

**PROYECTO DE INVESTIGACIÓN DE COLECCIONES Y FONDOS MUSEOGRÁFICOS**

**“DETERMINACIÓN DE LA ANTIGÜEDAD Y PROCEDENCIA DE LAS PLUMAS DE AVE ASOCIADAS  
A FARDOS YCHSMA EXCAVADOS POR EL PROYECTO ARQUEOLÓGICO PACHACAMAC-2005 EN  
EL SITIO DE PACHACÁMAC, PERÚ”**

**Informe Final**

**Presentado al Ministerio de Cultura del Perú por los doctores**

**Rafael Segura Llanos  
Universidad Antonio Ruíz de Montoya; Lima, Perú  
rafael.segura@uarm.pe**

**y**

**George Olah  
Universidad Nacional de Australia; Canberra, Australia  
george.olah@anu.edu.au**

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## 1. RESUMEN

Uno de los símbolos más prestigiosos de estatus entre las poblaciones prehispánicas de la costa y la sierra peruanas fueron sin duda alguna las plumas coloridas de aves exóticas de hábitats amazónicos. Sin embargo, poco sabemos sobre aspectos esenciales de la presencia documentada de estas plumas en regiones andinas no selváticas. ¿De qué aves específicamente se trata? ¿De qué parte de la selva amazónica proceden? ¿Cómo o bajo qué condiciones estos artículos arribaron a áreas tan distantes como la costa peruana? En esta línea de interés, este informe presenta los resultados de los análisis de datación radiocarbónica e isotópicos practicados en cinco muestras de plumas de loros (familia Psittacidae) procedentes de un contexto funerario llamado Tumba 1/2-'05 en Pachacamac, excavado en el año 2005 por el Proyecto Arqueológico Pachacamac. Los análisis confirman que las plumas se emplearon como adornos durante el período de ocupación Ychsma en el sitio, y revelan que las aves fueron traídas vivas a la costa, donde por algún tiempo proveyeron de plumas a las élites locales. Estos hallazgos plantean escenarios de adquisición de recursos y de contactos interregionales que superaron la formidable barrera de la cordillera de Andes siglos antes del surgimiento del imperio de los incas.

## 2. ANTECEDENTES, PROBLEMÁTICA Y OBJETIVOS DE LA INVESTIGACIÓN

Durante su temporada de campo de 2005, el Proyecto Arqueológico de Pachacamac (PAP) excavó una tumba de cámara (Tumba 1/2-'05) casi intacta ubicada en el cementerio Max Uhle frente al Templo Pintado, encontrando fardos de varios tamaños y estado de conservación (Shimada et al. 2010; Takigami et al. 2014). La datación por radiocarbono de los fardos, incluida los músculos conservados de los individuos momificados, los sitúa predominantemente entre los años 1000 y 1400 d.C. (Shimada et al. 2010; Takigami et al. 2014).

Algunos de los fardos más grandes fueron encontrados con un pequeño atado de plumas que todavía estaban unidas a la cabeza falsa. En otros casos, los atados de plumas se habían caído de los fardos. El hallazgo de estas plumas ofreció una excelente oportunidad para realizar análisis científicos encaminados a determinar la identidad y procedencia de las aves. En el año 2011, con el permiso de exportación de la Resolución Viceministerial No. 703-2011-VMPCIC-MC, los codirectores del PAP exportaron 25 pequeñas muestras de plumas de aves de la Tumba 1/2-'05 para (a) identificar taxonómicamente las aves correspondientes mediante análisis de ADN, y (b) demarcar las ubicaciones geográficas aproximadas de los hábitats de las aves identificadas.

En línea con estos objetivos, los análisis en el Laboratorio del Centro Australiano para ADN Antiguo (ACAD, por sus siglas en inglés) de la Universidad de Adelaida, Australia, permitieron identificar los genomas mitocondriales parciales de cinco especies: tres especies de guacamayos (*Ara macao*, *Ara ararauna* y *Ara chloropterus*) y un loro amazónico (*Amazona farinosa* cf. *farinosa*, *inornata*, *chapmani*), todos ellos con hábitat conocido en la selva amazónica, y una gaviota (*Xema sabini*) de la costa peruana (Segura et al. 2024).

Sin embargo, centrándonos en las plumas de los loros amazónicos (familia Psittacidae), nos propusimos realizar una determinación más certera de su antigüedad, y esclarecer si fueron adquiridas directamente de la Amazonía o bien de aves que fueron criadas en cautiverio en algún lugar de la costa. Para ello, se implementó una segunda fase de investigación que consistió en añadir al estudio cinco muestras de plumas de la Tumba 1/2-'05 para someterlos directamente a su datación radiocarbónica (AMS) y análisis de isótopos estables (no

radiactivos) de carbono, nitrógeno y oxígeno en Australia. El presente informe da cuenta de los resultados de tales análisis adicionales remitidos al equipo de investigación en agosto de 2025.

### **3. METODOLOGÍA APLICADA EN EL DESARROLLO DE LA INVESTIGACIÓN**

A continuación, se detalla de forma resumida el procedimiento realizado tanto en la selección de muestras en Perú como en los análisis en Australia.

#### Selección y exportación de muestras:

Siguiendo las recomendaciones del Museo de Sitio de Pachacamac, se implementó el Proyecto de Investigación de Colecciones y Fondos Museográficos *“Determinación de la antigüedad y procedencia de las plumas de ave asociadas a fardos Ychsma excavados por el Proyecto Arqueológico Pachacamac-2005 en el Sitio de Pachacámac, Perú”*, cuya ejecución fue autorizada a los doctores Rafael Segura Llanos y George Olah mediante las resoluciones directorales Nro. 000039-2024-DGM-VMPCIC/MC del 16.04.2024 y 000046-2024-DGM-VMPCIC/MC del 25.04.2024 (ver Anexo 1). El Dr. Segura supervisaría la correcta recolección y envío de las muestras en y desde Perú mientras que el Dr. Olah supervisaría la adecuada recepción y distribución de las plumas en los laboratorios designados, coordinaría su procesamiento y recopilaría los resultados en Australia. En concreto, este proyecto tuvo como único objetivo seleccionar cinco muestras de plumas de la Tumba 1/2-’05 para someterlos a los análisis destructivos referidos.

La búsqueda y selección de plumas adecuadas para el estudio se efectuó los días 25 de abril y 2 de mayo de 2024 en el almacén del Museo de Pachacamac donde se guardan los materiales arqueológicos excavados por el Proyecto Arqueológico Pachacamac - Temporada 2005 (almacenes localizados cerca del Puente Lurín). Con ayuda del inventario general de materiales del proyecto, el Dr. Segura abrió varias cajas hasta encontrar las plumas de la Tumba 1/2-’05. Estas fueron manipuladas cuidadosamente con guantes de látex estériles, desempolvadas (cuando fue necesario) con bombilla, fotografiadas y directamente colocadas dentro de bolsas estériles ziplock debidamente rotuladas. La búsqueda inicial se hizo con la presencia de la Lic. Rosangela Carrión Albán, especialista del Área de Registro y Manejo de Colecciones del Museo, y la posterior selección con la presencia, en todo momento, de un trabajador encargado por el museo. El muestreo priorizó: (a) el estado de conservación de las plumas, (b) el color como indicativo potencial de algunas de las especies de loros previamente identificadas mediante el análisis de ADN, (c) la presencia del cálamo o raquis, y (d) su ubicación segura dentro de la tumba, en algunos casos en directa asociación con algún fardo en particular. Las muestras seleccionadas se muestran en la Tabla 1.

Tabla 1  
Muestras de plumas seleccionadas de la Tumba 1/2-'05 de Pachacamac exportadas a Australia el 2024

	Nro. Registro	Trinchera	Rasgo o Tumba, temporada 2005	Peso (gr.)	Descripción	Detalles de contexto
1	11519	7	Tumba 1/2	2.8	Pluma de color verde. Longitud máx. 7.3 cm.	Pluma de penacho adherido a palo del Fardo C
2	11520	7	Tumba 1/2	2.7	Pluma con vetas de color naranja y azul. Longitud máx. 5 cm.	Interior de la tumba, pero sin asociación a fardo específico
3	11522	7	Tumba 1/2	3.2	Pluma de color naranja. Longitud máx. 9.5 cm.	Pluma de posible penacho asociado a Fardo A
4	12352	7	Tumba 1/2	2.3	Pluma de color amarillo. Longitud máx. 5.4 cm.	Pluma sobre segunda esterilla cubriendo Fardo U
5	12455	7	Tumba 1/2	3.3	Pluma de color naranja. Longitud máx. 12 cm.	Pluma sobre el piso de la tumba

Con base a esta lista y datos asociados, el Museo de Sitio de Pachacamac emitió el Acta de Entrega del 2 de mayo de 2024 a fin de que los investigadores puedan proceder al siguiente trámite de solicitud de exportación de muestras (ver Anexo 2). Tal solicitud fue resuelta con la Resolución Viceministerial Nro. 000147-2024-VMPCIC/MC del 31.05.2024 que autorizó el envío de las muestras a Australia mediante los servicios de courier de la empresa FedEx, específicamente a la ciudad de Canberra (ver Anexo 3). Las muestras salieron del país el 31 de julio del 2024 luego de tramitarse también un certificado internacional de pre-convención CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) ante SERFOR (Servicio Nacional Forestal y de Fauna Silvestre) del Ministerio de Desarrollo Agrario y Riego del Perú.

Procesamiento de las muestras en laboratorio:

***Datación radiocarbónica:*** Las cinco muestras de plumas fueron procesadas en el Laboratorio de Radiocarbono de la Universidad Nacional de Australia en Canberra (SANU) por el Professor Stewart Fallon (Research School of Earth Sciences). Esto consistió básicamente de un pretratamiento estándar de las muestras para descontaminarlas y luego en su datación mediante un espectrómetro de acelerador de masas de una sola fase (Fallon et al. 2010).

Finalmente, los fechados radiocarbónicos resultantes fueron calibrados con la curva SHCal20 mediante el programa OxCal v.4.4.4 (Hogg et al. 2020, Ramsey 2021).

**Análisis isotópico:** Las restantes porciones de las muestras de plumas fueron analizadas en el Laboratorio de Isótopos Estables de la Universidad Nacional de Australia en Canberra por el Dr. Hilary Stuart-Williams (Research School of Biology). Originalmente se había programado el análisis simultáneo de isótopos de carbono ( $\delta^{13}\text{C}$ ), nitrógeno ( $\delta^{15}\text{N}$ ) y oxígeno ( $\delta^{18}\text{O}$ ), pero las estimaciones de oxígeno no fueron realizadas por razones presupuestales. De todos modos, consideramos que los resultados de isótopos de carbono y nitrógeno fueron suficientes para nuestros propósitos específicos.

Después de un pretratamiento de limpieza, el contenido de C y N fue medido por combustión en un Analizador Elemental EA1110. El gas resultante de este procedimiento fue analizado con un Espectrómetro de Masas Isoprime. Seguidamente, los valores de  $\delta^{13}\text{C}$  y  $\delta^{15}\text{N}$  obtenidos de cada muestra fueron promediados, estimándose en cada caso la proporción C:N. En un paso posterior para nuestros objetivos con fines comparativos, estos valores fueron normalizados con aquellos reportados en colágeno óseo en los estudios análogos de Capriles et al. 2021 en el desierto de Atacama.

#### 4. RESULTADOS DE LA INVESTIGACIÓN

Para entender nuestros resultados, es necesario retomar brevemente los hallazgos más relevantes de los análisis de ADN en las muestras exportadas el 2011, pues ellos definieron la ruta de investigación con las muestras de plumas exportadas el 2024. Una exposición más detallada de estos resultados puede obtenerse en el artículo publicado adjunto (ver Anexo 4).

##### Resultados de los análisis de DNA

Con ayuda de los previos análisis de ADN endógeno y atributos morfológicos (tamaño y color) de las plumas (Segura et al. 2024), se pudo determinar la identidad taxonómica (a nivel de especie) de las aves de las que proceden las cinco muestras de plumas exportadas el 2024. Estas identificaciones se presentan en la Tabla 2.

Tabla 2

Identidad taxonómica de loros (fam. Psittacidae) a partir de las cinco muestras de plumas de la Tumba 1/2'05 de Pachacamac exportadas el 2024

Nro. Inventario PAP	Identificación Familia	Identificación Género-especie	Tipo de muestra	Contexto arqueológico
11519	Psittacidae	<i>Amazona farinosa</i>	Pluma	Tumba 1/2
11520	Psittacidae	<i>Ara macao</i>	Pluma	Tumba 1/2
11522	Psittacidae	<i>Ara chloropterus</i>	Pluma	Tumba 1/2
12352	Psittacidae	<i>Ara ararauna</i>	Pluma	Tumba 1/2
12455	Psittacidae	<i>Ara chloropterus</i>	Pluma	Tumba 1/2

##### Resultados de la datación radiocarbónica:

Las dataciones radiocarbónicas AMS obtenidas demuestran que los adornos de plumas son ampliamente contemporáneos con los fardos funerarios de la Tumba 1/2-'05, y que en conjunto todos estos restos anteceden al imperio de los incas en tanto se fechan principalmente entre los siglos XII y XIV, dentro del llamado Periodo Intermedio Tardío o Período de los Estados Regionales. La variedad de fechados dentro de este rango sugiere, preliminarmente, que los entierros fueron ocurriendo progresivamente dentro de la tumba, y

que durante todo este tiempo hubo un acceso continuado a plumas de origen extraregional. Los resultados se muestran en la Tabla 3.

