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Paleoindian settlement of the high-altitude Peruvian Andes

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interspecific hybridization; yet, such "reproductive character displacement" (*4*) seems an unlikely explanation for our results, as *A. carolinensis* and *A. sagrei* already differ markedly in species-recognition characteristics, males of both species nearly exclusively ignore heterospecific females in staged encounters (*25*), and the species have never been reported to successfully produce hybrids. We note, finally, that other mutually negative interactions such as apparent competition (*26*) and intraguild predation (*27*) could also produce divergence among overlapping species. These remain to be explored in this system, though some evidence exists for at least the latter (*17*).

Here, we have provided evidence from a replicated, natural system to support the long-held idea (*4*) that interspecific interactions between closely related species are an important force for evolutionary diversification (*2*). Moreover, we show that evolutionary hypotheses such as character displacement can be rigorously tested in real time following human-caused environmental change. Our results also demonstrate that native species may be able to respond evolutionarily to strong selective forces wrought by invaders. The extent to which the costs of invasions can be mitigated by evolutionary response remains to be determined (*28*), but studies such as this demonstrate the ongoing relevance of evolutionary biology to contemporary environmental issues.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/346/6208/463/suppl/DC1
Materials and Methods
Supplementary Acknowledgments
Figs. S1 and S2
Tables S1 to S7
References (*29*–*45*)

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NEW WORLD ARCHAEOLOGY

Paleoindian settlement of the high-altitude Peruvian Andes

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Study of human adaptation to extreme environments is important for understanding our cultural and genetic capacity for survival. The Pucuncho Basin in the southern Peruvian Andes contains the highest-altitude Pleistocene archaeological sites yet identified in the world, about 900 meters above confidently dated contemporary sites. The Pucuncho workshop site [4355 meters above sea level (masl)] includes two fishtail projectile points, which date to about 12.8 to 11.5 thousand years ago (ka). Cuncaicha rock shelter (4480 masl) has a robust, well-preserved, and well-dated occupation sequence spanning the past 12.4 thousand years (ky), with 21 dates older than 11.5 ka. Our results demonstrate that despite cold temperatures and low-oxygen conditions, hunter-gatherers colonized extreme high-altitude Andean environments in the Terminal Pleistocene, within about 2 ky of the initial entry of humans to South America.

Human settlement of high-altitude mountains and plateaus is among the most recent of our species' biogeographic expansions. Earth's highest-altitude lands, located in the Tibetan and Andean regions, pose numerous physiological challenges, including hypoxia (low-oxygen conditions), high solar radiation, cold temperatures, and high energetic costs of subsistence (*1*). These conditions are especially prevalent in the treeless landscapes higher than 4000 meters above sea level (masl), with little fuel for campfires, twice the sea-level caloric intake needed to maintain normal metabolic function (*2*), and O_2 partial pressure less than 60% that at sea level (*1*). Current archaeological models (*3*) emphasize these challenges to explain a lack of pre-Holocene [>11.5 thousand years ago (ka)] (*4*) archaeological evidence above 4000 masl on the Tibetan (*5*) and Andean (*6*) Plateaus.

In the Andes, human biogeographic expansion to high-altitude lands likely stemmed from adjacent areas in Peru (*6*), Chile (*7*), and Argentina (*8*) (Fig. 1A). By ~13.5 to 12.1 ka or earlier, foragers had settled the Pacific Coast (*9*–*13*) and the Southern Cone (*14*), and by ~12.7 to 11.3 ka groups occupied caves at ~2600 masl in central Peru (*15*, *16*) and up to 3300 masl in the Atacama Desert of northern Chile (*17*, *18*). In northwest Argentina, multiple sites at 3400 to 3800 masl date to ~12.0 ka, possibly as early as ~12.8 ka (*8*), although most pre-Holocene occupations have only single, unreplicated radiocarbon ages. Above 4000 masl, the earliest known Andean sites (table S1) date from the first millennium of the Holocene (*19*), with widespread occupation after ~9 ka (*6*–*8*) and earliest year-round settlement after ~7.1 ka (*20*).

