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# Diversified human dietary strategies and settlement patterns in the core of the Atacama Desert during the late Pleistocene-Holocene transition (~12.8 – 11.2 ka)

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ABSTRACT

Hunter-gatherers that spread after the Last Glacial Maximum, developed a wide range of strategies to cope with environments subject to major socio-ecological transformations. The Pampa del Tamarugal (PdT), in the hyperarid core of the Atacama Desert, was tied to episodic regional positive hydroclimate anomalies (Central Andean Pluvial Events, CAPE), which enhanced bioproductivity and marked diversity of resources that transformed the basin into an ecological refuge, well suited for hunting small and medium-sized fauna, gathering plants and firewood, and procuring types of lithic raw materials for tool production. Two distinct settlement systems were developed along Quebrada Maní wetlands and Pampa Ramaditas floodplains in the PdT basin, where excavations have yielded well-dated zooarchaeological and archaeological assemblages. Quebrada Maní (ca. 12.8–11.2 ka) functioned a seasonal residential camp under the protection and fertility of wetland and woodland. There, people captured, processed, and consumed a wide range of small and middle size fauna including rodents, birds, and guanacos. In contrast, at the slightly younger (ca. 12.4–11.3 ka) Pampa Ramaditas open riverine landscapes, people stablished short-term non-residential camps, consuming small game. We conclude that Pampa del Tamarugal played a key role in the early history of human dispersal and settlement in South America.

## 1. Introduction

After the Last Glacial Maximum (~26.0–20.0 ka BP[1]), different groups of hunter-gatherers developed social systems to cope with the planet's diverse ecosystems, which were undergoing profound ecological transformations (Nolan et al., 2018). The great variability of socio-

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[1] All dates are expressed in thousands of years (ka) calibrated.

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ecological systems that emerged at this time cannot be fully addressed by generalist theoretical models, as different socio-cultural adaptations occurred, even within similar ecosystems. The earliest hunter-gatherer groups to populate South America's varied ecosystems developed diversified and sophisticated livelihoods (Borrero, 2015; Braje et al., 2017; Lynch, 1988; Méndez et al., 2018; Politis et al., 2016). This entailed adjusting subsistence strategies and group size according to ecosystem characteristics and available resources.

Megafauna apparently went extinct in the high-altitude ecosystems of the Andes (or Andean Puna) before human arrival, according to recent chronological information obtained from megafaunal bone collagen and other proxies (Rozas-Davila et al., 2016; Villavicencio and Werdelin, 2018). In fact, faunal remains at early archaeological sites in the Puna suggest subsistence was based mainly on artiodactyls (camelids and deer) and rodents, such as in Salar de Punta Negra 6, Tuina 5, Cueva Bautista and Cuncaicha, among others (i.e. Capriles et al., 2016; Núñez et al., 2022; Rademaker et al., 2014). In contrast, solid evidence exists for megafaunal processing in various sites of the Argentinean Pampas such as Arroyo Seco 2 and Campo Laborde (Politis et al., 2016; 2019). Nevertheless, medium to small animals were consistently consumed in central Patagonia, as documented from archaeological deposits in sites such as Cueva Túnel or Alero El Puesto 1 (Martínez et al., 2016; Marchionni et al., 2022; Valiza Davis and Rindel, 2024).

On the western flank of the Andes, a similar contemporary mosaic of subsistence strategies has been documented. On the northern coast of Peru, the zooarchaeological assemblage from Huaca Prieta, a late Pleistocene human settlement associated with an early adaptation to the Pacific coast, includes deer, birds, and fish (Dillehay et al., 2012). In central Chile, the Tagua Tagua sites revealed the consumption of meat from waterfowl (mostly ducks), rodents (*Myocastor coypus*), and even amphibians (*Calyptocephalella* sp.), alongside well-documented evidence for megafauna exploitation, including Gomphotheriidae, Equidae, and Cervidae (Labarca et al., 2020; Labarca et al., 2024; Núñez et al., 1994). This is consistent with findings from other late Pleistocene archaeological sites in southern Chile, such as Tres Arroyos 1, Cueva del Medio, and Cueva Fell in southern Patagonia, where guanaco and, to a lesser extent, birds, rodents, and canids were more consumed than extinct taxa such as mylodons and equids (Humphrey et al., 1993; Labarca, 2016; Martin, 2022). Nevertheless, as in the Argentine Pampas, there are archaeological sites with faunal assemblages composed almost exclusively of megafauna, such as Monte Verde II, where a wide range of plant resources were also likely consumed and utilized (Dillehay, 1989). Acknowledging that the settlement systems of the Late Pleistocene-Early Holocene human foragers were much more complex and specialized than previously assumed, it is essential to understand how the earliest settlers of South America related to their available resources in a more integral and transformative way. To do this, research approaches are needed that document a wider range of contextualized resource utilization strategies as well as the potential effects of taphonomic processes.

As with the previous examples, human groups first inhabited the Pampa del Tamarugal (PdT) in northern Chile (Fig. 1) during the Pleistocene-Holocene transition (Latorre et al., 2013; Santoro et al., 2019). This period was characterized by significant paleoenvironmental changes in the low-elevation hyperarid basins of the Atacama Desert (de Porras et al., 2017; Gayo et al., 2012; Latorre et al., 2006; Nester et al., 2007; Orellana et al., 2023; Pfeiffer et al., 2018; Placzek et al., 2009; Quade et al., 2008; Rech et al., 2002; Ugalde et al., 2024a; Workman et al., 2020). Cultural assemblages at these early sites indicate that hunter-gatherers were part of a broader early Andean tradition with a complex mobility system that not only included locations on the coast as well as in the Puna, but also long-distance exchange networks that may have included the tropical rainforests of Bolivia and/or northwestern Argentina (Santoro et al., 2019). Animal bone remains were recovered in all of these sites and here we present a detailed zooarchaeological and taphonomic analysis of the faunal assemblages recovered from several late Pleistocene-Early Holocene archaeological sites in the PdT. The focus of this work is to provide a critical assessment of the following issues: (a) the taphonomic trajectories of the faunal remains; (b) biodiversity and food packages assembled by hunter-gatherer groups, and (c) interpretative models of subsistence systems and settlement patterns considering social and ecological factors.

## 2. Physical and archaeological setting

The PdT is a low elevation endorheic basin (19°17′–21°30′S) located between the western Andean slope and the Coastal Cordillera (Fig. 1). Situated in the low-lying Atacama Desert, this area receives minimal local precipitation (<5 mm/year), creating an expansive landscape with sparse and scarce plant and animal life (Arroyo et al., 1998), which is covered in places by a highly saline, organic-poor soil crust (Ewing et al., 2006; Finstad et al., 2014; Fletcher et al., 2012; Valdivia-Silva et al., 2012). Localized discharge of semi-perennial or ephemeral surface streams and mudflows, however, along with the outcropping of groundwater, creates patchy vegetation. Consequently, two types of modern plant communities exist along the PdT. Riparian environments are characterized by a moderately diverse plant assemblage that includes facultative phreatophytes (e.g., *Schinus molle*, *Geoffroea decorticans*), halophytes (*Distichlis spicata*, *Tessaria absinthioides*), and several hygrophytes (*Escallonia angustifolia*, *Morella pavonis*, *Baccharis scandens*, *Cortaderia atacamensis*) (Gajardo, 1994). In contrast, plant communities found across evaporative environments (e.g., salt pans) and alluvial fan-floodplains are less diverse, comprising exclusively phreatophytes (*Strombocarpa tamarugo*) and halophytes (*D. spicata*) (Faúndez, 2018; McRostie et al., 2017). Animal taxa are limited in diversity, with few mammals (*Thylamys pallidior*, *Lycalopex culpaeus*, *Ctenomys fulvus*, *Phyllotis darwini*), reptiles (*Tropidurus tarapacensis*, *Microlophus theresioides*), and birds (*Conirostrum tamarugense*, *Zonotrichia capensis*, *Tyto furcata*, among others) (SIMBIO, 2024).

A major pluvial event known as the Central Andean Pluvial Event (CAPE) occurred during the last glacial-interglacial transition across the Central Andes, including the highlands of the Atacama Desert (Quade et al. 2008). This event comprised two distinct positive hydroclimate anomalies, CAPE I (~18–14.5 ka) and CAPE II (~13.0–9.5 ka), separated by an arid phase relatively contemporaneous with the Ticaña event on the Bolivian altiplano (Sylvestre et al., 1999) and locally termed the "PdT Desiccation Event" (~14.5–13.0 ka) (Workman et al., 2020).

These pluvial phases significantly transformed the local hydrological and ecological conditions that define the present PdT hyperarid landscape. Despite the absence of local rainfall during CAPE I and CAPE II, surface perennial runoff and groundwater discharge increased substantially across the region. For instance, during CAPE I, runoff was likely sufficient to sustain wetlands and even small lakes with standing water in the distal western portions of the PdT basin (Pfeiffer et al., 2018). These hydrological shifts expanded riparian and wetland ecosystems, particularly in the southern part of the basin, where the QM and PR basins –our study area- are located, and where several extinct megafaunal remains have been found (de Porras et al., 2017; Gayo et al., 2012; Latorre et al., 2006; Nester et al., 2007; Orellana et al., 2023; Pfeiffer et al., 2018; Placzek et al., 2009; Quade et al., 2008; Rech et al., 2002; Ugalde et al., 2024a; Workman et al., 2020).

Following the arid Ticaña phase, the paleoenvironmental changes associated with CAPE II partially reestablished the riparian and wetland ecosystems of the PdT, which were then encountered by different groups of mobile hunter-gatherers (Caro et al., 2023; Casamiquela, 1969–70; Pfeiffer et al., 2018; Quezada, Varas, Vásquez, Sepúlveda, & Cifuentes, 2018). In contrast, the CAPE I positive hydroclimate anomaly appears to have been driven by increased summer rainfall, suggesting that peak biological productivity likely occurred during late summer or early fall. Consequently, the most favourable window for hunter-gatherer populations entry and settlement in the area would have coincided with these conditions. This temporal framework will later serve as a key

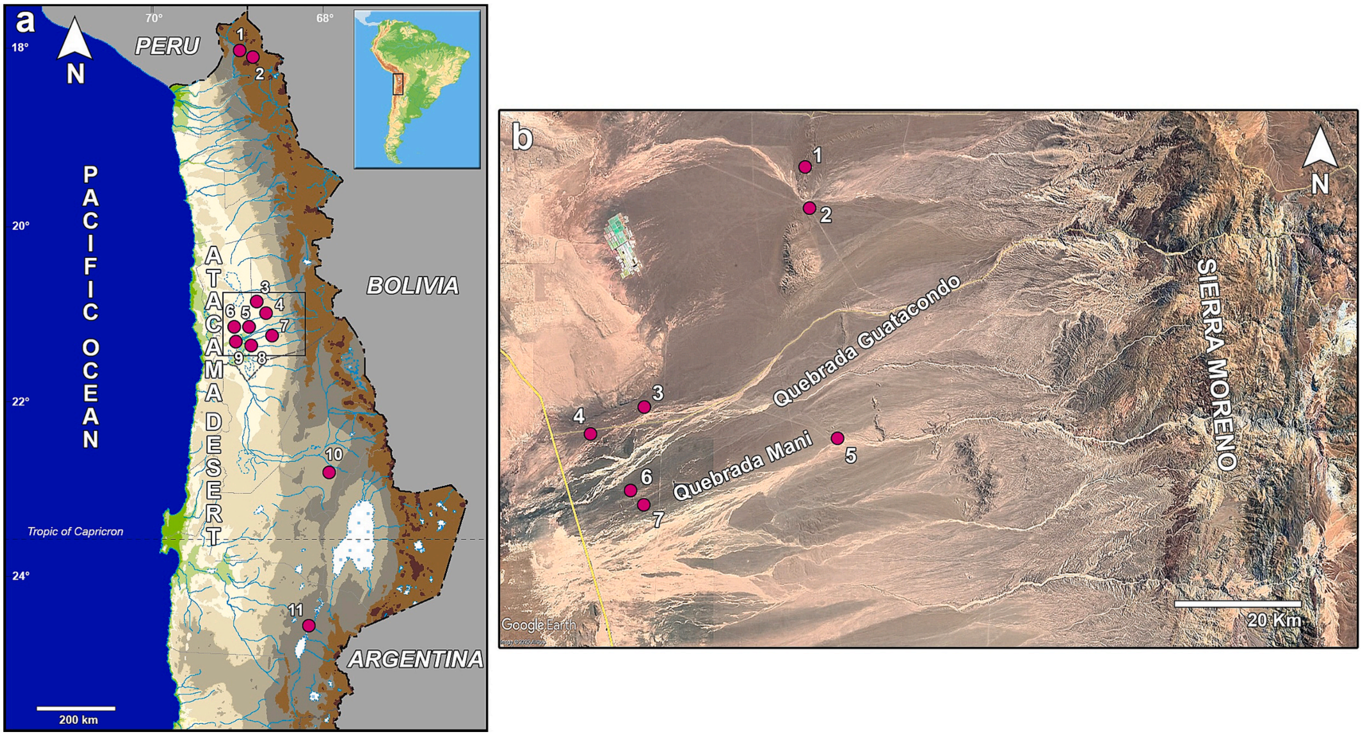

**Fig. 1.** (a): Study area and early archaeological sites from northern Chile mentioned in the text: (1) Patapatane; (2) Las Cuevas; (3) Quebrada Blanca; (4) Chipana-1; (5) Pampa Ramaditas 7 (PR7); (6) Pampa Ramaditas 5 (PR5); (7) Quebrada Maní 12c (QM12c); (8) Quebrada Maní 32 (QM32); (9) Quebrada Maní 35d (QM35d); (10) Tuina 5; (11) Punta Negra; (b): Archaeological sites in the alluvial fans of Quebrada Guatacondo and Quebrada Maní, and lithic quarries of Quebrada Blanca and Chipana: (1) Quebrada Blanca lithic quarry, (2) Chipana 1 lithic quarry; (3) PR7; (4) PR5; (5) QM12c; (6) QM35d; (7) QM32.

factor in analysing and interpreting the behavioural patterns of groups that inhabited the PdT during the Pleistocene-Holocene transition.

Several Paleoindigenous archaeological sites (i.e., early peopling sites) are closely linked with records that trace the local hydrological and ecological trajectory of Quebrada Maní (QM) and Pampa Ramaditas (PR) in the southern section of the PdT basin during CAPE II (Gayo et al., 2012; Herrera et al., 2023; Ugalde et al., 2024a). So far, no robust anthropogenic evidence contemporary to CAPE I or the Ticaña arid phase has been found (i.e. dates for CAPE I do exist, but they all correspond to only charcoal, where the “old wood” problem is common across the region; see Joly et al. 2017; Ugalde et al., 2024a). Archaeological sites are scattered from the proximal to the distal section of the QM alluvial fan, on the surface of ancient remnants of fluvial terraces formed during the late Miocene (T1) and Late Pleistocene (T2). Our previous studies of sites QM12c, QM32 and QM35d show that the recorded human occupations, although exhibiting clear palimpsests, correspond to the first waves of human migration that populated the Atacama during the Pleistocene-Holocene transition.