Tabla 3

Fechados radiocarbónicos de cinco muestras de plumas de loros (fam. Psittacidae) de la Tumba 1/2'05 de Pachacamac, exportadas el 2024

Nro. Inventario PAP	Lab ID	Tipo de muestra	Contexto arqueológico	Fecha-do BP <sup>14</sup> C	Error ±	Fechado calibrado 2σ (95%)
11519	SANU-78321	Pluma	Tumba 1/2	1000	18	1157-1265
11520	SANU-78119	Pluma	Tumba 1/2	751	18	1102-1225
11522	SANU-78120	Pluma	Tumba 1/2	837	18	1347-1457
12352	SANU-78121	Pluma	Tumba 1/2	909	18	1292-1350
12455	SANU-78123	Pluma	Tumba 1/2	886	18	1229-1295

Resultados de los análisis isotópicos:

Los análisis de ADN antiguo, exámenes filogenéticos, e identificación de los haplotipos de las plumas exportadas el 2011, y su comparación con los datos de las plumas de guacamayos modernos, incluyendo especímenes de Tambopata, también habían indicado de manera fehaciente una notoria diversidad genética, lo que es muy consistente con el escenario de que las aves fueron capturadas en su hábitat amazónico original. Para confirmar esta procedencia selvática, se procedió con los análisis isotópicos de C y N, ya que la proporción entre estos dos elementos permite determinar la composición de la dieta de los animales bajo estudio. Se esperaba que las mediciones fuesen consistentes con la dieta de las aves silvestres amazónicas. Sin embargo, los análisis isotópicos revelaron valores altos de  $\delta^{13}\text{C}$  y  $\delta^{15}\text{N}$  (Tabla 4), indicativos de una dieta muy distinta, particularmente basada en el consumo de plantas C4, un grupo de plantas que en la cordillera y costa de los Andes centrales está fuertemente representado por el maíz. De este modo, los datos genéticos e isotópicos combinados indican que los loros, y particularmente los guacamayos, que proveyeron de plumas coloridas a las poblaciones que se enterraban en Pachacamac fueron capturados en la selva amazónica. Subsiguientemente, ellos fueron transportados vivos a la costa donde fueron alimentados con una dieta propiamente costeña. La ausencia de datos publicados en más de un siglo de arqueología dando cuenta de jaulas, huevos o esqueletos de guacamayos en la costa fortalece la inferencia de que, al menos en Pachacamac, no hubo propiamente un programa de crianza de estas aves bien establecido a través del tiempo.

Tabla 4

Mediciones de isótopos estables de C y N en cinco muestras de plumas de loros (fam. Psittacidae) de la Tumba 1/2'05 de Pachacamac, exportadas el 2024

Nro. Inventario PAP	Lab ID	Tipo de muestra	Contexto arqueológico	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	C corregido	Proporción C:N
11519	SANU-78321	Pluma	Tumba 1/2	8.98	-7.64	-6.04	3.09
11520	SANU-78119	Pluma	Tumba 1/2	11.90	-10.20	-8.60	2.86
11522	SANU-78120	Pluma	Tumba 1/2	12.57	-8.15	-6.55	2.95
12352	SANU-78121	Pluma	Tumba 1/2	7.87	-9.47	-7.87	2.96
12455	SANU-78123	Pluma	Tumba 1/2	13.74	-8.67	-7.07	3.14

## 5. ACCIONES DE CONSERVACIÓN PREVENTIVA

Debido a la naturaleza y objetivos del proyecto de investigación no se realizaron intervenciones de conservación. Como corresponde, se efectuó una manipulación cuidadosa de las plumas seleccionadas para evitar su daño o contaminación, como brevemente se menciona en la sección 3 de este informe. Por otro lado, las muestras no regresaron a Perú pues, como se indicó en los permisos correspondientes, los exámenes realizados fueron de carácter destructivo.

## 6. CONCLUSIONES Y RECOMENDACIONES

Los resultados expuestos llevan a la conclusión de que los guacamayos cuyas plumas fueron usadas para adornar fardos funerarios de la tradición cultural Ychsma (1000 – 1450 d.C.) fueron capturados en algún lugar de la selva amazónica peruana y luego trasladados vivos a Pachacamac. Esto permite sostener que lejos de ser una sociedad carente de contactos extraregionales significativos, que es como tradicionalmente se ha caracterizado a la llamada cultura Ychsma, esta supo acceder a recursos de territorios muy distantes y ecológicamente muy diferentes durante gran parte de su desarrollo. Por supuesto, esto lleva a la obvia pregunta sobre bajo qué modelo y estrategias de adquisición esta población costeña tuvo acceso a los recursos mencionados. Aunque ya no forman parte de este informe, se debe mencionar que nuestros posteriores análisis y modelamientos espaciales con herramientas SIG plantean dos rutas alternativas de intercambio o movilización de las aves capturadas: desde la selva norte (región de la cultura Chachapoyas) hacia la costa norte, donde las sociedades Sicán (Lambayeque) y Chimú pudieron asumir un papel de intermediarios, dado que existe amplia evidencia de sus firmes contactos con las sociedades de la costa central, o desde la selva central a través de un corredor transversal a los Andes que conectó la región de Cerro de la Sal con Pachacamac. Mayores detalles y aspectos metodológicos sobre esta reconstrucción de rutas pueden ser revisados en el artículo publicado adjunto (ver Anexo 4).

## 7. EQUIPO DE INVESTIGADORES Y RESPONSABILIDADES

A continuación, se muestra una lista de especialistas con sus respectivas responsabilidades y afiliaciones institucionales.

- ◆ Dr. Rafael Segura Llanos ([rafael.segura@uarm.pe](mailto:rafael.segura@uarm.pe))  
Departamento de Ciencias Humanas  
Universidad Antonio Ruíz de Montoya  
Av. Paso de Los Andes 970, Pueblo Libre, Lima.  
web: <https://www.uarm.edu.pe/>  
Co-director del proyecto. Identificó las muestras de plumas apropiadas para el estudio propuesto, gestionó el permiso de exportación correspondiente y envió vía courier las muestras al Dr. Olah en Australia.
  
- ◆ Dr. George Olah ([george.olah@anu.edu.au](mailto:george.olah@anu.edu.au))  
Fenner School of Environment & Society  
The Australian National University  
Building 141, Linnaeus Way  
Canberra, ACT, 2600, Australia  
web: <https://researchers.anu.edu.au/researchers/olah-g>  
Co-director del proyecto. Recibió las muestras en Australia. Realizó una documentación escrita y fotográfica básica de las plumas y coordinó su procesamiento en laboratorio.

Recibió los resultados discutiéndolos con el equipo. Mantuvo estrecho contacto con el Dr. Segura.

- ◆ Dr. Stewart Fallon ([Stewart.Fallon@anu.edu.au](mailto:Stewart.Fallon@anu.edu.au))  
Laboratorio de Radiocarbono SANU (espectroscopía de masas con acelerador de partículas)  
Research School of Earth Sciences  
The Australian National University  
Building 142, Mills Road  
Canberra, ACT, 2600, Australia  
web: <https://earthsciences.anu.edu.au/research/facilities/anu-radiocarbon-laboratory>  
El Dr. Fallon supervisó la datación por radiocarbono de las muestras de plumas exportadas.
  
- ◆ Dr. Hilary Stuart-Williams ([hilary.stuart-williams@anu.edu.au](mailto:hilary.stuart-williams@anu.edu.au))  
Stable Isotope Laboratory, Research School of Biology  
The Australian National University  
Building 46, R.N. Robertson Building  
Canberra, ACT, 2600, Australia  
web: <https://biology.anu.edu.au/research/facilities/stable-isotope-laboratory>  
El Dr. Stuart-Williams supervisó el análisis de isótopos estables (carbono y nitrógeno) de las muestras de plumas exportadas.

## 8. INVENTARIO DE BIENES CULTURALES MUEBLES INVESTIGADOS

Los materiales estudiados se encuentran indicados en la Tabla 1.

## 9. MEDIOS DE DIFUSIÓN DE LA INVESTIGACIÓN

Los resultados acaban de ser publicados en la revista *Nature Communications* 17, 2117 (2026), bajo el título *Ancient DNA and spatial modeling reveal a pre-Inca trans-Andean parrot trade*. (<https://doi.org/10.1038/s41467-026-69167-9>), siendo el autor principal el Dr. Olah acompañado del equipo que participó en la investigación en las fases de excavación arqueológica (año 2005), análisis de ADN (exportación año 2011) y análisis radiométricos e isotópicos (exportación año 2024). Se adjunta copia del artículo en el Anexo 4. Asimismo, una serie de aspectos complementarios de la investigación se difunden en diversos websites dedicados a la divulgación científica. Se indican algunos ejemplos:

<https://communities.springernature.com/posts/feathers-of-the-rainforest-tracing-the-pre-inca-trade-of-amazonian-parrots-to-the-peruvian-coast>

<https://www.science.org/content/article/ancient-peruvians-transported-live-parrots-across-andes>

<https://www.popsci.com/science/ancient-parrot-trade-peru-inca/>

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**ARCHIVO FOTOGRÁFICO DEL PROCESO DE TRABAJO Y DE LOS BIENES CULTURALES MUEBLES  
INVESTIGADOS**



Figura 1: Área de excavación de la Tumba 1/2-'05 frente al Templo Pintado de Pachacamac.  
Excavación de la temporada 2005



Figura 2: Tumba 1/2-'05 con 34 fardos Ychsma en su interior. Varios de ellos con adornos de plumas



Figura 3: Penacho de plumas de guacamayo dentro de la Tumba 1/2-'05



Figura 4: Algunos adornos de plumas revisados durante el proceso de muestreo en Museo de Pachacamac

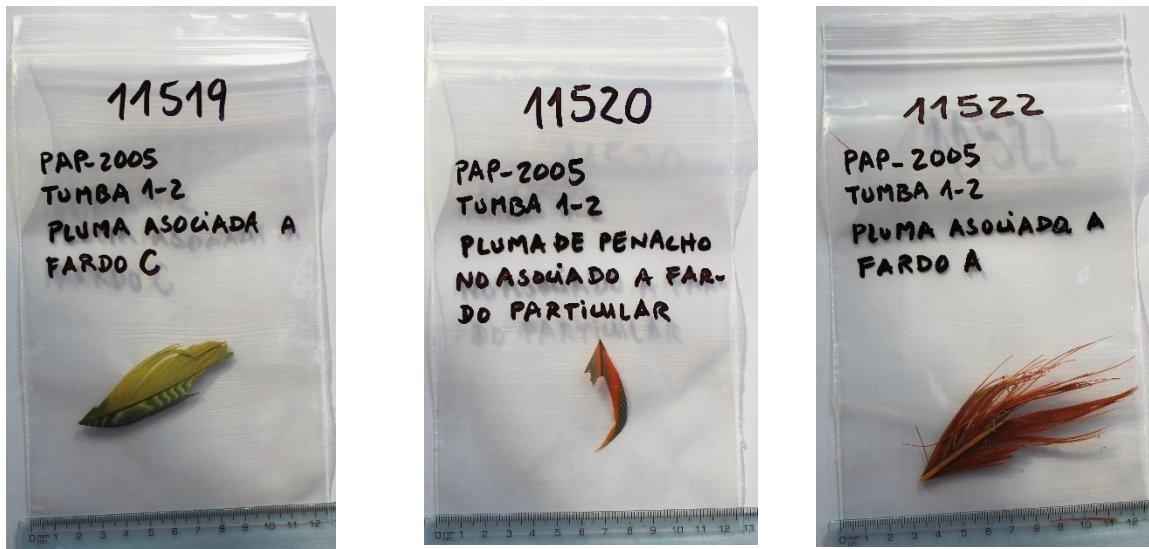


Figura 5: Muestras de plumas seleccionadas para exportación



Figura 6: Procesamiento de plumas en el Laboratorio del Centro Australiano para ADN Antiguo (ACAD)

# Ancient DNA and spatial modeling reveal a pre-Inca trans-Andean parrot trade

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George Olah <sup>1,2,10</sup> , Pere Bover <sup>3,4,10</sup> , Bastien Llamas <sup>5,6,7</sup>,  
Holly Heiniger <sup>5</sup>, Rafael Segura Llanos<sup>8</sup> & Izumi Shimada <sup>9</sup> 

Vibrant feathers from Amazonian parrots were among the most prestigious symbols of status in the pre-Hispanic Andes, yet their acquisition required traversing the formidable Andean mountain range. Here, we investigate feathers recovered from an intact, elite masonry tomb at the coastal religious center of Pachacamac, associated with the pre-Inca Ychsma culture that flourished during the Late Intermediate Period (ca. 1000–1470 CE). By integrating ancient DNA, stable isotope analysis, and spatial modeling, we reconstruct the complete journey of these feathers. Genomic data identify four distinct Amazonian parrot species (*Ara macao*, *A. ararauna*, *A. chloropterus*, *Amazona farinosa*) and reveal high genetic diversity, indicating extraction from wild populations rather than local breeding. Stable carbon and nitrogen isotope analysis reveals that these birds consumed a C4-rich coastal diet, demonstrating they were transported alive across the Andes and kept in the arid coast. Finally, we identify specific trans-Andean corridors used for this exchange by combining species distribution models of ancient habitats with landscape resistance modeling. Our findings reveal a sophisticated, managed trade network operated by the Ychsma through intermediaries, challenging views of pre-Inca regionalism and establishing a multidisciplinary toolkit for tracing ancient exchange.

The vibrant feathers of Amazonian parrots were highly prized goods in the ancient cultures of coastal Peru, essential for communicating status, power, and cosmology<sup>1–6</sup>. The reliable acquisition of these prestige goods from east of the Andes was a critical factor in the political economy of prominent coastal cultures such as Moche and Nasca as well as highland empires of the Wari and Inca<sup>7</sup>. However, the scale, organization, and specific routes of the trade networks that moved these items across one of the world's most formidable mountain

ranges before the rise of the Inca remain largely speculative. Resolving this requires identifying the geographic origins of the birds used to produce the ancient featherworks.

There is ample evidence of the long and extensive use of parrot feathers among pre-Hispanic cultures of the Andes<sup>1–3</sup>, Mesoamerica<sup>8</sup>, and in the American Southwest<sup>9</sup>. Within ancient Peru, parrots were represented sculpturally and/or in painting in the pottery styles ranging from Moche (Mochica; ca. 200–850 CE) and Middle Sicán (Classic

<sup>1</sup>Fenner School of Environment and Society, The Australian National University, Canberra, ACT, Australia. <sup>2</sup>King's Forensics, Department of Analytical, Environmental and Forensic Sciences, Faculty of Life Sciences and Medicine, King's College London, London, UK. <sup>3</sup>ARAID Foundation, Zaragoza, Spain.

