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Distribution of archaeological sites of Ancient Peru is linked to climatology and natural vegetation

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ABSTRACT

In this article, we try to discover a parallelism among climate and bioclimate belts, use of the territory, and previously studied plant communities, taking into account historical and archaeological data to find an answer as to how different cultures perceived the landscapes. After a statistical analysis generating a Sørensen dendrogram, we were able to observe how archaeological sites were ordered according to bioclimatic belts, crops, and human activity; the results of a canonical correspondence analysis (CCA) showed connections among archaeological sites, crops, products, and plant associations of the landscapes. Groups with the most humid climate represent areas with crops with a seasonal rain regime and shepherding of llamas and alpacas, while groups with the driest climate represent areas whose crops need irrigation. Notably, occidental slope areas with cactus associations present a terrace agricultural system irrigated by water springs, while sites near riparian plant associations are joined to vegetable gardens. Amazonian and Oriental Andean crops are present in the same bioclimatic belt in comparison to the coast. Using a minimal spanning tree (MST), hypothetical roads to exchange products between different crop areas could be traced with a high coincidence with the Inca Road (Qhapaq Ñan).

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Archaeological sites; bioclimatic belts; humidity interval; phytosociology; landscapes; Peru


Introduction

Landscapes denote a multidimensional abstraction of nature as a result of an interaction between historical scenarios and their actual use (Linderman et al. 2006). The Andean Cordillera presents a high altitudinal and latitudinal environmental diversity, linked to the geological features originated from the Nazca Plate and the lifting of the Andes and, from another viewpoint, to the use of the territory since circa 10000 yr BP (Dillehay et al. 2007). Throughout the Pleistocene, cold and warm periods occurred with the ascent and descent of the paramo and puna vegetation, increasing the isolation processes and flora diversification (Hooghiemstra et al. 2006). The early and middle Holocene climate (10000–4000 yr BP) tended to be dry and warm (Salaverry Llosa 2006) coinciding with the beginning of human activity in the Andes (Dillehay et al. 2007) and Amazonia (Bush et al. 2007). These activities can be condensed into various scenarios that indicate climate divergence within the Peruvian territory: (i) In Amazonia several domesticated crops linked to warm climate were probably being cultivated by 10000–7000 yr BP, including yams

(*Dioscorea* L. sp.), arrowroot (*Maranta arundinacea* L.), bottle gourd (*Lagenaria siceraria* (Molina) Standl.), squash (*Cucurbita* L. sp. pl.), sweet potato (*Ipomoea batatas* (L.) Lam.), and manioc (*Manihot esculenta* Crantz) (Denevan 2007), (ii) Also maize (*Zea mays* L.) agriculture, which had been adopted by 6000 yr BP (Bush et al. 1989). Perry et al. (2006) evidenced a pre-ceramic settlement with maize agriculture around 4000 yr ago from the southern Peruvian Andes (3625 m asl), (iii) The chewing of tupa-coca (*Erythroxylum novogranatense* var. *truxillense* (Rusby) Plowman) had begun in northern Peru (500–1200 m asl) by at least 8000 yr BP (Dillehay et al. 2010), (iv) The origin and domestication of the cultivated potato (*Solanum tuberosum* L.) occurred in the humid highlands of Peru (3500–4500 m asl) during the early Holocene, but its large-scale dissemination was apparently initiated 2500 yr BP by the Tiwanaku culture (Morales Garzón 2007).

Mountain regions of tropical South America host diverse lowland and alpine floras with a high proportion of endemic species. The Peruvian flora is constituted by 2458 genera and about 18000 species with ca. 5500 endemic species (Brako and Zarucchi 1993). These species constitute part of plant communities that some authors have linked to climate,

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cultural territories, and volcanic events since the early 20th century (i.e., Weberbauer 1945; Tosi 1960; Galán de Mera et al. 1997; Schwarzer et al. 2010, Montesinos-Tubée and Mondragón 2013; Montesinos-Tubée et al. 2015; Montesinos-Tubée 2016, 2017; Chicalla-Rios 2017; Quipuscoa Silvestre et al. 2019; Galán de Mera et al. 2011a). Recently, throughout South America, several investigations have shown an altitudinal distribution of vegetation associations linked to intervals of climate indexes (i.e., Navarro and Maldonado 2005 for Bolivia; Luebert and Plischoff 2006 for Chile; Kuentz et al. 2007; Montesinos-Tubée et al. 2012, Galán de Mera et al., 2009, 2016, 2017, for Peru; Rodríguez et al. 2017 for Argentina), following the bioclimatic belts model of Rivas-Martínez (2017) and Rivas-Martínez et al. (1999). From another perspective, various studies have indicated how the Andean territory was used during pre-Hispanic cultures, as well as changes in the landscape during the Spanish colonization (Sluyter 2001). One of the most important contributions to the understanding of ethnohistorical Andean economic and subsistence systems is Murra's (Murra 2009) model of vertical control on the use of the territory. This model is concerned with an Andean ideal of simultaneous control of vertical archipelagoes, which are divided among groups that are geographically distant and which differ according to the complexity of economic and political organization. In the Murra model, different ethnic groups attempt to control the maximum number of ecological belts in an effort to achieve self-sufficiency. Systems of reciprocity and redistribution mark the internal economies of the communities, but trade may occur between the communities (Brush 1976). These human activity areas are part of bioclimatic belts, and different plant products and plant communities used for production and subsistence, can be found in them, leading us to consider how landscape was perceived by the Peruvian pre-Hispanic cultures and early Spanish colonization.

The aim of this work is to find a parallelism among climate, use of territory, and previous studied plant communities, taking into account historical and archaeological data seeking an answer to the following questions: 1. How are archaeological sites distributed in Peru linked to bioclimatic belts?, 2. Are archeological sites linked to the surrounding vegetation?, 3. How were vegetal products and plant communities used by Ancient Peruvians distributed?, and 4. What roads and territories were used by Ancient Peruvians to exchange products between different crop areas?

Data and methods

Choosing historical and archaeological data about the use of the territory

From the Holocene to the Inca Empire and early Spanish colonization, we have been able to gather numerous archeological plant discoveries and human activities. These have been compiled from the literature and our own field observations, from the Peruvian coast to the Amazonia (Appendix 1, [Supplementary material](#)), also using the archaeological sites listed by the Grupo Funcional de Elaboración de

Carpetas Temáticas (GFECT 2014) and relevant information obtained from the Instituto Nacional de Cultura office in Arequipa. Most of them were chosen from the Arequipa and Ica Departments, where we can find archaeological sites from the coast to the Coropuna volcanic system (6377 m asl). To compare these plant remains and human activities linked to natural plant associations of Arequipa and Ica with those of other Peruvian regions, we have also used information from the Cajamarca to Moquegua Departments as well as from the Amazonia. Archaeological sites are referenced in the maps of the [Figure 1](#). Cultural periods are according to Cáceres Macedo (2009).

Bioclimatic analysis and ecological variability

To examine relationships between climate and the human scenarios with plant remains and natural plant associations, the bioclimatic system of Rivas-Martínez (2017) and Rivas-Martínez et al. (1999) was implemented, with data for at least 30 years (Schwarz 2019), from several meteorological stations as near as possible to the archeological sites ([Table 1](#)). These data were compared with those shown by Salaverry Llosa (2006) to observe if there were significant differences between the present and the Holocene times.

