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Archaeogenomic identification of ancient plant and feather remains from Túcume, Peru

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ABSTRACT

The recovery of ancient DNA (aDNA) from non-mineralized archaeological materials remains a major methodological challenge, particularly in tropical and semi-arid environments where high temperature and humidity accelerate molecular degradation. We evaluated the feasibility of extracting, authenticating, and identifying aDNA from feathers and plant remains recovered at the Túcume Archaeological Complex, a major Lambayeque and later Inca administrative and ceremonial center on the northern coast of Peru. A total of 201 archaeological subsamples (126 feathers and 75 plant remains) were processed in a dedicated aDNA laboratory under strict contamination controls. DNA extraction followed protocols optimized for aDNA extraction, shallow shotgun sequencing data was generated, and metagenomic pipelines were used to assess authenticity and taxonomic assignment. DNA was retrieved from both avian and plant materials, showing highly fragmented molecules and, in some cases, characteristic deamination patterns consistent with aDNA. Although endogenous DNA content was generally low, in many cases it was sufficient for molecular classification in a subset of samples. Initial classifications were obtained for approximately 40 % of feather samples and 36 % of plant samples, with most assignments restricted to higher taxonomic levels (order or family). The recovery of authentic DNA from such challenging substrates demonstrates the methodological viability of archaeogenomic analysis under tropical-arid conditions, but also emphasizes the current limitations imposed by low endogenous DNA content, shallow sequencing, and incomplete reference databases. This study supports the idea that unconventional biological materials could be included with appropriate caution in future archaeogenomic research in Peru and other tropical regions.

1. Introduction

The study of ancient DNA (aDNA) has potential to transform research in environmental archaeology by enabling direct access to genetic information from past ecosystems. Through the analysis of degraded biological remains, it is now possible to reconstruct aspects of past biodiversity, trade, and cultural practices that are otherwise invisible in the archaeological record (Hofman et al., 2015; Przelomska et al., 2020).

Most methodological developments in aDNA studies have focused on bones and teeth, which preserve DNA more effectively due to their mineralized structure (Knapp & Hofreiter, 2010). In contrast, the recovery of DNA from materials such as feathers or plant tissues remains far more challenging. Feathers are composed primarily of keratin, with minimal cellular content and highly fragmented DNA, while plant tissues are often degraded by environmental exposure, microbial activity, and chemical decay (Kistler et al., 2020). Despite these difficulties, recent studies have shown that ancient remains from both types of material can yield authentic DNA when processed under specialized protocols (Bello et al., 2001; Speller et al., 2011; Rawlence et al., 2009). However, systematic archaeogenomic work on these materials, particularly under tropical and semi-arid climates, remains limited.

Feathers hold particular archaeological importance in Peru, where

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pre-Hispanic cultures used them in ornaments, textiles, and ritual paraphernalia that symbolized status and identity (Donnan, 2004; Bourget, 2006; King & Delgado Pérez, 2012). Comparable molecular analyses of feather artifacts have revealed cultural and trade patterns in other regions (Hartnup et al., 2011). These artifacts, sometimes crafted with feathers from exotic Amazonian species, provide tangible evidence of long-distance exchange networks across the Andes and to the coast (Capriles et al., 2021). Likewise, plant remains from northern coastal sites reveal information about subsistence, medicinal practices, and environmental management (Dillehay et al., 2007; Nistelberger et al., 2016). Yet, morphological identification alone is often inconclusive because diagnostic features are lost through charring, desiccation, or decomposition. Ancient DNA analysis offers a complementary route to determine the biological origin of such remains and reconstruct past human–environment interactions.

The northern coast of Peru presents additional challenges for biomolecular preservation. The region's high temperatures, seasonal rains, and intermittent flooding accelerate DNA degradation and promote microbial contamination (Sandweiss & Maasch, 2022). Moreover, many archaeologically important materials in this area were excavated before the implementation of molecular sampling protocols, often under suboptimal conditions for conservation. These environmental and logistical factors make northern Peru a critical test case for evaluating the lower limits of aDNA preservation in the tropics.

A major limitation for DNA-based taxonomic identification of archaeological materials in South America is the uneven representation of local species in genomic reference databases. The accuracy of taxonomic assignment depends heavily on the availability of well-curated sequences for regional taxa (Kocher et al., 2017), especially for Neotropical birds and plants, which remain poorly represented in public repositories (Arana et al., 2024). Incomplete reference datasets can hinder the detection of endemic or culturally significant species and limit broader ecological interpretations derived from ancient samples.

The Túcume Archaeological Complex on Peru's northern coast is renowned for its monumental pyramids and rich material assemblage and was a major population, administrative and ceremonial center for the Lambayeque culture, the Chimú, and later for the Inca civilization (Heyerdahl et al., 1995). Its monumental architecture, long occupational sequence, and historical association with debates on long-distance interaction along the Pacific coast have made it a landmark site in archaeology (Heyerdahl et al., 1995; Narváez, 2023). At Túcume, the challenge of taxonomic identification is archaeologically relevant because various avian and botanical remains formed part of ritual, economic, and technological practices associated with political authority, ceremonial activity, storage, provisioning, craft production, and urban life (Heyerdahl et al., 1995; Narváez, 2023). Its location within a region shaped by irrigation agriculture, El Niño-related environmental disruption, and repeated cultural transitions further makes it a relevant setting for examining how biological materials were selected, moved, and used within late pre-Hispanic coastal societies (Sandweiss & Maasch, 2022; Narváez, 2023). Thus, identifying the taxonomic origin of Túcume's biological remains can help clarify whether they reflect local resource use, specialized craft production, ritual selection, or the movement of plant and animal materials across the northern coast and beyond.