Whether genetic adaptations or environmental amelioration were necessary for high-altitude

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human settlement remains poorly understood. High-altitude regions are among the most remote and least archaeologically studied lands on the planet. Here, we report initial data from Terminal Pleistocene archaeological sites at nearly 4500 masl in the Peruvian Andes, the highest Pleistocene sites yet identified anywhere in the world. These sites extend the residence time of humans above 4000 masl by nearly a millennium, implying more moderate late-glacial Andean environments and greater physiological capabilities for Pleistocene humans than previously assumed.

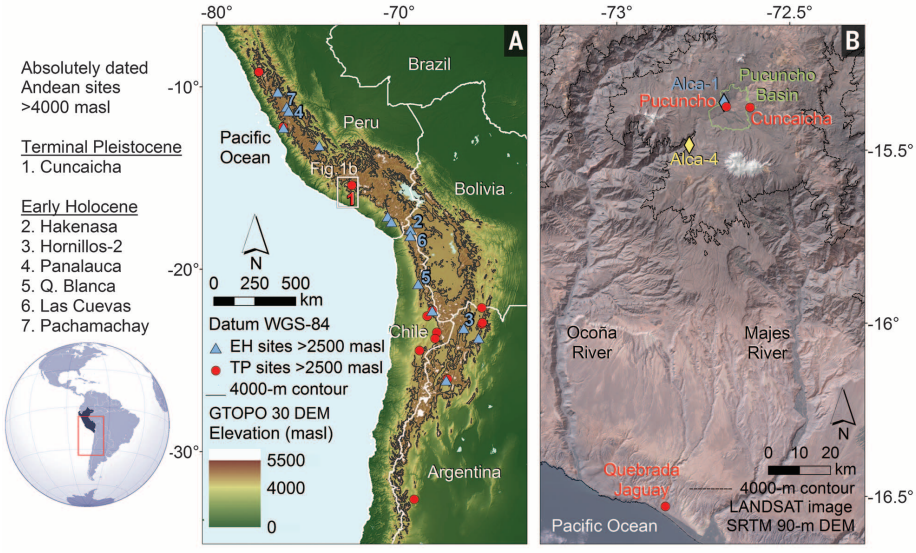

Fig. 1. Project area maps. (**A**) Andes showing Terminal Pleistocene and Early Holocene sites >2500 masl and >4000 masl (also see table S1). (**B**) Study area.