This bioclimatic model is based on thresholds of the thermicity index (It) versus the intervals of an annual humidity index (Io) coincident with altitudinal and latitudinal areas of flora and vegetation, including crops and the use of the territory. The thermicity index is based on mean annual temperature (T), and average maximum (M) and minimum (m) temperatures of the coldest month [$It = (T + M + m) / 10$]. The Io is a precipitation and temperature quotient ($Io = P / T_p \times 100$), where P is the annual precipitation, and T_p is the positive temperature or summed in degree tenths when $T > 0^\circ\text{C}$. Bioclimatic belts coincide with natural plant associations, and for Peru, six bioclimatic belts were defined and mapped by Galán de Mera (Galán de Mera et al. 2017): Infratropical ($It > 690$), thermotropical ($It = 490$ to 690), mesotropical ($It = 320$ to 490), supratropical ($It = 160$ to 320), orotropical ($It = 50$ to 160), and cryrotropical ($It < 50$). Io intervals are the following: Ultrahyperarid ($Io < 0.2$), hyperarid ($Io = 0.2$ to 0.4), arid ($Io = 0.4$ to 1.0), semiarid ($Io = 1.0$ to 2.0), dry ($Io = 2.0$ to 3.6), subhumid ($Io = 3.6$ to 6), humid ($Io = 6.0$ to 12.0), hyperhumid ($Io = 12.0$ to 24.0), and ultrahyperhumid ($Io > 24.0$).

Natural plant associations near archeological sites

Plant associations were observed near archaeological sites following several previously published works on vegetation in Southern, Central and Northern Peru ([Table 2](#)), which follow the phytosociology method (Braun-Blanquet 1932) and the International Code of Phytosociological Nomenclature (Weber et al. 2000) for vegetation classification. The phytosociology method lets us to synthesize the vegetation of a landscape, and can be used to define biogeographical units with a cartographic delimitation of the vegetation, in addition to suitably compiled and mapped bioclimatic and soil factors (Rivas-Martínez et al. 2011), as well as anthropology

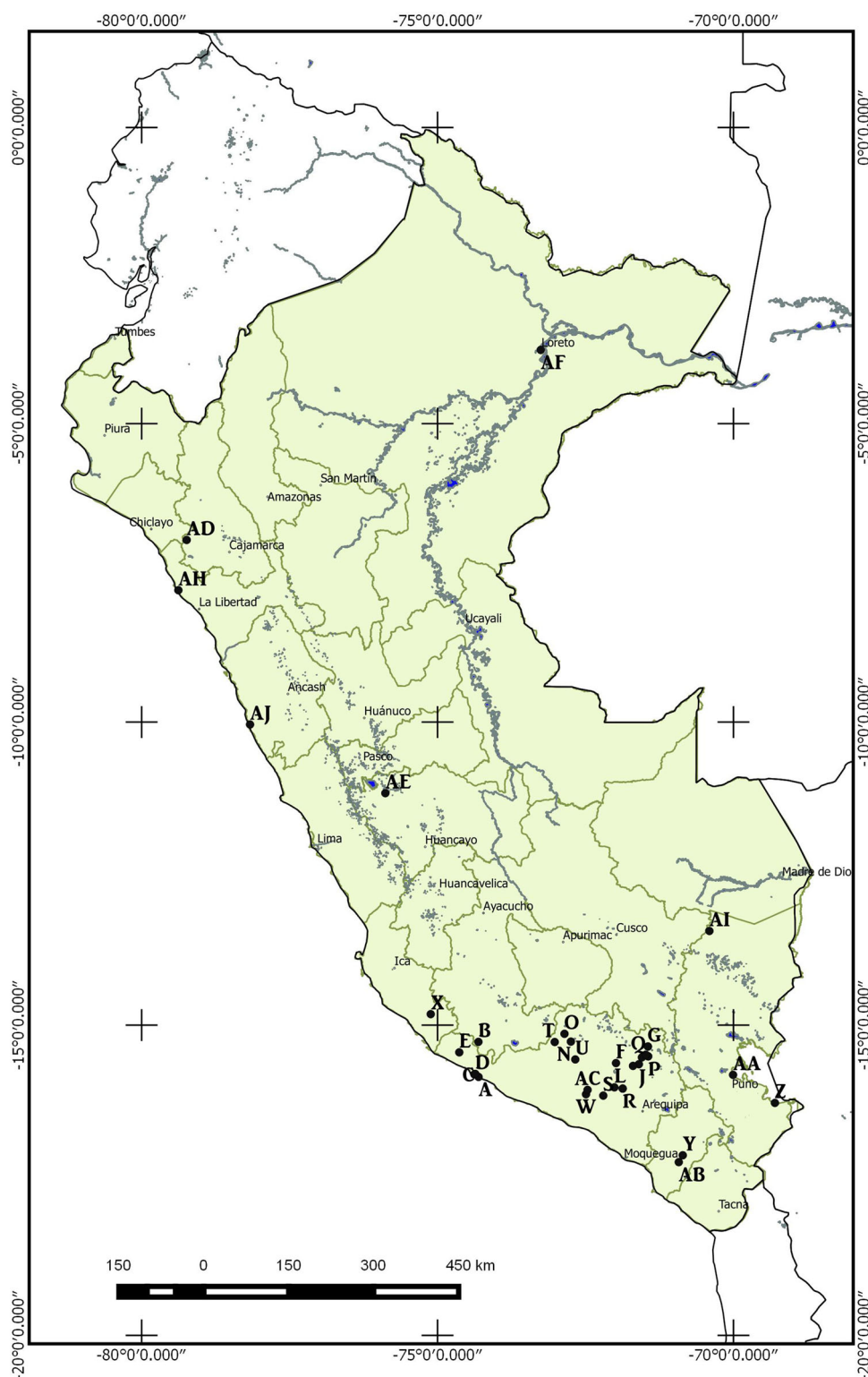


Figure 1. Map of Peru with geo-referenced archaeological sites. AJ, Punta Salina (Huarney, Ancash); A, Quebrada de la Vaca, Sileta, Caleta (Atiquipa, Arequipa); B, Inca road (Atiquipa, Arequipa); C, Atiquipa (Atiquipa, Arequipa); D, Pampamarca (Atiquipa, Arequipa); E, Acarí River (Acarí, Arequipa); F, Achachiwa (Cabanaconde, Arequipa); G, Tisco (Tisco, Arequipa); H, Sibayo 1 (Sibayo, Arequipa); I, Callalli 1 (Callalli, Arequipa); J, Chivay (Chivay, Arequipa); K, Tuti (Tuti, Arequipa); L, Lluta (Lluta, Arequipa); M, Achoma (Achoma, Arequipa); R, Huanca 1 (Huanca, Arequipa); N, Wayñuna (Cotahuasi, Arequipa); O, Tenahaha (Cotahuasi, Arequipa); P, Callalli 2 (Callalli, Arequipa); Q, Sibayo 2 (Sibayo, Arequipa); AC, Beringa (Majes, Arequipa); S, Huacán (Majes, Arequipa); T, Velinga (Cotahuasi, Arequipa); U, Coropuna (Viraco, Arequipa); V, Huanca 2 (Huanca, Arequipa); W, La Real (Aplao, Arequipa); AD, Nanchoc (San Miguel, Cajamarca); X, Cahuachi (Nazca, Ica); AE, Telarmachay (San Pedro de Cajas, Junín); AH, Huaca Prieta (Magdalena de Cao, La Libertad); AF, Iquitos (Loreto); Y, Cerro Baúl (Torata, Moquegua); AB, Chen Chen (Moquegua, Moquegua); Z, Pomata (Pomata, Puno); AA, Puno (Puno, Puno); AI, San Gabán (Puno).

and cultural features linked to the vegetation of a territory (Vicente Orellana and Galán de Mera 2003 and Buxó and Piqué 2008 in the Iberian Peninsula; Frosch and Deil 2011 in

Chile; Montesinos-Tubée and Mondragón 2013 and Montesinos-Tubée 2016, 2017 in Peru). Plant names and authorships are based on IPNI (2020).

Table 1. Archaeological sites, altitude, climatic data, and bioclimatic diagnosis in the meteorological stations consulted.

