations (University of Lund batch #3862, 9666 ± 2123 spores per tablet). A minimum of 300 terrestrial pollen grains were counted in each sample. For diatoms, a minimum of 300 valves were counted in each sample.
Data collection	The sediment core was collected by MBB and BGV. Pollen analysis was performed by CMÅ, diatom analysis was performed by FM-B, charcoal analysis was performed by MB, extended maize counts were performed by C-JF, XRF analysis was performed by LCP, and loss-on-ignition analysis was performed by FM-B. The sediment chemistry was analyzed using an Avaatech XRF (x-ray fluorescence) core scanner. A Zeiss Axioskop photomicroscope at magnifications of ×400 and ×630 was used for pollen analysis and at a magnification of ×1000 for diatom analysis. An Olympus stereoscope at magnifications of ×20 and ×32 was used for charcoal analysis. Pollen and diatoms were identified using the reference collection at Florida Institute of Technology, published materials, and online databases.
Timing and spatial scale	The sediment core was collected in July 2010 and data collection was undertaken throughout 2015-2019.
Data exclusions	All data is recorded in the raw count data.
Reproducibility	Recounts were undertaken in a number of samples to insure no notable differences between data collected.
Randomization	Randomization was not relevant to this study as the individual samples represent the environment at a specific point in time.
Blinding	Blinding was not relevant to this study. The data used were environmental proxies in a sediment record at various periods in time.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

## Field work, collection and transport

Field conditions	Field work was undertaken in a montane-forest setting on the eastern slopes of the Central Andes. The field work location has a mean monthly temperatures range between 15.5 and 17°C with precipitation in excess of 3200–4000 mm.
Location	Laguna de los Condores (6°51'03.02"S, 77°41'43.28"W) is located at 2860 meters above sea level in a deep, forested valley. The lake is c. 2.3 km by 700 m and has a maximum water depth of 60 m. A glacial-aged moraine forms a steep and shaded northern shoreline, while 100 m-high cliffs form the southern shore. The montane forest currently occupies the valley and the north-facing slopes over the crest of the moraine are maintained for grazing.



Access and import/export	Access to Laguna de los Condores was provided by the community of Leymebamba, Peru.
Disturbance	The sediment core was taken from the centre and the deepest point of the lake. All of the equipment used in the extraction of the lake sediments were removed from the site. No plants or animals were disturbed.

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

### Materials & experimental systems

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input type="checkbox"/>	<input checked="" type="checkbox"/> Palaeontology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data

### Methods

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging

## Palaeontology

Specimen provenance	Sediment subsamples containing the extracted fossil palynomorphs (pollen, charcoal, diatoms, sediment chemistry) were collected from lake sediments retrieved from Laguna de los Condores situated near Leymebamba, Peru.
Specimen deposition	Samples and microscope slides are stored and accessible at Florida Institute of Technology in the Institute for Global Ecology.
Dating methods	The chronology of the sediment core from Laguna de los Condores was established on 10 bulk sediment samples and one wood macrofossil sample using $^{14}\text{C}$ accelerator mass spectrometry. An age-depth model was generated using the package 'bacon' in R (3.5.2) and the IntCal13 calibration curve. The result of the radiocarbon dating is shown in Supplementary Table 1 and in Extended Data 1.
<input checked="" type="checkbox"/> Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.	