

Holocene Vegetation History from Fossil Rodent Middens near Arequipa, Peru

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Rodent (*Abrocoma*, *Lagidium*, *Phyllotis*) middens collected from 2350 to 2750 m elevation near Arequipa, Peru (16°S), provide an ~9600-yr vegetation history of the northern Atacama Desert, based on identification of >50 species of plant macrofossils. These midden florae show considerable stability throughout the Holocene, with slightly more mesophytic plant assemblages in the middle Holocene. Unlike the southwestern United States, rodent middens of mid-Holocene age are common. In the Arequipa area, the midden record does not reflect any effects of a mid-Holocene mega drought proposed from the extreme lowstand (100 m below modern levels, >6000 to 3500 yr B.P.) of Lake Titicaca, only 200 km east of Arequipa. This is perhaps not surprising, given other evidence for wetter summers on the Pacific slope of the Andes during the middle Holocene as well as the poor correlation of summer rainfall among modern weather stations in the central Andes-Atacama Desert. The apparent difference in paleoclimatic reconstructions suggests that it is premature to relate changes observed during the Holocene to changes in El Niño Southern Oscillation modes. © 2001 University of Washington.

Key Words: paleovegetation; Holocene; Atacama Desert.

INTRODUCTION

Paleoclimatic records from the central Andes and Atacama Desert are vital to understanding the history of the South American summer monsoon (SASM), and hence the role of the tropics in South American climate variability. The northern Atacama Desert in southern Peru, downwind of key paleorecords such as sediment records from Lake Titicaca (Wirmann and De Oliveira, 1987; Cross *et al.*, 2000; Rowe *et al.*, in press) and ice core records from Nevado Sajama (Thompson *et al.*, 1998) and at the southern end of the tropical rainfall belt, is especially well situated for such investigations. To date, paleoclimate records from high-altitude lakes, salt lake basins (salars), glacial landforms, ice cores, and alluvial and wetland deposits have provided data on the hydrologic history of the central Andes. Very little is known, however, about the vegetation history of the central Andes south of Lago Junín (11°S, Hansen *et al.*, 1994), with the exception of palynological studies at Lake Titicaca (Ybert, 1992) and Laguna Seca (Baied and Wheeler, 1993). Here, we report on rich plant macrofossil assemblages from fossil rodent middens near Arequipa, the first such midden study in Peru.

As in western North America and other arid regions of the world (Betancourt *et al.*, 1990), rodent middens are abundantly preserved in rock crevices and shelters of the Atacama Desert (Betancourt *et al.*, 2000b). Radiocarbon chronologies from terrestrial plant material in middens are unaffected by reservoir effects that typically afflict lacustrine studies in the central Andes. These deposits also provide higher taxonomic and spatial resolution than other paleobotanical records but are stratigraphically discontinuous, thus representing only “snapshots” of floral assemblages through time. The excellent preservation of plant remains affords high taxonomic resolution, thus also providing an opportunity for biogeographic inferences at the species level, and possibly to the genome level with current advances in molecular biology.

In southern Peru, rodent middens akin to North American packrat middens are made by *Lagidium peruanum* (Mountain Viscacha: CHINCHILLIDAE), *Abrocoma cinerea* (ABROCOMDAE), and several species of *Phyllotis* (Lear-eared mice: CRICETIDAE) including *P. xanthopygus*, *P. limatus*, and *P. magister* (Steppan, 1998). The large *L. peruanum*, weighing 900–1600 g, normally inhabits dry, rocky areas between ~3000 and 5000 m (spotted as low as 2500 m during our field season), has a foraging range of 75 m, and eats most plant species growing within its range (Pearson and Ralph, 1978). *Phyllotis* (20–100 g) live in rocky or brushy habitats between 0 and 5000 m and have foraging ranges of ~35–70 m (Pearson and Ralph, 1978). Like *Lagidium*, *Phyllotis* has a varied diet consisting of grasses, forbs, seeds, and insects (Pizzimenti and De Salle, 1980). Generalized diets, along with the collection of plant materials for nest and den construction, ensure that midden assemblages are fairly representative of hillslope vegetation within the foraging ranges of the animals.

STUDY AREA

The study area is located at intermediate elevations on the Pacific slope of the Cordillera Occidental of the Andes, near the city of Arequipa (2350 m) and within 100 km of the sea (Figs. 1 and 2). Elevation increases rapidly to more than 4000 m to the north and northeast within the 30 km² study area. The area is underlain by Cretaceous and Tertiary igneous intrusive rocks and marine sediments, Tertiary and Quaternary volcanic rocks (primarily ignimbrites), and Quaternary eolian and alluvial sediments. Several volcanoes rising more than 6000 m punctuate the landscape.

Precipitation in the northern Atacama (15°–24°S) occurs primarily during the austral summer and corresponds to the seasonal development of the SASM. During summer, the Intertropical Convergence Zone (ITCZ) migrates southward following the thermal equator, and deep convective heating occurs over the Amazon Basin. A thermally induced low in the lower troposphere intensifies the moisture-laden easterly trade winds, which cross the equator, develop a north–northwesterly flow along the eastern slope of the Andes, and turn cyclonically over