Archaeological deposits are shallow and surficial, i.e., ≤ 56 cm deep. Site QM12c, located atop the oldest alluvial terrace (T1), was formed after people excavated and disturbed an unusual desert pavement, probably developed during the Pliocene and early Pleistocene (Amundson et al., 2012; Ewing et al., 2006; Ugalde et al., 2020), with wooden stakes to set up a tent or similar structure. The location was selected as it was near a perennial river with hygrophytes and riparian vegetation, surrounded by a wetland. This occupation has been dated to ~ 12.8–11.6 ka, with dates on charcoal, wood and wooden tools, annual plant material, camelid dung and bone collagen, and marine shell. We adopted this strategy of dating as many different materials as possible for all the PdT sites, to ensure we were not just dating the use of old wood (see Joly et al., 2017; Ugalde et al., 2024) (Table 1). A Bayesian chronological model based on the 23 radiocarbon dates available for QM12 reveals distinct phases of residential occupations spanning 1,000 years (Ugalde et al., 2024). Hundreds of lithic tools, including stemmed, triangular projectile points of different types, are distributed across the surface and subsoil. A prepared hearth was discovered, along with lithic material (including obsidian), pigments, imported marine shells probably used as ornaments, camelid bones, pointed wooden stakes and potentially the proximal end of an atlatl dart. Anthracological analyses show that the inhabitants selectively used peppertrees (*S. molle*) and native willows (*M. pavonis*) for firewood, and excluded other woody species (Herrera, 2023; Joly et al., 2017; Latorre et al., 2013; Santoro et al., 2019; Ugalde et al., 2024a).

QM32 and QM35d sites are situated 21 km southwest of QM12c. Both are located on erosional remnants along the distal section of the QM fluvial fan (Fig. 1). QM32 was intermittently occupied between ~ 12.2 and 11.2 ka, spanning 700 years (Ugalde et al., 2024a; Ugalde et al., 2024b;) according to 20 radiocarbon dates on plant material, charcoal, dung, wood (including an imported species), and yarn (Table 1). It features a diverse assemblage that includes dispersed burned features, *in situ* lithic tools, and both plant and animal remains sourced from local and distant zones. For instance, it includes modified fibres derived from *Vicugna vicugna*, *Lama guanicoe*, a chinchillid rodent, and even human hair (Santoro et al., 2019). In addition, a wood fragment of undefined function was recovered (and dated), and identified as the silk floss tree (cf. *Ceiba speciosa*) (Mandakovic, 2018; Ugalde et al., 2024a). This species is native to the tropical forests east of the Andes, and its presence at the site suggests that the people who frequented it had access, or were part of, long-distance exchange networks that may have extended the tropical zones of Bolivia, northwestern Argentina and, eventually, even further afield (Santoro et al., 2019). The site also contains gastropods and bivalves from the Pacific Ocean, but these were only found on the surface and remain undated (Santoro et al., 2019; Ugalde et al., 2024a).

The QM35d site formed on top of a coppice dune, which was also altered through the excavation of a fire feature. This site shows a more continuous occupation without clear breaks between ~ 11.9 and 11.2 ka, as suggested by seven radiocarbon dates on bone collagen and wood

**Table 1**
Radiocarbon dates associated with sites QM12, QM35d, QM32, PR5 and PR7, as they appear in Latorre et al. 2013; Herrera et al. 2019; Ugalde et al. 2020 and Ugalde, Joly, et al. 2024. Terrestrial samples were all recalibrated with OxCal 4.4., SHCal20 curve, at 95.4% confidence.

| Site | Lab Code | Level | Material | 14C | 1σ error | Lower cal BP | Upper cal BP | Median cal BP | Reference |
|---|---|---|---|---|---|---|---|---|---|
| QM12c | UCIAMS-84346 | 1 | Charcoal | 12,420 | 35 | 14,145 | 14,730 | 14,410 | Latorre et al. 2013 |
| QM12c | UGAMS-7049 | 1 | Charcoal | 10,800 | 30 | 12,665 | 12,735 | 12,700 | Latorre et al. 2013 |
| QM12c | UCIAMS-89016 | 2 | Charcoal | 13,920 | 40 | 16,570 | 17,025 | 16,810 | Latorre et al. 2013 |
| QM12c | UCIAMS-89015 | 2 | Plant material | 10,080 | 25 | 11,350 | 11,750 | 11,530 | Latorre et al. 2013 |
| QM12c | UCIAMS-89019 | 2 | Plant material | 10,505 | 25 | 12,115 | 12,550 | 12,420 | Latorre et al. 2013 |
| QM12c | UCIAMS-89020 | 2 | Plant material | 10,120 | 25 | 11,400 | 11,805 | 11,645 | Latorre et al. 2013 |
| QM12c | UCIAMS-89-458 | 2 | Marine shell | 10,655 | 25 | 12,160 | 12,225 | 12,200 | Latorre et al. 2013 |
| QM12c | UGAMS-8241 | 3 | Wooden stake | 10,130 | 30 | 11,395 | 11,920 | 11,660 | Latorre et al. 2013 |
| QM12c | UGAMS-8242 | 3 | Wooden stake | 10,220 | 30 | 11,710 | 12,015 | 11,865 | Latorre et al. 2013 |
| QM12c | UGAMS-8243 | 3 | Wooden stake | 10,340 | 30 | 11,835 | 12,375 | 12,040 | Latorre et al. 2013 |
| QM12c | UCIAMS-89017 | 3 | Plant material | 10,160 | 25 | 11,410 | 11,980 | 11,740 | Latorre et al. 2013 |
| QM12c | UCIAMS-89022 | 3 | Camelid dung | 10,360 | 30 | 11,945 | 12,390 | 12,100 | Latorre et al. 2013 |
| QM12c | UCIAMS-89018 | 4/feat 13 | Charcoal | 10,930 | 30 | 12,700 | 12,815 | 12,750 | Latorre et al. 2013 |
| QM12c | UCIAMS-89021 | 4 | Plant material | 10,165 | 25 | 11,980 | 11,500 | 11,750 | Latorre et al. 2013 |
| QM12c | UCIAMS-84347 | 5 | Charcoal | 10,365 | 25 | 11,955 | 12,385 | 12,105 | Latorre et al. 2013 |
| QM12c | UGAMS-7050 | 5 | Charcoal | 10,210 | 30 | 11,645 | 12,010 | 11,850 | Latorre et al. 2013 |
| QM12c-NE | AA-112846 | 1 | Charcoal | 11,892 | 60 | 13,485 | 13,790 | 13,660 | Ugalde et al. 2020 |
| QM12c-NE | AA-112847 | 2 | Charcoal | 14,449 | 75 | 17,310 | 17,840 | 17,560 | Ugalde et al. 2020 |
| QM12c-NE | AA-112848 | 3 | Charcoal | 10,370 | 30 | 11,965 | 12,395 | 12,140 | Ugalde et al. 2020 |
| QM12c-NE | AA-112463 | 3 | Bone collagen | 10,212 | 50 | 11,610 | 12,035 | 11,840 | Ugalde et al. 2020 |
| QM12c-NE | AA-112551 | 4 | Wooden stake | 10,110 | 30 | 11,395 | 11,805 | 11,615 | Ugalde et al. 2020 |
| QM12d | AA-112546 | 2 | Charcoal | 10,200 | 30 | 11,640 | 12,000 | 11,830 | Ugalde et al. 2020 |
| QM12d | AA112547 | 2 | Charcoal | 10,210 | 30 | 11,645 | 12,010 | 11,850 | Ugalde et al. 2020 |
| QM32 | UCIAMS-134394 | 3 | Plant material | 9290 | 510 | 9270 | 12,370 | 10,550 | Herrera et al. 2019 |
| QM32 | UCIAMS-134395 | 4 | Plant material | 10,445 | 45 | 12,040 | 12,430 | 12,240 | Herrera et al. 2019 |
| QM32 | UCIAMS-134396 | 1 | Plant material | 10,085 | 35 | 11,340 | 11,760 | 11,540 | Herrera et al. 2019 |
| QM32 | UCIAMS-134397 | 1B | Plant material | 10,005 | 45 | 11,245 | 11,690 | 11,390 | Herrera et al. 2019 |
| QM32 | UCIAMS-134405 | 2B | Plant material | 10,210 | 35 | 11,640 | 12,015 | 11,845 | Herrera et al. 2019 |
| QM32 | UCIAMS-134399 | 2B/feat 2 | Plant material | 10,180 | 40 | 11,415 | 12,010 | 11,780 | Herrera et al. 2019 |
| QM32 | UCIAMS-134400 | 4 | Charcoal | 12,540 | 60 | 14,290 | 15,070 | 14,715 | Herrera et al. 2019 |
| QM32 | UCIAMS-134401 | 3 | Charcoal | 12,580 | 50 | 14,415 | 15,125 | 14,835 | Herrera et al. 2019 |
| QM32 | UCIAMS-134402 | 1 | Charcoal | 10,205 | 35 | 11,630 | 12,010 | 11,835 | Herrera et al. 2019 |
| QM32 | UCIAMS-134403 | 1 | Charcoal | 10,220 | 40 | 11,645 | 12,025 | 11,860 | Herrera et al. 2019 |
| QM32 | UCIAMS-134404 | 1B | Charcoal | 10,215 | 45 | 11,625 | 12,025 | 11,845 | Herrera et al. 2019 |
| QM32 | UCIAMS-134405 | 2B | Charcoal | 10,210 | 45 | 11,620 | 12,025 | 11,840 | Herrera et al. 2019 |
| QM32 | UCIAMS-134406 | 1 | Charcoal | 10,195 | 35 | 11,620 | 12,005 | 11,815 | Herrera et al. 2019 |
| QM32 | UCIAMS-134417 | 2B/feat2 | Rodent pellet | 10,115 | 35 | 11,360 | 11,820 | 11,625 | Herrera et al. 2019 |
| QM32 | UCIAMS-134418 | 2B/feat2 | Hair cordage | 10,040 | 35 | 11,270 | 11,700 | 11,465 | Herrera et al. 2019 |
| QM32 | UGAMS-61420 | S2E9/L1 | Wood | 9865 | 33 | 11,185 | 11,271 | 11,228 | Ugalde et al., 2024a |
| QM32 | UGAMS-61421 | S2E9/L2 | Wood | 10,082 | 30 | 11,320 | 11,756 | 11,530 | Ugalde et al., 2024a |
| QM32 | UGAMS-61429 | S2E8/L2 | Yarn (Camelidae) | 9874 | 36 | 11,185 | 11,310 | 11,232 | Ugalde et al., 2024a |
| QM32 | UGAMS-61428 | S1E8/L2 | Yarn (Camelidae) | 10,057 | 28 | 11,307 | 11,711 | 11,480 | Ugalde et al., 2024a |
| QM32 | AA-115362 | S88W45 | Wood (*Ceiba* sp.) | 10,260 | 20 | 11,900 | 11,960 | 11,840 | Ugalde et al., 2024a |
| QM35d | D-AMS-028064 | 4 | Bone collagen | 9886 | 41 | 11,185 | 11,345 | 11,245 | Herrera et al. 2019 |
| QM35d | D-AMS-028-065 | 3 | Bone collagen | 10,044 | 39 | 11,270 | 11,705 | 11,475 | Herrera et al. 2019 |
| QM35d | D-AMS-028066 | 5 | Bone collagen | 10,160 | 40 | 11,405 | 11,980 | 11,735 | Herrera et al. 2019 |
| QM35d | D-AMS-028067 | 6 | Bone collagen | 10,002 | 45 | 11,245 | 11,615 | 11,385 | Herrera et al. 2019 |
| QM35d | D-AMS-028068 | 2 | Bone collagen | 9828 | 49 | 11,105 | 11,290 | 11,210 | Herrera et al. 2019 |
| QM35d | D-AMS-028069 | 7 | Bone collagen | 10,089 | 37 | 11,340 | 11,760 | 11,550 | Herrera et al. 2019 |
| QM35d | D-AMS-028070 | 8 | Bone collagen | 10,189 | 40 | 11,505 | 12,010 | 11,800 | Herrera et al. 2019 |
| QM35d | UGAMS-61425 | 8 | Wood (root) | 9774 | 31 | 10,897 | 11,240 | 11,182 | Ugalde et al. 2024a |
| PR5 | UCIAMS-165640 | 1A/feat 1 | Plant material | 10,370 | 30 | 11,965 | 12,390 | 12,140 | Herrera et al. 2019 |
| PR5 | UCIAMS-165641 | 1A/feat 1 | Charcoal | 14,160 | 45 | 16,975 | 17,410 | 17,180 | Herrera et al. 2019 |
| PR5 | UCIAMS-165642 | 1B/feat 3 | Plant material | 10,425 | 30 | 12,055 | 12,410 | 12,225 | Herrera et al. 2019 |
| PR5 | UGAMS-61413 | N0E0/L2 | Charcoal | 14,193 | 35 | 17,074 | 17,360 | 17,211 | Ugalde et al., 2024a |
| PR5 | UGAMS-61414 | N0E0/L2 | Charcoal | 14,228 | 35 | 17,090 | 17,380 | 17,233 | Ugalde et al., 2024a |
| PR5 | UGAMS-61417 | N0E0/L3 | Wood | 10,342 | 32 | 11,889 | 12,435 | 12,046 | Ugalde et al., 2024a |
| PR5 | UGAMS-61415 | N0E0/L3 | Charcoal | 13,737 | 36 | 16,375 | 16,766 | 16,567 | Ugalde et al., 2024a |
| PR5 | UGAMS-61416 | N0E0/L3 | Charcoal | 13,959 | 47 | 16,706 | 17,068 | 16,937 | Ugalde et al., 2024a |
| PR5 | UGAMS-61426 | S2W5/L6 | Charcoal | 12,563 | 32 | 14,508 | 15,703 | 14,868 | Ugalde et al., 2024a |
| PR7 | UCIAMS-165643 | 1A/feat 1 | Charcoal | 10,105 | 30 | 11,365 | 11,795 | 11,600 | Herrera et al. 2019 |
| PR7 | UCIAMS-165644 | 1A/feat 2 | Wood | 10,010 | 80 | 11,230 | 11,760 | 11,455 | Herrera et al. 2019 |
| PR7 | UGAMS-61407 | N1E0/L1 | Charcoal | 10,199 | 28 | 11,646 | 11,925 | 11,808 | Ugalde et al., 2024a |
| PR7 | UGAMS-61406 | N1E0/L1 | Charcoal | 10,231 | 30 | 11,761 | 11,943 | 11,860 | Ugalde et al., 2024a |
| PR7 | UGAMS-61418 | N1E0/L2 | Wood | 10,080 | 31 | 11,319 | 11,755 | 11,527 | Ugalde et al., 2024a |
| PR7 | UGAMS-61427 | N1E0/L2 | Hair (Camelidae) | 10,101 | 28 | 11,327 | 11,763 | 11,604 | Ugalde et al., 2024a |
| PR7 | UGAMS-61408 | N1W1/L2 | Charcoal | 10,185 | 30 | 11,637 | 11,923 | 11,793 | Ugalde et al., 2024a |
| PR7 | UGAMS-61423 | N1W1/L2 | Bone apatite (Caviomorpha) | 9929 | 33 | 11,202 | 11,603 | 11,266 | Ugalde et al., 2024a |
| PR7 | UGAMS-61422 | N1W1/L2 | Bone apatite (Camelidae) | 10,024 | 30 | 11,267 | 11,629 | 11,461 | Ugalde et al., 2024a |
| PR7 | UGAMS-61409 | N1W1/L2 | Charcoal | 10,087 | 28 | 11,321 | 11,758 | 11,538 | Ugalde et al., 2024a |
| PR7 | UGAMS-61412 | N1W1/L3 | Charcoal | 10,108 | 29 | 11,326 | 11,830 | 11,636 | Ugalde et al., 2024a |
| PR7 | UGAMS-61411 | N1W1/L3 | Charcoal | 10,151 | 30 | 11,352 | 11,845 | 11,735 | Ugalde et al., 2024a |
| PR7 | UGAMS-61410 | N1W1/L3 | Charcoal | 10,378 | 30 | 11,966 | 12,459 | 12,149 | Ugalde et al., 2024a |