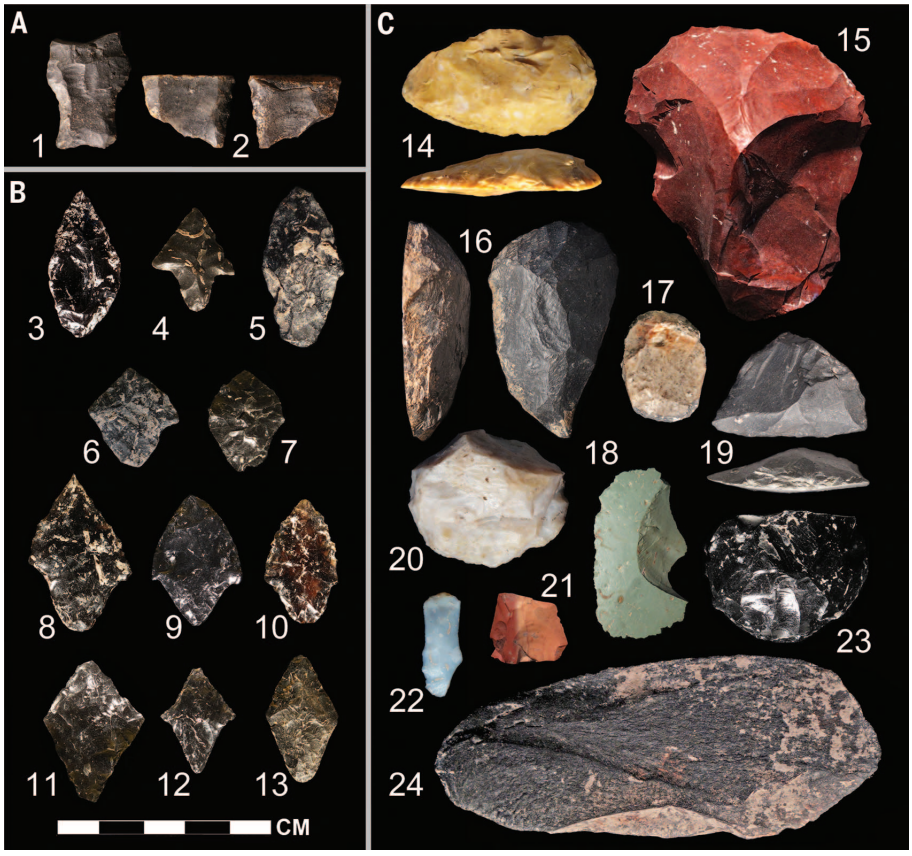

Fig. 2. Terminal Pleistocene lithic artifacts. From (**A**) Pucuncho workshop (1 and 2) and (**B** and **C**) Cuncaicha rock shelter (3 to 24) (also see table S4). (B) Projectile points (3 to 13) illustrated in stratigraphic order. (C) Selected tools and debitage (14 to 24) illustrating diverse forms and raw materials.

We discovered the Pucuncho and Cuncaicha archaeological sites (Fig. 1B and fig. S1) after mapping of the Alca obsidian source (*21*), predictive modeling (*22*), and systematic reconnaissance of the volcanic plateau bounded by the Cotahuasi and Colca canyons of southern Peru (*23*). In the heart of this plateau, the 132-km^2 Pucuncho Basin contains grassland and wetland habitats and thousands of domesticated camelids. The modern annual mean temperature at Pucuncho is 3°C, and prevailing easterly airflow maintains a semiarid climate, with 600 to 800 mm of annual precipitation primarily during the December to March wet season (*24*).

The Pucuncho open-air workshop site (4355 masl) on the basin's west edge was situated to exploit Alca-1 and Alca-5 obsidian pyroclasts eroding from an alluvial fan. The workshop includes debitage and 260 formal tools, including projectile points and nondiagnostic bifaces, unifacial scrapers, and other tools. Two fluted fishtail projectile point bases made of local fine-grained andesite and Alca-5 obsidian (Fig. 2A) are diagnostic to ~12.8 to 11.5 ka (*25*); the Pucuncho fishtails are the highest fluted points yet discovered in the Americas. Pucuncho likely provided the Alca-1 obsidian in contexts dated ~13.4 to 10.2 ka at Quebrada Jaguay, a Terminal Pleistocene fishing settlement ~150 km south on the Pacific Coast (*9*) (Fig. 1B). Because no geologic mechanism can transport Alca-1 obsidian to the coast, Quebrada Jaguay's inhabitants either visited the source or obtained obsidian via exchange.

Seven km east of the Pucuncho site, the Cuncaicha workshop site (4445 masl) occupies an alluvial fan where Alca-5 and Alca-7 obsidian pyroclasts crop out. This surface palimpsest contains debitage and more than 500 projectile points and nondiagnostic bifaces, scrapers, and other unifacial tools, representing thousands of years of episodic occupation. Above the alluvial fan is Cuncaicha rock shelter (4480 masl), comprising two north-facing alcoves formed by slab exfoliation of the andesite bedrock. Both alcoves exhibit sooted ceilings, rock art, and anthropogenic floor sediments, indicating use as campsites. The rock shelter is protected from westerly winds and offers a commanding view of wetland and grassland habitats.

Our investigations at Cuncaicha rock shelter sampled the minimum volume needed to document the stratigraphy and establish a precise absolute chronology of occupation. Ground-penetrating radar revealed collapsed roof slabs and depth of sediments to bedrock, allowing targeted excavations. Sediments are ~1.2 m deep, both within the shelter and outside the drip line over ~150 m^2. We excavated 5.5 m^2 (<4%) of these deposits in 2010 and 2012 (fig. S2).