<sup>4</sup>Instituto Universitario de Investigación en Ciencias Ambientales (IUCA), Grupo Aragosaurus, Universidad de Zaragoza, Zaragoza, Spain. <sup>5</sup>Australian Centre for Ancient DNA, School of Biological Sciences, Environment Institute, Adelaide University, Adelaide, SA, Australia. <sup>6</sup>National Centre for Indigenous Genomics, Australian National University, Canberra, ACT, Australia. <sup>7</sup>Indigenous Genomics, The Kids Research Institute Australia, Adelaide, SA, Australia. <sup>8</sup>Departamento de Ciencias Humanas, Universidad Antonio Ruiz de Montoya, Lima, Peru. <sup>9</sup>School of Anthropology, Political Science, and Sociology, Southern Illinois University, Carbondale, IL, USA. <sup>10</sup>These authors contributed equally: George Olah, Pere Bover. ✉e-mail: [george.olah@anu.edu.au](mailto:george.olah@anu.edu.au); [pbover@unizar.es](mailto:pbover@unizar.es); [ishimada@siu.edu](mailto:ishimada@siu.edu)

Lambayeque; 900–1100 CE) on the north coast, to Paracas (ca. 800–100 BCE) and Nasca (ca. 100 BCE–650 CE) on the south coast<sup>10,11</sup>. The direct indications of the important roles and values of parrots and their feathers are their preserved remains from well-documented archaeological contexts, especially as “feathered cloth”<sup>1–3,6</sup>. For making these ornaments, only less than 2% of all bird species in the Amazon region were used, most commonly parrots<sup>12</sup>.

In Andean scholarship, Amazonia is indeed often considered as a source of raw materials including bird feathers<sup>7</sup>. The rise of well-organized, late pre-Hispanic Arawak exchange/trade network (perhaps starting as early as 500 CE) to collect and distribute the desired Amazonian resources could have been critical for a reliable supply of the desired bird feathers out of Amazonia. Conservative estimates describe a trapping zone of ~100,000 km<sup>2</sup> to supply millions of Amazonian birds to the highlands for the Wari and Inca empires<sup>7</sup>. Transporting goods a great distance by land and/or sea raises the question of the high costs involved. The rarity and high esteem of exotic feathers in funerary ornaments of the central coast of Peru hint to a high value that paid off transporting from a far.

Here, we investigate a unique collection of feathered ornaments recovered from an intact, elite Ychsma culture tomb (ca. 1000–1470 CE) at the paramount religious center of Pachacamac, on the central coast of Peru<sup>13–15</sup>. Excavated from the Sacred Precinct in front of the Painted Temple—the same area of Max Uhle’s pioneering work that defined the Andean chronological framework<sup>16–19</sup>—the tomb contained 34 funerary bundles with five large ones adorned with bundled brilliant parrot feathers. While parrots (Psittaciformes) are a diverse tropical order<sup>20,21</sup>, and many species are native to the Neotropics, visual identification of processed feathers is often limited to broad categories like macaw (mainly *Ara* sp.) or Amazon parrot (*Amazona* sp.), precluding precise species identification and provenance. This limitation has historically hindered our ability to reconstruct ancient trade dynamics.

To overcome this challenge, we developed a cross-disciplinary approach integrating archaeological data with advanced biomolecular, geochemical, and computational modeling techniques. While ancient DNA (aDNA) can be recovered from feathers<sup>22,23</sup>, its application to fragile archaeological artifacts has been rare. Using targeted enrichment and high-throughput sequencing optimized for degraded material<sup>24,25</sup>, we successfully extracted aDNA from feather barb fragments. We combined these genetic identifications with stable isotope analysis ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ), AMS radiocarbon dating, and spatial modeling to pinpoint the taxonomic identity, diet, and geographic origin of the birds.

This study uses a multi-proxy approach to resolve the long-standing questions of provenance and procurement for these exotic feathers. We test the central hypothesis that the Ychsma, a regional coastal polity, sourced these feathers from wild Amazonian populations, a scenario that would require a carefully coordinated, long-distance trade network. By integrating ancient DNA for species identification, stable isotopes for dietary reconstruction, and species distribution and landscape modeling to map potential routes, we aim to provide direct evidence for the scale and nature of trans-Andean trade by a non-imperial society. This framework allows us to quantitatively test the economic and social connectivity between the Andes and Amazonia before the Inca Empire.

## Results

### An elite Ychsma tomb at a sacred coastal center

The famed religious-funerary center of Pachacamac, situated in the hyper-arid coastal desert of Peru—a region characterized by enduring aridity, punctuated by rains accompanying periodic El Niño Southern Oscillation (ENSO) events—presents a rare window into the sacred ritual practices of Andean societies. With tens of thousands of graves looted since the beginning of the Spanish colonial era and before the advent of scientific archaeology, the 2005 discovery of an intact Ychsma tomb in the Uhle Cemetery was an exceptional event (Fig. 1).

The funerary bundles—varying in size and construction—were prepared to emulate the appearance of the deceased in their formal, high-status look<sup>26</sup>. The most important personages were interred in large bundles featuring a decorated “false head”, often accompanied by cinnabar-painted wooden masks and striking feather headdresses, readily recognizable markers of elite status on the pre-Inca coast<sup>27,28</sup>. These feather ornaments, the focus of our study, were attached to the back of the false heads (Fig. 1f).

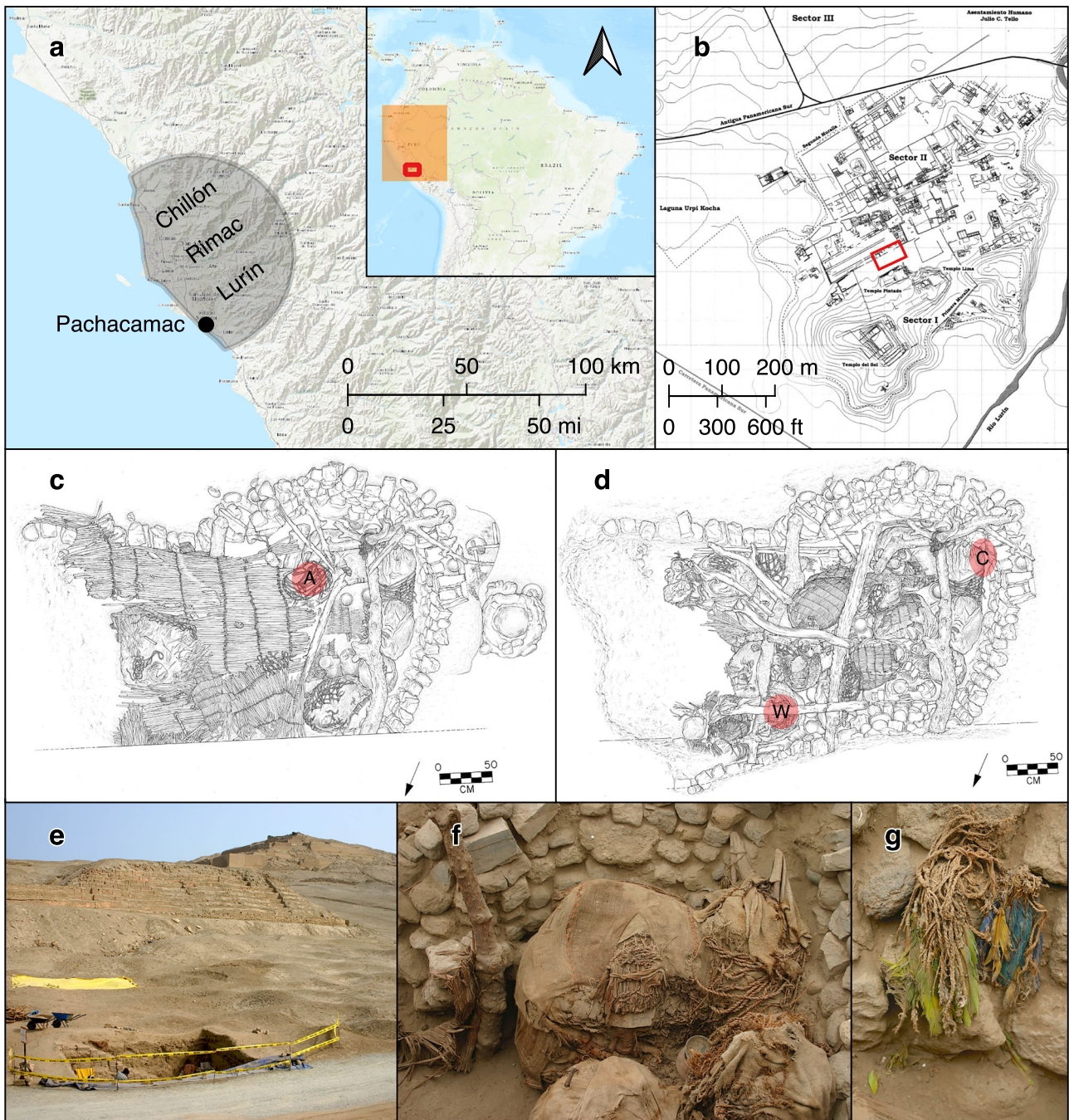
To establish a firm chronology for these artifacts, we conducted accelerator mass spectrometry (AMS) <sup>14</sup>C dating (see “Methods”). A series of feather samples from the ornaments yielded calibrated ages ranging from 1102 to 1457 CE (2 $\sigma$ ; Supplementary Table 1). These dates, combined with previous dating of textiles and human remains from the tomb and associated ceramics, securely place the burials in the period between ca. 1000 to 1400 CE<sup>29</sup>. This timeline firmly attributes the tomb to the Ychsma, a confederation of politically autonomous chiefdoms that flourished on the central coast during the Late Intermediate Period (ca. 1000–1470 CE), after the collapse of the Wari Empire and before subjugation by the Inca<sup>30,31</sup>. The Ychsma established a distinct regional identity, with Pachacamac serving as their undisputed religious epicenter<sup>14,32</sup>.

While societies of this era are often defined by their conflicts and regionalism, there is growing evidence that they did not develop in isolation<sup>33</sup>. The presence of these vibrant feather ornaments—presumably made from tropical birds—suggests significant long-distance contact. However, identifying the species and geographic origin of these birds, and thus the trade routes they represent, is often impossible through visual or macroscopic analysis alone<sup>34</sup>. We therefore turned to archaeogenetics to unlock the history preserved within the feathers themselves.

### Ancient DNA reveals a mix of local and Amazonian birds

To accurately determine the species used in the Pachacamac ornaments, we conducted genomic analysis on 25 ancient feathers sourced from eight different locations within the deposit (see “Methods” and Supplementary Data 1 for a detailed list of samples and their specific bundle provenance, whenever available). Working in the ancient DNA laboratory of the Australian Centre for Ancient DNA (ACAD, Adelaide University, Australia), we used targeted enrichment to sequence mitochondrial DNA from feather fragments (see “Methods”), which allows for robust identification even from degraded archaeological material<sup>35,36</sup>. The validated results show that the Ychsma utilized an avian assemblage sourced from two vastly different ecosystems. The colorful feathers belonged to four large parrot species (Fig. 2, Supplementary Figs. 1–7, and Supplementary Data 2–11): the Scarlet Macaw (*Ara macao*; haplogroup H4), Red-and-green Macaw (*Ara chloropterus*), Blue-and-yellow Macaw (*Ara ararauna*; haplogroup East = HE), and the Mealy Amazon (*Amazona farinosa*). In a single notable exception, one white feather was identified as a Sabine’s Gull (*Xema sabini*), a crow-sized seabird (Supplementary Figs. 1h and 8).

Phylogenetic and haplotype analyses provided further geographic context. The ancient macaw and Amazon parrot partial mitochondrial genomes consistently clustered with subspecies and haplogroups found today in the eastern regions of Peru and broader South America<sup>37,38</sup> (Fig. 3, and Supplementary Figs. 3–7). This genetic evidence creates a stark dichotomy in the origins of the birds. The Sabine’s Gull is an arctic breeder that winters along the Peruvian coast, making it a local resource for the Ychsma people within the rich Humboldt Current upwelling zone<sup>39</sup>. In sharp contrast, all four identified parrot species are native to lowland tropical rainforests and palm swamps located hundreds of kilometers to the east, on the other side of the Andes Mountains<sup>20</sup>. The unambiguous identification of this Amazonian avifauna confirms that the Ychsma society, centered on the arid coast, maintained extensive trans-Andes connections. This discovery raises a critical question regarding logistics: were these exotic



**Fig. 1 | Archaeological context of the Ychsma burials at Pachacamac.** **a** Map of Peru showing the Pachacamac Archaeological Site within the estimated territory of the Ychsma culture (gray shading) and our extended study area on the inlet map (orange shading). Map was created using QGIS v3.3 with ESRI World Topo as basemap. **b** Plan of the Pachacamac Sacred Precinct, with the location of Tomb 1/2 highlighted in red. **c, d** Drawings of the upper and lower layers of Tomb 1/

2, respectively, showing the arrangement of funerary bundles. The highlighted bundles with red indicate the location of bundles mentioned in this study. **e** The 2005 excavation in progress in front of the Painted Temple (also known as Temple of Pachacamac). **f** Funerary Bundles B and C in situ in the lower level of the tomb. **g** A representative feather ornament from Bundle C, composed of feather bundles tied to cotton cords. Photos by I. Shimada.