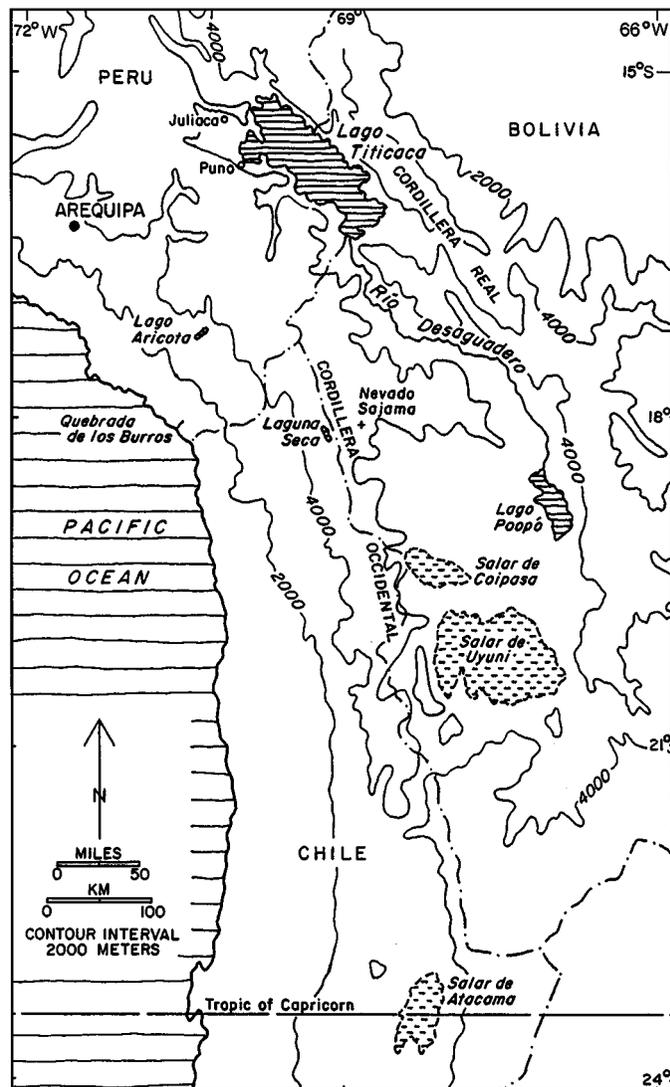


FIG. 1. Map of the subtropical Andes with the location of Arequipa and other study sites mentioned in the text.

the Gran Chaco from 20° to 30°S (Zhou and Lau, 1998). The Bolivian High, an upper tropospheric anticyclone, develops over the Bolivian Altiplano as a result of latent heat released by the convective activity in the Amazon, Central Andes, and South Atlantic Convergence Zone (SACZ; Lenters and Cook, 1997). Interannual variability in summer precipitation is partly influenced by El Niño Southern Oscillation (ENSO) and the strength and position of the Bolivian High and SACZ (Lenters and Cook, 1999). By contrast, rainfall in the southern Atacama (25°–30°S) occurs primarily during winter when weakening of the southeast Pacific anticyclone allows polar fronts and cutoff low-pressure cells to penetrate northward (Miller, 1976).

Arequipa receives an annual average of 100 mm of precipitation. Seasonal and interannual variability is evident in a three-dimensional graph of historical monthly precipitation for Arequipa constructed from Global Historical Climatology Network

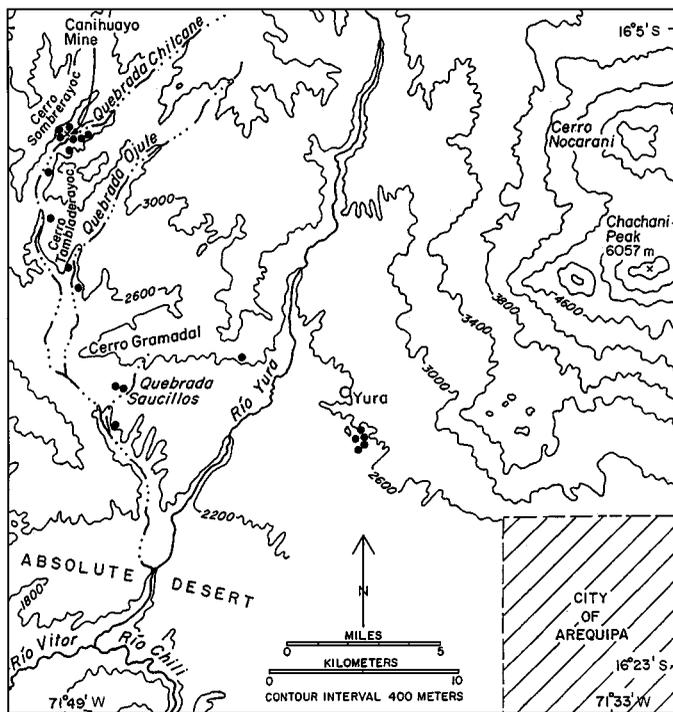


FIG. 2. Map of the study area northwest of Arequipa, Peru. Circles indicate midden locations.

(GHCN; <http://ncdc.noaa.gov/ghcn/ghcn.SELECT.html>) data (Fig. 3). Most of the region's moisture originates from SASM storms spilling over the Andes between December and March (percentage of mean annual rainfall is 80% at 4495 m and 91% at 2150 m). The lower percentage of precipitation occurring between December and March at higher elevations is due to an extension of the summer rainy season into November and April. If these months are included, >90% of mean annual precipitation falls during the summer at all sites. An exception is the brief period in the 1950s and 1960s when significant amounts of win-

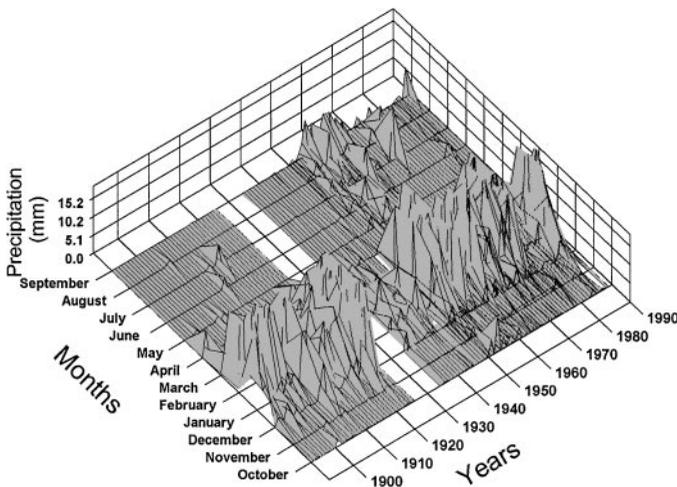


FIG. 3. Three-dimensional graph of monthly precipitation for Arequipa. White strip in center of graph reflects years for which no data were available.

ter precipitation occurred in Arequipa. This precipitation also appears to have originated primarily from the Amazon Basin, with the largest winter rainfall events in Arequipa corresponding to large peaks in monthly precipitation at one or more Altiplano stations (La Paz, Juliaca, Cuzco, Puno). Precipitation gradients with elevation are primarily a function of distance from the Andean crest. This is due to a lack of rising air masses on the Pacific slope of the Andes, while the few depleted orographic storms that cross the Andes rain out at high elevations, creating a steep decrease in precipitation with decreasing elevation. For every ~100-m decrease in elevation there is a 26-mm decrease in precipitation [$y = 3.8225x + 2343$ ($r^2 = 0.94$, $p < 0.01$)]. Vegetation in the area is primarily limited by precipitation, and plant communities change rapidly along the steep elevation–precipitation gradient. Vegetation classification and characteristic species follow Linares (1996). A list of plant taxa and families appears in Table 1.