Peruvian Department	District	Meteorological station and distance to archeological sites (Km)		h (m)	T	M	m	It	P	Tp	Io	Bioclimatic diagnosis
		Archeological sites	distance to archeological sites (Km)									
Ancash	Huarmey	Punta Salina	Huarmey (3.34)	25	19.3	20.8	13.2	533	9	2319	0	Thermotropical ultrahyperarid
Arequipa	Atiquipa	Quebrada de la Vaca, Sileta, Caleta	Atiquipa (10.27)	0	19.2	20.3	11.7	512	1	2303	0	Thermotropical ultrahyperarid
Arequipa	Atiquipa	Inca road	Chala (05.89)	20	19.7	19.7	13.3	527	2	2364	0	Thermotropical ultrahyperarid
Arequipa	Atiquipa	Atiquipa	Atiquipa (01.06)	400	19.2	20.3	11.7	512	1	2303	0	Thermotropical ultrahyperarid
Arequipa	Atiquipa	Pampamarca	Atiquipa Reserva (0.0)	1282	19.2	20.3	11.7	512	369	2303	1.6	Thermotropical semiarid
Arequipa	Acari	Acari River	Acari (0.0)	200	20.0	21.3	12.1	534	3	2402	0	Thermotropical ultrahyperarid
Arequipa	Cabanaconde	Achachiwa	Cabanaconde (0.95)	3320	10.7	18.6	-1.7	276	344	1286	2.6	Supratropical dry
Arequipa	Tisco	Tisco	Tisco (0.0)	4232	5.2	13.2	-9.7	87	696	618	11.2	Orotropical humid
Arequipa	Sibayo	Sibayo	Sibayo (0.0)	3919	8.2	16.2	-6.3	181	567	983	5.7	Supratropical subhumid
Arequipa	Callalli	Callalli	Callalli (0.0)	3887	8.1	16.1	-6.4	178	560	969	5.7	Supratropical subhumid
Arequipa	Chivay	Chivay	Chivay (0.0)	3713	9.0	16.9	-4.7	212	448	1008	4.1	Supratropical subhumid
Arequipa	Tuti	Tuti	Tuti (0.0)	3858	7.8	15.7	-6.5	170	536	933	5.7	Supratropical subhumid
Arequipa	Lluta	Lluta	Lluta (0.0)	3182	11.5	19.2	-0.2	305	137	1383	0.9	Supratropical arid
Arequipa	Achoma	Achoma	Achoma (0.0)	3503	9.9	17.7	-3.3	243	400	1184	3.3	Supratropical arid
Arequipa	Huanca	Huanca	Huanca (0.0)	3078	12.1	20.7	2.4	352	130	1455	0.8	Mesotropical arid
Arequipa	Cotahuasi	Wayñuna	Huilla (0.0)	3625	12.3	19.7	0.7	327	524	1480	3.5	Mesotropical dry
Arequipa	Cotahuasi	Tenahaha	Alca (9.0)	3200	13.0	20.4	1.6	350	433	1563	2.7	Mesotropical dry
Arequipa	Majes	Beringa	Aplao (03.33)	700	20.2	23.6	12.8	566	18	2420	0.0	Thermotropical ultrahyperarid
Arequipa	Majes	Huacán	El Pedregal (15.0)	1984	19.1	25.1	9.8	540	3	2293	0.0	Thermotropical ultrahyperarid
Arequipa	Cotahuasi	Velinga	Quechua (06.69)	1967	18.3	24.2	8.6	511	80	2196	0.3	Thermotropical Hyperarid
Arequipa	Viraco	Coropuna	Imata (169.49)	5600	2.8	10.9	-11	27	535	334	16.0	Cryotropical hyperhumid
Arequipa	Aplao	La Real	Huancarqui (04.21)	589	20.2	23.6	12.8	566	19	2428	0.0	Thermotropical ultrahyperarid
Cajamarca	San Miguel	Nanchoc	Nanchoc (0.0)	500	22.3	25.3	14.5	621	106	2677	0.3	Thermotropical Semiarid
Ica	Nazca	Cahuachi	Nazca (19.61)	400	20.9	25.3	7.9	541	4	2507	0.0	Thermotropical ultrahyperarid
Junín	San Pedro de Cajas	Telarmachay	San Pedro de Cajas (8.0)	4420	5.8	12.9	-4.1	146	802	697	11.5	Orotropical humid
La Libertad	Magdalena de Cao	Huaca Prieta	Magdalena de Cao (04.23)	8	19.9	22.2	13.7	558	7	2388	0.0	Thermotropical ultrahyperarid
Loreto	Iquitos	-	Iquitos (0.0)	104	26.1	30.4	20.5	770	2976	3431	8.6	Infertropical humid
Moquegua	Torata	Cerro Baúl	Torata (4.4)	2584	14.8	20.9	4.5	402	38	1772	0.2	Mesotropical hyperarid
Moquegua	Moquegua	Chen Chen	Moquegua (0.0)	1452	18.2	21.8	7.7	515	25	2054	0.1	Thermotropical ultrahyperarid
Puno	Pomata	Pomata	Pomata (1.44)	3960	8.9	14.1	-1.0	220	811	1066	7.6	Supratropical humid
Puno	Puno	Puno	Puno (0.0)	3832	8.4	14.2	-2.3	203	696	1008	6.9	Supratropical humid
Puno	San Gabán	-	San Gabán (0.0)	650	23.3	25.9	16.6	658	5224	2791	18.7	Thermotropical hyperhumid

Notes: H, altitude (m), T, mean annual temperature (°C); M, mean highest temperature of the coldest month (°C); m, mean lowest temperature of the coldest month (°C); It, thermicity index; P, annual precipitation (mm); Tp, positive temperature (°C); Io, annual humidity index.

Table 2. Plant associations and some alliances in the surroundings of the studied archaeological sites.

Plant associations	CCA abbreviation	Main diagnostic species	Bibliographic references	Archaeological sites	District	Department
Acacio <i>macracanthae- Tecometum guarumis</i>	ACA-GUA	<i>Bulnesia retamo</i> , <i>Scutia spicata</i> , <i>Tecoma fulva subsp. guarume</i> , <i>Vallesia glabra</i>	Galán de Mera et al. (2009)	Cahuachi	Nazca	Ica
Amazonian rain forests	RAIN	--	--	--	Iquitos and other Amazonian localities San Gabán	Loreto Puno
<i>Baccharito salicifoliae- Gynerietum sagittati</i>	BAC-GYN	<i>Baccharis salicina</i> , <i>Equisetum giganteum</i> , <i>Gynerium sagittatum</i> , <i>Tessaria integrifolia</i>	Galán de Mera et al. (2004)	Huaca Prieta	Magdalena de Cao	La Libertad
<i>Bacopo monnieri- Typhetum domingensis</i>	BAC-TYP	<i>Bacopa monnieri</i> , <i>Paspalum vaginatum</i> , <i>Schoenoplectus americanus</i> , <i>Phragmites australis</i> , <i>Typha domingensis</i>	Galán de Mera (1995)	Huaca Prieta	Magdalena de Cao	La Libertad
<i>Caesalpinio spinosae- Myrcianthetum ferreyrae</i>	CAE-MYR	<i>Caesalpinia spinosa</i> , <i>Citharexylum flexuosum</i> , <i>Croton alniifolius</i> , <i>Myrcianthes ferreyrae</i> , <i>Randia rotundifolia</i>	Galán de Mera et al. (2009)	Pampamarca	Atiquipa	Arequipa
<i>Crotono ruiziani- Acacietum macracanthae</i>	CRO-ACA	<i>Acacia macracantha</i> , <i>Bursera graveolens</i> , <i>Croton ruizianus</i> , <i>Espositoa lanata</i> , <i>Eriotheca ruizii</i> , <i>Onoseris odorata</i> ,	Galán de Mera et al. (2016)	Nanchoc	San Miguel	Cajamarca
<i>Dunalia spinosae- Baccharitetum latifoliae</i>	DUN-BAC	<i>Baccharis latifolia</i> , <i>Cantua buxifolia</i> , <i>Dunalia spinosa</i> , <i>Mutisia acuminata</i> , <i>Ophryosporus peruvianus</i>	Galán de Mera et al. (2003)	Achachiwa Chivay Lluta Achoma Wayñuna Tenahaha Huanca	Cabanaconde Chivay Lluta Achoma Cotahuasi Cotahuasi Huanca	Arequipa Arequipa Arequipa Arequipa Arequipa Arequipa
<i>Equiseto gigantei- Salicetum humboldtianae</i>	EQU-SAL	<i>Baccharis salicina</i> , <i>Equisetum giganteum</i> , <i>Pityrogramma trifoliata</i> , <i>Salix humboldtiana</i>	Galán de Mera et al. (2004)	Acarí River Cahuachi Huaca Prieta	Acarí Nazca Magdalena de Cao	Arequipa Ica La Libertad
<i>Festuco dolichophyllae- Calamagrostietum antonianae</i>	FES-CAL	<i>Calamagrostis rigida</i> , <i>Festuca dolichophylla</i> , <i>Novenia acaulis</i> , <i>Senecio evacoides</i> , <i>Trisetum spicatum</i>	Gutte (1985)	Telarmachay Pomata Puno	San Pedro de Cajas Pomata Puno	Junín Puno Puno
<i>Neoraimondio arequipensis- Browningietum viridis</i>	NEO-BRO	<i>Browningia viridis</i> , <i>Melocactus peruvianus</i> , <i>Neoraimondia arequipensis</i> , <i>Oreocereus hempelianus</i> , <i>Weberbauerocereus rauhii</i>	Galán de Mera et al. (2011a)	Velinga	Cotahuasi	Arequipa
<i>Nicotiano paniculatae- Urocarpidetum peruviani</i>	NIC-URO	<i>Malva parviflora</i> , <i>Nicotiana paniculata</i> , <i>Sisymbrium peruvianum</i> , <i>Urocarpidium peruvianum</i>	Müller (1985)	Cahuachi	Nazca	Ica
<i>Nolanion spathulatae associations</i>	NOL	<i>Lupinus mollendoensis</i> , <i>Nolana pallidula</i> , <i>N. spathulata</i> , <i>Palaua dissecta</i> , <i>Tetragonia vestita</i> , <i>Weberbauerella brongniartoides</i>	Galán de Mera et al. (2011a)	Inca Road, Atiquipa	Atiquipa	Arequipa
<i>Nototricho obcuneatae- Xenophylletum poposi</i>	NOTO	<i>Anthochloa lepidula</i> , <i>Dielsiochloa floribunda</i> , <i>Nototriche obcuneata</i> , <i>Xenophyllum poposum</i>	Galán de Mera et al. (2003)	Coropuna	Viraco	Arequipa
<i>Parastrephio quadrangularis- Festucetum dolichophyllae</i>	PAR-FES	<i>Festuca dolichophylla</i> , <i>Parastrephia quadrangularis</i> , <i>Poa candamoana</i> , <i>Senecio spinosus</i>	Galán de Mera et al. (2011a)	Tisco Sibayo Callalli Tuti	Tisco Sibayo Callalli Tuti	Arequipa Arequipa Arequipa Arequipa
	SCH-ACA			Punta Salina	Huarmey	Ancash