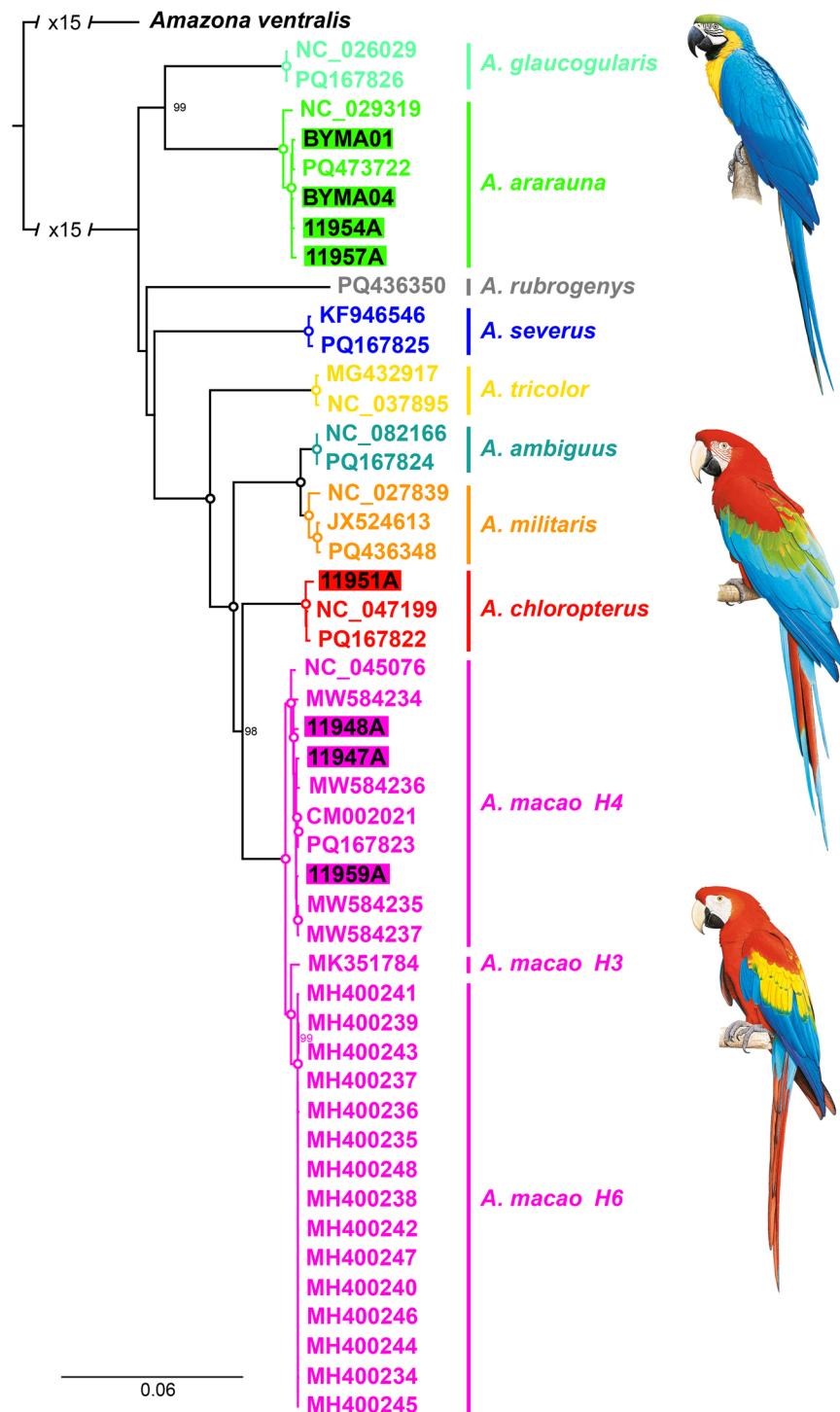
birds bred locally, or were they procured from their distant, wild habitats?

#### Genetic and isotopic data reveal wild origins and a coastal diet

The discovery of Amazonian parrots on the Peruvian coast begs the question of their procurement. One possibility is local captive breeding—a practice attested elsewhere in the pre-Hispanic Americas. At sites like Paquimé in Mexico<sup>40,41</sup> and in the Mimbres region of the American Southwest<sup>42</sup>, archaeologists have found direct evidence of

macaw breeding programs, including adobe cages, eggshells, and skeletons of captive birds dating to ca. 1100–1450 CE. Critically, these captive populations exhibit very low genetic diversity, a hallmark of inbred stocks<sup>43</sup>. To test this hypothesis at Pachacamac, we analyzed both the genetic diversity and the stable isotopic signatures of the ancient feathers.

The genetic evidence provides a clear verdict against local breeding. The mitochondrial genomes of the three ancient Scarlet Macaw feathers from Pachacamac were highly variable (Supplementary

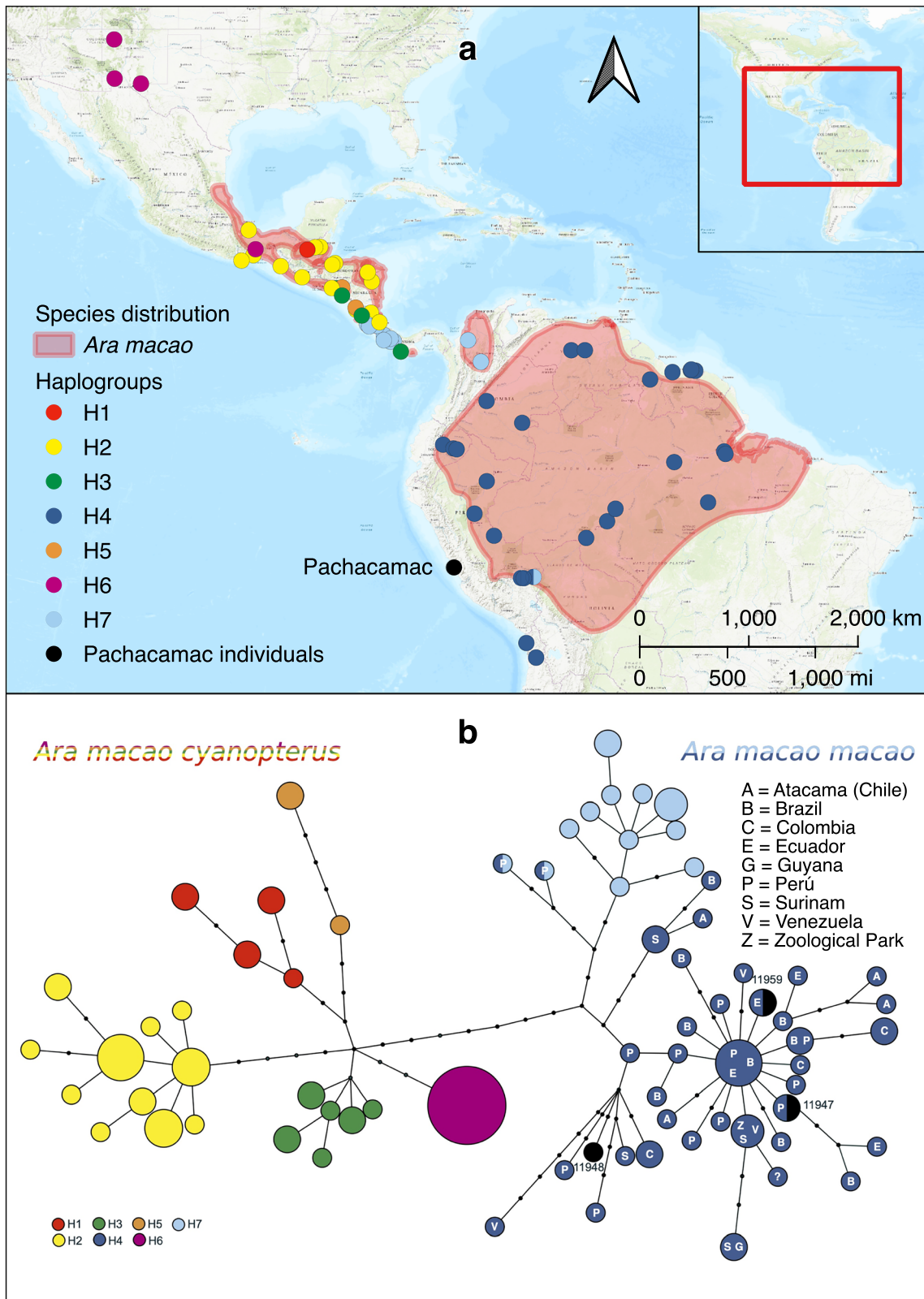


**Fig. 2 | Phylogenetic identification of ancient macaw feathers.** Maximum Likelihood tree based on mitochondrial genome sequences (15,455 bp), showing the placement of the six ancient feather samples from Pachacamac within the macaw genus *Ara*. The analysis confirms the identity of the samples as *Ara ararauna*, *A. chloropterus*, and *A. macao* (illustrated respectively from top to bottom, scaled relative to each other). The tree includes sequences from modern Peruvian *Ara*

*ararauna* macaw samples (BYMA01, BYMA04) and other reference specimens ( $n = 48$ , including outgroup). Numbers at nodes indicate bootstrap support; circles denote 100% support. Samples from this study are highlighted. Illustrations [by Luis Sanz] courtesy of Cornell Lab of Ornithology, from Birds of the World (<https://doi.org/10.2173/bow>).

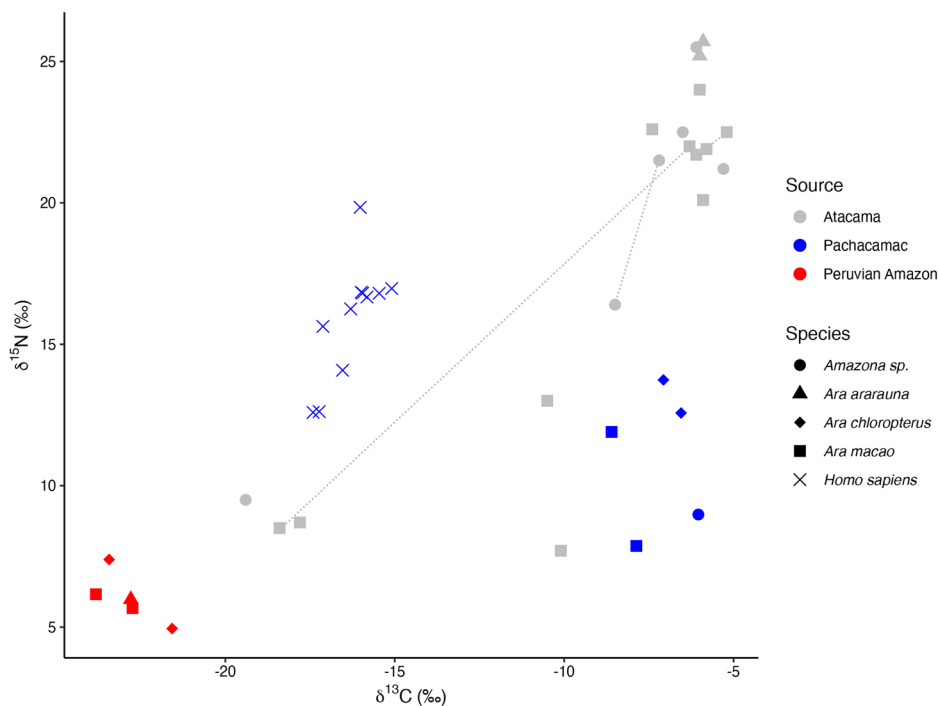
Table 2), defined by a high nucleotide diversity ( $\pi = 0.00223$ ) for these individuals. The average nucleotide diversity ( $n = 31$ ) reported for our H4 haplogroup in the wild is 0.00231 (SD = 0.00032), although using a smaller amount of mitochondrial data (~2200 bp)<sup>37</sup>. Furthermore, our value is also comparable to wild-sourced ancient macaws from other sites (Atacama Desert;  $\pi = 0.00272$ ) and dramatically exceeding the

near-zero ( $\pi = 0.00005$ ) diversity found in the known pre-Hispanic captive breeding colonies in the American Southwest<sup>4,43</sup>. Based on this stark relative difference from captive and match with wild populations, the genetic pattern strongly indicates that the Pachacamac feathers were sourced not from a small, local breeding program, but from a large, wild Amazonian population.



**Fig. 3 | Haplogroup analysis of ancient Scarlet Macaw feathers.** **a** Map showing the modern distribution of the Scarlet Macaw (*Ara macao*)<sup>121</sup> and the geographic locations of samples used in the network analysis (created by using QGIS v3.3 with ESRI World Topo as basemap). **b** Haplogroup network placing the three ancient Pachacamac samples (in black) firmly within Haplogroup 4.

This haplogroup is associated with the widespread South American subspecies, *A. m. macao*. The network is based on mitochondrial gene sequences from 121 modern and ancient individuals, with colors corresponding to previously identified haplogroups<sup>37</sup>.



**Fig. 4 | Isotopic evidence for a non-rainforest diet.** Plot of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope values from ancient samples from Pachacamac (blue), modern wild Amazonian parrots (red), and ancient parrots from the Atacama with a known captive diet (grey). The distinct isotopic signature of the Pachacamac feathers, which differs from the wild Amazonian samples, indicates a

local diet that included C4 plants possibly fertilized by seabird guano. Human data from Pachacamac are from ref. 29 and parrot data from Atacama are from ref. 4 (Supplementary Data 12). Dashed lines connect pairs of values from the same individual (see explanation in ref. 4). Values were standardized to collagen<sup>112,113</sup>.

While the genetics point to a wild origin, stable isotope analysis of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) revealed that the birds were not living in the rainforest when these feathers grew. Five ancient Pachacamac feathers tested (Supplementary Table 1) had enriched  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values ( $-10.20$  to  $-7.64\%$  and  $7.87$  to  $13.74\%$  raw values, respectively) that are distinct from modern parrots living in the Amazonian rainforest (Fig. 4, and Supplementary Data 12). This isotopic signature of the ancient feathers provides a dietary “snapshot” consistent with the consumption of C4 plants (such as maize) possibly fertilized by seabird guano, indicating the birds were sustained on a coastal diet during the specific period when these feathers grew.