Consequently, this study tests the feasibility of DNA extraction and identification from feathers and plant remains recovered at the Túcume site. By combining strict contamination controls with metagenomic bioinformatic pipelines, we assess the extent to which authentic DNA can be recovered from highly degraded samples in a tropical-arid environment. Specifically, we ask whether: (i) authentic DNA can be recovered and authenticated from archaeological feathers and plant remains from Túcume; (ii) metagenomic taxonomic assignment can improve the identification of these otherwise difficult-to-identify materials; and (iii) these molecular identifications can contribute to archaeological questions concerning resource use, ritual practice, craft production, and the movement of biological materials in late pre-Hispanic Túcume. This work demonstrates the methodological potential of feather and plant aDNA for better understanding Peruvian archaeology and emphasizes the need for better representation of Peruvian and Neotropical taxa in existing genomic/DNA reference databases to improve taxonomic resolution and reliability in future studies.

2. Methodology

2.1. Archaeological context and sample collection

The biological materials analyzed in this study were recovered from the Túcume Archaeological Complex, located in the lower La Leche Valley at the base of Cerro Purgatorio, Lambayeque, northern Peru (Fig. 1). Túcume was a preeminent late pre-Hispanic urban and ceremonial center, serving as a regional capital that spanned the Lambayeque, Chimú, and Inca periods (ca. CE 1000–1532). The site is situated within an arid coastal landscape, historically transformed into a highly productive agricultural hub through extensive irrigation systems and the management of dry forest and maritime resources. The complex comprises 26 monumental adobe pyramids (huacas), expansive plazas, and specialized domestic and craft-production sectors that have been excavated intermittently between 1990 and 2021 (Heyerdahl et al., 1995; Narváez, 2023). Samples analyzed here originated from both the northern and southern sectors of the complex, including Templo de la Piedra Sagrada, Huaca Larga, Plaza Central, Huaca I, Vivienda, Cementerio Los Gavilanes, Huaca Las Balsas and Huaca Las Abejas (Fig. 1). These locations represent a diverse range of functional contexts, from elite funerary chambers and ritual offerings to domestic refuse and storage areas. Feathers and plant remains were typically found in primary and secondary deposits, where they were often associated with textiles, ceramics, and other organic materials. All samples were registered under unique museum accession numbers and stored in controlled conditions to minimize further deterioration.

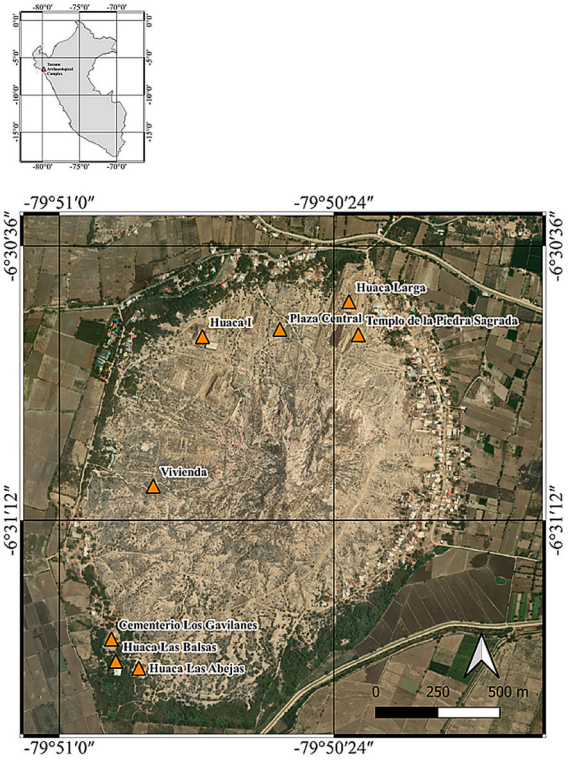

Fig. 1. Map showing the location of the Túcume Archaeological Complex within Peru, and the locations of sites from which the analyzed samples were collected.

2.2. Selection and preparation of subsamples

To minimize contamination, subsampling followed strict decontamination protocols (Supplementary Material 1). Tools were disinfected with 10 % sodium hypochlorite and then 70 % ethanol between samples, and nitrile gloves were used for each handling. Representative fragments were isolated, placed in sterile 2-mL vials, labeled with a unique code, and photographed prior to packing and shipment. Transport to a European research institution was conducted under official authorization from the Peruvian Ministry of Culture. All materials were kept refrigerated until processing.

In total, 201 archaeological subsamples relevant to this study were collected (Fig. 2), comprising 126 feather samples and 75 plant remains. The feather samples originated from a variety of artifacts and contexts, including textiles, ornaments, and isolated fragments recovered from ceremonial and domestic deposits. The plant remains encompassed leaves, fruits, seeds, stems, and wood, representing both dicotyledonous and monocotyledonous taxa, including members of the Poaceae family. All subsamples were subsequently processed for DNA extraction and sequencing under strict aDNA laboratory conditions.

2.3. Laboratory analysis and DNA extraction

The samples were processed in a dedicated paleo-genomics laboratory under strict aDNA laboratory protocols (Llamas et al., 2017). Before DNA extraction, the samples underwent a cleaning process to remove surface contaminants and minimize the presence of exogenous DNA. Each sample was washed with a 10 % diluted sodium hypochlorite solution, followed by rinses with ethanol and ultrapure molecular biology-grade water to eliminate disinfectant residues. Next, the samples were incubated in 750 μL of digestion buffer supplemented with 20 μL of Proteinase K (20 mg/mL), SDS 2 % w/v, Tris-HCl (pH 8.0) 10 mM, CaCl2, EDTA (pH 8.0) 2.5 mM, NaCl 10 mM, and DTT 40 mM (Campos & Gilbert, 2019). The incubation was carried out on a shaking plate at 56 °C for 12–48 h.