(continued)

Table 2. Continued.

Plant associations	CCA abbreviation	Main diagnostic species	Bibliographic references	Archaeological sites	District	Department
<i>Schino mollis</i> - <i>Acacietum</i> <i>macracanthae</i>		<i>Acacia macracantha</i> , <i>Bulnesia retamo</i> , <i>Pluchea chingoyo</i> , <i>Prosopis pallida</i> , <i>Schinus molle</i>	Galán de Mera et al. (2002)			
<i>Schino mollis</i> - <i>Tecometum</i> <i>arequipensis</i>	SCH-ARE	<i>Acacia macracantha</i> , <i>Fuertesimalva echinata</i> , <i>Schinus molle</i> , <i>Tecoma</i> <i>fulva</i> subsp. <i>arequipensis</i>	Galán de Mera et al. (2009)	Cerro Baúl Chen Chen	Torata Moquegua	Moquegua Moquegua
<i>Schino mollis</i> - <i>Tecometum</i> <i>tanaeciiflorae</i>	SCH-TAN	<i>Acacia macracantha</i> , <i>Schinus molle</i> , <i>Tecoma</i> <i>fulva</i> subsp. <i>tanaeciiflora</i>	Galán de Mera et al. (2009)	Huanca Tenahaha Beringa La Real	Huanca Cotahuasi Majes Aplao	Arequipa Arequipa Arequipa Arequipa
Seaweeds	SWE	–	–	Quebrada de la Vaca, Sileta, Caleta	Atiquipa	Arequipa
<i>Tillandsia latifoliae</i> associations	TIL	<i>Tillandsia latifolia</i> , <i>T.</i> <i>purpurea</i> , <i>T. straminea</i>	Müller (1985)	Huaca Prieta	Magdalena de Cao	La Libertad
<i>Weberbauerocero</i> <i>rauhii</i> - <i>Browningietum</i> <i>candelaris</i>	RAU-BRO	<i>Browningia candelaris</i> , <i>Haageocereus</i> <i>platinospinus</i> , <i>Neoraimondia</i> <i>arequipensis</i> , <i>Weberbauerocereus</i> <i>rauhii</i>	Galán de Mera et al. (2009)	Cahuachi	Nazca	Ica
<i>Weberbauerocero</i> <i>rauhii</i> - <i>Corryocactetum</i> <i>brevistylis</i>	WEB-COR	<i>Armatocereus riomajensis</i> , <i>Corryocactus brevistylus</i> , <i>Euphorbia apurimacensis</i> <i>Weberbauerocereus</i> <i>rauhii</i>	Galán de Mera et al. (2009)	Huanca Huacán	Huanca Majes	Arequipa Arequipa
<i>Weberbauerocero</i> <i>torataensis</i> - <i>Corryocactetum</i> <i>brevistylis</i>	TOR-COR	<i>Bougainvillea spinosa</i> , <i>Corryocactus brevistylus</i> , <i>Malesherbia ardens</i> , <i>Weberbauerocereus</i> <i>torataensis</i>	Galán de Mera et al. (2009)	Cerro Baúl	Torata	Moquegua
<i>Weberbauerocero</i> <i>weberbaueri</i> - <i>Browningietum</i> <i>candelaris</i>	WER-BRO	<i>Browningia candelaris</i> , <i>Cumulopuntia sphaerica</i> , <i>Neoraimondia</i> <i>arequipensis</i> , <i>Weberbauerocereus</i> <i>weberbaueri</i>	Galán de Mera et al. (2009)	Chen Chen	Moquegua	Moquegua

Statistical analysis

To show how the archaeological sites are grouped, a matrix with presences/absences of plant remains and plant communities was performed, and using a classification with the Sørensen index and paired group linkage method, a dendrogram was generated (DEN). Linked to this dendrogram, we have produced a minimal spanning tree (MST) using Euclidean distance among sites, and correlating it with a map generated by QGIS 3.0.1 software (QGIS Development Team 2018), in order to implement a hypothesis about areas and roads used by the Peruvian ancient cultures to inter-change products. To arrange archaeological sites, representative plant remains, human activities, and plants associations with respect to It, Io and altitude in m asl (h) as environmental variables, a canonical correspondence analysis (CCA) was implemented. Statistical analysis was performed using PAST 3.18 software (Hammer 1999–2019).