of a probable tree root (Ugalde et al., 2024a; Ugalde et al., 2024b) (Table 1). It contains the highest abundance of *in situ* tree stumps found in relation to archaeological sites in the PdT, corresponding to subfossil records of a tree grove of both phreatophyte (*S. tamarugo*) and riparian (*S. molle*) trees (Ugalde et al., 2024a). Hunter-gatherer groups utilized this grove by camping underneath the tree canopy and establishing at least one shelter that we have identified (Joly et al., 2017; Ugalde et al., 2024a). Lithic assemblages stand out as the only site where all four technical stages of projectile points are present: bifacial blanks, bifaces, preforms and projectile points of the Punta Negra style (del Castilllo, 2019; Herrera, 2021, 2023), but also the local Escallonia-Patapatane type (del Castillo, 2019; Ugalde 2023). Diverse activities carried out at this site suggest a relatively long-term, likely residential occupation, representing a traditional pampa settlement by people adapted to the hyperarid climate and exhibiting cultural expressions distinct from other Atacama groups (del Castillo, 2019; Ugalde et al., 2024a).

Pampa Ramaditas (PR), located at the distal section of the alluvial fan of Quebrada de Guatacondo, was a treeless floodplain during the Pleistocene–Holocene transition (Ugalde et al., 2024a). Two surficial Paleoindigenous archaeological sites (PR5, PR7) have been excavated and dated (Ugalde et al., 2024a), situated on old remnant surfaces, which are slightly elevated compared to braided channels and aeolian blowouts of the flood plain (Ugalde et al., 2020; Ugalde, 2023). PR5 and PR7 were occupied ephemerally, likely serving as hunting grounds during single phases of activities dated to ∼ 12.4 –12 ka and ∼ 11.9–11.3 ka, respectively (Ugalde et al., 2024a), which may be explained due to the lack of nearby wetlands and tree groves. PR7 has 13 dates on wood, charcoal, camelid hair, and rodent and camelid bone apatite (Table 1). Bone collagen was not well-preserved enough to be extracted and dated, a common problem in sites where soil salts have heavily weathered bones (Straulino Mainou et al., 2025). Bioapatite dates, however, coincide with dates on other materials and do not seem to be contaminated due to lack of organic soils or soils rich in carbonates. Surficial lithic tools, including projectile point types, knives, scrapers, side-scrapers, and notched scrapers, occur at both sites (Herrera, 2021, 2023; Ugalde, 2023). Beneath the surface, dispersed burned features, along with vertebrate bones, wooden artifacts, and wood fragments have been recovered. The absence of prepared hearths and the occurrence of finished lithic tools and plant fiber cordage at PR5-neither of which are associated with manufacturing remains-suggest a non-residential occupation of short duration (Alday, 2021; Herrera, 2023; Ugalde et al., 2024a). A Punta Negra type projectile point found *in situ* also suggests that this ephemeral camp may have been related to hunter-gatherer groups from the interior basins of the Intermediate Depression, located in the central and southern Atacama Desert (Ugalde, 2023). The site also includes both local and imported plant materials, such as twisted fibres used for making spliced yarn and cordage (Alday, 2021), as well as wood fragments attributed to species native to tropical areas on the eastern slope of the Andes (*Erythrina* sp. or *Ceiba* sp., Mandakovic, 2018). For this site, we have only dated plant material, charcoal, and wood, resulting in a poor understanding of the timing for human occupation, which so far mostly incorrectly dates to CAPE I, except for one date for a piece of wood (Table 1). The PR7 site features a prepared fireplace characterized by a small round structure filled with ashes, surrounded by dispersed charcoal, partially burned wooden sticks, and burned camelid bones (Ugalde et al., 2024a).

## 3. Materials and methods

A total of 24,309 specimens of faunal remains collected from archaeological deposits from sites QM12c, QM32, QM35d, PR5, and PR7 were analysed. All archaeological and zooarchaeological specimens were either collected *in situ* or by dry-sifting (0.2 cm mesh) and sorted and classified in the laboratory. Excavation units with the highest number of specimens were selected for sites QM32 and QM35d, representing 75 % and 77 % of the total number of excavation units, respectively. In contrast, 100 % of the faunal remains were studied from the other sites. Given the shallowness of the deposits and the likely mixing of the artifacts and ecofacts over a relatively brief period, as indicated by the $^{14}$C dates and sequence models (Table 1; Ugalde et al. 2024a), we have treated all excavation levels as part of a single archaeological unit at each site. All deposits with archaeological materials occur in Holocene aeolian sands, or to a lesser degree, floodplain deposits, which covered older Pleistocene surfaces or active Byz or Byzm soil horizons, where humans settled. Consequently, all archaeological materials were deposited in dominantly aeolian sands, making it impossible to separate or distinguish distinct occupational levels.

The Number of Specimens (NSP) and the Number of Identified Specimens (NISP) served as the fundamental counting units (Grayson, 1984). Bone specimens were identified using reference collections of modern fauna housed at the Laboratorio de Arqueología y Paleoambiente (Universidad de Tarapacá), along with personal collections (RL). Detailed anatomical and taxonomic identification of the vertebrate remains was carried out considering all bone and dental fragments showing diagnostic anatomical features (i.e., tuberosities, articular facets, nutritional foramina, and enamel distribution). Additional recognizable characteristics, including curvature, cross-section morphology, thickness, size, and morphology of the occlusal surface, were also considered (Mengoni-Goñalons, 1999).

Osteometrical analyses were applied to the Camelidae family, aiming to identify size differences between the two wild species: *Lama guanicoe* and *Vicugna vicugna* (Cartajena et al., 2007; Kent, 1982; Yacobaccio, 2021). Given the fragmentary nature of the sample, only the first phalanges, tarsal and carpal bones of adult individuals were measured, following the protocol of (Izeta and collaborators (2009)). Anterior and posterior phalanges were classified using a combined methodological procedure from Kent (1982) and Cartajena and colleagues (2007). Qualitative variations in size between specimens were expressed in bivariate plots. Comparative metrical data were sourced from Cartajena and colleagues (2007), Izeta et al. (2009), and Le Neün et al. (2023). Following Kaufmann parameters (2009), Camelidae mortality profiles were assessed through dental eruption and epiphyseal fusion.

Correspondence Analysis (CA) was conducted to determine taxonomic similarities/divergences between sites. This method is effective in positioning both samples and taxa within a unified low-dimensional space, facilitating the interpretation of complex relationships within data (Beh and Lombardo, 2014). CA was used to simultaneously plot the analyzed sites alongside their represented taxa. Specifically, taxa were positioned near the samples in which they were found, and conversely, samples were placed close to the taxa they contained. Furthermore, samples with comparable taxonomic compositions were clustered together, while taxa with similar distributions across samples were positioned close to each other. This spatial arrangement is based on chi-squared distances to reveal the structure of the dataset, such as the association of specific taxa to specific locations.

Measures for taxonomic diversity in terms of richness and evenness were also estimated. The Number of Taxa Identified (NTAXA) was used as a proxy for richness. We employed the quotient between NSP and m$^3$ excavated on each site as a proxy for bone discard intensity, assuming that more recurrent/residential occupations would result in more bone specimens discarded when compared to ephemeral/logistic stations.

The Shannon homogeneity index –using NISP- was calculated with the formula $\Sigma\, pi \ln pi/\ln S$, where S represents the total number of taxa and Pi is the standardized proportion of specimens belonging to taxon i (Lyman, 2008). Additionally, the Number of Unidentified Specimens (NUSP) was categorized into three types: long bone, flat bone, and spongy fragments. The age distribution of camelid specimens was categorized into young (indicated by unfused epiphyses, presence of metaphyses, porous bones, or unmarked articular facets), adults (characterized by fused epiphyses, well-established articular facets, and nonporous bones), and undetermined.

Body-part profiles were quantified by the Minimum Number of

Elements (MNE), which was derived from the NISP (Lyman, 2008). To standardize the MNE, we employed Minimal Anatomical Units (MAU) and their percentage of survivorship (%MAU) (Binford, 1978). MAU was also grouped in anatomical regions based on Stiner (1991), by recognizing that the anatomical elements are often subject to anthropogenic manipulation and transport in articulated segments. The Minimum Number of Individuals (MNI) was determined from the highest MNE value considering sizes and ages of specimens (Lyman, 2008). To evaluate whether the camelid sample is density-mediated, we correlated the %MAU with structural mineral density values of *Lama* spp. taken from Stahl (1999). The camelid body-part profiles were also analyzed in terms of their economic utility by considering the Guanaco Meat Utility Index (GMUI) and the Standardized Meat and Marrow Index (SMMI) (Borrero, 1990), both of which are correlated with the %MAU. Following Faith and Gordon (2007), the results of the economic utility correlations were supplemented with the Shannon Evenness Index, applied specifically to bone sets with high element survival MAU tallies (Cleghorn and Marean, 2004).

To detect modifications caused by animals and/or humans on bone surfaces, specimens were examined at low magnification (up to 50x). High-resolution imaging techniques were used to examine the morphological characteristics and possible taphonomic alterations of a small rodent sample, composed of 12 identified specimens (NISP = 12). This included the use of an AURIGA compact field emission scanning electron microscope (SEM), as well as transmission electron microscopy (FESEM-SEM) and focused ion beam microscopy (FIB-SEM), available at the Electron Microscopy Unit of Universidad Austral de Chile. Non-human animal modifications include marks by carnivore teeth (i.e., punctures, pits, scores, and furrowing; Binford, 1980), as well as marks by rodents (Lyman, 1994) and signs of digestion (mainly pitting, Andrews, 1990). The intensity of these modifications was also recorded following Andrews (1990). Other biotic and abiotic modifications included weathering (segmented into cracking and discoloration), as well as polishing, trampling and root etching, were examined and recorded (Behrensmeyer, 1978; Fernández-Jalvo and Andrews, 2016; Lyman, 1994).

Human modifications caused by cutting, scrapping, percussion cuts and their byproducts (such as bone flakes), as well as burning were recorded. This also included observation of burning (Domínguez-Rodrigo et al., 2009; Gifford-Gonzalez, 2018; Stiner et al., 1995). The location, orientation and frequency of each human modification were documented and used to reconstruct butchering and culinary practices. Anthropogenic alterations were also evaluated in unidentifiable specimens and quantified separately from those that were made on taxonomically identified specimens.

To investigate taphonomic categories across different archaeological sites, we used the Bray-Curtis dissimilarity metric based on its effectiveness in handling compositional data and its sensitivity to variations in the abundance of taphonomic categories (Ricotta and Podani, 2017). We calculated pairwise Bray-Curtis dissimilarity scores between all site pairs and generated a matrix that served as input for a Principal Coordinates Analysis (PCoA). PCoA was used to display the multivariate taphonomic data in a two-dimensional space and visualize relationships among sites (Legendre and Legendre, 2012).

Bone fractures were categorized broadly as “fresh” and “dry”, with each category assessed based on the fracture’s angle (oblique, acute, or straight) and outline (curved or transverse) (Villa and Mahieu, 1991). The maximum length of long bones –whether identifiable or unidentifiable- was measured. To assess the similarities between these fragmentation categories, we first calculated a distance matrix based on the Bray-Curtis dissimilarity metric, which quantifies the compositional differences in fragmentation categories. A PCoA was then applied to the Bray-Curtis distance matrix to visualize the relationships among the sites. This analysis aimed to map the distance matrices of the original high-dimensional data into a lower-dimensional space, while preserving the distances between data points as accurately as possible to highlight these relationships. For this analysis, a two-dimensional configuration was selected to observe the patterns in fragmentation data across sites. NISP/NSP and MNE/NISP ratios were also calculated, and their relationships between sites were examined using cluster analysis.

## 4. Hunter-gatherer settlement and zooarchaeology

Based on the diversity of analyses carried out, we assessed a range of interpretative possibilities to reconstruct the subsistence and settlement systems at the PdT. We depart from Binford’s (1980) classical model for hunter-gatherer mobility and settlement based on the residential and logistic continuum, with two distinct extreme mobility patterns where the “base camp” plays a central role. Regardless of whether the camp is relocated to access resources or resources are brought to the camp, the base camp serves as the primary living area for the group, where most daily activities occur. In contrast, a “task camp” pertaining to the logistic model is designated for specific activities, related to resource gathering, with only a portion of the group engaging in these activities (Binford, 1980; Kelly, 1992). Thus, by examining the diversity of activities carried out in a site or group of sites, it is possible to infer whether the archaeological deposits were primarily residential or logistic (Moclán et al., 2021).

Another critical aspect of site functionality is the duration of occupation. Base camps can be occupied for relatively shorter periods in the residential model or for longer durations in the logistical model. In contrast, logistical camps are always occupied for shorter periods (Binford, 1978, 1980). Short and long-term camps can be distinguished archaeologically based on the intensity of discarding materials (e.g., Costamagno et al., 2006; Marín et al., 2019; Moclán et al., 2021), whereas residential or base camps feature a wider range of activities, which can be expressed in low or high quantities of archaeological materials. Logistical camps are characterized by a low diversity of activities and a minimal number of archaeological materials.