Below ~2400 m the hyperarid “Absolute Desert” is marked by the near absence of vegetation. Matorral Desert with columnar cacti occurs between 2400 and 2800 m. Xerophytic shrubs (*Ambrosia fruticosa*, *Gochmatia arequipensis*, *Encelia canescens*, *Balbisia weberbaueri*, *Krameria lappaceae*), columnar cacti (several species of *Corryocactus*, *Oreocereus*, *Haageocereus*, and *Weberbauerocereus*), and small herbs and grasses (*Monnina ramosa*, *Mastigostila* sp., *Eragrostis peruviana*, *Urocarpidium sephardae*, and *Spergularia stenocarpa*) characterize this community. Between 2800 and 3300 m, vegetation consists of Matorral (shrubland) Desert with columnar cacti and Pajonal. This community contains the shrubs *Tarasa operculata*, *Diplostephium tacorense*, and *Adesmia spinosissima* in addition to a mixture of species from the Matorral Desert and Pajonal (grassland). The Pajonal, a high-altitude grassland found between 3300 and 4000 m, is characterized by *Stipa obtusa*, *Baccharis*, *Parastrephia*, *Tetraglochin strictum*, *Plantago monticola*, *Urocarpidium sephardae*, and *Cardionema ramossissima*. Between 4000 and 4300 m the bunch grasses *Festuca orthophylla* and *Stipa ichu* dominate the Pajonal–Pastizal vegetative community. The Pajonal–Pastizal gives way to Tolar–Pajonal above 4300 m. The vegetation in this zone includes *Stipa ichu*, *Calamagrostis*, and spiny shrubs known as Tolar with species in the genera *Parastrephia*, *Senecio*, *Baccharis*, and *Tetraglochin*. Finally, above 4500 m dispersed cushion plants (*Azorella compacta*), grasses (*Stipa*, *Festuca*, *Calamagrostis*), and shrubs (*Parastrephia* and *Senecio*) form the Almohadillada–Caespitosa community.

METHODS

Fifty-nine rodent middens were collected within a 30-km² area northwest of Arequipa, Peru (Table 2). Middens were collected from 2350 to 2600 m and 2600 to 2750 m (Matorral Desert) and processed and analyzed according to well-established procedures (Spaulding *et al.*, 1990). Macrofossil abundances were quantified on a relative scale of 1 to 5. Plant reference materials used to identify midden taxa were collected

TABLE 1
List of Plant Taxa and Families Mentioned in Text

Aizoaceae	Caryophyllaceae	Poaceae
<i>Tetragonia</i> sp.	<i>Cardionema ramosissima</i>	<i>Andropogon flavescens</i>
Anacardiaceae	<i>Spergularia stenocarpa</i>	<i>Aristida peruviana</i>
<i>Schinus molle</i>	Chenopodiaceae	<i>Bouteloua simplex</i>
Apiaceae	<i>Atriplex</i> sp.	<i>Bromus trinitii</i>
<i>Azorella compacta</i>	<i>Chenopodium</i> sp.	<i>Calamagrostis</i> sp.
Asteraceae	Cyperaceae	<i>Enneapogon desvauxii</i>
<i>Ambrosia fruticosa</i>	Cyperaceae	<i>Nassella pubiflora</i>
<i>Baccharis</i> sp.	Ephedraceae	<i>Munroa decumbens</i>
<i>Bidens</i> sp.	<i>Ephedra americana</i>	<i>Poa</i> sp.
<i>Chuquiraga</i> sp.	Fabaceae	<i>Eragrostis peruviana</i>
<i>Diplosteghium</i>	<i>Adesmia spinosissima</i>	<i>Festuca orthophylla</i>
<i>tacorense</i>	<i>Adesmia</i> sp.	<i>Stipa ichu</i>
<i>Encelia canescens</i>	<i>Crotalaria incana</i> var.	<i>Stipa annua</i>
<i>Galinsoga</i> cf.	<i>incana</i>	<i>Stipa macbridei</i>
<i>parviflora</i>	cf. <i>Hoffmannseggia</i> sp.	<i>Stipa obtusa</i>
<i>Gochmatia arequipensis</i>	<i>Lupinus</i> sp.	<i>Stipa</i> sp.
<i>Grindelia</i> sp.	Geraniaceae	Polygalaceae
<i>Parastrephia</i> sp.	<i>Balbisia weberbaueri</i>	<i>Monnina ramosa</i>
<i>Senecio</i> sp.	Hydrophyllaceae	Polygonaceae
<i>Tagetes multiflora</i>	<i>Nama dichotomum</i>	<i>Chorizanthe</i> sp.
Boraginaceae	<i>Phacelia</i> sp.	Portulacaceae
<i>Cryptantha</i> sp.	Iridaceae	<i>Calendrinia</i> sp.
<i>Pectocarya laterifolia</i>	<i>Mastigostila</i> sp.	<i>Cistanthes</i> sp.
<i>Tiquilia</i> sp.	Krameriaceae	Rosaceae
Brassicaceae	<i>Krameria lappaceae</i>	<i>Tetraglochin strictum</i>
<i>Descuriana</i> sp.	Malvaceae	Rubiaceae
<i>Lepidium</i> sp.	<i>Cristaria</i> sp.	<i>Galium</i> cf. <i>aparine</i>
<i>Sisymbrium</i> sp.	<i>Tarasa operculata</i>	Scrophulariaceae
Bromeliaceae	<i>Urocarpidium sephardae</i>	<i>Castilleja</i> sp.
<i>Tillandsia</i> sp.	<i>Urocarpidium</i> sp.	Solanaceae
Cactaceae	Nyctaginaceae	<i>Lycopersicon</i> sp.
<i>Arequipa hempeliana</i>	<i>Allionia incarnata</i>	<i>Solanum</i> sp.
<i>Corryocactus</i> cf.	<i>Mirabilis</i> sp.	Urticaceae
<i>brevistylus</i>	Plantaginaceae	<i>Parietaria debilis</i>
<i>Erdisia meyenii</i>	<i>Plantago monticola</i>	
<i>Haageocereus</i> sp.	<i>Plantago</i> sp.	
<i>Neoraimondia</i>		
<i>arequipensis</i>		
<i>Opuntia sphaerica</i>		
<i>Opuntia ignescens</i>		
<i>Oreocereus</i> sp.		
<i>Weberbauerocereus</i> sp.		