The apparent paradox between the birds’ wild genetic origin and their coastal dietary signature is resolved by a model of capture and transport. The high genetic diversity shows they were hatched in the wild, while the coastal isotopic signature shows they were kept in captivity on the coast for an extended period. This model of capturing wild birds and transporting them live across the Andes to be reared in coastal settlements is documented nearly 1,000 km south in the Atacama Desert of Chile, where isotopic data also confirmed a local maize-based diet for exotic parrots<sup>4</sup>. This conclusion is further supported by the complete lack of archaeological evidence for breeding at Pachacamac (no cages, skeletons, or eggshells) and a coastal climate ill-suited for breeding tropical parrots<sup>26,44</sup>. The combined evidence refutes the local breeding hypothesis and points to a sophisticated system capable of capturing live birds in the Amazon and moving them across one of the world’s most formidable mountain ranges.

### Modeling the trans-Andean feather trade

Having established that the Ychsma sourced wild parrots from the Amazon, we sought to identify the trade routes that made this continental-scale procurement possible. We used two computational

modeling approaches. First, we applied machine-learning species distribution models (SDMs) to reconstruct the parrots’ potential distributions around 1000 CE<sup>45</sup>. Second, we used landscape resistance modeling, based on circuit theory<sup>46</sup>, to map the paths of least resistance for humans between the Ychsma heartland and 10 contemporary sites in the Andes and Amazon, selected a priori for their importance as trade hubs or as potential sourcing locations for the parrots (Table 1). Our models accounted for elevation, the navigability of rivers, and the potential for seafaring (see “Methods”).

The hindcasted SDMs confirmed that the four identified parrot species’ habitats were restricted to the eastern side of the Andes, primarily in the wet tropics of the Amazon Basin, creating a vast and formidable barrier to the coast (Fig. 5a, and Supplementary Fig. 9). The landscape resistance models then identified two primary, highly plausible corridors for traversing this barrier (Fig. 5b–d).

The first was a northern route, connecting the Ychsma to the powerful north-coast polities of the Chimú (capital at Chan Chan) and Sicán (a.k.a. Lambayeque; capital at Sicán). These centers consistently appeared as low-resistance nodes in our models (Supplementary Table 3). This route is strongly supported by archaeological evidence for long-standing interaction between the north coast and the Amazon. These ties have deep historical roots, with earlier Moche iconography often depicting Amazonian species, and were later maintained by the Chimú and Sicán, who are known to have had outposts and trade relationships with the Chachapoyas people of the upper Amazonian slopes, a region inhabited by the identified parrots and whose people were known for their bird-capturing skills<sup>47–52</sup>. This suggests a sophisticated, multi-stage network: birds sourced by the Chachapoyas could have been traded to either the Sicán or Chimú (where the captive birds might have been reared at a larger scale) and then transported south to Pachacamac via established coastal routes. The documented geopolitical expansions of the Chimú polity north- and southward along the Peruvian coast during

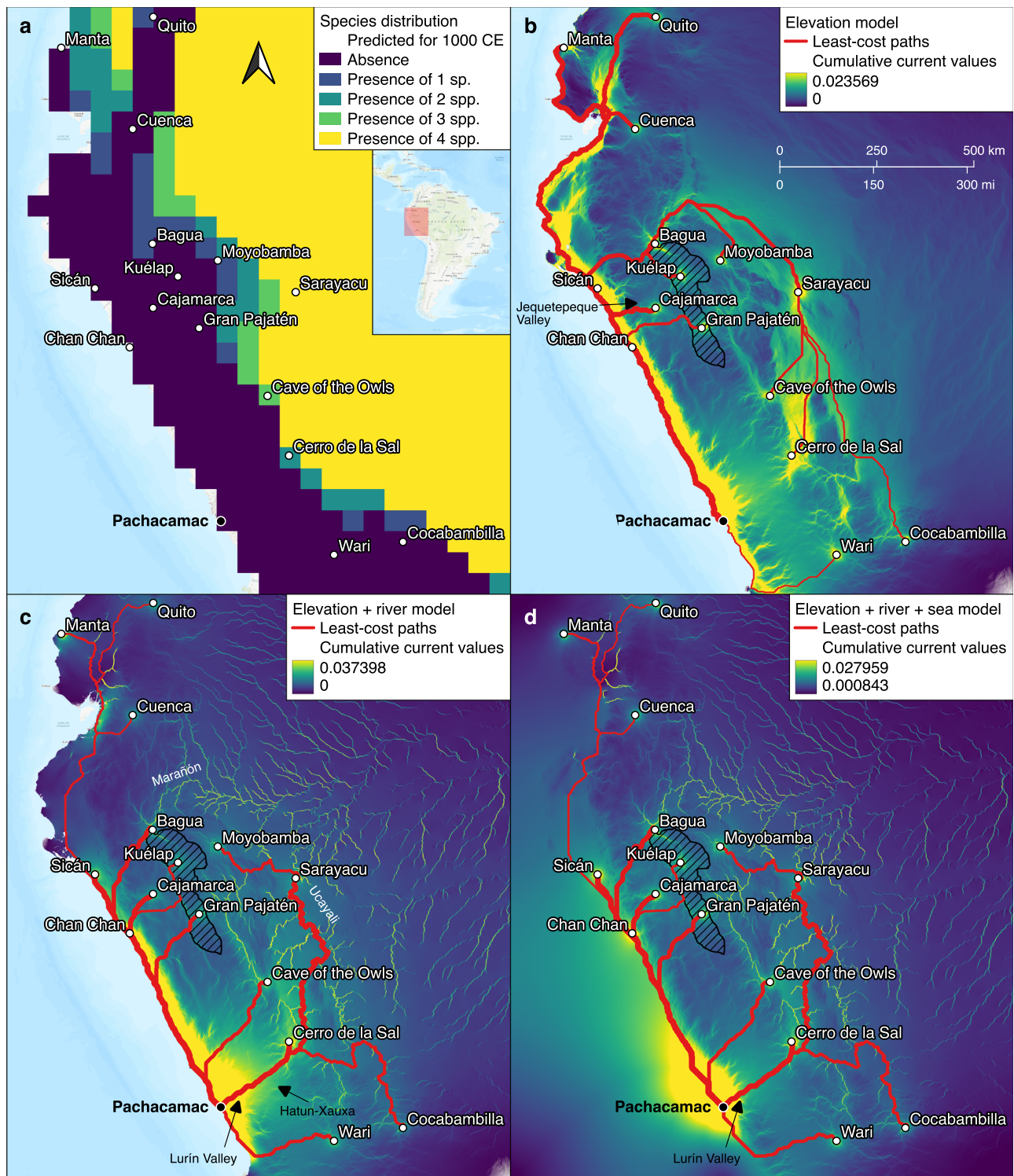
**Table 1 | Key sites contemporary to the Ychsma culture for trade modeling**

Location	CMS Lat	CMS long	Relevance
Bagua	5°38'8"S	78°31'46"W	A trade route connecting the Amazonian lowlands with the Cuenca Basin passed through the high Andes of southern Ecuador and northern Peru, via the trade center of Bagua on the Peruvian side. From this point, trade with the Amazonian lowlands along the Río Marañón was still active during the 1500s CE <sup>135</sup> .
Cajamarca	7°10'0"S	78°31'0"W	The intermontane basin (ca. 2750 m asl) of Cajamarca was the core area of the persistent pre-Hispanic cultural tradition of the same name that can be traced back to ca. 200 BCE <sup>136</sup> . For much of its existence, Cajamarca interacted with the neighboring coastal areas and upper Amazonia, perhaps serving as interregional traders, taking advantage of strategic geographic locations along the major east-west routes <sup>50,52,137,138</sup> . It had an alliance with the Chimú Empire in face of the Inca expansion northward <sup>115</sup> .
Cave of the Owls	9°16'1"S	75°47'8"W	Monzón Coarse Ware (related to Yarinacocha) were uncovered at the Cave of the Owls site (near the modern city of Tingo María). The dating of this phase has been approximated to 1000–1500 CE <sup>139</sup> .
Cerro de la Sal	10°41'28"S	75°16'23"W	Centered on the extraction of salt at Cerro de la Sal, trade routes reached out in all directions, following the Ene, Tambo, Perené, and Apurímac Rivers. The Ucayali route was a key link in the transport of merchandise between the Andean highlands and the lowland rainforest and was predominantly occupied by Arawak-speakers at the time of contact. As late as the 1960s, the pre-Andine Arawaks northeast of Cerro de la Sal still engaged in an intense trade along the mountain slopes, exchanging items such as knives, dogs, baby-slings, achiote, salt, machetes, pots, bows, arrows, and cash <sup>140</sup> .
Chan Chan	8°6'21"S	79°4'28"W	The Chimú Empire (1200–1470 CE) succeeded the Moche and Sicán cultures and conquered much of the Peruvian coast before it was conquered by the Incas <sup>53,54,115</sup> . They engaged in fishing, agriculture, craft work, and trade. The trade of <i>Spondylus</i> shell was integral to the expanding political power and economy of the Chimú as much as the Sicán <sup>141</sup> . Chan Chan is the vast capital of the Chimú Empire comprised mainly by 13 gigantic “royal compounds” in the lower Moche Valley (near the modern city of Trujillo).
Cocabambilla	12°45'6"S	72°33'14"W	During the 1500s CE, some Piro groups conducted three-month trading expeditions along the Ucayali, reaching as far as Cocabambilla, more than 300 km from their home. At Cocabambilla, parrots, cotton cushmas, cedar, canoes, gum, resins, and turtle oil were exchanged for metal tools, salt, and cloth <sup>142,143</sup> .
Cuenca	2°53'51"S	79°0'13"W	The Cañari culture (500 CE until the Inca conquest) was found in the Cuenca Basin, Ecuador. The Cañari believed that their ancestors were the snake and the macaw. They used both sides of the Ecuadorean Andean slopes to trade e.g., cotton and salt with lowland groups <sup>144</sup> . Another route connecting the lowlands with the Cuenca Basin passed through the high Andes of southern Ecuador and northern Peru, via the trade center of Bagua on the Peruvian side <sup>145</sup> . Trade with the Amazonian lowlands along the Río Marañón was still active during the 1500s <sup>135</sup> .
Gran Pajatén	7°38'56"S	77°25'5"W	Gran Pajatén is a major archaeological site in the Río Abiseo National Park that is situated between two major tributaries of the Amazon River, Marañón and Huallaga. The visible masonry architecture largely pertains to the Chachapoyas culture that was subjugated by the Incas around 1460–70 CE, although evidence of earlier occupations dating back to ca. 200 BCE exists <sup>146–149</sup> . The Chimú Empire and the Chachapoyas may have had a trading relationship <sup>150–152</sup> .
Kuélap	6°25'5"S	77°55'24"W	The monumental walled settlement of Kuélap is commonly considered to be the population and political center of the Chachapoyas culture of the Late Intermediate (900–1470 CE) and Late Horizon (1470–1535 CE) periods <sup>149,153,154</sup> . Its geographic location at a mid-level altitude (at ca. 3000 m asl) and between the coast and the upper Amazonia allowed residents to exploit resources from lower and higher elevations as well as to serve as economic intermediaries throughout the “Three Worlds of the Andes”.
Manta	0°57'30"S	80°42'30"W	The Manteño-Huancavelica culture (600–1530 CE), centered around the modern city of Manta on the south-central coast of Ecuador, contained mainly agriculturists who also specialized in diving for <i>Spondylus</i> and other large tropical marine shell and making beads from them. There is archaeological and ethnohistorical information pointing to trade between the Manteño-Huancavelica and the Sicán and the Chimú cultures <sup>155,156</sup> .
Moyobamba	6°2'5"S	76°58'22"W	The Jebero seems to have been an important link in the trading connections across this part of Amazonia. They traded regularly with the Spaniards in Moyobamba, exchanging captives for iron tools that were passed on to the Cocama in exchange for canoes and clothing <sup>157</sup> .
Pachacamac	12°15'24"S	76°54'01"W	Focus of the study.
Quito	0°13'12"S	78°30'45"W	The Quito culture (500 BCE – 1470 CE) was found at present day Quito and traded with the coast. There are ethnohistorical sources that speak of semi-autonomous “merchants” or traders known as <i>mindaláes</i> who worked for native lords of the Ecuadorean highlands around the time of the Incas <sup>158,159</sup> .
Sarayacu	6°47'25"S	75°6'50"W	In the 1800s and possibly well before that, the Piro traded parrots and monkeys for iron tools at Sarayacu <sup>160</sup> .
Sicán	6°41'59"S	79°54'8"W	The Sicán culture (850–1375 CE) inhabited what is now the north coast of Peru (centered in modern-day Lambayeque region). Their trade networks appear to have been unprecedented in range and goods involved ( <i>Spondylus</i> shell, emeralds, feathers, and other minerals were imported), which helped to insure the spread of Sicán religion and polity outside of the Lambayeque and La Leche Valleys <sup>161</sup> . They also could have controlled the transport methods in addition to the goods being traded.
Wari	13°03'38"S	74°11'56"W	Trade between the Wari (Huari) Empire and the Amazonian lowland areas along the Apurímac, Ene, Tambo, and Ucayali Rivers was intense <sup>162</sup> .

Name, GPS coordinates, and relevance of locations for trade between the Andes and Western Amazonia, with corresponding references.

the period of ca. 1250 to 1400 CE<sup>53</sup>, however, strongly suggest that it was the expansive Chimú Empire that served as the north coast nexus in the inferred multi-stage trade network. Not only the Chimú conquered the Sicán by 1375–1400 CE and interacted with the contemporaneous Ychsma<sup>54</sup>, but their production and usage of feathered objects seems to have been unprecedented<sup>3</sup>. Max Uhle even recovered a well-preserved Chimú feathered crown at Pachacamac during his pioneering fieldwork there (Supplementary Fig. 10).