To evaluate and discuss the functionality of the archaeological sites of the PdT we selected several zooarchaeological proxies in light of the theoretical frame summarized above: (1) Discard Rate (NISP/m3): Where a higher rate is expected in long-term residential occupations compared to short-term residential occupations or logistical camps; (2) Taxonomic Diversity (NTAXA): Residential camps (whether long-term or short-term), will show a wider array of exploited taxa compared to a logistical camp. Additionally, logistical camps are expected to have a higher proportion of easily captured taxa due to the expedient nature of the settlement; (3) Evenness related to NTAXA: Residential camps will exhibit a higher evenness in species representation compared to a logistical camp; (4) Frequencies of anatomical parts: Residential camps, particularly regarding camelids, would produce whole carcasses if the hunting prey was located near the base camp (unconstrained strategy, Faith and Gordon, 2007). If the hunting prey was farther away, elements with high economic yield would likely be dominant (Binford, 1978; Lupo, 2001, 2006; O’Connell et al., 1988, 1991; White, 1953). The distance between the hunting spot and the base camp would determine the transport strategy, whether bulk, unbiased, or gourmet (Binford, 1978; Metcalfe and Jones, 1988). In logistical camps (specifically hunting camp), the opposite utility curves are expected, with low economic yield elements dominating the assemblages (e.g., skulls, mandibles, distal limb bones) (Costamagno et al., 2006; Enloe, 2004; Marín et al., 2019; Metcalfe and Jones, 1988); (5) Manufacturing debris: in a residential or permanent camp, we expect to find bone manufacturing debris, indicative of bone tool or ornament preparation. Although we recognize that various factors and ranges of variation could affect the identification of these processes, we believe that they are helpful for identifying general patterns in the zooarchaeological assemblages.

## 5. Results

A total of 2,429 specimens were taxonomically identified, representing 11.09 % of the total sample. Important differences were observed among the sites (Table 2), but these differences were not statistically significant in relation to the excavated volume of the sites ($r_s = 0.4$; $p = 0.483$). We analyzed similar volumes at QM12c and QM35d (3.27 and 3.39 $m^3$, respectively), but the specimen deposition rate (NSP/$m^3$) is markedly different (827.5 and 4872.8, respectively). Important differences were also observed between QM32 and PR7. Whereas only 0.71 $m^3$ were documented in the former, 1.18 $m^3$ were observed in the latter, displaying very different specimen deposition rates (NSP/$m^3$ = 5004.2 and 807.6, respectively) (Table 2).

### 5.1. Taxonomic composition

A total of 13 taxa were identified, including reptiles, birds, and mammals (Table 3). The sample, however, is dominated by mammals (NISP = 94.75 %), and particularly camelids and caviomorph rodents. Few camelid bones were measured (NISP = 9) due to the sample's fragmentary condition and the high frequencies of unfused bones (see below). The osteometric data suggest that only the *Lama* genus is represented among the camelid remains (Supplementary Data 1), but most of the identified remains that were not measured could be qualitatively included in this genus. However, a couple of small bones coming from QM12c could be tentatively assigned to the *Vicugna* genus.

At least two caviomorph rodent taxa were identified. Craniometric data (i.e., interorbital width) indicate the presence of cf. *Abrocoma cinerea*. In turn, the scarce remains of *Ctenomys* were identifiable only to genus. Given the current distribution of the group, they likely correspond to *Ctenomys fulvus* (SIMBIO, 2004).

A total of six bird taxa were identified, including two groups of waterfowl: teals (Anatidae) and grebes (Podicipedidae). Dove remains were specifically assigned to *Zenaida meloda*. Accipitridae and Strigidae families were also determined, but only the pygmy owl (*Glaucidium* sp.) was positively identified (Jaramillo, 2005) (Table 3).

Significant variation was determined in the frequency of the identified taxa. These differences are evident when grouping the sample (NISP) into five main taxonomic categories: camelids, caviomorph rodents, cricetid rodents, birds, and reptiles (Fig. 2a). Camelids are the most frequent taxa in the QM sites but are scarce or completely absent in the PR sites, where rodents dominate. However, if MNI is considered, rodents surpass camelids in QM sites, except for QM12c, whereas no rodents were observed (Table 3). Among the camelids, *L. guanicoe* is the most represented taxon. In contrast, *V. vicugna* has limited representation, occurring only at QM12c. Among the caviomorph rodents, cf. *Abrocoma cinerea* was recorded at all the sites except QM12c. *Ctenomys* sp. was identified only at QM32 and PR5, albeit in a very low frequency. Birds were recovered from all sites, *Z. meloda* being the most represented species, and primarily at QM35d and QM32. Raptors were recorded at nearly all sites (Table 3).

In terms of taxonomic richness, QM35d exhibits the highest number of identified taxa (NTAXA = 9), followed by QM32 (NTAXA = 7). Remaining sites are comparatively less diverse, with only three or four taxa identified. These values are not directly related to sample size, since a relatively similar number of specimens were identified in QM32 and PR5, but the NTAXA is markedly different (NTAXA = 7 and 4, respectively). Similarly, the same number of identified taxa was estimated for QM12 and PR5, despite their NISP being 51 and 193, respectively. PR7 presents the highest evenness (0.783), while QM32 (0.575) and QM35d (0.538) have intermediate values. In contrast, PR5 (0.213) and QM12c (0.175) display the lowest evenness values.

**Table 3**
Summary of identified taxa (NISP/MNI) from PdT sites.

| Taxa | QM12c | QM32 | QM35d | PR5 | PR7 | Total |
|---|---|---|---|---|---|---|
| *Lama guanicoe* | 8/1 | 6/1 | 35/2 | 0 | 1/1 | 50/5 |
| cf. *Vicugna vicugna* | 2/1 | 0 | 0 | 0 | 0 | 2/1 |
| Camelidae undetermined | 39/1 | 129/2 | 873/4 | 0 | 7 | 1,048/7 |
| cf. *Abrocoma cinerea* | 0 | 10/2 | 218/24 | 86/17 | 12/1 | 326/44 |
| *Ctenomys* sp. | 0 | 0 | 0 | 2/1 | 0 | 2/1 |
| Caviomorpha undetermined | 1/1 | 56/2 | 682 | 93/9 | 11 | 843/12 |
| Cricetidae undetermined | 0 | 4/1 | 18/2 | 6/1 | 0 | 28/4 |
| *Lycalopex* sp. | 0 | 0 | 3/1 | 0 | 0 | 3/1 |
| *Zenaida meloda* | 0 | 1/1 | 20/4 | 0 | 0 | 21/5 |
| *Glaucidium* sp. | 0 | 0 | 2/1 | 0 | 0 | 2/1 |
| Strigidae undetermined | 0 | 0 | 0 | 1/1 | 0 | 1/1 |
| Accipitridae undetermined | 0 | 1/1 | 0 | 0 | 0 | 1/1 |
| Anatidae undetermined | 0 | 0 | 0 | 0 | 1/1 | 1/1 |
| Podicipediformes undetermined | 0 | 0 | 1/1 | 0 | 0 | 1/1 |
| Passeriformes undetermined | 0 | 1/1 | 4/1 | 0 | 0 | 5/2 |
| Birds undetermined | 1/1 | 1 | 8 | 3 | 3 | 16/1 |
| Lacertilia undetermined | 0 | 0 | 77/6 | 2/1 | 0 | 79/7 |
| Total | 51/5 | 209/11 | 1,941/46 | 193/30 | 35/3 | 2,429/95 |

CA analysis confirms the taxonomic distinctions among the archaeological sites. The first dimension (axis) mainly separates camelids from cricetids and caviomorphs, indicating a meaningful taxonomic division in the dataset. The second dimension distinguishes birds from reptiles and carnivores. Notably, the first axis effectively separates sites PR5 and PR7 from QM35d, QM32, and QM12. There is also a marked difference between QM12c and QM32/QM3d (Fig. 2b). Pairwise comparisons between sites reveal that camelids and caviomorphs are the main taxa explaining the differences between these groupings. However, between PR5 and PR7, the difference is skewed towards caviomorphs (Fig. 2b).

### 5.2. Fragmentation and surface bone modifications

Bone surface modifications indicate that both natural and anthropogenic agents altered the assemblages, but with low incidence (Supplementary Data 2). The PCoA that considers all taphonomic modifications (Fig. 3a) reveals that the first axis primarily separates QM35d and PR7 from the other sites. The second axis discriminated QM35d from PR7, placing them apart from a cluster formed by QM32, PR5, and QM12c.

In QM12c, almost one-third of the sample shows signs of weathering (Fig. 3b). At the other sites, percentages of altered bones are less than 9

**Table 2**
Summary of the quantitative indices of the faunal remains of the PdT.

| Site | Excavated $m^3$ | NISP | NUSP | NSP | % NISP | NSP/$m^3$ | NISP/$m^3$ |
|---|---|---|---|---|---|---|---|
| QM12c | 3.27 | 51 | 2,655 | 2,706 | 1.88 | 827.5 | 15.5 |
| QM32 | 0.71 | 209 | 3,344 | 3,553 | 5.88 | 5004.2 | 294.3 |
| QM35d | 3.39 | 1,941 | 14,578 | 16,519 | 11.75 | 4872.8 | 572.5 |
| PR5 | 1.18 | 193 | 760 | 953 | 20.25 | 807.6 | 163.5 |
| PR7 | 0.43 | 35 | 550 | 585 | 5.98 | 1360.4 | 81.3 |
| Total | | 2,429 | 21,887 | 24,309 | | | |

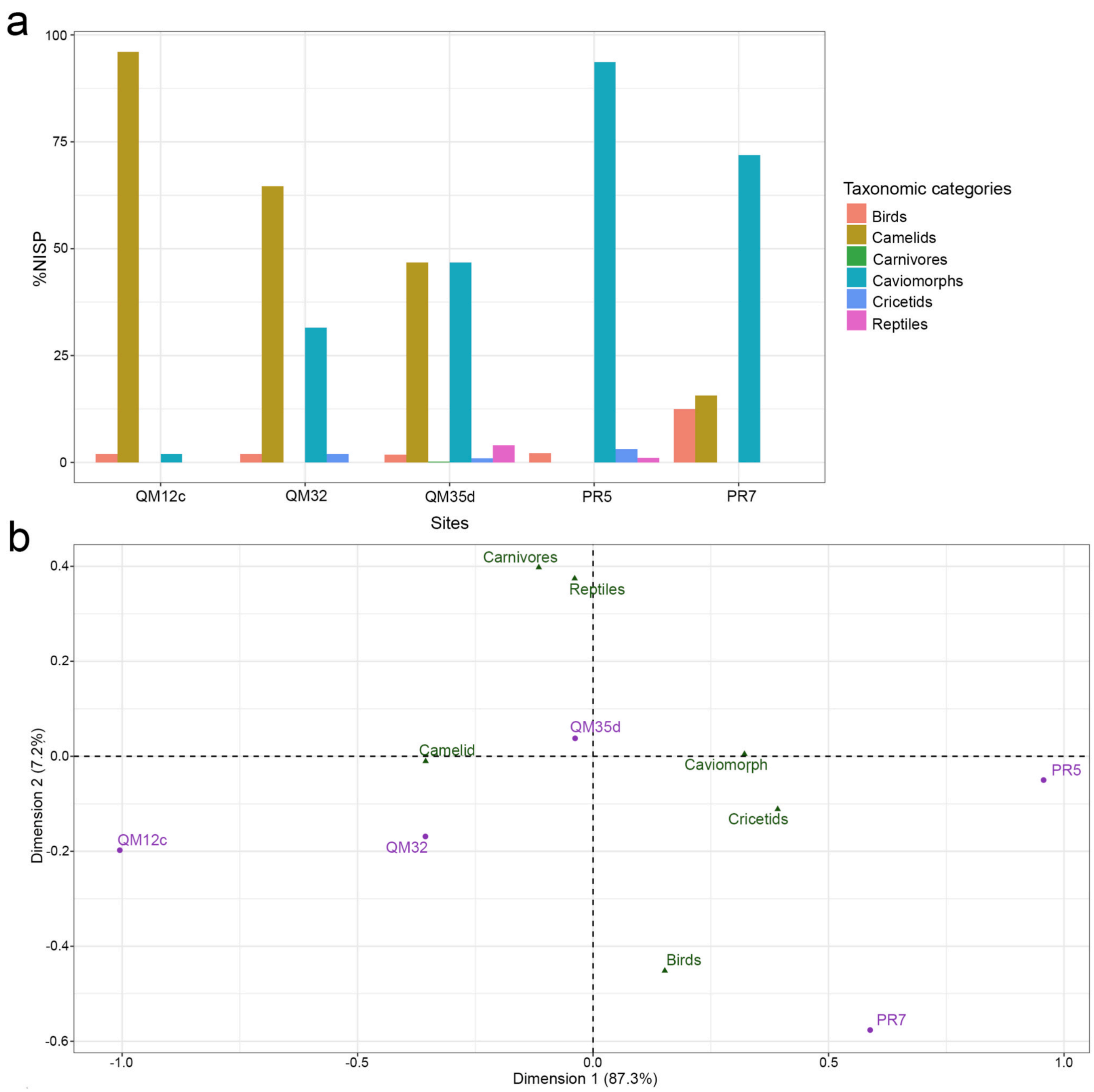

**Fig. 2.** (a) Relative abundance (%NISP) of general taxonomic categories; (b) correspondence analysis considering the same taxonomic categories.

%. At all sites, including QM12c, most of the damaged bones show weathering stages 1, 2 and 3. Stage 3, however, is absent at the PR sites and is minimally represented at the QM sites. Most of the weathered bones belong to camelids, with rodent specimens showing virtually no signs of weathering. Of the 89 weathered fragments identified, only ten (NISP = 10.11 %) correspond to caviomorph rodents, six of which were recovered from PR5.

Discoloration, which can also be attributed to surface exposure, is more prevalent in QM, especially in the QM12c sample (NISP = 13.63 %). Whereas the PR assemblages exhibit low values, with PR7 showing no discolored bones. Polished bones were recorded exclusively for the QM sites, in low proportions (NISP $<$ 4 %). Carnivore tooth marks are scarce, appearing only in QM32 (NISP = 2). Rodent gnawing marks were recorded only at QM35d (NISP = 1).

Bones exhibiting evidence of digestive corrosion (i.e., pitting) were documented at all sites, except QM12c. In QM35d, all the modified bones belong to small taxa, primarily affecting caviomorph rodent bones (NISP = 19; MNI = 3). Of the altered bones from QM35d, 77.27 % were classified in the light category (Andrews, 1990), while the remaining sample fell into the moderate category. In QM32, all the bones with acid marks (NISP = 3, MNI = 3) were attributed to Caviomorphs and were classified as the light category. PR5 had only one Caviomorph bone with moderate acid marks. PR7 contains one Caviomorph and one Anatidae, which exhibited light and moderate modifications, respectively (Fig. 4).