Atacama. More than 50 taxa from 23 families were identified, comparable in taxonomic resolution to recent packrat midden studies in North America (e.g., Betancourt *et al.*, 2000a). The relative abundances of macrofossils from the middens (after Spaulding *et al.*, 1990) are shown in Figure 4. The sites are divided into elevations above and below 2600 m. This division corresponds to a transition within present Matorral Desert, with vegetation above ~2600 m characterized by a noticeable increase in plant cover, especially large shrubs.

Several patterns characterize the vegetation history of both the lower and higher elevation sites. Most notable is the stability and dominance of cacti throughout the Holocene, especially *Corryocactus* cf. *brevistylus*, *Opuntia sphaerica*, *Arequipa hempeliana*, and the *Cereus* cacti (*Weberbauerocereus*, *Oreocereus*, and *Haageocereus* were indistinguishable in midden materials). *Pectocarya laterifolia*, *Plantago* sp., *Solanum* sp., and *Tagetes multiflora*, are also persistent and abundant in the midden record at all elevations. In addition, many species occur only during the periods where middens are clustered, from 0 to 1000 cal yr B.P. and 2800 to 9560 cal yr B.P. These include annuals (*Castilleja* sp., *Cryptantha* sp., *Galinsoga* cf. *parviflora*, *Lepidium* sp., *Monnina ramosa*, *Parietaria debilis*, *Sisymbrium* sp.), small cacti (*Erdisia meyenii*, *Opuntia ignescens*), C₄ annual grasses (*Bouteloua simplex*, *Munroa decumbens*, *Stipa ichu*), and perennials (*Allionia incarnata*, *Baccharis* sp., *Chorizanthe* sp., *Encelia canescens*, *Crotalaria incana* var. *incana*, *Grindelia* sp., *Phacelia* sp., and *Tillandsia* sp.).

At the lower-elevation sites, vegetation changes noticeably around 2800 cal yr B.P. with the disappearance or increased rarity of *Galium* cf. *aparine*, *Urocarpidium* sp., *Allionia incarnata*, *Chenopodium* sp., *Chorizanthe* sp., *Lycopersicon* sp., *Tetragonia* sp., *Bromus trinitii*, and *Mirabilis* sp. All of these species, however, persisted at higher elevation sites except for *Allionia incarnata*, *Chorizanthe* sp., and *Mirabilis* sp., which are rare or absent above 2600 m during the entire Holocene. At or shortly after 2800 cal yr B.P., *Tiquilia* sp., *Munroa decumbens*, *Stipa annua*, and *Ephedra americana* first appear, while *Opuntia sphaerica*, *Tarasa operculata*, *Enneapogon desvauxii*, and *Krameria lappaceae* increase markedly in abundance. *Ambrosia fruticosa* and *Atriplex* sp. are present and abundant throughout the Holocene at these sites.

Vegetation at higher elevation sites appears more stable than at the lower sites. Here, *Galium* cf. *aparine*, *Lycopersicon* sp., *Calandrinia* sp., *Chenopodium* sp., *Tagetes multiflora*, *Urocarpidium* sp., and *Bromus trinitii* all persist during the Holocene. However, a lack of middens between 3380 and 670 cal yr B.P. from higher sites makes it impossible to assess whether vegetation remained stable or experienced change comparable to the lower elevation sites during this period. One noticeable occurrence at higher elevation sites is the appearance of *Stipa ichu* and *Opuntia ignescens* during the mid-Holocene around 5000–4500 cal yr B.P. Both of these species are characteristic of higher elevations and represent the largest shifts in species distributions (450 m and 750 m, respectively) in our study.

from field sites and from the herbarium at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos in Lima, Peru. Plants presently growing within 100 m of the midden sites were identified in the field or collected and later identified at the Museo de Historia Natural. Calib 4.0 (Stuiver and Reimer, 1993) was used to correct for ¹³C fractionation and convert all corrected dates to calibrated ages.

RESULTS

Radiocarbon dates from 38 middens provide a record of vegetation history in southern Peru spanning ~9600 cal yr B.P. (Table 2). The macrofossil record from the rodent middens provides one of the first paleovegetation records from the northern