We dated the Cuncaicha sequence using large-mammal bone specimens in direct association with abundant, unequivocal artifacts. Faunal and other organic remains exhibit outstanding preservation in this cold, dry setting. Moreover, dating large bone specimens avoided the risk of sampling remains vertically translocated by rodent bioturbation, a process shown to affect Andean rock

shelters elsewhere (*15*). Geoarchaeological analysis indicates only small-scale cryo- and bioturbation of deposits (*26*) (fig. S4).

We obtained 35 accelerator mass spectrometry (AMS) ages at three laboratories using distinct pretreatment protocols on bone collagen (*26*) (table S2). Dates on split samples at multiple laboratories are statistically indistinguishable. The AMS-dated bone specimens are in correct stratigraphic order, without reversals. Cuncaicha rock shelter contains occupation components corresponding with five distinct strata (fig. S3). Hiatuses correspond with clear stratigraphic signatures and are well constrained with AMS ages (Table 1 and table S2).

Feature 12-4 (an organic-rich pit containing artifacts) yielded the oldest reproduced ages, ~12.4 to 11.8 ka (n = 2 AMS ages). Stratum 5 is composed largely of carbonates, likely derived from anthropogenic burning of plants, including the local, resinous *Azorella compacta* (*26*) (fig. S5). Terminal Pleistocene-age deposits lack visible stratigraphic divisions. We grouped and averaged AMS ages by excavation level (Table 1). The positive age-depth relationship (Fig. 3) suggests episodic deposition ~12.4 to 11.4 ka (n = 19 AMS ages). The upper contact of stratum 5 is sharp and distinct, likely formed during an occupation hiatus ~11.4 to 9.5 ka. Stratum 4 corresponds to a brief, robust Early Holocene occupation ~9.5 to 9.3 ka (n = 6 AMS ages), followed by a ~3.6 thousand year (ky) mid-Holocene hiatus. Stratum 3 includes distinct late-Middle Holocene occupations dated ~5.7 to 5.5 ka (n = 3 AMS ages) and ~5.5 to 5.1 ka (n = 3 AMS ages). Strata 1 and 2 represent brief, episodic uses of the shelter within the past ~2.2 ky (n = 2 AMS ages) (table S2).

Cuncaicha contains a rich assemblage of ceramics; chipped-stone tools, cores, and debitage; faunal material; bone beads and quartz crystals; and fragments of red ochre (table S3). Ceramics, which locally date <4 ka (*27*), were found only in Late Holocene strata 1 and 2. Temporal affiliations for the 153 projectile points found throughout the stratigraphy (*23*, *28*) are consistent with the AMS chronology. A complete lithic operational chain is present at Cuncaicha shelter and the workshop below. Most lithic tools and debitage at Cuncaicha are made from locally available Alca-1, -5, and -7 obsidian, andesite, and jasper. Lithic tools indicate hunting and butchering activities, consistent with the limited subsistence options on the plateau.

The inhabitants of Cuncaicha hunted vicuña (*Vicugna vicugna mensalis*), guanaco (*Lama guanaco*), and taruka (*Hippocamelus antisensis*) (tables S5 and S6). Preliminary analysis of camelid age profiles suggests predation at the end of the rainy season when vicuña are born (March and April) and possibly during the dry season (May to November) when vicuña bands aggregate (*29*). The even representation of mammal fore- and hindlimb elements indicates dismembering of whole carcasses at the shelter. First and second phalanges are abundant, and the skinning of animals to the toes attests to careful processing of all animal foods, including meat and fat within the bone.

We recovered small, fragmented charred plant remains from sediments (*26*). Most abundant are woody twigs, stems, and root wood, consistent with burning small shrubs and *Azorella compacta*. Also present are charred fragments of parenchymous storage tissue (fig. S6). Their vitreous appearance indicates that these are starchy roots and/or tubers (*30*), likely gathered from lower elevations and brought to the site for consumption (*26*).

Cuncaicha is ~40 to 50 km from elevations ≤2500 masl, so it is unlikely that the site was merely a logistical station for the collection and processing of lithic material, meat, and hides for transport to low-elevation base camps. Together, the quantity and diversity of early tool types; the emphasis on local lithic materials, animals, and combustible fuel; the presence of starchy roots and/or tubers; and the location in the heart of the plateau suggest that Cuncaicha was a base camp.