Following complete digestion of the specimen, the samples were centrifuged at maximum speed (13,000–14,000 rpm) for 5 min in a benchtop microcentrifuge to separate solid residues from the supernatant. The supernatant was carefully transferred to a clean 2 mL tube for subsequent purification. Following digestion, DNA purification was performed in two successive steps with one volume of phenol:chloroform:isoamyl alcohol (25:24:1), and a final step using chloroform (purity > 99.8 %) to remove proteins and impurities. In each step, the content was thoroughly mixed before centrifuging at maximum speed for 5 min, and recovering the upper aqueous layer containing the DNA. Finally, the purified DNA underwent a concentration and cleaning process using the MinElute PCR Purification Kit (Qiagen), following the manufacturer's instructions, to ensure the removal of contaminants and obtain high-quality DNA for further analysis.

2.4. Library construction and sequencing preparation

Once the extracted DNA was quantified using fluorometry (Qubit), the construction of Illumina-compatible double-stranded DNA libraries was carried out using the BEST (Blunt-End Single-Tube) library preparation protocol, which optimizes adapter ligation in a single tube and minimizes purification steps to maximize DNA recovery from highly degraded material (Carøe et al., 2018). Libraries were subsequently amplified and indexed with a custom set of dual unique primers, using AmpliTaq Gold polymerase according to the manufacturer's instructions.

The PCR reaction mixture in a final volume of 100 μL contained 1X AmpliTaq Gold buffer, 2.5 mM $MgCl_2$, 0.2 mM each dNTP, 0.2 μM forward primer, 0.2 μM reverse primer, 0.4 mg/mL bovine serum albumin, and 0.05 U/μL AmpliTaq Gold polymerase. The PCR cycling conditions were as follows: initial denaturation at 95 °C for 10 min, followed by a sample-specific number of cycles of denaturation at 95 °C for 30 s, annealing at 60 °C for 60 s, extension at 72 °C for 45 s, and a final extension at 72 °C for 5 min. The optimal number of amplification cycles for each sample was estimated using quantitative PCR (qPCR) using the same PCR conditions as for indexing the libraries. The indexed libraries were then purified and size-selected with SPRI beads (Cytiva Sera-Mag or AMPure XP) using a beads:DNA ratio of 1.2:1.0. Molarity and fragment length distribution for each amplified library were estimated using High Sensitivity D1000 ScreenTape assay (Agilent) on a 4200 TapeStation instrument (Agilent). Finally, libraries were pooled equimolarly and sequenced by Novogene Europe on the Illumina NovaSeq X platform in 150-bp paired-end format and aiming to generate a mean of 2.5 Gbp raw sequencing data per sample.

2.5. Contamination considerations

Given the high risk of contamination in aDNA analysis, strict measures were implemented to ensure result integrity. All work was conducted in a positively pressurized paleo-genomics lab equipped with HEPA air filtration systems, laminar flow hoods and strict access

Fig. 2. Representative archaeological samples analyzed in this study. The left panel shows feather fragments from sample MST2-218, and the right panel shows desiccated seeds from sample MST2-382.

protocols. Throughout the procedure, sterilized protective clothing was worn, including full-body protective suits, double gloves, face masks, and hair covers. Additionally, all materials and work surfaces were periodically disinfected with 5 % sodium hypochlorite to prevent both sample cross-contamination and environmental contamination.

2.6. Bioinformatic analysis

The principal sequencing data analysis included preprocessing of reads to remove adapters, filter out low-quality reads, and eliminate PCR duplicates, and then performing taxonomic classification of the obtained sequences. This workflow followed a metagenomic approach without an *a priori* species assumption developed for large-scale metagenomic data processing in environmental samples (https://www.github.com/miwipe/Holi). In the preprocessing phase, adapters and low-quality regions were removed using cutadapt (Martin, 2011), discarding reads shorter than 30 nucleotides after trimming. Paired-end reads were further trimmed and aligned using AdapterRemoval v2.0 (Schubert et al., 2016) to identify and collapse paired sequencing reads with an overlap of at least 11 bp, retaining afterwards only collapsed and unpaired reads. Subsequently, the String Graph Assembler (SGA) (Simpson & Durbin, 2010) tools *preprocess*, *index*, and *filter* were used to remove duplicate sequences and low-complexity sequences such as those containing poly-nucleotide tracts or microsatellites.

A high degree of DNA fragmentation and low endogenous yields were expected due to the harsh environmental and storage conditions in the area (Sandweiss & Maasch, 2022). For this reason, rigorous authentication criteria were applied to all sequence data for the decontamination and taxonomic classification. First, filtered reads were subjected to a k-*mer*-based classification approach with Kraken2 (Wood et al., 2019) using the plusPF microorganism database, and reads classified as microorganisms were discarded from the analyses. Next, a competitive mapping approach was conducted against the microbial Genome Taxonomy Database (GTDB) (Parks et al., 2022) and custom reference databases using Bowtie2 (Langmead & Salzberg, 2012) to estimate the closest matching lineages.

The reference databases for feather and plant samples consisted of Aves and Magnoliopsida sequences, respectively. The former integrated publicly available sequences and region-specific mitogenomes from Neotropical birds. To overcome the challenges of using nuclear data that are often misassembled or contain microbial contamination, only organelle genomes were used under the assumption that these assemblies are less contaminated and error-prone. For this we queried the NCBI nucleotide database using the Entrez Direct (EDirect) command-line tools (NCBI). For birds, 6,263 complete or partial mitochondrial genomes were downloaded on 2025–06-28 (search term Aves[ORGN] AND mitochondrion[TITL] AND (complete[TITL] OR partial [TITL] AND 0:20000[SLEN]) and combined with the assembled contigs from 214 newly-sequenced Neotropical bird mitogenomes deposited in Dryad (https://doi.org/10.5061/dryad.dbrv15fht). Similarly, Magnoliopsida complete chloroplast genomes with total lengths between 50–250 kbp were retrieved (search term Magnoliopsida[ORGN] AND chloroplast [TITL] AND complete[TITL] AND 50000:250000[SLEN], on 2025–05-28), retaining only one sequence per species within genera distributed in Peru (based on the World Checklist of Vascular Plants (WCVP)). A total of 17,769 chloroplast sequences were retained in the custom database.