TABLE 2
Radiocarbon Dates and Locations of Rodent Middens

Midden Designation	Material dated	¹⁴ C age (yr B.P.)	SD	δ ¹³ C (‰)	Calibrated (2σ) age range (yr B.P.)	Lab No.	Latitude (°S)	Longitude (°W)	Elevation (m)	Slope aspect	Rock type	Vertebrates
Canihuayo Mine 739A	grass stems	6980	70	-18.5	7926-7590	AA34544	16°08'	71°49'	2850	W	LS	Thpa, Abci, Phli, TR
Canihuayo Mine 739B	fecal pellets	3240	80	-23.5	3625-3172	GX25846	16°08'	71°49'	2850	W	LS	Phli
Canihuayo Mine 739C	fecal pellets	6870	100	-22.7	7820-7476	AA34598	16°08'	71°49'	2850	W	LS	UR
Cerro Gramadal 735	fecal pellets	815	45	-20.9	773-571	AA34596	16°14.601'	71°43.569'	2515	SW	SS	UR
Cerro Sombreyoc 771B	fecal pellets	150	40	-25.8	270-0	GX26355	16°07.662'	71°49.084'	2750	NNE	LS	UR
Cerro Sombreyoc 772	grass florets	195	40	-23.8	283-0	AA36327	16°07.685'	71°49.126'	2750	NNW	LS	UR
Cerro Sombreyoc 773	grass florets	735	40	-22.0	671-551	AA36328	16°07.861'	71°49.154'	2750	E	LS	UR
Cerro Sombreyoc 775	fecal pellets	120	95	-24.2	293-0	GX25844	16°07.861'	71°49.154'	2750	E	LS	Abci
Cerro Sombreyoc 776B	fecal pellets	4870	60	-23.0	5647-5328	AA34542	16°07.861'	71°49.154'	2750	E	LS	Phli
Cerro Sombreyoc 776D	fecal pellets	5400	55	-24.8	6278-5935	AA34539	16°07.861'	71°49.154'	2750	E	LS	Aksu
Cerro Sombreyoc 774	fecal pellets	415	40	-24.2	504-302	AA34536	16°07.861'	71°49.154'	2750	E	LS	UR
Quebrada Chilcane 758B	fecal pellets	0	N/A	-26.0	N/A	GX25838	16°07.816'	71°48.920'	2750	SSE	LS	Phli
Quebrada Chilcane 759A	fecal pellets	3290	60	-23.9	3627-3273	GX26356	16°07.825'	71°48.846'	2750	SSE	LS	UR
Quebrada Chilcane 759B	fecal pellets	3715	90	-22.5	4234-3694	AA34599	16°07.825'	71°48.846'	2750	SSE	LS	Thpa, Phli
Quebrada Chilcane 759C	fecal pellets	770	60	-25.3	729-550	GX26356	16°07.825'	71°48.846'	2750	SSE	LS	TR
Quebrada Chilcane 760A	grass stems	4375	50	-22.0	5025-4825	AA34540	16°07.768'	71°48.790'	2750	ESE	LS	UR, TR
Quebrada Chilcane 760B	grass stems	4365	50	-10.1	4968-4713	AA34541	16°07.768'	71°48.790'	2750	ESE	LS	Thpa, TR
Quebrada Chilcane 765	cactus seeds	450	45	-26.7	514-309	AA34597	16°07.719'	71°49.002'	2750	WNW	LS	Phli, Chsa, UR
Quebrada Chilcane 769	fecal pellets	140	40	-24.9	267-0	AA36323	16°07.419'	71°49.000'	2750	WNW	LS	UR
Quebrada Ojule 730A	grass stems	8465	75	-22.4	9532-9146	AA34545	16°12.177'	71°48.930'	2580	NW	CONG	Phli
Quebrada Ojule 730B	wood	8470	65	-10.9	9530-9155	AA36325	16°12.177'	71°48.930'	2580	NW	CONG	Phli
Quebrada Ojule 730D	fecal pellets	6560	70	-25.3	7559-7267	AA34595	16°12.177'	71°48.930'	2580	NW	CONG	UR
Quebrada Ojule 731	fecal pellets	5920	55	-21.0	6790-6498	AA34537	16°12.177'	71°48.930'	2580	NW	SS	Phli
Quebrada Ojule 732	fecal pellets	110	40	-18.3	255-0	AA36322	16°12.177'	71°48.930'	2580	NW	SS	UR
Quebrada Ojule 733	grass florets	3445	40	-9.6	3693-3473	AA36324	16°12.177'	71°48.930'	2580	NW	SS	UR
Quebrada Ojule 734	cactus seeds	4930	45	-10.3	5657-5485	AA36326	16°12.177'	71°48.930'	2580	NW	SS	Phli
Quebrada Ojule 756A	wood	8560	75	-23.9	9552-9327	AA34601	16°12.177'	71°48.930'	2580	NW	CONG	Abci, Phma
Quebrada Ojule 756B	wood	7010	190	-17.3	8159-7432	GX25839	16°12.177'	71°48.930'	2580	NW	CONG	Abci, Phli, UR
Quebrada Saucillos 711B	fecal pellets	2800	45	-20.0	2922-2751	AA34538	16°15.256'	71°47.361'	2350	SSW	IG	Phli
Quebrada Saucillos 740A	fecal pellets	845	70	-24.2	881-565	GX25843	16°14.896'	71°47.669'	2378	E	IG	UR
Quebrada Saucillos 757	fecal pellets	825	70	-22.3	789-560	AA34600	16°15.913'	71°47.492'	2351	ESE	IG	UR
Yura 750	fecal pellets	515	65	-22.1	617-315	GX25840	16°16.357'	71°40.063'	2600	NNW	IG	Aksu
Yura 751	fecal pellets	910	65	-22.7	921-661	GX25841	16°16.307'	71°40.063'	2600	NNW	IG	Phli, UR, TR
Yura 752	fecal pellets	1090	110	-23.3	1173-692	GX25847	16°16.252'	71°39.919'	2600	NW	IG	UR
Yura 753	fecal pellets	330	70	-23.7	481-1	GX25835	16°16.252'	71°39.919'	2600	NW	IG	UR
Yura 754	fecal pellets	1420	110	-22.7	1507-994	GX25836	16°16.167'	71°40.42'	2600	NW	IG	Abci, Phli
Yura 755	fecal pellets	330	100	-22.8	511-0	GX25837	16°16.167'	71°40.42'	2600	NW	IG	UR

For Rock Type, LS = limestone, SS = sandstone, CONG = conglomerate, IG = ignimbrite. For Vertebrates, Thpa = *Thylamys pallidior*, Abci = *Abrocoma cinerea*, Phli = *Phyllotis limatus*, Phma = *Phyllotis magister*, Aksu = *Akodon subfuscus*, Chsa = *Chinchillula sahamae*, TR = *Tropiduridae*, UR = *Unidentifiable Rodent remains*.

Midden ages show a clustering between 0–1000 cal yr B.P. and 2800–9560 cal yr B.P. In other midden studies (Webb and Betancourt, 1990; Betancourt *et al.*, 1993; Spaulding, 1995), clusters of radiocarbon dates have been interpreted as either sampling bias for middens of a particular age or variability in ecosystem productivity and midden formation. In Peru, we sampled all middens encountered in the field, thus offsetting any sampling bias. As a first approximation, we suggest that greater abundance of middens during certain times reflects wetter, more productive periods. We recognize that this interpretation will be tested as more middens are collected and dated in southern Peru.