Results

Similarity between archaeological sites

Figure 2 is a dendrogram showing the closeness among archaeological sites, based on plant remains, animals or human

activities. U-Coropuna, D-Pampamarca, A-Quebrada de la Vaca, Y-Cerro Baúl, and E-Rio Acarí present the lowest similarity with a minimum of plant remains or activities. In the Coropuna, only an Inca irrigation infrastructure, *Caesalpinia spinosa* (Molina) Kuntze crop remains in Pampamarca, as well as *Indigofera suffruticosa* Mill. in Rio Acarí was found; in Quebrada de Vaca only a seaweed extraction site was reported. F-Achachiwa to T-Velinga is a group where *Chenopodium quinoa* Willd., *Solanum tuberosum* and *Zea mays* farming was the main human activity, according to the bibliographic references and some of our own observations (Appendix 1, Supplementary material). In the F-Achachiwa to I-Callalli group, the sites belong to supratropical and orotropical bioclimatic belts, except O-Tenahaha, which belongs to mesotropical belt, but which is joined to supra-orotropical sites because *Chenopodium quinoa*, *Solanum tuberosum* and *Zea mays* remains were found, and additionally, with a higher humidity than in the R-T group. The R-Huanca to T-Velinga are meso-thermotropical with low humidity sites, and therefore, with *Zea mays* farming by irrigation (Figure 3a). P-Callalli 2 to AB-Chen-Chen is a group where camelids were constantly documented; P, Q-Sibayo, Z-Pomata and AA-Puno are supra-tropical sites, and AE-Telarmachay is orotropical, while

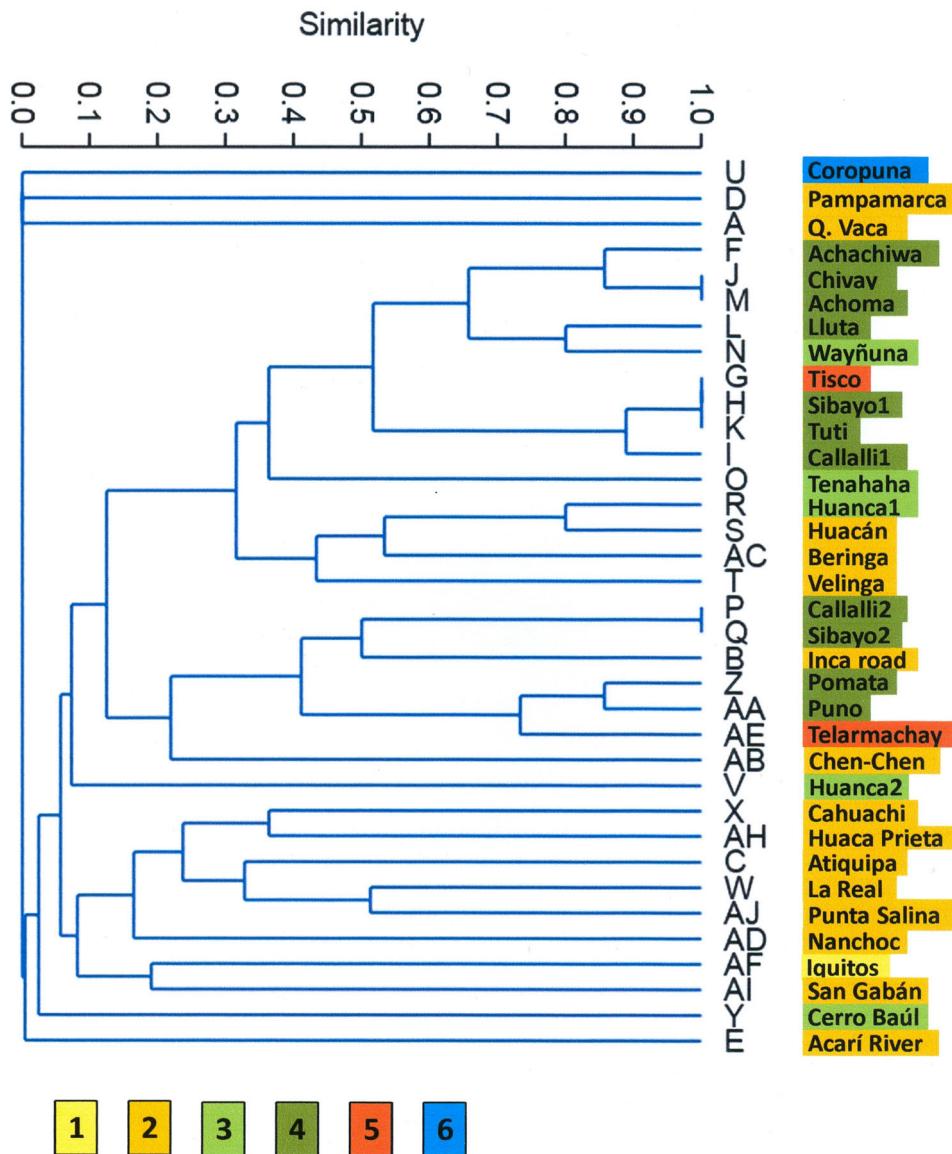


Figure 2. Dendrogram showing the closeness between the different selected archaeological sites. Letters are the same that in Figure 1. Bioclimatic belts: 1, infratropical; 2, thermotropical; 3, mesotropical; 4, supratropical; 5, orotropical; and 6, cryrotropical.

B-Camino Inca and AB-Chen-Chen are thermotropical points situated near the foggy coastal hills. This bioclimatic succession reflects the transhumance with camelids between the Andean heights and the coast. The branche V-Huanca 2 is isolated in the dendrogram due to the presence of *Cantua buxifolia* Lam., *Mutisia acuminata* Ruiz & Pav. and *Salvia oppositiflora* Ruiz & Pav. shrub communities, these being common in the surroundings of Inca ruin sites (Figure 3b). Finally, the group X-Cahuachi to AD-Nanchoc are thermotropical archaeological coastal sites with *Zea mays* remains (Figure 3c) and plant remains from Amazonia, as *Canna edulis* Ker Gawl., *Ipomoea batatas*, or *Manihot sculenta*, and from the North, as *Erythroxylum novogranatense* var. *truxillense* (Figure 3d). AI-San Gabán (thermotropical) and AF-Iquitos (infratropical) represent two Amazonian regions where many products originate.

Minimal spanning tree (MST) shows a geographical relationship among different sites (Figure 4a) taking into account that AF-Iquitos and AI-San Gabán represent an Amazonian region, respectively infratropical and thermotropical. The

distance between AF-Iquitos and AH-Huaca Prieta means a road from Amazonia to the northern coast, as well as AI-San Gabán and AC-Beringa in the southern Peruvian Andes. Occidental Andean slopes – AC-Beringa, D-Pampamarca, T-Velinga, S-Huacán – are connected with medium altitudes such as O-Tenahaha, R-Huanca or N-Wayñuna, where corn crops are very extended, and from here to the highlands with llamas, alpacas and potato crops – Z-Pomata, AA-Puno, Q- Sibayo, K-Tuti, and P-Callalli 2. This itinerary can be plotted in a map (Figure 4b) showing a parallelism with the occidental and southern Andean sketch of the Inca Road (Qhapaq Ñan) across the desert and between the coast to the Amazonia respectively.

Arranging archaeological sites vs environmental variables

Results from the CCA ordination (Figure 5) show how the archaeological sites are grouped according to their plant