The second was a more direct central route, connecting Pachacamac eastward across the Andes to the highlands, specifically toward the region of Cerro de la Sal. This corridor was particularly favored in models that included river travel (Fig. 5c). This route aligns with ethnohistorical accounts of the Yánesha, an Arawak-speaking group who inhabited this Amazonian region and traveled along these same paths to the central coast valleys for trade and exchange<sup>55,56</sup>. This corridor essentially represents an early iteration of a route later formalized by



**Fig. 5 | Modeling potential pre-Inca trade routes.** **a** Predicted habitats for the four identified Amazonian parrot species around 1000 CE. Hindcasted species distribution models show that suitable habitats were restricted to the eastern side of the Andes, far from the coastal Pachacamac site. **b–d** Landscape resistance models of potential trade corridors connecting key sourcing sites to the Ychsma coastal heartland. In these models, yellow indicates high conductance (easy travel) and

dark blue indicates high resistance (difficult travel). The models are based on elevation alone (**b**); elevation plus navigable rivers as low-resistance corridors (**c**); and elevation, rivers, and potential sea routes (**d**). Red lines show the calculated least-cost paths, and the hashed area highlights the Chachapoya region<sup>150</sup>, a plausible source area for traded birds. Maps were created using QGIS v3.3.

the Inca as part of their Qhapaq Ñan imperial road system<sup>57</sup>. Of note, our models showed that maritime trade, despite its documented use for other goods, offered no significant advantage for procuring Amazonian feathers (Fig. 5d).

## Discussion

By integrating ancient genomics, isotopic analysis, and spatial modeling, we have traced the journey of feathers from Amazonia to an elite tomb on the Pacific coast during the Late Intermediate Period of the

Andean chronology. Our results provide direct evidence that the Ychsma culture, long before the Inca empire, participated in a sophisticated trade network that spanned the Andes. We show that they sourced live parrots from genetically diverse wild populations in the Amazon, transported them over hundreds of kilometers either through their own direct networks or via powerful intermediaries, and sustained them on a coastal diet.

Our application of spatial modeling, supported by archaeological and ethnohistoric data, identifies two independent and highly plausible trade corridors that made this possible: a northern route leveraging particularly the powerful Chimú polity and to a lesser extent, the Sicán polity, as intermediaries; and a direct central route connecting the coast to Arawak-speaking groups in the central highlands. The existence of these robust networks fundamentally challenges the view of this era as a period of frequent conflicts and regionalism, revealing instead a complex mosaic of long-distance interaction and economic integration operating outside of a pan-Andean imperial structure.

This cross-disciplinary approach provides a powerful toolkit for archaeology. It moves beyond qualitative inference to quantitatively model ancient trade routes and interaction spheres. This framework, particularly suited for organic artifacts, can be applied to enigmatic materials from archaeological contexts worldwide, holding the promise of redrawing the map of ancient economies and revealing the true extent of connectivity between the world's past cultures. This study also provided a deep historical context for a human fascination with colorful parrots that today drives a destructive illegal trade threatening their very survival.

## Methods

### Study sites and sample collection

The ancient feather samples were all recovered during a 2005 excavation in the Uhle Cemetery in front of the sacred Painted Temple at the famed pre-Hispanic religious center of Pachacamac on the central coast of Peru (Fig. 1). The 2005 fieldworks by the Pachacamac Archaeological Project (PAP) co-directed by Izumi Shimada and Rafael Segura Llanos were authorized by the National Institute of Culture of Peru (Resolución Directoral Nacional No. 919). Guided by results of their prior ground-penetrating radar survey, Shimada and his team excavated a large, intact, stone-lined, chamber tomb (Fig. 1c–e), 2.25 m (N–S) × 3.27 m (E–W) in dimension in Trench 7 within the Uhle Cemetery<sup>26,29</sup>. The tomb contained 34 well-preserved funerary bundles organized into two levels, seven in the upper (Fig. 1c) and 27 in the lower levels (Fig. 1d). Isotope and mtDNA analyzes of skeletal/dental samples of the deceased inside these bundles and associated artifacts (particularly ceramic styles) revealed that the deceased came from different communities on the central coast (lower reaches of coastal valleys) and the cis-Andean slopes (higher, interior portions) of the same valleys, including the Chillón, Rimac, and Lurín<sup>26</sup>.

Strontium isotope (<sup>87</sup>Sr/<sup>86</sup>Sr) analysis of bones from 26 individuals excavated in Trench 7 at the Uhle Cemetery and the neutron activation analysis of sherds from the adjacent Pilgrims Plaza both indicate that they were derived from at least three distinct locations<sup>26</sup>. To locate these sites, a comparative study of the ceramic vessels associated with the funerary bundles in Trench 7 was conducted, providing an independent confirmation of the analytical findings. It has revealed, that in addition to Ychsma domestic vessels occurring widely on the central coast, at least two jars—with heart-shaped body, a short globular neck, a pair of symmetrically placed strap handles, and brown paste (Supplementary Fig. 11)—are most likely derived from mid to upper valleys of the central to south-central coast from Rimac to Mala (see Plates 10-4066, 4289, 4291, and p116 in ref. 58, Fig. 3 in ref. 59, and ref. 60). The bundles were most likely brought on a litter (stretcher) to Pachacamac for the honor of being interred close to the venerated deity.

Examination of the 20 bundles—specifically those unfolded or partially exposed due to degradation—identified three infants, while the rest were adults aged ~22–61 years. The adult mortuary bundles (e.g., Bundles B, C, and W) were constructed using a complex, multi-layered technique. This process began by wrapping the flexed body in a cotton shroud (Fig. 1c, d). In the most elaborate examples (Bundles B and C; Fig. 1f), the deceased was clothed in a high-quality tunic woven from camelid fiber, with the cranium secured in decorated textiles. This primary wrapping was subsequently enclosed within a coarse netting made of braided junco or *Scirpus* sp. reeds. To create volume and shape, the spaces within and around this netting were packed with raw cotton bolls, bundled reeds, and other vegetative matter. Successive layers of cotton bags or large textiles were applied, repeating the stuffing and wrapping process to achieve the final dimensions. Structural stability was provided by inserting vertical cane or wooden supports along the flanks of the bundle after the formation of the third or fourth layer. The exterior was finished with a large textile sack simulating a tunic. A “false head” (constructed from a cloth bag filled with reed bundles and vegetation) was often stitched onto the top of the bundle. Due to the relatively poor state of preservation and ethical consideration of preserving some for future studies, not all bundles were opened. Consequently, Bundles A and C were neither unbundled nor radiocarbon-dated.

The site of Pachacamac being the preeminent religious-funerary center close to the city of Lima was subjected to intense grave looting—particularly targeting bundles of elite/wealthy individuals—since early Colonial era until the 20th century. Uhle<sup>15</sup>, who conducted the first scientific excavation of Pachacamac and often regarded as the father of the scientific archaeology in the Andes, considered that the great majority of an estimated 60,000 to 80,000 pre-Hispanic burials in six cemeteries that once existed at the site had been looted prior to his work<sup>26,61,62</sup>. In the Sacred Precinct toward the southern corner of the site, Uhle<sup>15</sup> (see Figs. 2–5 in ref. 15) uncovered at least 50 relatively well-preserved funerary bundles (dating from Late Lima, ca. 600–650 CE to the Late Horizon, ca. 1470–1533 CE) in his excavations in areas (including cemeteries) around the sacred temples (Painted and Sun Temples). Many of these bundles did not preserve well and generally speaking, Uhle did not detail how these bundles were prepared<sup>61</sup>. He did not illustrate any of the excavated bundles, but there is a photograph (The Uhle Pachacamac Collections at the University of Pennsylvania Museum) that presumably he took of the back of a relatively well-preserved bundle, apparently taken in the field soon after its excavation, that is dressed in a striking feather-covered cloak. A bundle of large feathers is tied to the back of its false head. Subsequent archaeological projects largely focused on clearing the top of these and other temples in the same zone, finding a handful of offering burials without any feather ornaments. The long-standing Ychsma Project directed by P. Eeckhout, on the other hand, has focused on the history, organization, and functions of the inferred Ychsma royal palaces (“Pyramids with Ramps”) in the central sector of the site, and since 1993 has “uncovered several hundred burials” of diverse age groups, both sexes, and those of unknown age and sex of predominantly Late Intermediate and Late Horizon date (ca. 1000–1500 CE)<sup>63–67</sup>. There are no mentions of any feather ornaments associated with these late pre-Hispanic individuals. They have been interpreted as either sacrificial victims to the Ychsma/Pachacamac deity or those who long suffered from health problems and were brought to the site to be divinely healed<sup>64,67</sup>. In addition, there is a well-preserved funerary bundle attributed to have been found (by looters) at Pachacamac and currently at the Ethnological Museum in Berlin, Germany (Inventory No. Berlin-VA 60382) that has a false head decorated with large yellow feathers on its back. It appears to be late pre-Hispanic in date.

The funerary bundles in these tombs belonged to the Ychsma culture, which is widely regarded as a late pre-Hispanic confederation of ethnic chiefdoms or kingdoms (known ethnohistorically *señorios* or

*curacazgos*) on the central coast. They were politically autonomous but acted as a religious community through the shared veneration of Ychsma (also spelled Ichma, Ichmay, or Ishma)<sup>30,31</sup> that was renamed as Pachacamac during the Inca domination of the site<sup>68–73</sup>. Its political composition probably accounted for the variability in funerary bundle construction<sup>74,75</sup>. Ychsma became recognizable ca. 1000 CE or somewhat earlier and was later subjugated by the Inca Empire around 1460 CE<sup>29</sup>. Its territory covered the lower and partially middle portions of the valleys of Chillón, Rimac, and Lurín (Fig. 1a) with the sites of Maranga (Rimac Valley) and Pachacamac (Lurín Valley) serving the political and religious epicenters, respectively<sup>14,32,76,77</sup>. This time period—after the Wari and before the Inca Empire—is known as the Late Intermediate Period (1000–1476 CE) or Period of Regional States, in which Andean cultures develop a strong self-identity in their respective territories. These regionalized cultures somewhat also expand their territories but incomparable to the pan-Andean integration processes led by the Wari or the Incas.

Visual and macroscopic identification of feathers is often challenging, especially with old and/or poorly preserved samples<sup>78</sup>. Even with extensive ornithological expertise, especially in parrots, we were only able to identify some of the samples as macaws (*Ara* sp.) and Amazon parrots (*Amazona* sp.) but given the condition of the feathers and their similarity within each genus, explicit species identification was not always possible.

A subset of 25 ancient feathers from ornaments (Fig. 1g) in funerary bundles (see details in Supplementary Data 1) from the Ychsma period (1000–1470 cal. CE) were selected for the genetic analysis<sup>29</sup> and sampled. To contribute to the preservation of the funerary bundles, feathers were not obtained directly from them, except samples #11938–11946 from Bundle C (Fig. 1f, and Supplementary Fig. 12). Whereas all feathers certainly came from the excavated funerary bundles, source of some feathers (Supplementary Data 1) could be identified and inferred according to their position on tomb floors and the immediate proximity to the bundles (e.g., samples #11947–11948 from Bundle W and samples #11949–11951 from Bundle A). Samples #11960 and #11961 were obtained from an excavation cut (Cut 1) into Layer 1 (near the modern surface) of the NE–NW sector in the large Trench T7, suggesting that these samples came from a looted burial or funerary bundle with a feather head ornament. The feather samples were placed into zip-lock bags or Eppendorf tubes, marked with a unique identifier, and sent to the paleogenomics laboratory of the ACAD, Adelaide University (Australia). Exportation of the feather samples used in this study was granted by the Ministry of Culture (Resolución Viceministerial No. 703-2011-VMPCIC-MC and 147-2024-VMPCIC-MC) and the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) in Peru (CITES permit No. 24-PE-005991-SP).

Blood samples from macaw nestlings were collected in 2010, using jugular venipuncture in the Bahuaja-Sonene National Park, southeastern Peru, following procedures approved by the Institutional Animal Care and Use Committee of the Texas A&M University (Animal Use Permit No. AUP 2009-215), and stored in 70% ethanol<sup>78,79</sup>. The sample S1109 from a female Scarlet Macaw *A. macao* nestling was used to generate mtDNA baits for capturing DNA sequences from the ancient feathers having been visually identified as belonging to macaws and Amazon parrots. Samples BYMA01 and BYMA04 from two Blue-and-yellow Macaw *Ara ararauna* nestlings were used for reference of the Peruvian haplogroup. Molted feather samples from parrots and macaws were also collected from the same region and in the Tambopata National Reserve, and used as reference for stable isotope analysis.

All modern samples were collected under research permits from the Servicio Nacional de Areas Naturales Protegidas (SERNANP) in Peru (Resolución Jefatural No. 001-2010-SERNANP-DGANP-PNBS and Resolución del Jefe de la Reserva Nacional Tambopata No. 001-2010-SERNANP-DGANP-JEF). For the transportation of modern blood and

feather samples, CITES permits were provided by SERFOR in Peru (export permit No. 15-PE-000448-SP) and the Wildlife Trade and Biosecurity Branch of the Department of Environment in Australia (import permit No. PWS2015-AU-001508). Genetic access to the samples was granted by SERFOR in Peru (Resolución de Dirección General No. 013-2016-SERFOR-DGGSPFFS).

### DNA extraction, sequencing, and blasting

**Modern DNA.** Fresh DNA from the modern blood samples was extracted using general salting out protocol and DNAzol (Invitrogen) at the genetic laboratories of The Australian National University in Canberra, Australia<sup>79</sup>. TrueSeq Nano Double-Stranded libraries (DSL) of samples BYMA01 and BYMA04 were constructed at Macrogen (South Korea) and shotgun sequenced in a NovaSeqX (150 bp paired-end). Adapter sequences from sequencing results were trimmed using “fastp” v0.20.1<sup>80</sup> and paired-end reads were mapped to the *A. ararauna* mitochondrial genome (GenBank accession number NC\_029319) using BWA v0.7.17 “mem” algorithm<sup>81</sup> with stringent mapping parameters (options -B 8 -O 10,10 -E 4,4 -T 80 -k 50). Duplicated reads were filtered out using samtools “rmdup”<sup>82</sup>. A mitochondrial genome 75% majority consensus for each sample was generated using Geneious v7.1.7<sup>83</sup>, only calling nucleotides for positions with a coverage depth  $\geq 3\times$  (other positions were called as N; see Supplementary Data 5). The complete mitochondrial genome sequences for BYMA01 (coverage depth 23.2 $\times$ ) and BYMA04 (coverage depth 10.5 $\times$ ) were deposited to GenBank under accession numbers PV816315 and PV816316, respectively.