The Pucuncho Basin constituted a high-altitude oasis ideal for a specialized hunting (and later, herding) adaptation. Vicuña births coinciding with the end of the wet season and maintenance of permanent territories by vicuña bands (*29*) would have permitted predictable scheduling of subsistence activities and year-round plateau residence (*31*). However, wet-season storms and the risk of hypothermia, as well as maintenance of extended

Table 1. Average AMS ages from Cuncaicha rock shelter. Component abbreviations: LMH, Late-Middle Holocene; EH, Early Holocene; TP, Terminal Pleistocene. Two Late Holocene AMS ages were not averaged and are reported in table S2. Stratigraphic abbreviations: L, Level; F, Feature. CALIB 7.0.0 (*39*) reports the test statistic T for a series of uncalibrated ^{14}C ages from the same stratigraphic context (n) having a X^2 distribution with $n - 1$ degrees of freedom (df) under the null hypothesis of no difference with respect to a threshold of $\alpha = 0.05$ (*40*). Weighted means were calculated for statistically indistinguishable groups of stratigraphically equivalent ages and calibrated using SHCal13 (*41*). ^{14}C yr B.P., radiocarbon years before the present. 68%/95% cal B.P., 68% and 95% probability age range in calendar years before the present.

Component	Context	*n*	df	*T*	0.05	^{14}C yr B.P.	68% cal B.P.	95% cal B.P.
LMH-II	30–33 cm	3	2	1.2	6.0	4614 ± 36	5446–5302	5466–5088
LMH-I	40–45 cm	3	2	0.8	6.0	4867 ± 37	5644–5586	5660–5484
EH	50–62 cm	6	5	2.0	11.1	8420 ± 34	9486–9432	9525–9324
TP	L.8-8b, 77–79 cm	3	2	0.5	6.0	10,074 ± 57	11,764–11,406	11,964–11,346
TP	L.9, 79–83 cm	3	2	0.2	6.0	10,073 ± 49	11,760–11,408	11,958–11,357
TP	L.11, 90–98 cm	2	1	0.1	3.8	10,182 ± 50	11,982–11,769	12,067–11,641
TP	L.12, 98–108 cm	2	1	0.8	3.8	10,191 ± 32	11,980–11,822	12,036–11,761
TP	L.13, 108–115 cm	7	6	7.8	12.6	10,228 ± 18	11,953–11,809	12,004–11,759
TP	F.12-4 base	2	1	0.2	3.8	10,345 ± 71	12,386–11,953	12,411–11,822

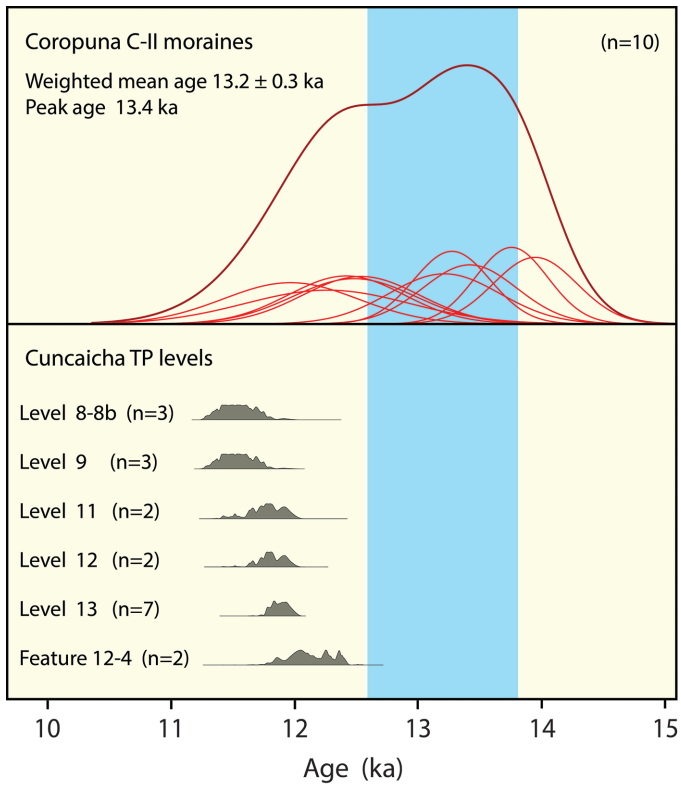

Fig. 3. Nevado Coropuna ^{3}He ages from C-II moraines and average AMS ages from Cuncaicha rock shelter Terminal Pleistocene levels. Blue bar shows 95% range of C-II weighted mean age.