Taxonomic nomenclature for avian sequences was standardized according to the International Ornithological Community (IOC) World Bird List v15.1 (Gill et al., 2025); while for plants, nomenclature followed the Angiosperm Phylogeny Website v14 (Missouri Botanical Garden, n.d.). Taxonomic classification was performed using a lowest common ancestor (LCA) algorithm, and authenticity of aDNA was verified through characteristic deamination patterns and short read lengths. To ensure reliability, only taxa supported by at least 10 reads were retained for further analyses as explained below, following established minimum-read thresholds for trustworthy identification. However, filtered data may still contain exogenous or modern DNA, meaning not all sequences necessarily correspond to the original species of the sample. Therefore, taxonomic classifications were further curated and validated using the alignment filtering, LCA assignment, and genome-mapping approaches described below.

The resulting alignments were filtered using bam-filter (https://github.com/genomewalker/bam-filter) to remove poorly aligned reads and problematic reference sequences, minimizing the influence of non-diagnostic or ambiguous regions on taxonomic assignments. The filters required alignments to be at least 90 % of the read length (−A 90) and have at least 90 % sequence identity to their matches in the reference database (−a 90). Additional filtering criteria included a minimum read count (−n 3), expected breadth ratio (−b 0.8), normalized entropy (−e 0.75), and normalized Gini coefficient (−g 0.6). Filtered alignment files for each dataset were compressed using metaDMG's compressbam algorithm (Michelsen et al., 2022) and respectively merged with the compressed GTDB alignment results. Taxonomic LCA assignments were performed using ngsLCA (Wang et al., 2022), requiring between 95–100 % similarity (−simscore low 0.95 −simscorehigh 1). NgsLCA evaluates all alignments for each read and assigns taxonomy at different levels depending on the distance of the taxa involved (e.g., a read from highly-conserved regions, where alignments could span multiple taxa, are likely to be assigned to higher ranks such as class or order). All runs were repeated once, omitting the initial alignment filtering step to compare results from reference sequences discarded due to a low number of reads not reaching the filtering criteria.

Lastly, in cases where the taxonomic identity was assigned with at least 10 reads to an LCA with available close relative reference genomes, the sample's raw reads were trimmed and mapped using PALEOMIX v1.3.7 (Schubert et al., 2016) to the available nuclear and organellar genome assemblies of all species under the genus or family of the identified LCA. Ancient DNA authenticity was corroborated using mapDamage2 (Jónsson et al., 2013). Mapping statistics were obtained from the PALEOMIX summary file.

2.7. Genomic database

To evaluate potential reference bias, we conducted a comprehensive review of the NCBI nucleotide and genome databases (Benson et al., 2018) to determine the availability of genomic resources for bird species relevant to South American archaeology. To assemble this list, we performed a systematic survey of published archaeological and zooarchaeological studies documenting avian species from South American contexts. Each species reported in these sources was then cross-referenced against NCBI to assess whether nuclear and mitochondrial genome assemblies were available. All species included in this assessment, along with their bibliographic sources and NCBI accession codes, are presented in Table 4, which serves as the full reference dataset for this component of the analysis.

3. Results

3.1. Genomic DNA extraction and sequencing

DNA was successfully extracted from 126 feather samples and 75 plant samples. DNA concentration varied significantly among the different sample types. Feather samples showed values ranging from $<$ 0.05 ng/μL to 126 ng/μL, and plant samples ranged from $<$ 0.05 ng/μL to 54 ng/μL (Table S1). Samples were screened via shallow shotgun Illumina sequencing, yielding a total output of 353.58 Gbp and 155.64 Gbp, respectively (Table S1).

The preprocessing of sequencing reads resulted in a significant reduction in the amount of retained data due to the removal of unusable or redundant regions. Read filtering led to an average per-sample data reduction of 91.74 % for feathers and 92.78 % for plants, leaving a usable data volume of 9.47 Gbp and 9.07 Gbp, respectively, for taxonomic

assignment analyses (Table S1).

3.2. Taxonomic identification

Taxonomic assignment followed an initial metagenomic approach using competitive alignments to organelle genomes and posterior nuclear genome mapping for each identified family or genus. For feathers, 50 out of 126 samples (40 %) attained an initial classification, from which 15 were at the genus level, 28 at the family level, and 7 to higher ranks. There was a notable difference in classifications among sites. Samples from the northern areas, Huaca Larga and Templo de la Piedra Sagrada, were predominantly assigned to the order Passeriformes, including families such as Tyrannidae, Thamnophilidae, and Emberizidae. In contrast, samples from the Vivienda sector showed a broader diversity of avian taxa, encompassing orders including Anseriformes, Galliformes, Columbiformes, Cuculiformes, Strigiformes, Accipitriformes, Suliformes, and Passeriformes (Table 1).

For plants, 27 out of 75 (36 %) samples attained an initial classification, from which 4 were at the genus level, 12 at the family level, 1 at the subfamily level, and 10 to higher ranks (Table 2). In Huaca Larga, the only identified sample was assigned to Mesangiospermae. Samples from Huaca Las Abejas included assignments to Mesangiospermae, Lamiids, and Eudicotyledoneae, as well as taxa such as Lauraceae, Poaceae, Mimosoideae, Annonaceae, Malvaceae, and Fabaceae. At Huaca Las Balsas, sequences were classified within Pentapetalae, Eudicotyledoneae, and Monocotyledoneae, whereas samples from Plaza Central were assigned to Pentapetalae, Eudicotyledoneae, and the family Poaceae (Table 2). None of the plant samples from Huaca I (n = 1) or Cementerio Los Gavilanes (n = 3) attained a taxonomic assignment.