Anthropogenic modifications were recorded across all the analyzed sites and detected in either identifiable or unidentifiable specimens. These included several alterations related to carcass reduction and consumption. Cut marks were observed exclusively at the QM sites, while anthropogenic percussion (e.g., flake scars, percussion notches, and flakes) was documented in all sites except PR5 (Tables 4 and 5). Among the identifiable samples, all human modifications were recorded in camelid bones. In the unidentified assemblage, anthropogenic marks

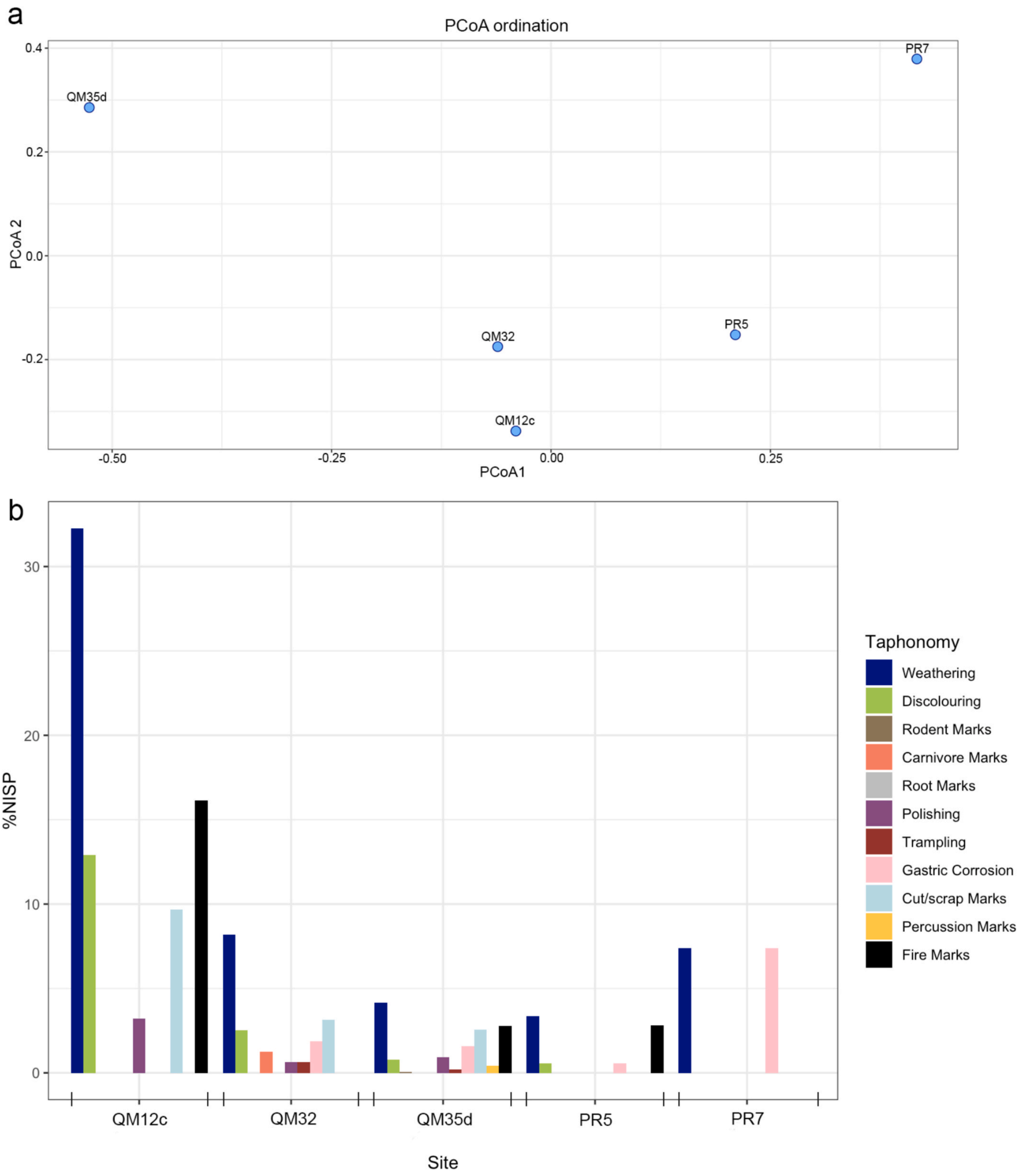

**Fig. 3.** (a) Principal Coordinates Analysis (PCoA) of bone surface modifications (BSM); (b) relative frequencies (%NISP) of BSM.

were found on bones of thickness and size compatible with large mammals, likely camelids. The limited representation of these modifications in PR5 and PR7 is likely related to the significant presence of rodents. The location, orientation, and frequencies of cut marks (e.g., Binford, 1980; Costamagno et al., 2019) indicate that skinning, dismembering, defleshing, and likely evisceration activities were performed at the sites. When using the number of marked bones as a proxy for processing intensity, it is evident that axial and posterior limb bones were butchered more frequently than anterior limb bones. Dismembering emerged as the most common processing activity, followed by defleshing (Table 4, Fig. 5a and b).

Percussion marks were recorded mainly at the QM35d site and were

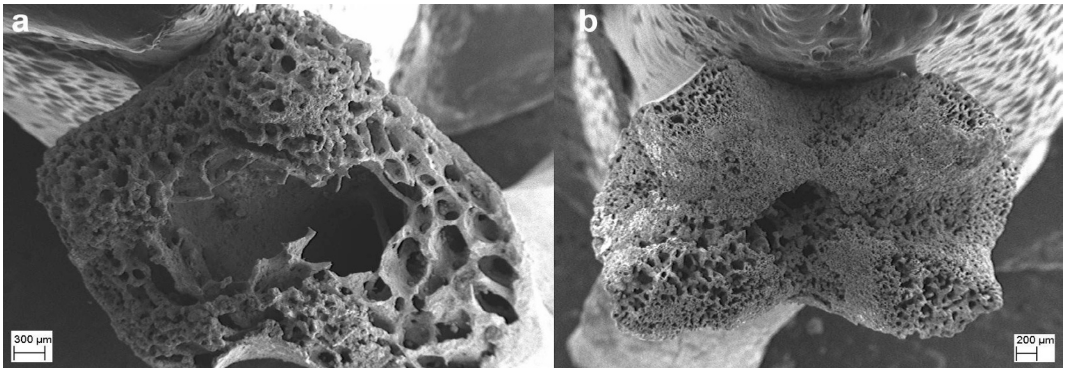

**Fig. 4.** Gastric corrosion on caviomorph bone remains including a proximal humerus (a) and a distal femur (b) from QM35d.

found on both anterior and posterior limb bones (Table 5, Fig. 5c). Each bone exhibited only one negative scar, except for a radius-ulna, which showed two percussion negatives located on the dorsal and palmar surfaces. The extent of the impact point varied, ranging from 29.6 to 8.9 mm, suggesting the use of different percussion techniques. Five of the six specimens also displayed cut marks. Additionally, several bone flakes were documented (Fig. 5d), even in QM32 and PR7, where no percussion marks were observed.

No bone tools were identified in the studied samples; however, evidence of bone tool manufacture was found at QM35d. This evidence consists of manufacturing waste from a camelid scapular blade, featuring a deep transverse incision that culminates in a fracture. Despite the anthropogenic nature of the assemblages, fire marks are scarce, except for QM12c (Fig. 3). For the QM35d sample, most of the fire marks are carbonized (NISP = 39; NISP = 67.2 %), while a small portion is calcined (NISP = 15; NISP = 25.8 %), displaying a gray or white coloring. When categorized by taxa, camelids represent the most burned group (NISP = 35; NISP = 60.3 %) (Fig. 5e), followed by caviomorph rodents (NISP = 22; NISP = 37.9 %) and birds (NISP = 1; NISP = 1.7 %). Generally, the bones are not completely burned, mainly exhibiting localized fire damage. The fragmentation of the samples limits a more detailed analysis of the fire mark locations.

Nearly half of the burned camelid subsample in QM35d consists of molar fragments (NISP = 15; NISP = 42.8 %), while the remaining identified elements include axial elements (mandible, vertebrae) or appendicular elements (radius-ulna, phalanx). In contrast, the burned subset of caviomorph rodents is more varied, including cranial remains, long bones, scapular and pelvic girdle, and teeth, without a clear trend like was observed in camelids. Burned bones from QM12c (NISP = 5) and QM32 (NISP = 4) seem to follow the same pattern as QM35d since most of them are dental fragments (NISP = 4 in both cases).

The fracture type was recorded in 299 long bone specimens, most coming from QM32 (NISP = 49) and QM35d (NISP = 216) (Supplementary Data 3). The sample shows relatively similar values across sites, with more green fractures (60 %) recorded than dry fractures (40 %). The only exception is QM12c, which had a lower proportion of fresh fractures. Cases of combined fracture types were rare. Among green fractures, helicoidal and diagonal were the most prevalent categories. An exception is observed in PR5, where longitudinal and transverse fractures are well represented, likely due to the exclusive presence of rodents. Dry fractures are more diverse, with the longitudinal/transversal and jagged categories dominating across all assemblages except for PR5 (Supplementary Data 3).

Fragmentation of long bones was observed in identified and unidentified specimens. Among the QM assemblages, QM12c exhibits the highest degree of fragmentation, with 87.2 % of long bones measuring < 2 cm in length and no specimens > 7 cm (Fig. 6a, Supplementary Data 4). In comparison, specimens < 2 cm were less common in QM32 (NSP = 69.9 %) and QM35d (NSP = 68.3 %). QM35d, in contrast to all other sites, included larger specimens ranging from 9 to 15 cm. Lastly, PR5 appeared to be more fragmented than PR7, with 73.3 % of its elements measuring < 2 cm compared to 52 % in this size range for PR7. Fragments > 3 cm are absent in PR5.

PCoA results reveal several key relationships regarding fragmentation patterns among sites (Fig. 6b). Sites PR5 and PR7 appear closely related, indicating quite similar fragmentation profiles. Similarly, QM32 and QM12c cluster together, reflecting comparable fragmentation patterns. Notably, the position of QM35d on the PCoA plot stands out; the second axis distinctly separates QM35d, suggesting it has a less fragmented sample compared to other sites. The SIMPER analysis supports these findings. Overall, the categories “0–1 cm”, “1–2 cm” and “2–3 cm” contributed most significantly to the differences between sites, as these are the most prevalent among the samples.

Sample fragmentation can also be evaluated using the NISP/NSP and MNE/NISP ratios. The NISP/NSP values varied significantly, forming a gradient with QM12c at the lower end and PR5 at the higher end. Conversely, the MNE/NISP proportion is relatively consistent across all sites, except for PR7, which exhibits comparably high values (Fig. 7a). The low NISP/NSP and MNE/NISP values indicate that QM12c has the most fragmented sample. PR7 and, to a lesser extent, PR5 are less fragmented, as shown by their higher NISP/MNE and MNE/NISP values, respectively. QM32 and QM35d occupy an intermediate position in terms of fragmentation. The cluster analysis reveals that QM32 and QM35d are the most closely related samples. PR5 is more related to the QM sites, but the most significant distance is observed between PR7 and the other sites (Fig. 7b).

Fragmentation was also calculated by examining each skeletal element individually through the MNE/NISP ratios of all camelid elements identified in QM35d (Supplementary Data 5). The average fragmentation is 0.33; consequently, elements with lower values are considered more fragmented. Values above 0.33 mean the opposite. When considering the 25th and 75th percentiles, a bone with values below 0.18 is classified as heavily fragmented, whereas those with values above 0.5 can be regarded as nearly complete. The bones of the skull and ribs are highly fragmented due to their thin and flat consistency. Among limb bones, metapodials are less fractured compared to humerus, radius-ulna, and femur. Phalanges and tarsal/carpal bones (including astragalus and calcaneus) exhibit the least fragmentation (Supplementary Data 5). The correlation between MNE/NISP and SMMI is significantly negative ($r_s = -0.531$; $p < 0.05$), suggesting that bones with lower economic yield tend to be more complete.

### 5.3. *Skeletal-element and mortality profiles*

The frequencies of the anatomical units in caviomorph rodents indicate that the skull and mandible are particularly abundant in QM32, QM35d, and PR5. In the latter site, cranial remains dominate (Fig. 8a, Supplementary Data 6). In contrast, in QM35d the anatomical

**Table 4**
Summary of cut marks recorded on different animal bone specimens.

| Site | Element | Location | NISP | Activity |
|---|---|---|---|---|
| QM35d | Mandible | Ramus, lateral face, near to condyle | 1 | Dismembering |
| | Mandible | Ramus, medial face | 1 | Defleshing |
| | Mandible | Oral, towards basal | 1 | Skinning |
| | Hyoid | Dorsal | 1 | Dismembering |
| | Cervical vertebrate | Articular facet | 1 | Dismembering |
| | Thoracic vertebrate | Base of the spine, external face of the arch | 1 | Dismembering & defleshing |
| | Lumbar vertebrate | Body | 2 | Evisceration? |
| | Lumbar vertebrate | Transverse process | 2 | Defleshing |
| | Rib | Dorsal face, near to costal facet | 3 | Dismembering |
| | Rib | Body | 4 | Defleshing |
| | Humerus | Medial diaphysis | 1 | Defleshing |
| | Humerus | Posterior distal, near to olecranon fossa | 1 | Dismembering & defleshing |
| | Radius-ulna | Medial diaphysis | 1 | Defleshing |
| | 3rd carpal | Dorsal face | 1 | Dismembering |
| | Coxal | Neck of illion | 1 | Dismembering |
| | Coxal | Rim of acetabulum | 2 | Dismembering |
| | Femur | Proximal diaphysis, towards posterior | 1 | Defleshing |
| | Femur | Distal diaphysis towards posterior | 2 | Defleshing |
| | Tibia | Proximal diaphysis, towards lateral | 1 | Defleshing |
| | Metatarsus | Anterior/lateral diaphysis | 2 | Skinning |
| | Metapodial | Anterior diaphysis | 1 | Undetermined |
| QM35 | Astragalus | Medical face towards distal | 1 | Dismembering |
| | Calcaneus | Body, plantar face | 1 | Dismembering |
| | Phalanx 1 | Diaphysis Px/Ds | 3 | Dismembering |
| | Flat bone | Undetermined | 2 | Undetermined |
| | Long bone | Undetermined | 9 | Undetermined |
| | Spongy bone | Undetermined | 2 | Undetermined |
| QM12c | Metacarpus | Anterior diaphysis | 1 | Skinning |
| | Femur | Media diaphysis towards posterior | 1 | Defleshing |
| | Long bone | Undetermined | 1 | Undetermined |
| QM32 | Mandible | Base of the ramus | 1 | Defleshing |
| | Thoracic vertebra | Base of the spine, transverse process | 1 | Defleshing |
| | Radius-ulna | Distal diaphysis towards posterior | 1 | Defleshing |
| | Metapodial | Anterior diaphysis | 1 | Undetermined |
| | Phalanx 1 | Posterior diaphysis | 1 | Dismembering |
| | Long bone | Undetermined | 4 | Undetermined |
| **Total** | | | 61 | |