**Ancient DNA.** All ancient DNA extractions and library constructions were performed at the dedicated ancient DNA laboratory at ACAD, Australia.

Fragments from the 25 feathers from the Ychsma tomb were cut into tiny pieces using scissors (amount of feathers used ranged between 10 and 210 mg; see details in Supplementary Data 1). DNA from these feather samples was extracted following ref. 35. Shortly, digestion step was performed for each feather using 4 ml of a buffer containing 75 mM Tris pH 8.0, 50 mM NaCl (Sigma-Aldrich), 2 mg Proteinase K (Life Technologies), 50 mM DTT (Promega), and 0.75% SDS (Life Technologies), and digested for 1 h under constant rotation at 55 °C. Samples were then centrifuged at 3085  $\times g$  (4600 r.p.m.) for 1 min and the supernatant was pipetted into 16 ml of a modified QG buffer containing 91% QG buffer (Qiagen), 1.3% Triton X-100 (Sigma-Aldrich), 25 mM NaCl (Sigma-Aldrich), 0.17 M Sodium Acetate (Sigma-Aldrich), and 100  $\mu$ l of silicon dioxide solution<sup>84</sup>, and left for 1 h at room temperature under constant rotation. Samples were centrifuged at 3085  $\times g$  (4600 r.p.m.) for 5 min to pellet the silica suspension, discarding supernatant. This silica pellet was washed three times in 80% ethanol and centrifuged at 18,215  $\times g$  (13,000 r.p.m.) for 1 min, and finally air dried for 30 min and resuspended in 120  $\mu$ l of a pre-warmed (at 50 °C) mix of EB buffer (Qiagen) and 0.05% Tween 20, and incubated for 10 min. A final volume of 120  $\mu$ l of DNA extract was obtained after centrifugation at 18,215  $\times g$  (13,000 r.p.m.) for 1 min. A negative control was included for all extractions.

Partial-UDG treated<sup>85</sup> DSL were constructed following the protocol by ref. 86 using modifications in ref.<sup>87</sup>, which uses truncated Illumina adapters with a 7-mer barcode on both P5 and P7, and using AmpliTaq Gold (Invitrogen) for final library amplification. In-house synthesized RNA captures for mitochondrial enrichment were constructed using genomic DNA from the *Ara macao macao* sample S1109 following ref. 36, and libraries were enriched for mitochondrial DNA following ref. 88. Enriched libraries were finally sequenced in an Illumina NextSeq platform (mid-output, 150 bp paired-end).

Resulting sequencing reads were demultiplexed according to both P5 and P7 barcode sequences using Sabre v1.0 (<https://github.com/najoshi/sabre>), adapter sequences were removed using AdapterRemoval v2.3.0<sup>89</sup>, and paired reads were collapsed (merged) into a

single read when overlapping by 11 nucleotides, discarding reads shorter than 30 bp.

Collapsed reads of each sample were initially mapped to the *A. macao* mitochondrial genome (GenBank accession number CM002021) using BWA v0.7.17 backtrack algorithm<sup>81</sup> and using mapping parameters for ancient samples (options: -l 1024, -n 0.01, -o 2). Duplicated reads were filtered out using FilterUniqueSAMCons.py<sup>90</sup>. A 75% majority consensus was then generated using Geneious v7.1.7<sup>83</sup>, only calling nucleotides for positions with a coverage depth  $\geq 3\times$  (other positions were called as N). Longest contigs (>50 bp) obtained for each sample with at least 50 reads mapped (Supplementary Data 2) were BLASTn<sup>91</sup> analyzed to identify them taxonomically. Thus, a subsequent mapping to mitochondrial genome of *Amazona aestiva* (NC\_033336), *Ara ararauna* (NC\_029319), *A. macao* (NC\_045076), *A. chloropterus* (NC\_047199), and *Larus brunnicephalus* (JX155863) was performed for those samples assigned to *Amazona ventralis*, *Ara ararauna*, *A. macao*, *A. chloropterus*, and *Larus crassirostris* by BLASTn, respectively. Iterative mapping to those references was then performed generating an intermediate 75% majority consensus sequence in Geneious retaining the reference allele at positions with coverage depth  $< 3\times$ . The new consensus sequences were then used as the references for a new round of mapping following the process described above. Once no more reads were mapped, a final 75% majority consensus was then generated using Geneious, only calling nucleotides for positions with a coverage depth  $\geq 3\times$  (other positions were called as N). Ancient DNA damage pattern was assessed using mapDamage v2.2.1<sup>92</sup>.

Archaeogenetics results indicate that from the 25 feathers analyzed, eight provided enough endogenous DNA for taxonomic identification (Supplementary Fig. 1, and Supplementary Data 2–4). Ancient DNA damage analyzes for these samples display the expected patterns for sequencing libraries partially repaired with UDG (Supplementary Fig. 2).

### Phylogenetic and haplogroup network analyses

To construct the different datasets for the species identification of the samples, just the samples covering at least 50% of the reference in the BWA mapping (independently of the coverage depth of the final consensus sequence) were used, except in the case of sample #11942 (~30%), identified as *Amazona* sp., as it was the only sample from this species with more than 50 reads mapped in the preliminary mapping to *Ara macao*. The sequence datasets were constructed to both verify the species identification of the samples furnishing enough DNA and to identify haplogroup for samples from which haplotype data were available (i.e., *Ara macao* and *A. ararauna*). Datasets were generated by aligning the corresponding sequences using MUSCLE<sup>93</sup> implemented in Geneious v7.1.7<sup>83</sup>. Maximum Likelihood (ML) phylogenetic analyzes for *Ara* and Laridae datasets were performed using IQTREE2<sup>94</sup>, implementing substitution models as estimated by ModelFinder in IQTREE2 in both the partitioned (*Ara* mitochondrial genome dataset and *A. macao* network dataset, see below) and unpartitioned data (using option -m TEST, in Laridae and *Ara ararauna* phylogenetic trees), with node support values estimated by performing 1000 ultrafast bootstrap replicates<sup>95</sup>. Maximum Likelihood analyzes for *Amazona* unpartitioned datasets were performed using RAxML 8.2.11<sup>96</sup> with node support values estimated by performing 100 bootstrap replicates. Haplogroup networks for *Ara macao* and *A. ararauna* were estimated using Fitchi<sup>97</sup>.

**Ara species identification.** Macaws are a polyphyletic group (consisting of six genera) and the largest sized parrots in the Neotropics with 16 species still extant in the wild, although many of them threatened by extinction today<sup>98</sup>. Samples from Pachacamac initially identified as belonging to *Ara* spp. provided partial mitochondrial genome sequences ranging from 12.3 to 96.8% of reference coverage and with a coverage depth ranging from 0.2 to 11.4 $\times$ . A dataset was constructed

using available *Ara* spp. mitochondrial genomes in GenBank (Supplementary Data 6) and partial mitogenomes from feather samples providing a minimum reference coverage of 50% (i.e., samples #11954 and #11957 after mapping to *A. ararauna*, sample #11951 after mapping to *A. chloropterus*, and samples #11947, #11948, and #11959 after mapping to *A. macao*; Supplementary Data 3). The 39 mitochondrial genome sequences of *Ara* species (available in GenBank) and our newly generated *Ara* sequences (six ancient individuals and the two modern *A. ararauna* BYMA01 and BYMA04) were aligned using MUSCLE in Geneious, using *Amazona ventralis* as outgroup (Supplementary Data 6), and the Control Region gene was removed. The dataset was divided in Protein Coding Genes (PCGs), *12S\_rRNA*, *16S\_rRNA*, and *tRNAs*. PCGs were further partitioned in codon positions (Supplementary Data 7) using DAMBE v7.0.5<sup>99</sup>. Final dataset contained 48 individuals and was 15,455 bp long.

The ML phylogenetic analysis using mitochondrial genomes of *Ara* spp. (Fig. 2) confirms the preliminary BLASTn identification of feather samples, with unambiguous assignment [i.e., Maximum Likelihood Bootstrap (MLB) = 100] of samples #11954 and #11957 as *A. ararauna*, sample #11951 as *A. chloropterus*, and samples #11947, #11948, and #11959 as *A. macao*.

**Ara macao and A. ararauna haplogroup networks.** The concatenated alignment of mitochondrial genes *12S\_rRNA*, *16S\_rRNA*, *COXI*, and *CYTB*, and the corresponding data from complete and partial mitochondrial genomes from *A. macao* specimens available in GenBank (Supplementary Data 8) was used to construct a network to identify the haplogroup of samples #11947, #11948, and #11959. This dataset was also partitioned in *12S\_rRNA*, *16S\_rRNA*, and PCGs (further divided in codon positions using DAMBE; Supplementary Data 7). Haplogroups within *A. macao* were used following refs. 37, 43. The dataset contained 125 individuals of length 2243 bp.

Haplogroup network analysis of *A. macao* (Fig. 3, and Supplementary Fig. 3), as well as the mitochondrial genome phylogeny, confirmed the three ancient *A. macao* feathers belong to haplogroup H4 (but MLB = 86), which is one of two haplogroups characteristic of *A. macao macao*.

An alignment of 1290 bp and 55 individuals using the available *A. ararauna* mitochondrial CR longer than 500 bp and corresponding CR sequences from mitochondrial genomes available in GenBank (Supplementary Data 9), as well as the two sequences of modern individuals (BYMA01 and BYMA04) obtained here and partial sequences from samples #11954 and #11957, was used to generate a haplogroup network for the species. The Eastern/Western haplogroups (HE/HW) are based on ref. 100.

The *A. ararauna* haplogroup network analysis using partial sequences of the mitochondrial control region (Supplementary Figs. 4 and 5) showed that the two ancient feathers (#11954 and #11957) belong to the same haplogroup, which is related to the HE haplogroup. Modern sample BYMA01 is closely related to Eastern h6 and h23 haplotypes, and BYMA04 forms a single haplotype also within the HE haplogroup related to the other Peruvian samples. However, all the currently available Control Region gene information is from Brazilian individuals or of unknown origin (except the four Peruvian individuals analyzed here), so it is not possible to establish more accurate relationships with populations from other South American countries.

**Ara macao nucleotide diversity.** Nucleotide diversity was calculated for *A. macao* using DnaSP v5.10.1<sup>101</sup> and the complete mitochondrial genomes divided in different sets based on haplogroup identification and specimen availability. The analysis was performed for all individuals of H4 ( $n = 9$ , comprising both ancient and modern samples) and H6 haplogroups ( $n = 15$  with just ancient individuals from putative breeding colonies<sup>43</sup>). Three different subsets from the H4 haplogroup were analyzed: a subset including the Pachacamac samples ( $n = 3$ ),

another one including ancient samples from the Atacama Desert sourced from wild populations ( $n=4$ ), and a third one including modern samples ( $n=2$ ). An additional analysis was performed on H6 haplogroup removing sequence MH400234 (i.e.,  $n=14$ ), which includes about 35% of unknown positions (Ns).

The nucleotide diversity ( $\pi$ ) estimated for the *A. macao* mitochondrial genomes (Supplementary Table 2) is higher in the H4 (-0.002) than in H6 haplogroup individuals (-0.00005) coming from captive breeding colonies according to ref. 43. As expected, both nucleotide diversity and haplotype diversity (Hd) are lower in captive breeding individuals (Hd = 0.371 when using all H6 individuals, and Hd = 0.495 when removing the H6 individual with 35% Ns). In contrast, in the H4 sets of individuals, the Hd = 1 (i.e., one haplotype for each individual), suggesting that the four individuals studied from the Atacama Desert came from traded animals from different wild populations. The very similar nucleotide diversity of these Atacama individuals (0.00272) and the three Pachacamac individuals (0.00223), and the remarkably lower nucleotide diversity of the individuals coming from breeding colonies in the American Southwest (0.00005), suggest that the Peruvian individuals would have also come from wild populations.

**Laridae species identification.** A single dataset concatenating available sequences for mitochondrial genes *COXI*, *CYTB*, and *ND2* was generated to identify the Laridae species for sample #11960 by aligning selected genes obtained for the feather sample and the available gull *CYTB*, *COXI*, and *ND2* gene sequences, and corresponding sequences from mitochondrial genomes available in GenBank (Supplementary Data 10). One individual per species was selected, and when multiple sequences per gene were available, the longest one was selected. Specific names in this Laridae group follow the proposed taxonomy by ref. 102. Three tern species were also used (*Gelochelidon nilotica*, *Sterna hirundo*, and *Sternula albifrons*), as well as *Haematopus ater* and *Calidris pugnax* as outgroups. The final dataset contained 62 sequences of a total length of 3736 bp.

The white feather sample #11960 (Supplementary Fig. 1h) was identified as belonging to a Laridae species (Supplementary Data 1). The phylogenetic analyzes, which included most species of Laridae, place the feather within Sabine's Gull *Xema sabini* with high confidence (MLB = 100; Supplementary Fig. 8).

**Amazona species identification.** Although the amount of data retrieved for sample #11942 is very limited (see below), three different datasets were generated to infer the species identification of this sample. As no *CYTB* data were recovered from the ancient sample, the datasets used were obtained by aligning the sample #11942 sequences to *Amazona* sp. gene sequences for mitochondrial *COXI* [334 individuals (using *Ara macao* as outgroup), 1548 bp], *I2S\_rRNA* [74 individuals (*Ara ararauna* as outgroup), 391 bp], and *I6S\_rRNA* [72 individuals (*A. ararauna* as outgroup), 542 bp] genes (Supplementary Data 11).