Table 1
Initial LCA results from competitive mappings for feather samples. The number of samples that could be taxonomically assigned is indicated as *n*, expressed as assigned samples out of the total number of samples analyzed for each site sector.

Site sector	Metagenomic taxonomic assignment	Rank	Samples (n)
Huaca Larga (n = 15 of 44)	Neognathae	Infraclass	1
	Passeriformes	Order	2
	Passeriformes, Tyrannidae	Family	6
	Passeriformes, Thamnophilidae	Family	1
	Passeriformes, Emberizidae	Family	1
	Galliformes, *Phasianidae*	Family	3
	Columbiformes, Columbidae	Family	1
Templo de la Piedra Sagrada (n = 1 of 4)	Passeriformes, Tyrannidae	Family	1
Vivienda (n = 34 of 78)	Neognathae	Infraclass	1
	Neoaves	Superorder	2
	Strigiformes	Order	1
	Anseriformes, Anatidae	Family	8
	Columbiformes, Columbidae	Family	1
	Galliformes, Cracidae	Family	4
	Passeriformes, Thraupidae	Family	1
	Suliformes, Phalacrocoracidae, *Leucocarbo*	Genus	1
	Strigiformes, Strigidae	Family	1
	Anseriformes, Anatidae, *Cairina*	Genus	3
	Accipitriformes, Cathartidae, *Coragyps*	Genus	3
	Columbiformes, Columbidae, *Columba*	Genus	1
	Columbiformes, Columbidae, *Zenaida*	Genus	1
	Cuculiformes, Cuculidae, *Crotophaga*	Genus	1
	Passeriformes, Thraupidae, *Sporophila*	Genus	1
	Galliformes, *Phasianidae*, *Meleagris*	Genus	1
	Strigiformes, Strigidae, *Athene*	Genus	1
	Strigiformes, Strigidae, *Bubo*	Genus	1
	Passeriformes, Troglodytidae, *Campylorhynchus*	Genus	1

Table 2
Initial LCA results using a metagenomic approach for plant samples. The number of samples that could be taxonomically assigned is indicated as *n*.

Site sector	Metagenomic taxonomic assignment	Rank	Samples (n)
Huaca Larga (n = 1 of 1)	Mesangiospermae	Clade	1
Huaca Las Abejas (n = 20 of 48)	Mesangiospermae	Clade	2
	Lamiids	Clade	1
	Eudicotyledoneae	Clade	1
	Lauraceae	Family	2
	Poaceae	Family	9
	Mimosoideae	Subfamily	1
	Annonaceae, *Annona*	Genus	2
	Malvaceae, *Gossypium*	Genus	1
	Fabaceae, *Neltuma*	Genus	1
Huaca Las Balsas (n = 3 of 11)	Pentapetalae	Clade	1
	Eudicotyledoneae	Clade	1
	Monocotyledoneae	Clade	1
Plaza Central (n = 3 of 11)	Pentapetalae	Clade	1
	Eudicotyledoneae	Clade	1
	Poaceae	Family	1

For samples that attained a genus or family classification, a posterior genome mapping analysis was performed to all available nuclear and organellar genomes. This analysis allowed an authentication of the aDNA and an estimation of the endogenous DNA content (Table 3; Table S2), with most samples exhibiting low endogenous content yet retaining short fragment lengths (Fig. S1) and terminal deamination patterns characteristic of aDNA (Table S2, Fig. S2).

Sample MST2-183 had low numbers of mapped reads, either due to limited DNA recovery or the absence of corresponding reference genomes (e.g., birds of the genus *Athene*), exhibited inconsistent DNA damage profiles and could not be authenticated as ancient (Table 3, Fig. S2). A total of 42 libraries were excluded from downstream interpretation due to low mapped read numbers (< 10 reads). In contrast, samples with longer average fragment lengths and no clear damage pattern, such as MST2-377 (94.59 bp), are most likely to represent modern contamination (Table S1). The best sequence matches should not be interpreted as definitive species identifications, given the limited representation of local avian and plant taxa in current NCBI genomic databases. Nevertheless, in most cases where mapping included global representatives of the same family or genus, reads showed higher alignment to South American or broadly American species than to taxa distributed in other regions.

3.3. Genomic database

A group of 28 bird species recorded in South American archaeological contexts was analyzed to determine the availability of nuclear and mitochondrial genome assemblies in the NCBI database (Table 4). Additionally, bibliographic references from studies documenting these records are included.

The results indicate that 15 of the 28 bird species recorded in South American archaeological contexts are represented in public databases by nuclear genome assemblies, although several of these are incomplete or scaffold-level assemblies. Mitochondrial genome assemblies are available for 14 of the 28 species, although one is only partially assembled. Additionally, some species from South American archaeological contexts lack any complete nuclear or mitochondrial genome reference.

4. Discussion

The recovery of ancient DNA (aDNA) from archaeological organic

Table 3
LCA-informed genome mapping results for feather and plant samples. Species marked with an asterisk (*) are not naturally distributed in Peru. Ancient damage indicates the mismatch rate at the first mapped base on the 5′ end.