**Table 5**
Summary of percussion-induced modifications identified in different bone specimens.

| Site | Modification | Anatomical unit | Location | NSP |
|---|---|---|---|---|
| QM35d | Percussion notch | Femur | Proximal anterior diaphysis | 1 |
| | | Tibia | Proximal medial diaphysis | 1 |
| | | Radius-ulna | Medial diaphysis, anterior and posterior face | 1 |
| | | Metatarsus | Medial/posterior diaphysis | 2 |
| | | Metapodial | Medial lateral diaphysis | 1 |
| | | Long bone | Undetermined | 1 |
| | Bone flake | Long bone | Undetermined | 11 |
| | Flake scar | Long bone | Undetermined | 1 |
| QM32 | Bone flake | Long bone | Undetermined | 4 |
| PR7 | Bone flake | Long bone | Undetermined | 1 |
| Total | | | | 24 |

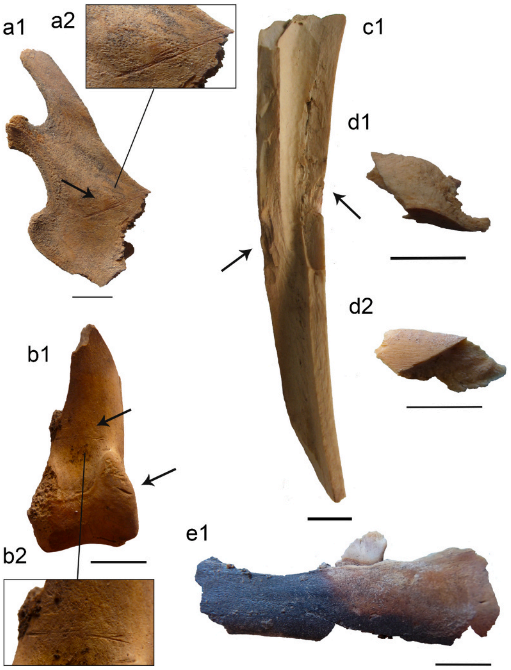

**Fig. 5.** Selected cultural modifications on camelid bones. (a1 and a2) cut marks on mandibular ramus (QM35d); (b1 and b2) cut marks on first phalanx (QM32); (c1) percussion marks on tibia (QM35d); (d1 and d2) bone flakes (QM35d); (e1) fire marks on mandible (QM35d) (scale = 1 cm).

representation is more diverse. Vertebrae and ribs are comparatively less frequent than bones of the appendicular skeleton. Hindlimb bones are more represented than forelimb ones (Fig. 8a, Supplementary Data 6). A correlation between both sites using the %MAU attests a statistically significant positive strong relationship ($r_s = 0.739$; $p = 0.04$).

The profile of the camelid bones in the QM35d sample indicates that almost the entire skeleton is represented, with no major element being underrepresented. The highest %MAU ($>35$) corresponds to bones of the axial and appendicular skeleton (i.e., skull, mandible, hyoid, humerus, radius-ulna, pelvis, femur, tibia, calcaneus, and phalanges 1 and 2) (Fig. 8b, Supplementary Data 5). Following Stiner's (1991) analytical segmentation, the profile of the skeletal elements of QM35d shows that the skull (including the mandible) is the most recorded segment. The neck and the thoracic segments are less represented than the lumbosacral portion. The rear limbs are more common than the front limbs.

These frequencies are not related to bone density, as no significant correlation was verified between %MAU and bone structural density (BMD) of all camelid bones (Stahl, 1999) ($r_s = 0{,}008$; $p = 0{,}968$). When considering the high survival elements (Cleghorn and Marean, 2004; Marean and Cleghorn, 2003), the results show a non-significant negative correlation ($r_s = -0.407$; $p = 0.213$), which means that less dense bones have a higher frequency. The correlation between %MAU and GMUI for all QM35d camelid bones is slightly positive but not significant ($r_s = 0.249$; $p = 0.262$), suggesting that transport decisions were not influenced by bone meat content. Similar results were obtained using the %MAU and SMMI ($r_s = 0.234$; $p = 0.294$). For high survival bones, no significant relationships were recorded for both indices ($r_s = 0.484$; $p = 0.155$; $r_s = 0.011$; $p = 0.755$, respectively). A high Shannon homogeneity index (0.895) was obtained for high survival bones.

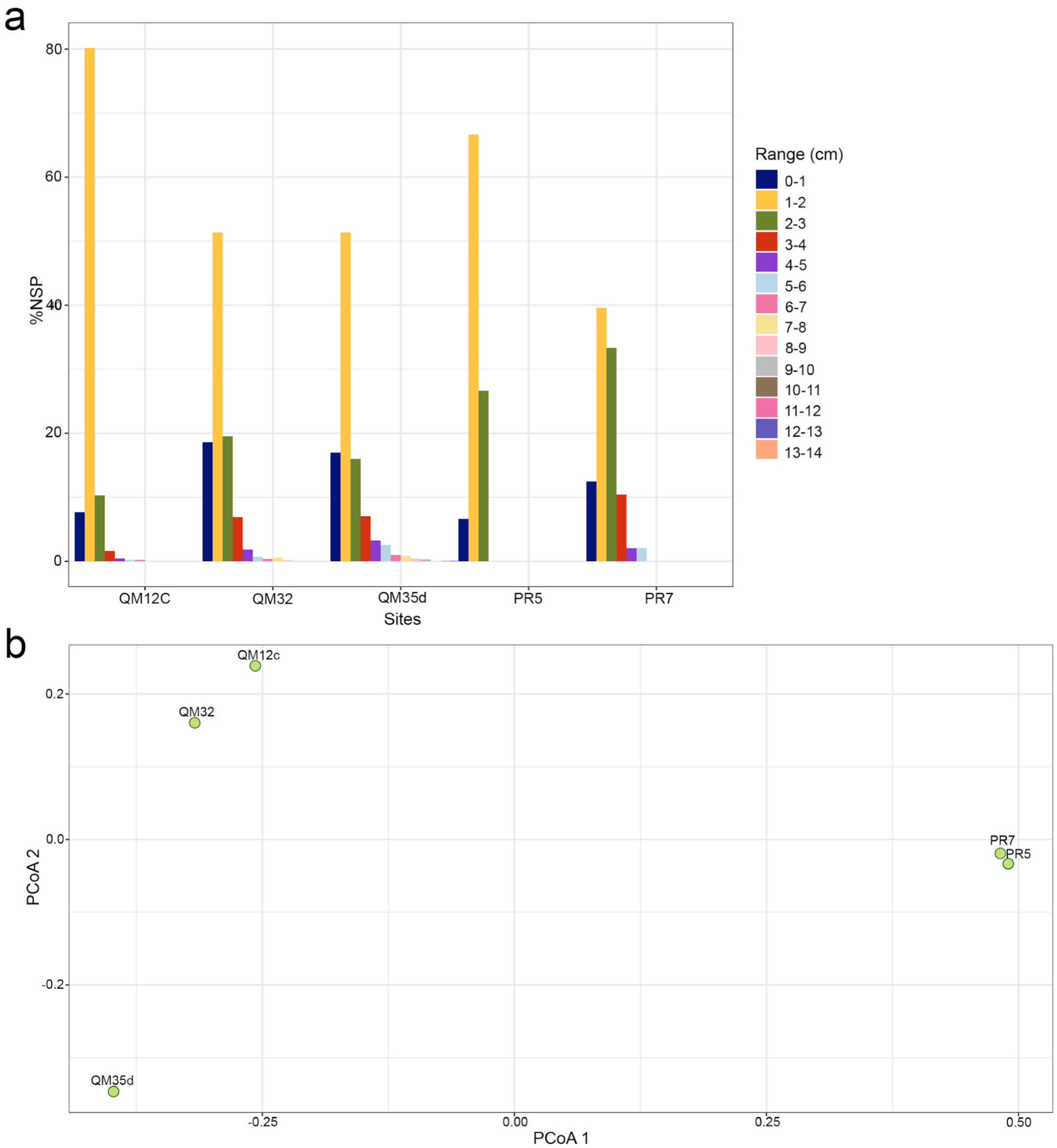

**Fig. 6.** (a) Relative frequencies (% NSP) of length's bones considering 1 cm interval; (b) NMDS considering length intervals.

The camelid sample from QM12c is dominated by small enamel fragments, with a notable absence of proximal long bones (humerus, femur), medial long bones (radius-ulna, tibia), shoulder and pelvic girdle, and ribs. In contrast, the profile of camelid skeletal elements in QM32 is more diverse and includes axial and appendicular bones. The most represented elements are the skull, the metacarpus and the first phalanx (Fig. 8a, Supplementary Data 5). Considering all camelid bones, there is no significant correlation between %MAU and VMD ($r_s = 0.3$, $p = 0.211$). A negative but not significant correlation was observed between GMUI and % MAU ($r_s = -0.241$; $p = 0.32$). There is a non-significant positive correlation between Meat and Marrow Index and % MAU ($r_s = 0.2$; $p = 0.41$). These results suggest that the selection of anatomical elements with moderate to low meat content, but high marrow yield was more frequent in QM32. The limited number of items identified precluded more detailed quantitative analyses of decisions about what was transported or left at the hunting scene.

Information on camelid age profile comes mostly from QM35d, with minor contributions from QM12c and QM32. In QM35d, there are six times more young specimens (i.e., unfused and/or porous bones) than adults, and young bones represent almost half of the sample

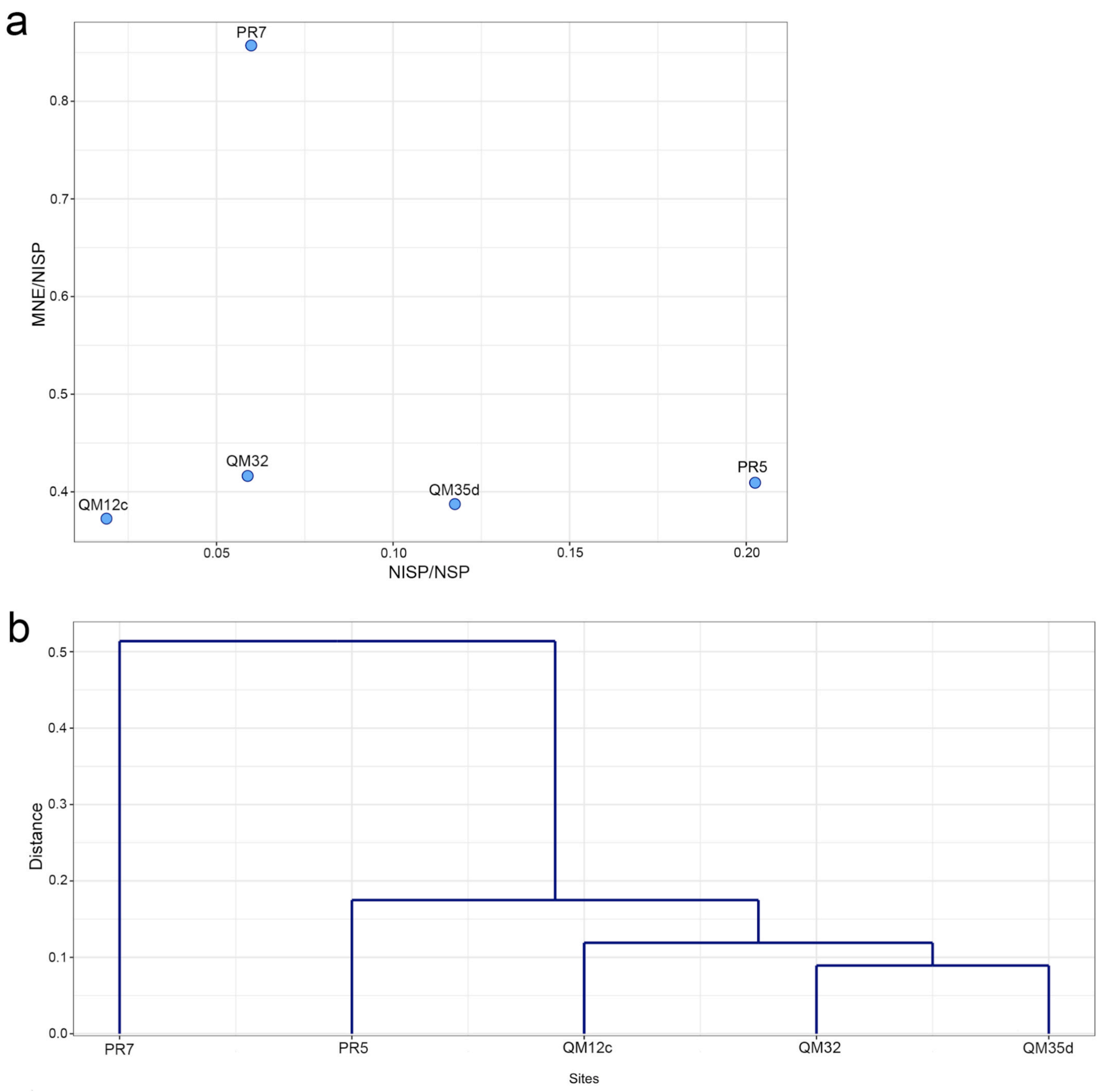

**Fig. 7.** Cluster analysis considering NISP/NSP and MNE/NISP proportions. (a) Biplot with NISP/NSP. (b) MNE/NISP proportions.

(Supplementary Data 7). At QM32, the numbers are more pronounced, with more than eleven young specimens for every adult. 34.07 % of the camelid sample was classified as juveniles. This proportion is lower than that of QM35d due to the higher frequency of indeterminate specimens. QM12c, in contrast, presents a higher number of adult camelid remains compared to the young specimens (Supplementary Data 7). The high frequency of young camelid remains is also reflected in the MNI. Considering the epiphyseal fusion sequence (Kaufmann, 2009), a single adult over three years old at the time of death was observed in QM12c and in PR7. At QM32, we found one adult and two juvenile specimens (i.e., an infant less than five months old and a juvenile less than 19 months old). In the QM35d sample, six individuals were identified: two adults, two juveniles and two infants less than three months old. One of these infants may correspond to a perinate, given the size and porosity of some of the bones.