Among vertebrate remains in the middens (Table 2), *Phyllotis limatus* and *Abrocoma cinerea* are the most common. No remains of *Lagidium peruanum* were found, suggesting that it may be less responsible for midden building than *P. limatus* and *A. cinerea*. *Chinchillula sahamae* and *Neotomys ebriosus*, found in only a few middens, are rare at elevations below 3500 m today. Likewise, *Oligoryzomys andinus* is restricted to areas adjacent to water and *Phyllotis magister* and *Akodon subfuscus*, although more independent of water, are not found in dry sites.

DISCUSSION

Elevational displacements of plant species found in middens should reflect shifts in easterly trade-wind intensity and tropical rainfall that spills over to the Pacific slope of the Andes. In this study, we found that several species were remarkably stable during the Holocene. Many species present in southern Peru have very large ecological amplitudes (i.e., broad elevational ranges), which may explain the observed stability. Across 500 m in elevation (~130-mm difference in precipitation) the more noticeable changes may be in community structure (species abundances) rather than community composition (species presence or absence). Macrofossil relative abundance, subject to several filters (animal preferences, distance to plants, duration of depositional episode, etc.), may or may not be sensitive to changes in plant community structure. Hence, the apparent stability in Holocene midden floras may mask actual instabilities in plant community structure. In addition, no middens were encountered from the Pleistocene–Holocene transition where the greatest instability in vegetation is expected.

Despite the relative stability, however, there does appear to be evidence for a wetter middle Holocene consistent with the greater frequency in midden ages and, hypothetically, ecosystem productivity during this time. Because productivity is limited primarily by rainfall in the Atacama, clusters of midden ¹⁴C dates should represent wetter periods during the Holocene, and a lack of dates should represent drier periods. This is supported by evidence from the southwestern United States, where the paucity of middens during the mid-Holocene (Webb and Betancourt, 1990) corresponds to a well-documented period of winter drought (Webb and Betancourt, 1990; Betancourt *et al.*, 1993; Spaulding,

1995). The occurrence of many species in middens only during these periods also indicates increased moisture, because an increase in species richness would be expected to occur during more productive periods. Finally, it appears that several higher elevation species retreated from lower elevations after 2800 cal yr B.P., implying increasing aridity from middle to late Holocene.

There is considerable disagreement among regional paleoclimate records regarding mid-Holocene precipitation levels, especially between high- and low-altitude sites (see Fig. 1 for locations of sites). Ice cores from Nevado Sajama, the highest altitude record at 6542 m, display high $\delta^{18}\text{O}$ values and dust concentrations between 9000 and 3000 yr B.P., interpreted as indicating aridity (Thompson *et al.*, 1998). Likewise, multiproxy studies of Lake Titicaca (3800-m elevation) show lake levels were about 100 m lower between >6000 and 3800 yr B.P. (Wirmann and De Oliveira, 1987; Cross *et al.*, 2000; Rowe *et al.*, in press). A mid-Holocene arid phase (undated, but correlated to the Titicaca record) is inferred for Laguna Seca (4500 m) based on $\delta^{18}\text{O}$ results from ostracods and authigenic carbonates (Schwalb *et al.*, 1999). Pollen analyses from this lake suggest aridity from about 7000–5000 yr B.P. and a moister period from 5000–3500 yr B.P. (Baied and Wheeler, 1993). This moist period is also seen in the Rio Desaguadero, Lake Titicaca's outlet into Lago Poopó and Salar de Coipasa and Salar de Uyuni. Fluvial terraces in the northern Rio Desaguadero valley mark an interval of high water from 4500 to 3900 yr B.P., which could be due to either spillover from the lake or local changes in precipitation when Titicaca was below the spill level (Baucom and Rigsby, 1999). Thus, while many Altiplano records indicate a mid-Holocene drought, others indicate increased moisture.

Evidence of a wet mid-Holocene is more common at sites on the Pacific slope of the Andes than on the Altiplano. A wet phase from 7100 to 3500 cal yr B.P. is seen in fossil rodent middens (2400–3200 m) and wetland deposits (2500–2700 m) near the Salar de Atacama in the central Atacama (22°–24°S) Desert (Betancourt *et al.*, 2000b). In addition, paleoshorelines of Lago Aricota (2800 m), on the Pacific slope ~170 km south of Arequipa, were highest between >7100 and 3500 cal yr B.P. (Placzek *et al.*, 2001). The catchment for Lake Aricota spans from 5000 to 2800 m, so this record integrates both high- and low-altitude precipitation. Thus, the mid-Holocene drought inferred from several Altiplano records is not visible in these records nor in our midden record of vegetation from southern Peru.

The discrepancies among records, especially between the Altiplano and Pacific slope, call into question assumptions about the regional coherence of summer precipitation in the central Andes. The predominance of summer-flowering plants in middens throughout the Holocene indicates that precipitation seasonality did not change. Changes in the strength of the SASM could be invoked to explain precipitation variability within the region during the mid-Holocene if storms have strong local, but not regional, effects. Linear regression of GHCN historical