Sample	Metagenomic ID	Best match	Number of unique reads	Endogenous fraction	Mean read length (bp)	Ancient damage
MST2-148	Anatidae sp.	NUCL: *Anas georgica* MITO: *Anas platyrhynchos (*)*	NUCL: 192,047; MITO: 1,334	6.58 %	51	0.034
MST2-158	*Bubo* sp.	NUCL: *Bubo virginianus* [a] MITO: *Bubo scandiacus (*)*	NUCL: 25,711; MITO: 80	2.84 %	48	0.14
MST2-172	*Leucocarbo* sp.	NUCL: *Nannopterum harrisi (*)* MITO: *Leucocarbo bougainvilliorum*	NUCL: 1720; MITO: 65	0.15 %	49	0.058
MST2-173	Anatidae sp.	NUCL: *Anas platyrhynchos (*)* MITO: *Anas platyrhynchos (*)*	NUCL: 5,792; MITO: 76	0.84 %	53	0.042
MST2-174	*Meleagris* sp.	NUCL: *Meleagris gallopavo (*)* MITO: *Meleagris gallopavo (*)*	NUCL: 4,093; MITO: 199	0.37 %	55	0.053
MST2-176	*Cairina* sp.	NUCL: *Cairina moschata* MITO: *Cairina moschata*	NUCL: 123,308; MITO: 1,356	14.03 %	54	0.038
MST2-177	Anatidae sp.	NUCL: *Anas flavirostris* MITO: *Anas platyrhynchos (*)*	NUCL: 4,789; MITO: 86	0.40 %	50	0.041
MST2-179	*Cairina* sp.	NUCL: *Cairina moschata* MITO: *Cairina moschata*	NUCL: 43,557; MITO: 12	4.45 %	56	0.021
MST2-183	*Athene* sp.	NUCL: *Athene cunicularia* MITO: *Athene cunicularia*	NUCL: 613; MITO: 21	0.04 %	52	0.03 (Noisy)
MST2-210	*Columba* sp.	NUCL: *Columba livia* MITO: *Columba livia*	NUCL: 81,785; MITO: 332	6.60 %	51	0.025
MST2-211	*Zenaida* sp.	NUCL: *Streptopelia decaocto (*)* MITO: *Zenaida auriculata*	NUCL: 34,281; MITO: 224	2.77 %	57	0.023
MST2-215	*Coragyps* sp.	NUCL: *Vultur gryphus* MITO: *Coragyps atratus*	NUCL: 3,493; MITO: 25	0.29 %	55	0.031
MST2-217	*Cairina* sp.	NUCL: *Cairina moschata* MITO: *Cairina moschata*	NUCL: 841,259; MITO: 233	63.79 %	56	0.049
MST2-218	*Campylorhynchus* sp.	NUCL: *Thryothorus ludovicianus (*)* MITO: *Campylorhynchus zonatus (*)*	NUCL: 197,932; MITO: 1,258	23.57 %	65	0.039
MST2-221	*Sporophila* sp.	NUCL: *Sporophila hypoxantha* MITO: *Sporophila minuta*	NUCL: 10,416; MITO: 81	0.92 %	58	0.031
MST2-341	Lauraceae	NUCL: *Umbellularia californica* CHLO: *Cassytha filiformis*	NUCL: 923; CHLO: 82	0.24 %	45	0.179
MST2-382	*Gossypium* sp.	NUCL: *Gossypium hirsutum (*)* CHLO: *Gossypium barbadense*	NUCL: 39,155; CHLO: 191	5.99 %	51	0.073

[a] *Bubo virginianus* in *sensu lato* includes *Bubo magellanicus*, which is present in Peru.

materials offers new opportunities to explore the biological and cultural dimensions of past societies. This study is primarily exploratory in nature, aiming to evaluate the feasibility and reliability of recovering and identifying aDNA from unconventional archaeological substrates. While previous aDNA research in Peru and other tropical regions has typically focused on human, bone, or dental remains (Nieves-Colón et al., 2018), which are known to preserve genetic material under adverse conditions (Hofreiter et al., 2001), this study shows that authentic DNA can be retrieved from a subset of materials that are highly susceptible to decay, such as feathers and plant matter, although recovery and taxonomic resolution were limited. These results support the potential of archaeogenomic research in tropical and semi-arid regions by demonstrating that feather and plant remains, two substrates rarely analyzed in these environmental contexts, can preserve authentic DNA despite their high susceptibility to degradation.

4.1. Factors influencing DNA preservation

DNA preservation in archaeological materials is influenced by a combination of intrinsic and extrinsic factors, including temperature, humidity, soil composition, and exposure to contaminants (Lindahl, 1993). Feathers, composed mainly of keratin and lacking living cells, retain only minimal amounts of endogenous DNA (Harvey et al., 2006) and are particularly vulnerable to fragmentation and hydrolytic damage. In contrast, plant tissues, despite their exposure to environmental degradation, can retain trace amounts of DNA within lignified or silicified structures (Schwörer et al., 2022), explaining the generally higher recovery observed in plant remains. Further challenges arise from DNA degradation, environmental exposure, and potential contamination with exogenous material (Knapp & Hofreiter, 2010). Moreover, archaeological materials from Túcume were excavated and stored before the implementation of sampling protocols for molecular studies, increasing the risk of exogenous contamination and chemical deterioration. These factors collectively may explain the variability in DNA preservation among the analyzed materials and sites. Nevertheless, the extraction and authentication of aDNA in a subset of feather and plant samples demonstrate that, even under suboptimal conservation conditions, molecular traces can survive for centuries when protected within microenvironments such as textile matrices, burial offerings, or compacted sediments.

4.2. Taxonomic identification and database constraints

Taxonomic assignment of aDNA sequences remains one of the most challenging aspects of archaeogenomic analysis, particularly when working with non-mineralized materials and poorly represented taxa (Cribdon et al., 2020). In this study, taxonomic classification was achieved for a subset of the analyzed feather and plant samples, including approximately 40 % of feather samples and 36 % of plant samples, confirming the presence of authentic ancient avian and botanical DNA. The specificity of taxonomic identification varied from high-level assignments (e.g., order or family) to genus-level classifications, depending on DNA preservation quality and the availability of suitable reference genomes.

The avian samples included taxa from a broad range of orders, such as Anseriformes, Galliformes, Columbiformes, Cuculiformes, Strigiformes, Accipitriformes, Suliformes, and Passeriformes, while the plant remains were primarily assigned to major clades such as Mesangiospermae, Eudicotyledoneae, and Monocotyledoneae, and to families including Lauraceae, Poaceae, and Malvaceae. These assignments provide preliminary molecular evidence for the biological diversity represented in the archaeological materials, consistent with the complex

Table 4
Avian species reported in archaeological contexts and the availability of genomic information. The bibliographic reference column indicates the study reporting each species from South American archaeological contexts.