When analyzing the feather preliminarily identified as *Amazona* sp. (sample #11942), just 9, 15.3, and 17.3% of the final alignments for *COXI*, *I2S\_rRNA*, and *I6S\_rRNA* *Amazona* datasets, respectively, were non-degenerate nucleotides. However, phylogenetic analyzes strongly support [MLB = 94 for *COXI* analysis (Supplementary Fig. 6), 94 for *I2S\_rRNA*, and 100 for *I6S\_rRNA* (Supplementary Fig. 7)] the attribution of this sample to the Mealy Amazon *Amazona farinosa* and probably to subspecies *A. f. farinosa*, *inornata*, or *chapmani*.

**Human contamination.** The BLASTn analysis of the longest contig after mapping for sample #11938 suggested possible contamination with human DNA (Supplementary Data 2). In order to verify if the DNA was potentially coming from the human buried in the funerary bundle, we remapped the sequencing reads for this sample to the human RSRS

mitochondrial genome<sup>103</sup>. Up to 1077 unique reads (covering 66% of the reference at a mean coverage depth of 5.3 $\times$  and with a mean mapped read length of 81.1 bp) were mapped, especially in those mitochondrial genome regions highly conserved across vertebrates (i.e., *I2S\_rRNA* and *I6S\_rRNA* genes). Analysis of the consensus sequence using the tool Haplocheck v1.3.1<sup>104</sup> from the Mitoverse platform (<https://mitoverse.readthedocs.io/>) identified the human haplogroup as H2a1, and there was no other source of human contamination (i.e., no ambiguity about H2a1 and no sequences that could come from another individual). H2a1 is a pan-Eurasian haplogroup found from Siberia to southern Spain<sup>105-108</sup>, indicating that the source of human DNA of that sample is a recent contamination that most probably occurred during excavation or sampling tasks. These results are compatible with the higher mean length of the reads mapped in comparison with the endogenous bird reads (81.1 bp versus <56 bp) and with the unclear damage pattern (Supplementary Fig. 13).

### Radiometric dating and stable isotope analysis

Radiocarbon dating was performed on five feather samples from Pachacamac (#11519, #11520, #11522, #12352, #12455; Supplementary Data 1) in the Radiocarbon Laboratory (SANU), Research School of Earth Sciences, The Australian National University (Australia). During a non-routine pre-treatment, the feathers were subjected to a sequential solvent wash followed by an acid-base-acid (ABA) protocol to remove a broad range of potential contaminants. The solvent wash consisted of immersing the sample in acetone, methanol, and dichloromethane (DCM). Following the solvent wash, the ABA protocol was performed as follows: samples were treated with 1M hydrochloric acid (HCl) for 30 min at 70 °C, then with 0.2M sodium hydroxide (NaOH) for 1 h at room temperature, and finally with 1M HCl for another 30 min at 70 °C. Radiocarbon dating was performed using a single-stage AMS system as described by ref. 109. This system provides high-precision measurements of radiocarbon content, providing reliable age determinations for the analyzed samples. We calibrated the results using the southern hemisphere calibration curve SHCal20<sup>110</sup> in Oxcal v4.4.4<sup>111</sup>. Calibrated current era (CE) years are presented in 95.4% (2 $\sigma$ ) ranges.

Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope contents were measured in five contemporary parrot feathers (collected in the Tambopata-Candamo area, Southeastern Peruvian Amazon) and the five feather samples from Pachacamac described earlier (Supplementary Data 1) in the Stable Isotope Laboratory, Research School of Biology, The Australian National University (Australia). After cleaning the feathers with three chloroform-methanol washes, the samples were dried, and their C and N contents were measured by combustion of the samples in an EA1110 elemental analyzer (CE Instruments, Milan, Italy) with the resulting gas analyzed by an Isoprime mass spectrometer (Micromass UK, Manchester, England). A mean for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values obtained for each sample was calculated. For comparative purposes, C and N isotope values for feather samples have been normalized to values obtained from bone collagen as in ref. 4 following ref. 112. For this reason, we added 2.8‰  $\delta^{13}\text{C}$  and subtracted 2.2‰  $\delta^{15}\text{N}$  in soft tissue samples and added 1.6‰  $\delta^{13}\text{C}$  to feather samples, which provided the data to generate a  $\delta^{13}\text{C}/\delta^{15}\text{N}$  plot using the bird samples studied here and the ones from ref. 4. For comparison with human samples, we also included data from previously analyzed human hair samples from Pachacamac<sup>29</sup>. C and N isotope values for human hair have been normalized for collagen following ref. 113, i.e., adding 1.2 ‰ to  $\delta^{15}\text{N}$  and 0.7 ‰ to  $\delta^{13}\text{C}$  values for hair keratin. Results of the five contemporary and five ancient feather samples are shown in Supplementary Table 1, Fig. 4, and Supplementary Data 12.

### GIS analyses

Considering that the present distribution of all identified parrot species includes Peru and some neighboring countries, and that maritime trade might have occurred in the region and time of interest, we

defined our geographical provenance investigation to a sensible catchment area around Pachacamac (82°W, 14°S, 70°E, 0°N) extending into the sea and the mainland (around 2 million km<sup>2</sup> in total). A southernmost limit of 14°S was selected, as available archaeological evidence strongly suggests a close and probably direct contact (establishing colonies or sending emissaries) with the north as far as the Lambayeque region but no evidence is known about contact with the south<sup>114–117</sup>.

**Hindcasted species distribution models.** SDMs were implemented with the application Wallace EcoMod<sup>45</sup> available from the “wallace” v2.1.0 R package in R v4.2.2<sup>118</sup>, which provides a freely available, open resource, and reproducible framework for species distribution modeling<sup>119</sup>. Occurrence data for the four parrot species identified in this study were downloaded from the Global Biodiversity Information Facility<sup>120</sup>, after the following filtering: observations were sourced from the eBird Observation Dataset, the basis of record field was “made by humans”, with coordinates without geospatial issues (e.g., invalid or zero coordinates, country-coordinate mismatch, coordinate out of range, etc.), within the distributional range of each species in Peru, as defined by the expert-derived range maps from BirdLife International<sup>121</sup>.

Environmental data were obtained with “pastclim” v1.2<sup>122</sup> from the Krapp et al. (2021) dataset<sup>123</sup> for 17 standard bioclimatic variables (bio02 and bio03 not being available) with a resolution of 0.5° for the present (for training) and 1000 CE (for projection). Occurrence data within the same cells of bioclimatic variables used and within 10 km of each other (spatial thinning) were also removed with “spThin” v0.2.0<sup>124</sup>.

For modeling, we first defined a training background of the country borders of Peru with a 0.5° buffer, then used “wallace” to randomly sample 532 background points. We then built SDMs using the algorithm Maxent<sup>125</sup>, which estimates the species’ responses to environmental variables<sup>126,127</sup>. We tuned the complexity of models by testing a set of feature classes (L = linear, LQ = linear-quadratic, H = hinge, LQH = linear-quadratic-hinge, and LQHP = linear-quadratic-hinge-product) with a regularization multiplier of value 1 (the default penalty against complexity in Maxent), without clamping (i.e., unconstrained extrapolation). We selected optimal model complexity settings by choosing the model with a delta AICc of 0.

We transferred the optimal models to the environmental variables for the year 1000 CE in our study area (defined above). We made model predictions with the “cloglog” transformation<sup>128</sup>, which is bounded between 0 and 1. Continuous predictions of habitat suitability were converted into binary predictions that indicate presence/absence predictions for each species using the “10 percentile” threshold, omitting all regions with habitat suitability lower than the suitability values for the lowest 10% of occurrence records within Peru. The executable R code that can reproduce the analysis with Wallace and raw data are available in Figshare (<https://doi.org/10.6084/m9.figshare.24665697>).

The machine-learning hindcasted species distribution reconstruction of the identified psittacine species’ distributions for 1000 CE did not find optimal climatic conditions in Pachacamac or between the Pacific coastline and the western slopes of the Andes for any of these species (Supplementary Fig. 9). The predicted distributions 1000 years ago were similar to their present-day ranges in the wet tropics, mainly in the Amazon Basin up to the eastern slopes of the Andes (Fig. 5a).

**Resistance maps and least-cost paths of trade routes.** Three landscape resistance models were developed to examine how topography affected potential trade routes between Pachacamac and other contemporary settlements (~1000–1500 CE) in the Peruvian Andes and Western Amazon regions. Such models are routinely used in landscape ecology studies<sup>129,130</sup> but, to the best of our knowledge, they have not been applied to archaeology. Each map was compiled on a separate

raster grid of 1-km resolution in QGIS v3.3<sup>131</sup>. The study area was defined as the valleys of Chillón, Rimac, and Lurín (Ychsma homeland) as the most probable sources of the funerary bundles<sup>26,29</sup> with a rectangle catchment area defined above.

The resistance maps included (i) an elevation model, based on the Global Multi-resolution Terrain Elevation Data 2010<sup>132</sup> with resistance values of meters above sea level, investigating the effect of topography on trade routes; (ii) an elevation + river model, including potentially navigable rivers for small boats (around 5–15 meters minimum extent) in South America<sup>133</sup>, with resistance values of “1” given to the cells with navigable rivers and “1000” outside of this zone, and summed with the overlapping elevation values to investigate the influence of river transport; and (iii) an elevation + river + sea model, including the sea level surface (with resistance values of “1000” to match the scale of the previous model) as potentially navigable routes for maritime trade.

Ten sites—contemporary to the Ychsma culture—were selected either within the predicted presence of the birds 1000 CE or outside their range but regarded as important trade hubs in that time (listed with details in Table 1). CIRCUITSCAPE v5.0<sup>46</sup> was used in the Julia programming language to generate landscape resistance values based on circuit theory<sup>134</sup>, between the Ychsma homeland and the 10 a priori selected sites, taking into account all possible pathways. A pairwise modeling approach was used to calculate resistance values, and cumulative current maps were generated for each resistance model to identify areas that contribute most to connectivity between sites. In this framework, “resistance” represents the difficulty of movement across a given landscape feature (e.g., high elevation poses high resistance), and “current” represents the modeled flow of movement, with high-current areas indicating the most probable corridors. Maps were visualized in QGIS v3.3, and overlaid with the potential present distribution predictions of parrot species<sup>121</sup> identified by the archaeogenomic analyzes. To complement the connectivity maps, we also identified the single most efficient routes. While CIRCUITSCAPE excels at modeling broad corridors by considering all possible pathways simultaneously, it does not generate a single least-cost path. Therefore, to identify the single route of minimum cumulative resistance, we used the same resistance raster maps in the Least-Cost Path v1.1 plugin in QGIS v3.3 to calculate paths between Pachacamac and the a priori sites. This dual approach allowed us to visualize both the most probable regions for movement and the most efficient path within those regions.

In the first scenario, when we only accounted for elevation in the model, Chan Chan and Sicán (on the coast), and Sarayacu (in the Amazon Basin) were assigned with the lowest resistance values (Supplementary Table 3) connecting to the Ychsma homeland (Fig. 5b), while the lowest cost paths were assigned to Chan Chan, Sicán, and Manta (Supplementary Table 3), indicating a coastal transit route (Fig. 5b). Sarayacu was also located within (or at the border of) the predicted past distribution of all four parrot species (Supplementary Fig. 9).

In the second scenario, when navigable rivers were added to the elevation model as highly “conductive” pathways, Sarayacu had the lowest resistance values (Supplementary Table 3) through a trans-Andean pathway (Fig. 5c), while Chan Chan, Sicán, and Cerro de la Sal had the lowest cost path values calculated (Supplementary Table 3). Cerro de la Sal (at the foothills of the Andes on the Amazonian side) was also located within (or right at the border of) the predicted distribution of all four parrot species in 1000 CE (Supplementary Fig. 9).

In the third scenario, when seafaring was also considered on top of the previous models, Chan Chan, Sicán, and Sarayacu showed the lowest resistance values (Supplementary Table 3, and Fig. 5d), while Chan Chan, Sicán, and Cerro de la Sal had the lowest cost path values calculated (Supplementary Table 3). Both the river and the seafaring

models predicted to connect Cerro de la Sal with Pachacamac directly through the Andes, even though it is isolated from the central coast by mountains over 5000 m above sea level.

### Reporting summary

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

### Data availability

New sequences obtained by this study are available at the National Center for Biotechnology Information (NCBI) GenBank, Sequence Read Archive (SRA), and Figshare (see Supplementary Data 13 for accession codes and links). Previously published sequences used in this study for phylogeny reconstructions are listed in Supplementary Data 2–6 and 8–11. Sequences with more than 50% of Ns (given that GenBank does not permit the deposition of such sequences), alignments of the ten Maximum Likelihood (ML) analyzes in Phylip format, and the radiocarbon results are available in Figshare (<https://doi.org/10.6084/m9.figshare.24665697>). All other data are provided in the Supplementary Data sheets. Source Data for Fig. 4 can be found in Supplementary Data 12. The original archaeological samples are permanently curated and accessible at the Museo de Sitio de Pachacamac in Peru (Mg. Denise Pozzi-Escot, [museopachacamac@cultura.gob.pe](mailto:museopachacamac@cultura.gob.pe)). Remaining samples from living birds are stored at freezers of the Research School of Biology, The Australian National University.

### Code availability

Code for the hindcasted species distribution and landscape resistance models are available in Figshare at <https://doi.org/10.6084/m9.figshare.24665697>.

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- analyzed stable isotope results and prepared all visualization. I.S., R.S.L., and G.O. administered the project and acquired permits. I.S., G.O., and P.B. acquired fundings. I.S. and B.L. performed supervisory roles. All authors contributed to the writing of the paper and reviewed the manuscript.

### Competing interests

The authors declare no competing interests.

### Additional information

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**Correspondence** and requests for materials should be addressed to George Olah, Pere Bover or Izumi Shimada.

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### Author contributions

G.O. and I.S. conceived the work. I.S. and R.S.L. conducted the archaeological research and collected ancient feathers. G.O. collected and extracted DNA from modern samples, and sampled feathers for aDNA analysis. P.B., H.H., and B.L. extracted and sequenced aDNA. G.O. performed spatial modeling, P.B. analyzed DNA results. G.O. and P.B.