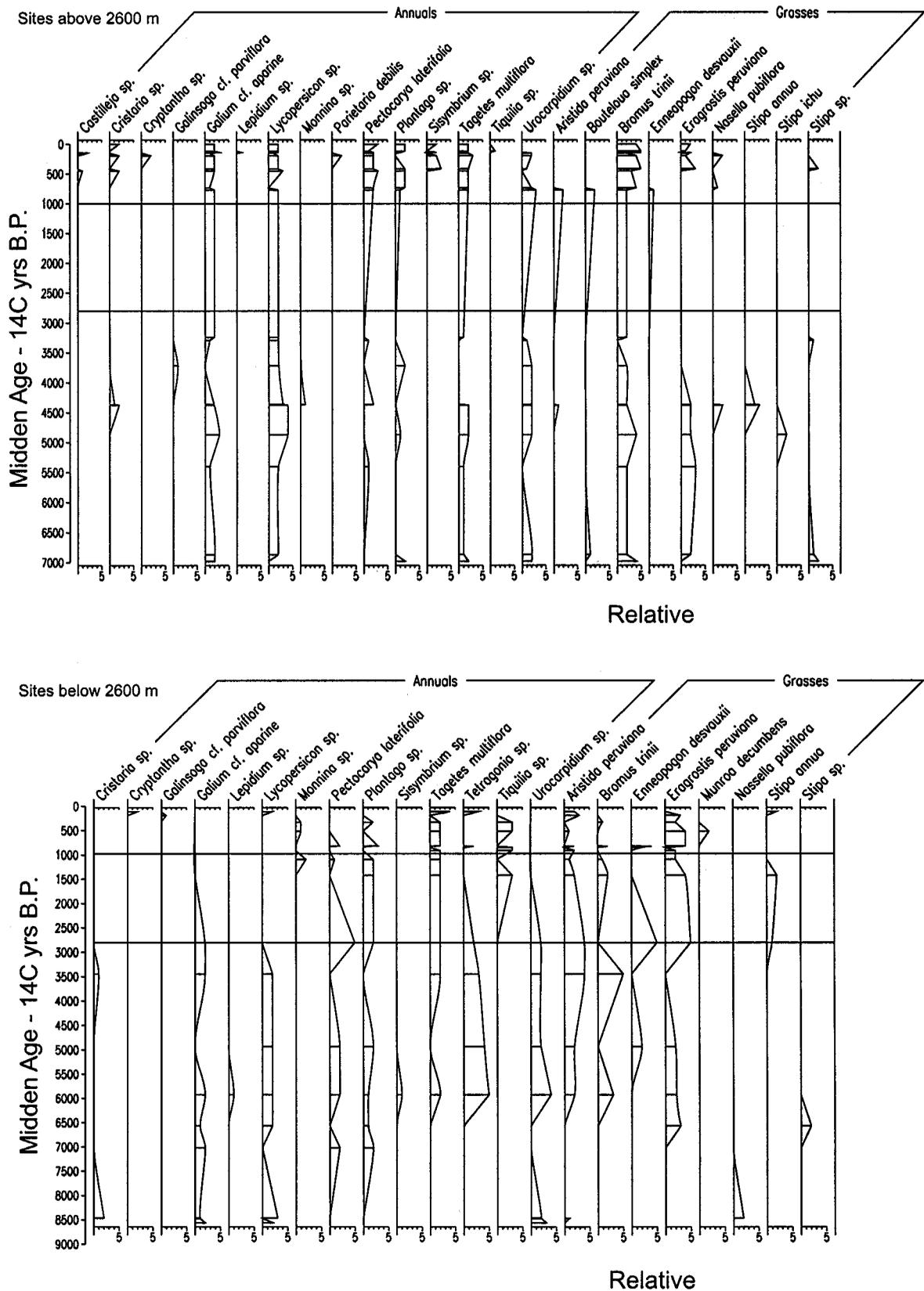


FIG. 4. Relative abundance of macrofossils through time for sites above and below 2600 m, where 0 = absent, 1 = rare, 5 = most abundant. Short horizontal bars within the abundance curves indicate midden dates. The horizontal lines spanning the width of the graphs indicate vegetation patterns discussed in text.