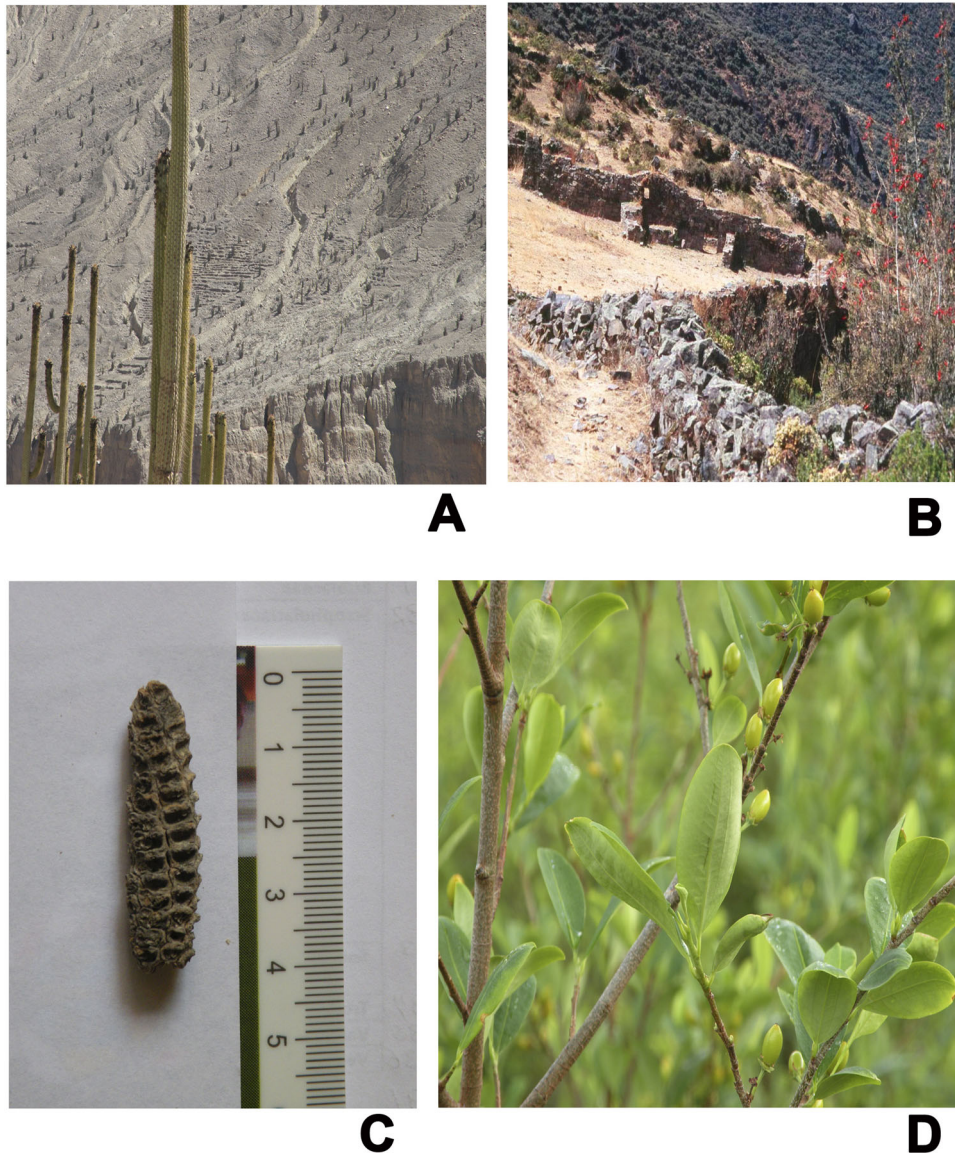


Figure 3. Some archaeological sites and important plant elements for ancient cultures of Peru. A, Wari terraces in Velinga (Arequipa) behind *Neoraimondio arequipensis*-*Browningietum viridis* association; B, Inca ruins in the highlands of Lima, with *Cantua buxifolia* to the right; C, Ancient corncob from Aplao in Arequipa; D, *Erythroxylum novogranatense* var. *truxillense* ("tupa coca") from the Marañón valley.

remains, animals and plant associations representing their landscapes, correlated with the thermicity index (It), the humidity index (Io) and the altitude as environmental variables. Group A belongs to supra- and orotropical belts, where camelids (camel) and *Zea mays* (*Zea*), *Chenopodium quinoa* (Che qui), and *Solanum tuberosum* (Sol tub) can be found, and the principal landscape is grasslands of *Parastrephio quadrangularis-Festucetum dolichophyllae* (PAR-FES) in the South and *Festuco dolichophyllae-Calamagrostietum antonianae* (FES-CAL) associations in the center. Group B is the mesotropical group with *Zea mays*, where the sites on the left – N-Waynuña and O-Tenahaha – are more humid than the ones on the right – R-Huanca, V-Huacán, and Y-Cerro Baúl, whose landscapes contain a very xerophytic vegetation, such as *Schino mollis-Tecometum arequipensis* (SCH-ARE), *Weberbauerocereo torataensis-Corryocactetum brevistyli* (TOR-COR), and *Schino mollis-Tecometum tanaeciiflorae* (SCH-TAN), and thus irrigation is necessary for agriculture; *Dunalio spinosae-Baccharidetum*

latifoliae (DUN-BAC) is near V-Huanca because irrigation canals can be found, and *Cantua buxifolia* (Can bux) was cultivated in the surroundings of the archaeological sites as an ornamental shrub.

Groups C and D belong to the occidental Andean and coastal thermotropical belt, where Amazonian products, such as *Bunchosia armeniaca* DC. (Bun arm), *Capsicum baccatum* L. (Cap bac), *Cucurbita ficifolia* Bouché (Cuc fic), *C. moschata* Duchesne (Cuc mos), *Indigofera suffruticosa* (Ind suf), *Inga feuillei* DC. (Ing feu), *Ipomoea batatas* (Ipo bat), *Lagenaria siceraria* (Lag sic), *Persea americana* Mill. (Per ame), and *Psidium guajava* L. (Psi gua) often appear. All these crops, being situated in Figure 5 between two kinds of natural vegetations, need irrigation: above the horizontal axis, we find, especially, several xerophytic cactus associations (group C) such as *Neoraimondio arequipensis-Browningietum viridis* (NEO-BRO), *Weberbauerocereo weberbaueri-Browningietum candelaris* (WER-BRO), and *Weberbauerocereo rauhii-*

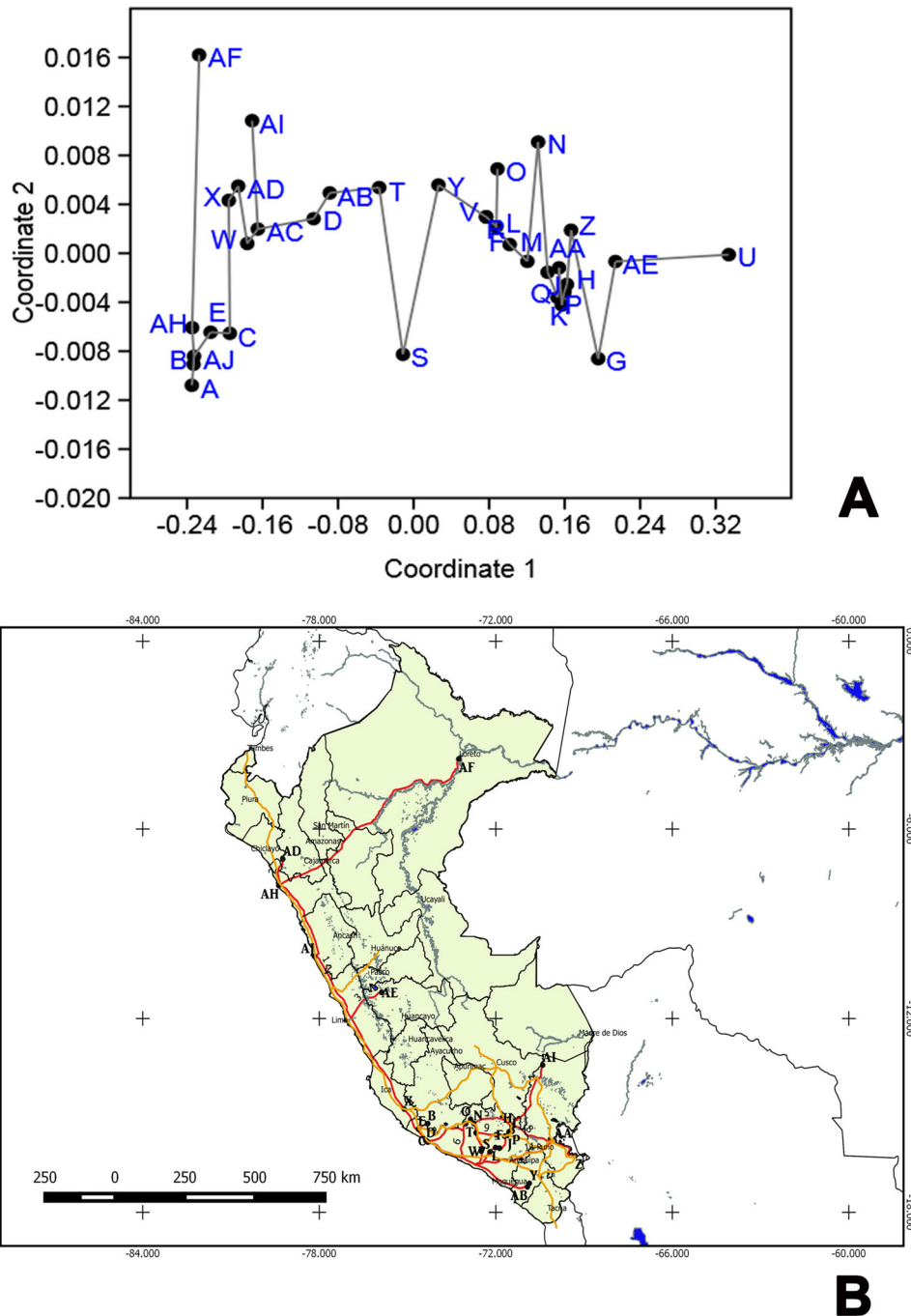


Figure 4. Geographic relationships among the different studied sites. A, Minimal spanning tree (MST) showing distances (letters are the same that in Figure 1); B, Map with the coastal Inca Road and some branches (in yellow) indicated by Guijarro and Gargate (2014), and the hypothetical roads (in red) with the archaeological sites referenced in the Figure 1 (black dots and capital letters).