social networks and collection of edible plant resources, may have encouraged regular descents to lower elevations.

Lithic tools and debitage of nonlocal fine-grained rocks, some with stream-polished cortex (Fig. 2C), suggest that Terminal Pleistocene and Early Holocene plateau residents ventured periodically to high-energy rivers below the plateau. Formal tools of Alca-4 obsidian at Cuncaicha originated in outcrops near the plateau edge ~22 km southwest (*21*) (Fig. 1B). Contemporary sites at Quebrada Jaguay on the Pacific Coast contain Alca-1, -4, and -5 obsidian tools and debitage (*9*, *23*); the only source of these three obsidians is the Pucuncho Basin and surrounding plateau (*21*). The oldest dates at Quebrada Jaguay and Cuncaicha overlap at two standard deviations. These sites likely constitute end members in a coast-highland Paleoindian settlement system.

Pleistocene glaciers did not present a barrier to human migration and settlement of the Pucuncho Basin. Glacial-geologic records from adjacent Nevado Coropuna (*32*) suggest that local glaciers reached their late-Pleistocene maxima ~25 to 20 ka and even then did not encroach into the basin. After a relatively minor readvance ~13.4 ka (*26*) (Fig. 3 and table S7), glaciers again receded. Southward displacement of the intertropical convergence zone ~13.0 to 11.5 ka (*33*) probably resulted in increased wet-season precipitation. The arrival of humans to the Pucuncho Basin coincided with a period of warming climate and enhanced primary productivity in plateau habitats.

Our data do not support previous hypotheses, which suggested that climatic amelioration and a lengthy period of human adaptation were necessary for successful human colonization of the high Andes. The Pucuncho Basin sites postdate the oldest known South American lowland site, Monte Verde (*13*), by only ~2 ky. Because early settlement of high-altitude regions is understudied, additional Terminal Pleistocene sites above 4000 masl likely await discovery. The Pucuncho Basin sites suggest that Pleistocene humans lived successfully at extreme high altitude, initiating organismal selection (*34*), developmental functional adaptations (*35*), and lasting biogeographic expansion in the Andes. As new studies (*36*–*38*) identify potential genetic signatures of high-altitude adaptation in modern Andean populations, comparative genomic, physiologic, and archaeological research will be needed to understand when and how these adaptations evolved.

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SUPPLEMENTARY MATERIALS

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PLANT SCIENCE

Antheridiogen determines sex in ferns via a spatiotemporally split gibberellin synthesis pathway

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Some ferns possess the ability to control their sex ratio to maintain genetic variation in their colony with the aid of antheridiogen pheromones, antheridium (male organ)–inducing compounds that are related to gibberellin. We determined that ferns have evolved an antheridiogen-mediated communication system to produce males by modifying the gibberellin biosynthetic pathway, which is split between two individuals of different developmental stages in the colony. Antheridiogen acts as a bridge between them because it is more readily taken up by prothalli than bioactive gibberellin. The pathway initiates in early-maturing prothalli (gametophytes) within a colony, which produce antheridiogens and secrete them into the environment. After the secreted antheridiogen is absorbed by neighboring late-maturing prothalli, it is modified in to bioactive gibberellin to trigger male organ formation.

Genetic diversity affords a competitive advantage to a particular species. Homosporous ferns have evolved a mechanism to favor cross-fertilization by controlling the sex ratio among individuals or prothalli within the population with the aid of antheridiogens. Antheridiogens are pheromones released in the aqueous environment by early-maturing fern prothalli in a colony, and they cause neighboring late-maturing prothalli in the colony to