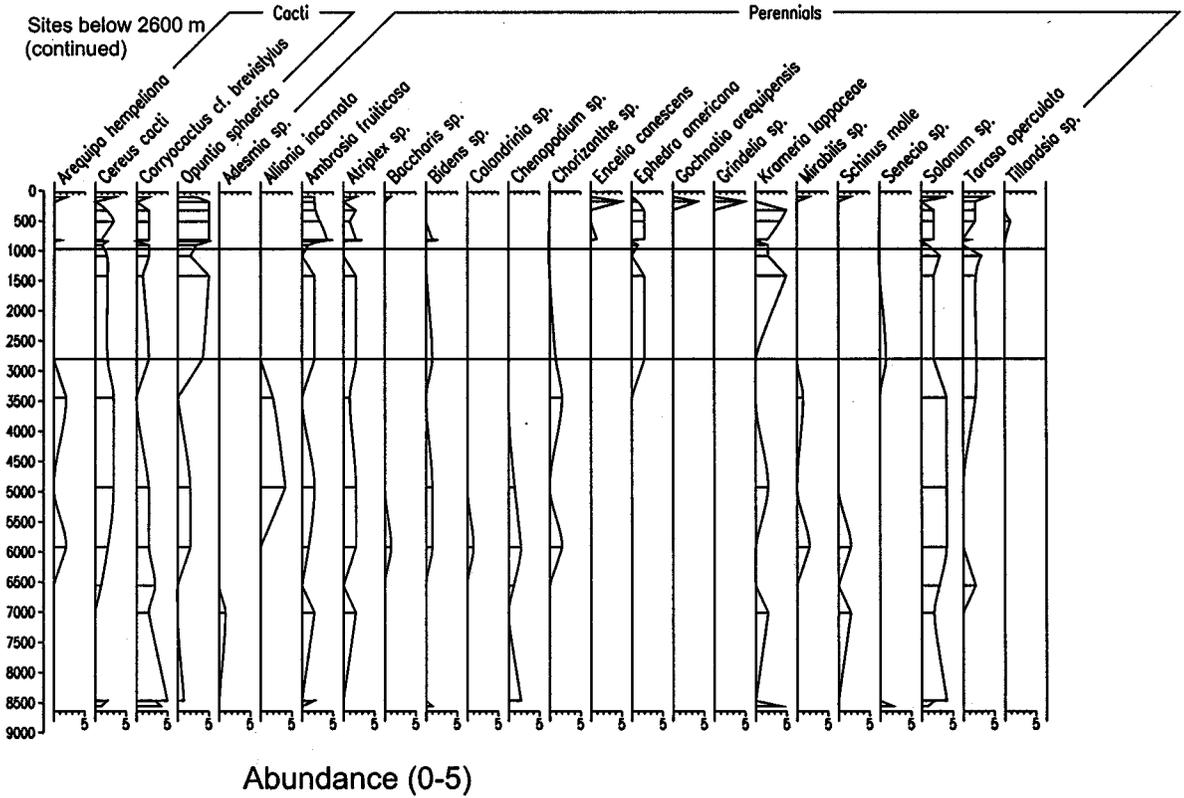
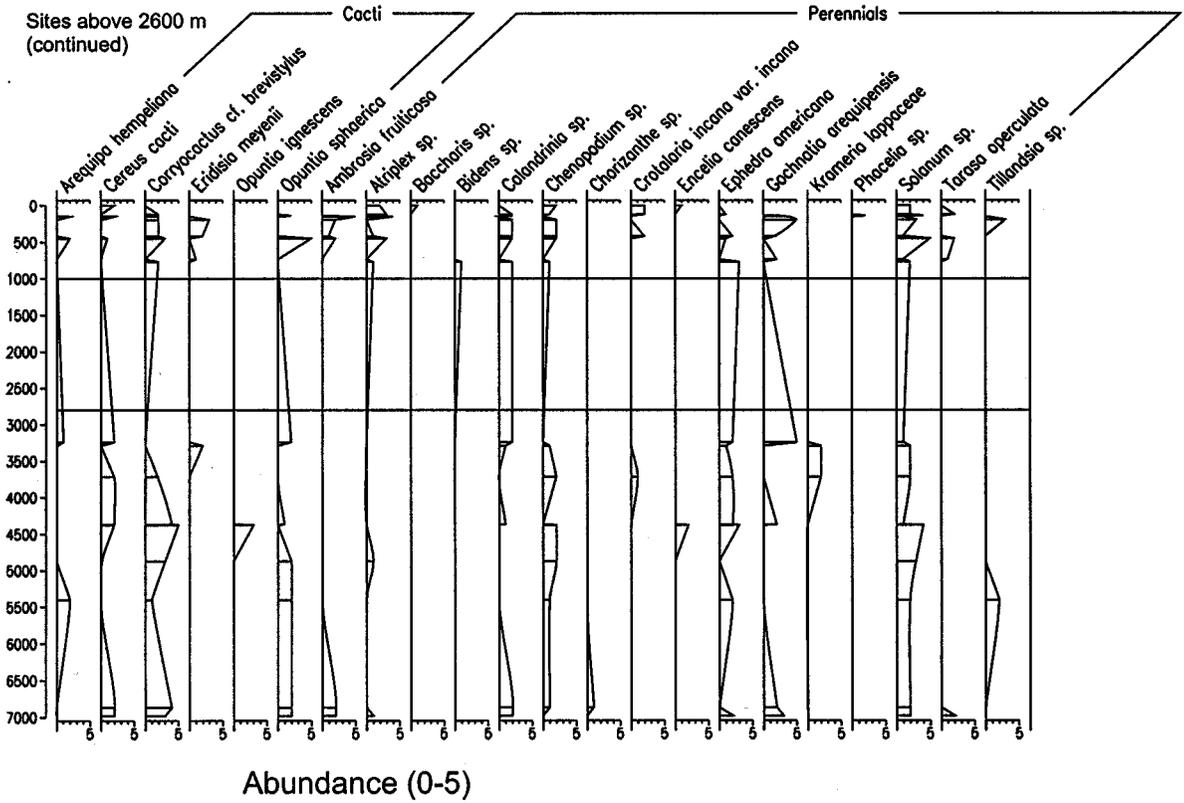


FIG. 4—Continued

summer (December–March) precipitation values from Arequipa and Puno (Lake Titicaca) shows little similarity ($r^2 = 0.17$, $p = 0.128$) between stations. The apparent greater correlation during some winter months (August, $r^2 = 0.695$, $p < 0.0001$) is due to the fact that Arequipa and Puno receive no winter precipitation except during rare years when a few frontal storms bias the correlation. Juliaca and Puno, located only 50 km apart on the shores of Lake Titicaca, exhibit no better correlation than do Arequipa and Puno ($r^2 = 0.18$, $p = 0.120$).

As in other monsoonal areas of the world, the sparse weather station network in the central Andes may be inadequate to capture regional-scale patterns in summer precipitation. Convective storms with narrow tracks (<10 km wide) can easily miss one station and hit another, particularly when stations are more than 100 km apart. Thus, the SASM may have highly variable local effects that confound regional interpretations. Changes in SASM storm tracks during the mid-Holocene could explain why precipitation increased in some areas and decreased in others. It is also possible that the disparities between the records may be due to dating problems or differing response times of the various systems—oceans, big and small lakes, rivers, water tables, and vegetation.

Precipitation variation in the central Andes also has been linked to long-term ENSO behavior. El Niño episodes during the austral summer produce rainfall anomalies over most of tropical South America, with flooding common along the coasts of Ecuador, Peru, and central Chile but reduced rainfall at higher elevations (>1000 m) on the Pacific slope and Altiplano. Paleoclimatic studies in the area consistently show that sea-surface temperatures were lower and ENSO variability was weak or absent during the mid-Holocene (Keefer *et al.*, 1998; Fontugne *et al.*, 1999; Rodbell *et al.*, 1999; Cane *et al.*, 2000; Cole, 2001). One exception is the thermally anomalous molluscan assemblages, attributed to warm tropical water as far south as 10°S during the mid-Holocene by one author (Sandweiss *et al.*, 1996), but to local changes in coastal geomorphology by others (DeVries and Wells, 1990).

We recognize that the scarcity of weather stations and the strong local effects of convective precipitation render historical station data inadequate to capture regional patterns. Precipitation data from Arequipa, however, show that only three of the five wettest years occurred during El Niño events and none of the driest years occurred during La Niña events. The limited correspondence between ENSO and precipitation, in addition to the discordance between regional paleorecords, suggests that the relation between precipitation variation and long-term ENSO behavior remains speculative. These results indicate that continued investigation of paleoclimate records from the central Andes and Atacama Desert is necessary to fully understand regional climate variability and its large-scale forcing during the Holocene. In this study, well-dated fossil rodent middens provide the first paleobotanical record of its kind for Peru. This study also indicates great potential for future midden studies in the northern Atacama Desert and adjoining regions, which could play a key

role in clarifying past patterns of vegetation and climate variability in the central Andes.

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