Browningietum candelaris (RAU-BRO), while below, riverine plant associations (group D), such as *Baccharito salicifoliae-Gynerietum sagittati* (BAC-GYN), *Bacopo monnieri-Typhetum domingensis* (BAC-TYP), *Equiseto gigantei-Salicetum humboldtiana* (EQU-SAL), and *Schino mollis-Acacieta macracantha* (SCH-ACA) are present.

AF-Iquitos represents an infratropical Amazonian site where very gathered plants to lowlands were used, linked to rain forests such as *Paullinia cupana* Kunth (Pau cup), *Theobroma grandiflorum* (Willd. ex Spreng.) K. Schum. (The gra), and *Bertholletia excelsa* Bonpl. (Ber exc). Nevertheless, *Bixa orellana* L. (Bix ore) is displaced to the right in the

CCA, and it is an example of a domesticated plant that left the Amazonian borders to arrive at the Pacific coast, at least to Nazca archaeological sites. AI-San Gabán is an Amazonian hyperhumid region and, in consequence, very connected to the lo vector near *Ananas comosus* (L.) Merr. (Ana com) and *Erythroxylum coca* Lam. var. *coca* (Ery coc) as main domesticated plants very scarce as archaeological remains neither on the western slopes of the Andes nor on the coast. U-Coropuna is a cryotropical site with a glacial landscape and an ancient irrigation infrastructure with the *Nototricho obtusatae-Xenophylletum poposi* association (NOTO).

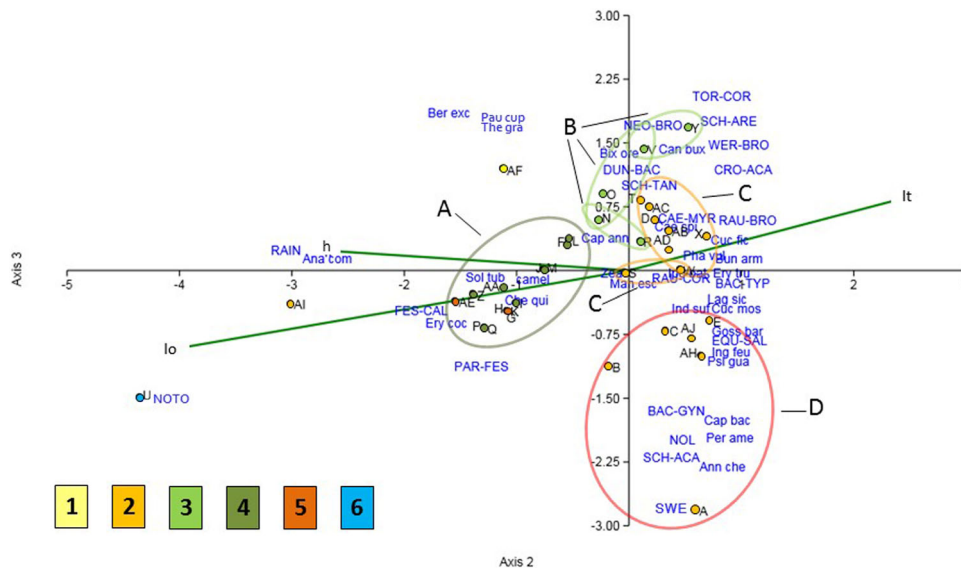


Figure 5. Canonical Correspondence Analysis (CCA) showing the groups formed between archaeological sites (letters are the same that in Figure 1), plant remains, camelids and plant associations that represent the surrounding landscapes, correlated with thermicity index (It), humidity index (Io) and altitude (h). Bioclimatic belts: 1, infratropical; 2, thermotropical; 3, mesotropical; 4, supratropical; 5, orotropical; and 6, cryotropical. Group A, supra- and orotropical archaeological sites; group B, mesotropical archaeological sites; group C, thermotropical archaeological sites near xerophytic cactus associations; and group D, thermotropical archaeological sites near riverine plant associations. Blue capital letters represent plant associations (see Table 2). Blue small letters represent plant remains, seaweeds, and camelids (see Results).

Discussion

Peru is a country where we find evidence of ancestral human activity (Whaley et al. 2010), linked to similar landscapes from pre-Hispanic periods (Beresford-Jones 2011), where camelids, transhumance and domesticating crops were very important, as Figures 2, 4a and 5 reflect. In the dendrogram (Figure 2) and in the CCA (Figure 5), sites such as P-Callalli 2, Q-Sibayo, Z-Pomata and AA-Puno are near the B-Inca Road, a thermotropical point on the coast, which shows the presence of camelids, and therefore, a transference of products between the highlands and the coast; and also a grassland searching for the animals when the highest belts are dry, due to the opposite rain period between the coast and the mountains with grasslands on the coastal hills (pastures of *Nolanion spathulatae* alliance) (Erickson 1992). This agrees with Lane et al. (2017) who recently underlined the presence of Nazca sites around 2000 m asl, perhaps to access or to interchange products, such as potato, with populations from the highlands. Also, the dendrogram and the CCA show several sites on the coast with plants from the eastern infratropical and thermotropical belts of Amazonia which, accordingly to Denevan (2007) and Beresford-Jones et al. (2011), were cultivated indicating a plant switch between the same bioclimate belts, but with different humidity ranges, of both Andean slopes, an idea previously developed by Gade (1999). On the coast, irrigation was very important (Rostworowski 2005) which allowed certain localities, such as C-Atiquipa, which were known to be used by pre-Inca and Inca cultures as production satellites, to carry some products toward the mesotropical to orotropical spaces of the mountains (Brush 1976; Canziani Amico 2009; Murra 2009). Additionally, Dillehay et al. (2007) supported the idea that *Arachis hypogaea* L. (*Ara hyp*), *Cucurbita moschata* (*Cuc mos*) and *Gossypium barbadense* L. (*Gos bar*) were cultivated in the

northern infra- and thermotropical belts from at least 8000 years ago, and afterwards were expanded to the South.

On the other hand, some plants are outlined in the CCA (Figure 5): *Erythroxyllum novogranatense* var. *truxillense* (*Ery tru*) – “tupa coca” – expanded to the South from the thermotropical western Andean slopes of northern Peru, from where archaeological records were found in Nanchoc (Cajamarca) by Dillehay et al. (2010), but an oriental origin in the dry lowlands of the Marañón valley is even probable (Plowman 1984). This dry condition favored crops in the western Andean region instead of *Erythroxyllum coca* var. *coca* (Bradley 2013) with an Amazonian origin (Clement et al. 2010). This distribution of cultivated *Erythroxyllum* P. Browne species is coincident with the CCA, where *E. novogranatense* var. *truxillense* is situated to the right of axis 2, between the thermotropical archaeological sites, near the xerophyllous cactus landscaped associations *Weberbauerocereo rauhii-Browningietum candelaris* (RAU-BRO) and *Weberbauerocero rauhii-Corryocactetum brevistyli* (RAU-COR) described by Galán de Mera et al. (2009), while *E. coca* var. *coca* is connected to the rain forests (RAIN) of *Cinchona micrantha* Ruiz & Pav. (Galán de Mera et al. 2017) to the left of axis 2.