Species	Nuclear genome	Mitochondrial genome	Bibliographic reference
Amazona aestiva	GCA_017639355.1, GCA_001420675.1*,GCA_026283685.1*	KT361659.1	Eeckhout, 2002; Capriles et al., 2021
Amazona farinosa	GCA_032353435.1*	Absent	Eeckhout, 2002; Gómez et al., 2017; Capriles et al., 2021
Amazona festiva	GCA_031763565.1*	Absent	Eeckhout, 2002
Amazona ochrocephala	GCA_039720435.1	CM077910.1, KM611467.1	Eeckhout, 2002; Gómez et al., 2017; Capriles et al., 2021
Ara ararauna	GCA_026284445.1, GCA_010014805.2	KF010315.1, PQ473722.1	Gómez et al., 2017; Capriles et al., 2021
Ara macao	GCA_026283635.1*, GCA_000400545.1*, GCA_000400695.1*	MK351783.1, MK351784.1, PQ167823.1	Gómez et al., 2017; Capriles et al., 2021
Ara severus	GCA_024733695.1*	PQ167825.1, KF946546.1	Eeckhout, 2002
Athene cunicularia	GCA_003259725.1*	Absent	Urquiza & Echevarria, 2018
Cairina moschata	GCA_048319975.1, GCA_018104995.1, GCA_009194515.1, GCA_049942535.1	NC_010965.1, MN356432.1	Gómez et al., 2017
Coragyps atratus	Absent	MN720440.1	Eeckhout, 2002
Cotinga cayana	Absent	Absent	Eeckhout, 2002
Molothrus oryzivorus	Absent	Absent	Gómez et al., 2017
Chloephaga melanoptera	Absent	Absent	Urquiza & Echevarria, 2018
Leucocarbo bougainvilliorum	Absent	Absent	deFrance, 2005
Nannopterum brasilianum	GCA_002174335.1*	KT626611.1	deFrance, 2005
Pharomachrus pavoninus	Absent	Absent	Eeckhout, 2002
Phoenicoparrus jamesi	Absent	Absent	Urquiza & Echevarria, 2018
Phoenicoparrus andinus	Absent	Absent	Urquiza & Echevarria, 2018
Phoenicopterus chilensis	Absent	Absent	Urquiza & Echevarria, 2018
Platalea ajaja	Absent	Absent	Eeckhout, 2002
Psittacara mitratus	GCA_026283805.1*	NC_082169, OR209190	Capriles et al., 2021
Rhea pennata	GCA_028389875.1, GCA_003342835.1	MN356430.1, AF338709.2	Urquiza & Echevarria, 2018
Rupicola peruvianus	Absent	MN602289.1	Gómez et al., 2017
Sula nebouxii	GCA_047404275.1*	Absent	deFrance, 2005
Sula variegata	GCA_038407235.1*	Absent	deFrance, 2005
Trogon melanurus	GCA_013399275.1*	MN356299.1	Gómez et al., 2017
Trogon personatus	Absent	MK060146.1**	Gómez et al., 2017
Trogon viridis	Absent	NC_011714.1	Eeckhout, 2002

*: Incomplete nuclear assemblies (scaffold-level or lacking chromosome-level data).**: Partial mitochondrial genome.

cultural and environmental context of the Túcume site. The identified avifauna span both marine-associated and terrestrial taxa, reflecting the broad environmental range of biological materials used at the site. Similarly, the plant families detected are consistent with the use of agricultural products and economically important plant resources in Lambayeque, Chimú, and Inca-period contexts (Dillehay et al., 2007; Narváez, 2023).

In a single case, sequence alignments matched a taxon not documented in pre-Hispanic Peru, namely *Meleagris gallopavo* (wild turkey), a North American species. This sample produced 4,093 unique nuclear reads and 199 unique mitochondrial reads assigned to *M. gallopavo*, with a low endogenous fraction of 0.37 %, a mean read length of 55 bp, and detectable terminal damage patterns consistent with degraded DNA. Given the exploratory nature of the study, this result may reflect modern contamination, post-contact introduction, or reference bias rather than definitive evidence for the presence of turkey in a pre-Columbian context. The possibility of reference bias is relevant because Peru lacks native *Phasianidae*, and the native Galliformes in the region belong instead to the families Cracidae and Odontophoridae (Gill et al., 2025). We therefore interpret MST2-174 conservatively as evidence for the detection of an unresolved galliform rather than definitive evidence for the presence of turkey in pre-Columbian Peru.

The limited representation of Neotropical birds and plants in global genomic databases (Arana et al., 2024; Marks et al., 2021) hinders species-level resolution and increases the likelihood of false positives when DNA fragments align with distant taxa that are better represented in reference datasets. Expanding genomic resources for Neotropical avifauna and flora is essential not only to enhance the reliability of molecular classifications but also to enable the reconstruction of past biodiversity and trade networks with greater precision. Developing region-specific reference panels that include endemic and culturally significant species would significantly strengthen future archaeogenomic research in South America.

4.3. Archaeological implications of the taxonomic assignments

The taxonomic assignments reported here should be interpreted cautiously, they provide a useful molecular perspective on the biological materials incorporated into different sectors of Túcume. This is particularly relevant because Túcume was not a single-function settlement, but a complex urban, political, and ceremonial center occupied during the Lambayeque, Chimú, and Inca periods (Heyerdahl et al., 1995; Narváez, 2023). The recovery of avian and plant DNA from these contexts helps to connect organic remains with broader questions concerning ritual practice, resource use, and the movement of materials across the northern coast of Peru.