## 6. Discussion

### 6.1. *Taxonomic composition*

Except for some small vertebrates (i.e., *Ctenomys* sp., *Zenaida meloda*), the zooarchaeological assemblages include taxa that are no longer found at the PdT (SIMBIO, 2024). These species probably became extirpated at the end of CAPE II (~9.5 ka early Holocene) or possibly earlier, as indicated by our radiocarbon dating of bones and fibres. At this time, a hyper-arid regime began, causing the disappearance of the hydroclimatic conditions that sustained the last remnants of flora and fauna in the PdT. The most striking case is that of cf. *A. cinerea* because of

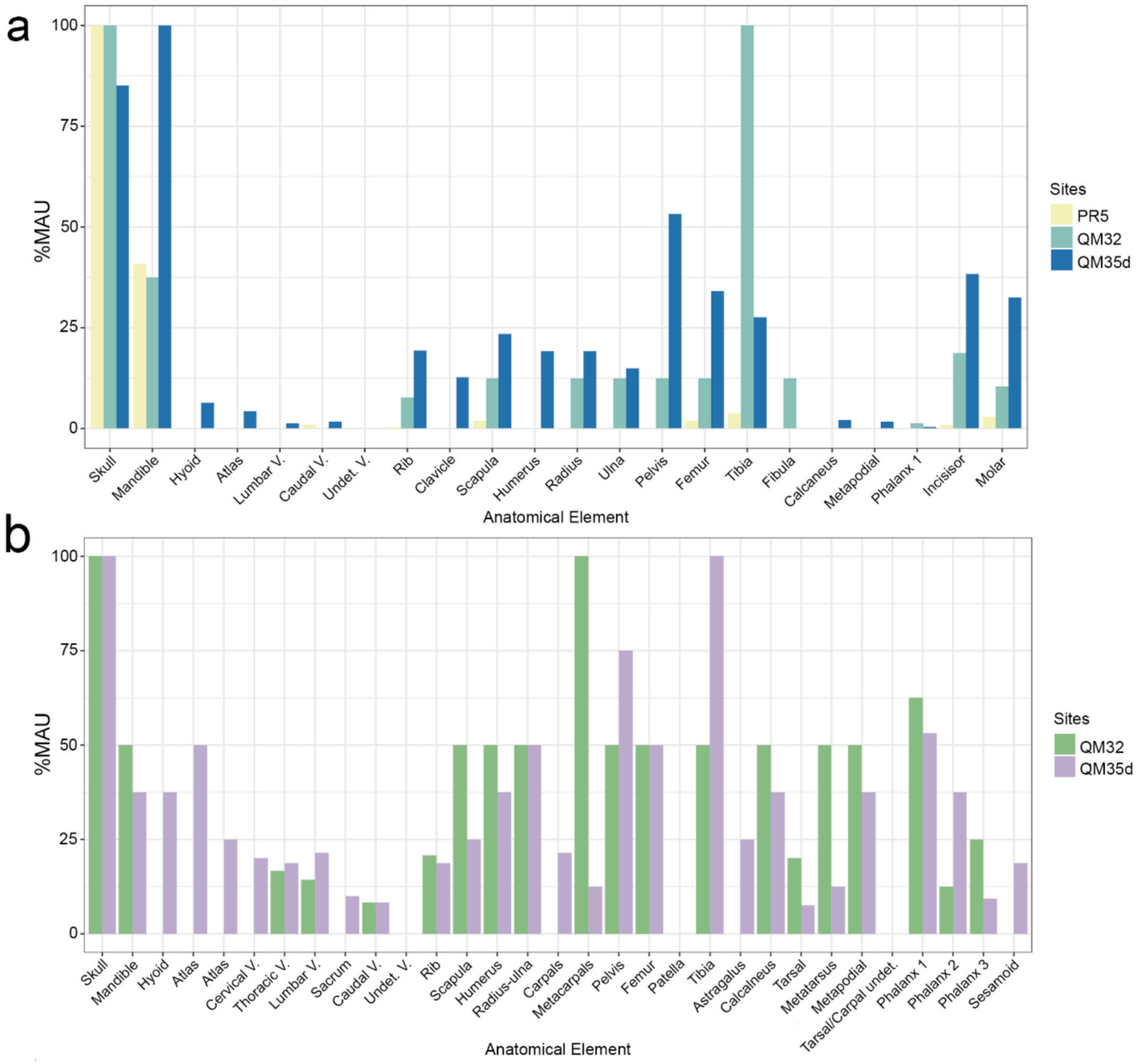

**Fig. 8.** Profiles of skeletal element (% MAU). (a) rodents; (b) camelids.

its non-migratory behaviour and its limited distribution area, today exclusively confined to high Andean rocky environments > 3,500 m asl (Braun and Mares, 2002; González-Pinilla et al. 2024; Iriarte, 2005; Latorre et al., 2002; Patton et al., 2015; Riveros-Riffo et al., 2025). Stable isotope analyses of rodent skeletal remains from archaeological sites at QM and PR indicate that they likely fed locally in the wetland and riparian environments of the PdT (Ugalde et al., 2024b).

*Vicugna vicugna* is another remarkable case. This medium-sized herbivore is currently present at high-Andean areas (3,800 to 5,000 m asl), and in favourable conditions (i.e., wet years), shows highly selective feeding behaviour and a marked sedentary lifestyle. No migratory circuits are known (Bonavia, 1996). Although its behaviour could have been different during the Pleistocene-Holocene transition, the limited number of *V. vicugna* bones at QM12c may indicate that parts of the animal were likely transported from higher elevations instead of being hunted locally. *Lama guanicoe* is also completely absent today from the PdT, despite being a highly adaptable herbivore. Currently, it is distributed fragmentarily along the western Andean slope between Peru and Patagonia. It migrates seasonally or remains in the same territory year-round, depending on the stability of the fodder that constitutes its generalized diet (Bonavia, 1996). *L. guanicoe* was probably a common dweller of the PdT in the past, and likely visited the basin seasonally, especially during the summer when the floodplain received overflow from the mountains (Workman et al., 2020). Stable isotope analyses on camelid bone remains reveal two isotopically distinct groups from different geographical origins in the PdT archaeological sites. The first group corresponds to a population of camelids of local origin. The second group of animals was from the Andean Puna (Ugalde et al., 2024b). The lack of species-level identification in this previous analysis prevents us from knowing whether the first group corresponded to guanacos and the second to vicuñas. However, stable isotope analyses of *V. vicugna* fleece indicate a relatively high consumption of $C_4$ plants and a relatively high $\delta^{15}N$ signal as well, suggesting that this fiber would have been anthropically transported from the Puna (> 4000 m) or from pre-

Puna (< 4000 m), where *D. spicata*, a $C_4$ plant, is abundant (Santoro et al., 2019; Ugalde et al., 2024b).

The archaeofaunal record of a diverse freshwater-associated waterfowl (such as teals and grebes) is further evidence of the existence of wetland and riparian environments at QM and PR, respectively. The most vegetated landscape that we have identified so far was concentrated in the wetland at QM35, which included trees that not only attracted pigeons and passerine birds, but also small nocturnal and diurnal raptors. In this landscape, foxes preyed on small birds, caviomorphs, cricetid rodents, and lizards.

We did not encounter any specimens morphologically or metrically comparable to extinct taxa known from the PdT, such as giant ground sloths (Megatheriidae), horses (Equidae), and wolves (Canidae). Furthermore, there is no paleontological record indicating that these megafaunas survived beyond CAPE I in the PdT (Caro et al., 2023; Frassinetti and Alberdi, 2001; Moreno et al., 1994; Straulino Mainou et al., 2025; Villavicencio et al., 2018; Workman et al., 2020). Direct dating of these bones is complex because they lack collagen, and the bioapatite fraction could have been contaminated by carbonate-rich groundwater that would have been present at the time of burial. We speculate that they possibly became extinct towards the end of this event, or during the PdT Desiccation Event (~14,5–13 ka), which began more than 1,500 years before the first human occupation at QM (Ugalde et al., 2024a).

These ideal hydrological and ecological conditions, however, began to disappear towards the end of CAPE II (Gayo et al., 2012; Nester et al., 2007), leading to the extirpation of some of the most common animal and plant taxa. During these profound environmental changes, the influence of human actions cannot be excluded, especially since, as an invasive species (Gurevitch and Padilla, 2004), humans may have contributed to significant but localized degradation of this otherwise pristine environment, for example, through the direct exploitation of plant and animal resources. Nevertheless, we cannot assume *a priori* that humans were detrimental everywhere they inhabited in the past. In fact, positive interactions, which could even be characterized as symbiosis (Fletcher et al., 2012; Yager et al. 2021), might better characterize the processes that occurred at the PdT. Based on our current evidence, it appears that humans at QM35 seemed to have known of the benefits of the *tamarugo* trees and restrained from cutting them down or using them for firewood.

The archaeofaunal evidence also seems to suggest that human impacts on these wetland ecosystems created synanthropic niches which attracted animals such as rodents and probably raptors and other scavengers to the trash heaps created by human camps (Baumann, 2023). Given the limited (as in concentrated) resource availability of the PdT, these processes could have been quite ecologically significant and could have initially buffered against some level of environmental unpredictability.

### 6.2. *Taphonomic trajectories*

Various taphonomic agents contributed differently to the taxa composition of the zooarchaeological assemblages from the PdT. Humans were the main agent for camelid skeletal remains accumulation, as demonstrated by fire, cut, and percussion marks, in varying proportions. This contrasts with the extremely low proportion of modification produced by non-human predators, such as carnivore or rodent tooth marks.

Taphonomic alterations in small vertebrates suggest a complex depositional history. Digestive marks, mainly detected on rodents, indicate that a minor portion of this subsample entered the archaeological deposits via non-human predators. Based on the frequency and intensity of gastric corrosion, predators are typically divided into three main groups: nocturnal raptors (Strigiformes, light-moderate intensity), diurnal raptors (mainly Falconiformes, moderate-severe intensity), and carnivores (heavy-extreme intensity) (Andrews, 1990; Fernández-Suárez et al., 2007). Acid marks occur at low frequencies, with 75 % of the affected remains categorized as light incidence, suggesting that Strigiformes were responsible for such modifications. Strigiform remains were identified at PR7 and QM35d. In the latter, the specimens correspond to *Glaucidium* sp., a pygmy-owl that hunts nocturnally and diurnally, preying on identified taxa such as caviomorph rodents (e.g., *Abrocoma*), cricetid rodents, passeriform birds, and lizards (Jiménez and Jaksić, 1989; Jiménez and Jaksic, 1993).

Rodent burrows found at QM32 and PR7 imply nesting and natural deaths at these sites during or shortly after human occupations, corroborated by radiocarbon dates on rodent bones at PR7 (Ugalde et al., 2024a). A burrow with cf. *Abrocoma cinerea* remains in PR7 slightly disturbed the site and was found next to a prepared fireplace (Ugalde et al., 2024a). Today, this rodent is only found in rocky landscapes (Iriarte, 2005; Mann Fischer, 1978) and does not occur in open environments with sandy substrates, such as the PdT. Other species, including *A. boliviensis* and *A. bennetti* are commonly associated with tree groves (Braun and Mares, 1996) and could also have taken advantage of the waste and disturbance generated by humans. No cut marks were observed on *Abrocoma*/ Caviomorpha remains, and only a few burned specimens were found at QM32, QM35d and PR5. However, actualistic and ethnographic records (e.g., Hesse, 1982; Medina et al., 2012) indicate that small and medium-sized rodents are typically not thoroughly processed prior to consumption, resulting in a low likelihood of finding cut or combustion marks. Cranial remains dominate the studied samples, especially at QM32 and PR5, which is a common anthropic pattern of discarding skulls and mandibles before consumption (Andrade and Fernández, 2017; Hesse, 1982; Simonetti and Cornejo, 1991). Another reason for their capture might have been for its fur, which is soft and warm akin to that of the chinchilla (*Chinchilla* spp., Mann Fischer, 1978; Wolffsohn, 1916).

Thus, the high frequency of cf. *A. cinerea* remains, which contrasts with the low incidence of other rodents that could also benefit from human activity (e.g., ctenomids and cricetids), leads us to suggest that most individuals of cf. *A. cinerea* were consumed and deposited anthropogenically. Moreover, natural deaths or non-human predator patterns would be expected to exhibit a more diverse range of anatomical frequencies (Andrade and Fernández, 2017; Andrews, 1990; Lopez, 2020). Thus, it appears that rodents were perhaps captured and slaughtered near or within the camps, suggesting that humans realized that their garbage was an attractive habitat for rodent families that reproduced *in situ*, generating a buffer source of protein that was easy to capture and consume (Hesse, 1984; Simonetti and Cornejo, 1991; Weissbrod et al., 2017).

Post-depositional processes were different between sites, resulting in slightly divergent taphonomic trajectories. QM12c exhibits the most fragmented assemblage, which is reflected in a low proportion of identified specimens (NISP/NSP), a low deposition ratio of identified specimens (NISP/$m^3$), and a limited number of taxa determined (NTAXA = 4). This site also has the highest proportion of eroded, polished and discoloured bones and the highest number of dry fractures, suggesting that non-human taphonomic agents were primarily responsible for this poor preservation. In addition, the bones show signs of having had prolonged exposure on the surface, which may be related to long periods of abandonment of the site. QM12c is located on the surface of a remnant of a Miocene fluvial terrace (Nester et al., 2007; Workman et al., 2020), which is not the case of the other sites. Due to protracted exposure to atmospheric conditions, which included some direct rainfall in the past (i.e. Pliocene, and early Pleistocene), this is the only site that shows the formation of a desert pavement and the development of a B horizon rich in extremely soluble salts (Ugalde et al., 2020), an indication that rainfall was very ephemeral and limited in time. We suspect that salts, especially in soils and sediments with a basic pH, along with other chemical and physical factors, such as bone burning by tossing them into the fires, are responsible for poor bone collagen preservation in the PdT.

In contrast, QM35d is the least fragmented assemblage, with the highest number of identified specimens and the highest total (NSP/m$^3$) and identified (NISP/m$^3$) specimen deposition ratios. This site has the lowest proportion of non-biological agents but shows a comparatively high incidence of fresh fractures and percussion marks; features that we estimate are related to anthropogenic reduction.

Unlike QM12c, the site shows a low proportion of modifications associated with weathering, which would mean that after its abandonment the remains were covered relatively rapidly by aeolian sands that formed a coppice dune; a deposit that is not rich in either salts or acidic organic matter, which also led to a good bone collagen preservation. The proportions of weathered and discoloured specimens in QM32 fall between QM12c and QM35d. Similarly, the proportions of identified specimens, the deposition ratio of identified specimens, taxonomic diversity, and fragmentation reflect this trend, which we interpret as the effect of local cultural and environmental factors.