A hypothetical itinerary for “tupa coca” can be drawn considering the minimal spanning tree (MST) and the map of the Figure 4b. Leastways, here, the AF-Iquitos points, representing Amazonian oriental territories, and AH-Huaca Prieta are connected, as well as other sites on the coast (Bird and Hyslop 1985). Thus, this hypothetical itinerary is coincident with the coastal Inca Road (Qhapaq Ñan) and its principal branch in the Cajamarca Department joining the Marañón Valley lowlands and the coast, as Plowman (1984) also suggested. Later, “tupa coca” reached Ica and Arequipa Departments in the South (Guijarro and Gargate 2014).

Annona cherimola Mill. (*Ann che*), *Gossypium barbadense* (*Gos bar*), and *Indigofera suffruticosa* (*Ind suf*) appear in the

CCA near the riverine plant associations of the hyperarid coast, *Schino mollis-Acacietaum macracanthae* (Galán de Mera et al. 2002), *Baccharito salicifoliae-Gynerietum sagittati* and *Equiseto gigantei-Salicetum humboldtiana* (Galán de Mera et al. 2004; Montesinos-Tubée and Mondragón 2013), this meaning an irrigated agriculture for these plants. *A. cherimola* and *G. barbadense* expanded to the South from the western slopes of northern Peru. Thermotropical dry forests of northern Peru were the source of cherimoya agriculture from the Pre-ceramic period (4000yr BP), as well as the Moche (1800–1300yr BP) and Chimú (1000–800yr BP) cultures (Bonavia et al. 2004). *G. barbadense* had already been cultivated for at least 8000 years (Dillehay et al. 2007), but was later recorded from the central coast of Peru dating to 5500yr BP (Wendel et al. 2010), tracing an expansion road along the coast (Figure 4b). *Indigofera suffruticosa*, an oriental plant in Peru (Tropicos 2019), was cultivated by the Nazca culture for cotton dye weaves (Beresford-Jones et al. 2011; Carvalho et al. 2014), and today we can find remains of this crop in the Acarí basin (Arequipa) in the humid soils of the *Equiseto gigantei-Salicetum humboldtiana* *indigoferetosum suffruticosae* subassociation (Montesinos-Tubée and Mondragón 2013). The hypothetical road plotted in Figure 4b presents numerous branches to the South such as the secondary routes of the Inca Road across the Cotahuasi Valley and near the Parinacochas lagoon, connecting the coast of Ica and Arequipa to the Urubamba Valley (Cusco), and the Amazonia (Guijarro and Gargate 2014); perhaps these routes were an entrance for Amazonian products into the southern Peruvian coast, which also is coincident with Wernke et al. (2017) in the area of the Qhapaq Ñan, in Southern Peru. This idea is also supported by the dendrogram (Figure 2) and by the minimal spanning tree (Figure 4a), where the E-Acarí River site belongs to the thermotropical group of the coast with close connections to the Amazonian localities.

Archaeological sites also contain plant remains belonging to the surrounding plant associations (Table 2). Remains of riparian woodlands of the plant associations *Equiseto gigantei-Salicetum humboldtiana* (EQU-SAL), *Acacio macracanthae-Tecometaum guarumis* (ACA-GUA), and *Schino mollis-Acacietaum macracanthae* (SCH-ACA) (Galán de Mera et al. 2009), and herb vegetation of the *Nicotiano paniculatae-Urocarpidietum peruviani* (NIC-URO) and *Bacopo monnieri-Typhetum dominicensis* (BAC-TYP) associations are frequent (Galán de Mera 1995; Galán de Mera et al. 2002, Galán de Mera et al. 2009). For example in X-Cahuachi (Ica), a town and ceremonial site of the Nazca, Wari and Inca cultures (Piacenza 2005). Moreover, using tree woods and rushes to roof buildings and for grazing, trees were planted to embank agricultural plots along their edges to retain seasonal floodwaters and protect against strong winds, and also the legume trees were used as nitrogen-fixing improvers (Whaley et al. 2010). Other plants, such as *Argemone subfusiformis* G.B. Ownbey and *Datura innoxia* Mill. were used as medicine or in rituals (Piacenza 2005). Y-Cerro Baúl (Moquegua) is a mesotropical hyperarid site, located between coastal localities in the dendrogram (Figure 2), and in the CCA (Figure 5) in the B group

near *Schino mollis-Tecometaum arequipensis* (SCH-ARE), and *Weberbauerocereo torataensis-Corryocactetum brevistyli* (TOR-COR) associations (Galán de Mera et al. 2009), coinciding with the use of fruits of *Schinus molle* L. to obtain fermented beverages (Goldstein et al. 2009). *Neoraimondia arequipensis* (Meyen) Backeb. is a thermotropical bio-indicator belonging to the *Weberbauerocereo-Browningietum candelaris* cactus associations (Galán de Mera et al. 2009) in the Andean western slopes and coastal hills, whose remains often appears in archeological sites as La Real (Arequipa) (Yépez Álvarez and Jennings 2012) or Chen Chen (Moquegua) (Blom 1999), its spines probably being used in textile activities, as Núñez et al. (2005) has also documented for other cacti in the Atacama region in Chile, even Piacenza (2005) has indicated *Echinopsis pachanoi* (Britton & Rose) H. Friedrich & G.D. Rowley ("San Pedro") in X-Cahuachi (Ica) as one of the plants used in religious rituals, clearly transported from the North, according to the distribution of this cactus (Ostolaza Nano 2014). In the group B of the CCA (Figure 5), shrubs of the *Dunalio spinosae-Baccharidetum latifoliae* (DUN-BAC) association are represented, which forms a unity with human settings around houses and terraces with maize in mesotropical and middle areas of supratropical belts (Galán de Mera et al. 2017, see also Montesinos-Tubée et al. 2012 for Moquegua), where *Cantua buxifolia* (Can bux) "Ccantu," which is a plant used in Inca agricultural rituals (Mulvany 2005), derives from (Figure 3b). Different branches of the dendrogram (Figure 2) and group A of the CCA (Figure 5) are sites of the upper supratropical belt with terraces and of the orotropical belt grasslands of *Parastrephio quadrangularis-Festucetum dolichophyllae* (PAR-FES) association (Galán de Mera et al. 2011a), where llamas and alpacas graze. This is an extended setting in the localities of the Colca Canyon – F-Achachiwa, M-Achoma, I-Callalli 1, J-Chivay, Q-Sibayo 2, G-Tisco, K-Tuti – since at least Wari times (Wernke 2003). Probably this use of grasslands is similar to those by the Wari State in Moquegua (Montesinos-Tubée et al. 2015), and Yarowilca culture (1018–486yr BP) between the departments of Ancash and Huánuco (Montesinos-Tubée 2016).

Finally, the CCA shows the AF-Iquitos locality as an infratropical humid region with rain forest near some plants such as *Bertholetia excelsa* (Ber exc), *Paullinia cupana* (Pau cup), and *Theobroma grandiflorum* (The gran), whose origin is the center of Amazonian basin, along the major white-water rivers, where the highest pre-conquest population densities developed (Clement et al. 2010). However, *Ananas comosus* (Ana com) and *Erythroxylum coca* var. *coca* (Ery coc) have an Amazonian peripheral origin (Clement et al. 2010, 2015) in the lower thermotropical belt, such as the AI-San Gabán region, but their remains have not been found in the archaeological sites of the Peruvian coast.

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Author contributions

Design of research: AGM & ELP; performance research: AGM, ELP, JMAG & JAVO; collection and organization of plants data from archaeological sites of Northern Peru: CRZ, FMR, ITM, JMQ; collection and organization of plants data from archaeological sites of Southern Peru: AGM, CTV, ELP, FVB & JAVO; review of geological and geomorphological data: CTV; bibliographical and herbarium queries at Real Jardín Botánico de Madrid: JMAG; construction of maps with QGIS and composition of images: ELP; manuscript writing: AGM & ELP; revised by all authors.

Disclosure statement

The authors declare that they have no conflict of interest.

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