The avian identifications suggest distinct patterns of use between site sectors. Huaca Larga and the Templo de la Piedra Sagrada were dominated by passerine identifications, particularly from the Tyrannidae family. This pattern is consistent with the highly ritualized nature of these spaces (Narváez, 2023). For example, in the Templo de la Piedra Sagrada, where human and camelid sacrifices are documented in relation to the final phases of occupation (Narváez, 2023), the presence of small passerine feathers may reflect their use in specialized offerings or the decoration of elite textiles (King & Delgado Pérez, 2012; Gómez et al., 2017). By contrast, identifications of avian remains from the Vivienda sector showed a broader taxonomic spectrum, including ducks (Anatidae), owls (*Bubo* sp.), and scavenging birds (*Coragyps* sp.), which may reflect a broader range of local or commonly available birds associated with residential, urban, or secondary depositional contexts.

Regarding botanical remains, the presence of Poaceae, *Gossypium*, *Annona*, and *Neltuma* provides molecular evidence consistent with the importance of cultivated, managed, and economically useful plants at the site. The identification of *Gossypium* is particularly relevant, given the importance of cotton in Andean textile production and in elite and ritual contexts at Túcume (Narváez, 2023). Furthermore, the presence of *Neltuma* reflects the persistent importance of the dry forest ecosystem, which provided fuel, timber for monumental construction, and seeds and wood used in domestic, construction, and possibly ritual contexts.

4.4. Methodological limitations and future directions

The analysis of highly degraded archaeological materials presents several methodological challenges that must be considered when interpreting the results. The first limitation concerns the quality and quantity of preserved DNA. Most feather and plant samples yielded low endogenous DNA content and highly fragmented molecules, which limited the potential depth of sequencing and thus reduced the number of reads available for taxonomic classification. Only taxa supported by sufficient read depth and characteristic aDNA damage profiles can be considered reliable, following conservative minimum-read thresholds to ensure that identifications reflect authentic sequences rather than spurious alignments. Although the application of strict authentication criteria minimized the impact of contamination, the low fraction of endogenous DNA remains a major constraint in archaeogenomic research. In such challenging cases, deeper sequencing could increase the recovery of informative reads, although this strategy may remain inefficient when endogenous DNA content is very low. Future efforts to target specific taxa with in-solution hybridization capture (Carpenter et al., 2013) may therefore offer a more efficient way forward.

A second major limitation arises from the fragmentary nature of genomic reference databases for South American taxa. The underrepresentation of regional species, particularly among Neotropical birds and plants, limited the resolution of taxonomic assignments and increased the probability of ambiguous or incorrect classifications. Recent progress in regional genomics (Sánchez-Vendizú et al., 2025) provides a valuable foundation for expanding genomic coverage of Peruvian biodiversity. Building on these efforts, future initiatives should prioritize the inclusion of native Andean and coastal taxa to create a more comprehensive genomic database for South America. Improved reference representation would not only enhance taxonomic assignment but also support the development of regionally appropriate hybridization capture baitsets, whose design depends on the availability of representative sequence data. Such developments will improve the accuracy of molecular identifications and enable the investigation of broader questions concerning species domestication, exchange networks, and biogeographic connectivity in the pre-Hispanic Andes.

Finally, there is a need for standardized field and storage procedures specifically designed for archaeogenomic sampling. Many of the samples analyzed in this study were collected before the establishment of protocols for protecting the molecular content of biological remains, which likely contributed to DNA degradation and the introduction of exogenous material. The implementation of systematic procedures will substantially improve DNA preservation and minimize contamination risks. A detailed protocol for field collection, cleaning, and preservation of organic archaeological samples is provided in English and Spanish in Supplementary Data 1.

4.5. Broader implications and cultural relevance

This study represents one of the first systematic attempts to recover and analyze aDNA from feathers and plant remains in archaeological contexts from the northern coast of Peru. The successful extraction and authentication of genetic material from a subset of these highly degradable substrates supports the feasibility of applying molecular techniques to a broader range of these archaeological materials than was previously assumed possible, while also making clear the limitations imposed by low endogenous DNA content and incomplete reference databases. By expanding the spectrum of analyzable specimens, this research contributes to the development of methodological frameworks for the study of tropical and semi-arid contexts, where DNA preservation has historically been considered limited. Beyond its methodological value, this study provides a foundation for future interdisciplinary research integrating molecular, archaeological, and ecological evidence. Such integration will enable more detailed reconstructions of past economies, ritual practices, and environmental management strategies across pre-Hispanic societies. Strengthening the representation of South American taxa in genomic databases will further enhance the resolution of taxonomic identifications and promote comparative studies across regions.

The advancement of archaeogenomics in Peru also carries broader implications for the conservation and understanding of the country's biocultural heritage. Ancient DNA research not only recovers biological information from the past but also provides a molecular record of the interactions between people and their environment. Building regional capacity for archaeogenomic analysis through collaborative networks, training programs, and the establishment of local genomic databases will foster greater autonomy in the study and preservation of Peru's archaeological legacy. These efforts will ultimately contribute to documenting, protecting, and revaluing the biological and cultural diversity of northern Peru.

CRediT authorship contribution statement

Juan Esteves: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Renato D. La Torre Ramirez:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Jacqueline Hernández:** Investigation, Formal analysis. **Alejandra Arana:** Writing – review & editing, Validation. **Jaime Morin-Lagos:** Supervision, Project administration, Methodology, Funding acquisition, Formal analysis. **Sarah L.F. Martin:** Methodology. **José M. Capriles:** Writing – review & editing. **Letty Salinas:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Alfredo Narváez:** Writing – review & editing, Validation, Resources, Project administration. **Bernarda Delgado:** Writing – review & editing, Validation, Resources, Project administration. **César Arana:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Michael D. Martin:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2026.105979.

Data availability

Raw sequencing data generated from the Túcume archaeological specimens will be deposited in the European Nucleotide Archive under project accession PRJEB114849. The Neotropical bird mitogenome reference sequences used in this study are available in Dryad at https://doi.org/10.5061/dryad.dbrv15fht.

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