The occurrence of trees during human occupation possibly helped to reduce wind erosion. After the total abandonment of the PdT (~9.5 ka), the roots of dead trees contributed to stabilize the deposit, protecting the cultural assemblages while the dune, formed during human occupation, continued to grow.

QM32 presents two key markers of greater mobility: the remains of *Ceiba* sp. wood brought from the tropical forest, and *V. vicugna* hair brought from mountainous areas. These foreign materials, coupled with the taxonomic diversity, may indicate a more cyclical or seasonal mobility pattern, which contrasts with the longer-stay mobility system, around summer, in QM35d. Longer periods of abandonment would have contributed to bone fragmentation, weathering, and discoloration.

Regarding site formation, QM32 was at the boundary of a wetland and grove, but the wetland soils were not as developed as in QM35; thus, salts were forming and cycling more intensely than at QM35. These chemical salt processes were less pronounced than at QM12c. The low density of trees at QM32 would have limited the formation of coppice dunes compared to QM35d.

Occupation PR5 could be considered as a non-intensive or infrequently visited campsite, given the low frequency of discarded bones (NSP/m$^3$) and their completeness, which resulted in a higher number of identified taxa (i.e., high NISP/NSP and NISP/m$^3$). In contrast, PR7 would have been occupied more intensively and recurrently than PR5, although less frequently than QM32 and QM35d. PR7 has a greater quantity of discarded bones, but the proportion of identified bones is lower. The elevated MNE/NISP ratio at PR7 can be attributed to the fact that most identified specimens are portions of elements rather than complete elements. The PR5 assemblage is more fragmented than that of PR7, but the high frequency of rodents in the former limits direct comparison. Both sites show a very low incidence of taphonomic modifications in the faunal assemblages, suggesting rapid post-occupational burial.

### 6.3. *Site function and seasonality*

Cluster analysis considering NSP/m$^3$, NISP/m$^3$, NTAXA, and evenness (excluding cricetids and reptiles due to their likely natural origin), distinguishes two groups of sites, closely matching their geographic distribution (Fig. 9). QM32 and QM35d contain a greater volume of discarded bones (indicated by NSP and NISP), a greater number of identified taxa with somewhat uniform distributions and representations. In contrast, PR5, QM12c and, to a lesser extent, PR7, show lower bone discard intensities, fewer identified taxa, and a predominance of one or two taxa per assemblage.

Skeletal parts do not show a correlation between the high survival bone set in QM35d and SMMI. Analysis of high-survival elements yielded a high Shannon uniformity index (0.895), indicating a relatively uniform distribution of skeletal elements that aligns with unbiased and bulk transport strategies (Binford, 1978). These results would indicate that QM35d hunter-gatherers did not select anatomical parts in the hunting area. Instead, *L. guanicoe* carcasses were transported to the camp in whole or near-whole for processing, consumption, and disposal. This also implied that the hunting activities occurred in proximity to this camp. For QM32, there was a non-significant negative correlation between GMUI and %MAU, which together with a slightly positive correlation between MAU and SMMI, suggests that some fleshy units were discarded outside the camp. Bones from QM35d show marks of skinning, dismembering, defleshing (the latter two features in almost equal proportions), and percussion, indicating that the whole processing of the carcasses, up to their discard, took place in the camp. It should also be noted that this is the only site where remains of bone artifact manufacture have been found *in situ*, although no specific bone instruments were identified.

Considering all these proxies, we propose that QM35d and QM32 functioned as long-term residential camps. Particularly, we estimate that QM35d was a residential camp recurrently occupied, considering its location next to a wetland where most of the variety of animals

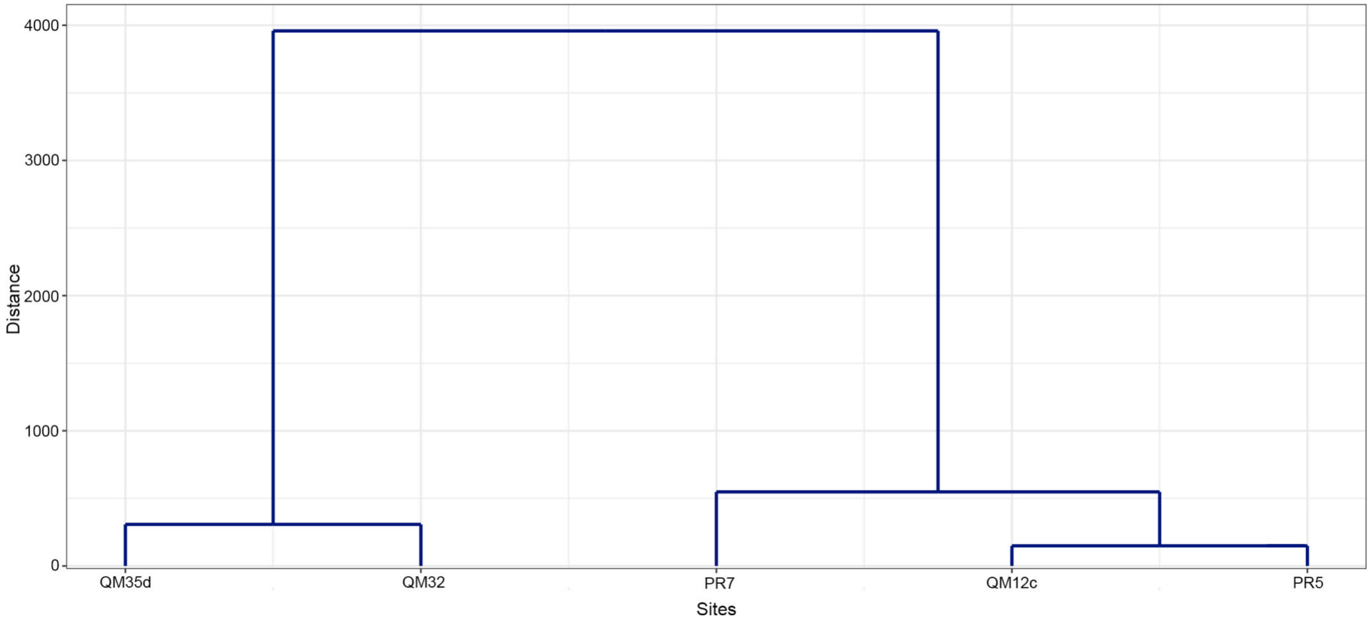

**Fig. 9.** Cluster analysis considering NSP/m$^3$, NISP/m$^3$, NTAXA and evenness.

consumed in the camp were concentrated, as well as fresh water. In addition, outside the wetland, the camp was in a grove area that provided protection and shelter to the hunter-gatherer groups that settled there (Ugalde et al., 2024a; Ugalde et al., 2024b). This interpretation is supported by the more complete operational sequences of the lithic assemblage (Herrera, 2021, 2023) and by radiocarbon phasing models.

The prevalence of young individuals in QM32 and QM35d (i.e., unfused and porous bones) is interpreted as a seasonal marker to indicate that the main sojourn would have occurred around the southern hemisphere summer months. Although the calving season of *L. guanicoe* varies throughout northern Chile, it always coincides with the warmest and rainiest season and therefore with the highest bioproductivity (González et al., 2006). We estimate that this period coincided with December to March, when runoff and groundwater discharge peak. The hunter-gatherer groups of the time, knowing very well the functioning of this ecosystem, settled at that time and concentrated their hunting actions on young camelid individuals born during the calving period of that season. If so, our hypothesis of a seasonal mobility system with permanent settlements in highly productive areas of the PdT, such as the paleo-wetland near QM35d, would be reaffirmed.

The “diversified portfolio of dietary strategies” found in QM35d and QM32 campsites was also reported for the Great Plains linked to coping with different ecosystems through a sequence of 13,000 years (Otárola-Castillo et al., 2020). In the case of the PdT, it does not seem feasible that the observed diversity was due to ecosystem limitations that forced a broadening dietary portfolio. On the contrary, it seems more plausible to us that the PdT offered suitable environmental conditions for hunting groups, as has been reported for Anatolia, where from ∼ 13.9 ka onwards a trend was detected to incorporate a greater number of taxa of differing sizes and behaviors, sustained by an overall improvement of the ecosystem (Atici, 2009).

With low numbers of taxa and the comparatively lower intensity of bone discard, the PR5 and PR7 campsites are interpreted as logistic or short-term residential camps. This behaviour would be related to the microecological characteristics of the distal section of the alluvial cone of the Quebrada de Guatacondo where the PR camps were located. There, a low-energy surface water environment, with no wetlands, gave rise to shrubby vegetation with very few trees, so it may have been less attractive, both for animals and humans, to settle there more permanently. The PR and QM alluvial fans, however, coalesce into each other at their distal ends and were under a similar climatic regime, so given the wide mobility pattern of camelids, they must have also roamed around PR.

The near absence of camelids and the high frequencies of rodents in the PR camps could be also explained through site function, since this area might have served as a stopping place for people in transit from the QM residential camps to the large stone quarries of Chipana 1 and Quebrada Blanca, or even the Pacific coast. Rodents are easier to capture than camelids, which require longer and more costly hunting strategies. Alternatively, it could be that people camped at PR during the fall or winter seasons, when the guanacos were more dispersed and out of the calving cycle. In any case, the excavated PR camps could have been key strategic stops for people coming from residential camps. These interpretations, however, do not explain the occurrence of several Punta Negra projectile points scattered at the PR surface (see del Castillo, 2019; Ugalde 2023). One possibility is that groups carrying Punta Negra projectile-point darts to hunt medium-sized animals (camelids) camped at different places and times within the PR, leaving behind ephemeral remains insufficient to become stratified archaeological sites. This situation will need to be revised with future explorations and excavations. The zooarchaeological data from QM12c seem to indicate short-term occupations, but this interpretation could be biased due to the taphonomic factors discussed above.

### *6.4. PdT and its relationship with other contemporary sites*

Based on the archaeological, ecological, and paleoecological data, we estimate that QM campsites were occupied during the most productive months, meaning from late summer or early fall, linked to the rainy season in the highland (December-May). Thus, the settlement and mobility system of these early hunter-gatherers integrated neighbouring and distant areas both toward the mountains (>80 km away) and the Pacific coast (60–80 km away). The link with the Andes is supported by the presence of *V. vicugna* and obsidian in QM12c, and *V. vicugna* fleece at QM32. Fragments or complete shells of small-sized sea mollusks are indicative of movement towards the coast (Santoro et al., 2019). Unfortunately, in the adjacent areas, no campsites have been found synchronous with those of the PdT, which limits the definition of a more precise supralocal mobility system.

The styles of projectile points recorded in the PdT campsites formally resemble the Patapatane and Las Cuevas styles described for the Dry Puna highland zone to the northeast of this basin (Osorio et al., 2017a). In turn, the Punta Negra style projectile points and one Tuina style projectile point trace a link to the Salt Puna highland area to the southeast of the PdT (see de Souza et al., 2022; Grosjean et al., 2005; Herrera, 2021; Loyola et al., 2017; Loyola et al., 2019; Núñez et al., 2002; Osorio et al., 2017a; Osorio et al., 2017b; Santoro, 1989; Santoro and Núñez, 1987). Given the low human population density of the period (Gayo et al., 2015), we estimate that the procurement of raw materials and other goods from long distances, along with the reproduction of tool forms across a wide geographic area, likely involved both direct and indirect exchange networks. This may account for the far-distant connections that brought pieces of *Ceiba* sp. wood to the PdT (Santoro et al., 2019). Based on this, we propose the existence of larger social interaction spheres and regional territoriality, as suggested for other Late Pleistocene to early Holocene hunter-gatherer groups, such as in the Levant (Byrd et al., 2016).

It is important to note that the projectile point styles were distributed differentially across the campsites of QM and PR, which may suggest that hunter-gatherer groups with distinct cultural backgrounds and settlement systems converged at the PdT, potentially occupying separate spaces. The PR hunter-gatherers mainly used Punta Negra point style manufactured in the siliceous rock from the Chipana 1 quarry, while in QM Escallonia-Patapatane and Las Cuevas point styles were more common (del Castillo, 2019; Herrera, 2021; Latorre et al., 2013; Loyola et al., 2017; Osorio et al., 2017a; Ugalde, 2023; Ugalde et al., 2024a). According to the radiocarbon dates, both areas were apparently occupied synchronously during some intervals between ∼ 12.2–11.2 ka, but it is impossible to know for sure if both groups coincided, because of radiocarbon’s intrinsic uncertainty ranges. If the two groups did indeed interact, given that the PR and QM camps were separated by several kilometres (Fig. 1), there was no direct (face-to-face) and immediate contact between the two groups. The separation, however, was close enough to avoid social isolation and reduce being left out of local and regional collaborative networks (Seong and Kim, 2022). Even if both groups did not coincide during the same season, we estimate that the proximity of their campsites would have been sufficient to know if the other group had recently been in the area; key information to verify that the mobility circuit to the PdT was still viable.

The subsistence strategies documented in the PdT do not differ from those reported for the nearby highlands. There, hunter-gatherers consumed the same faunal package integrated by camelids, rodents, and birds (Cartajena et al., 2014; Cartajena et al., 2007; Osorio et al., 2017b). Only in the Dry Puna have marginal marine imports been identified (Osorio et al., 2017a). Evidence of extinct megamammals is nonexistent in the zooarchaeological record, except for a possible Equidae sacrum fragment in Tuina 5 (Cartajena et al., 2007). Both archaeological and paleontological data indicate that large mammals were either extinct or extirpated by the time of human arrival in the ecosystems of the Atacama Desert.

Our zooarchaeological analyses indicate that the Late Pleistocene and early Holocene inhabitants of the PdT selected a diverse range of animals for food consumption and other purposes. These records also show a complete absence of now-extinct megamammals, suggesting that human activity was not a driving factor in their extinction in this area. People arrived at the PdT around ~ 12.8 ka, and abandoned it around ~ 11.2 ka, several centuries before the beginning of its complete ecological demise at ~ 9.5 ka. Probably, the gradual reduction of surface runoff during the summer rainy season must have affected the plant productivity, which would have impacted animal diversity, especially camelids, potentially coming down from the mountain ranges to the PdT. In this process of deterioration of the basin's ecology, the role of humans as an invasive species is an issue that requires further examination. The lack of water was probably the main factor for these hunter-gatherers, much more sensitive to gradual ecological changes, to opt early on to abandon their camps and not return to the PdT.

The diversified range of dietary strategies provided by hunting activities consisted of camelids (mainly *L. guanicoe*) along with a variety of rodents and birds (e.g., cf. *Abrocoma cinerea*, *Ctenomys* sp., teals and grebes) whose remains were anthropogenically and differentially introduced into the campsites of the QM and PR localities.

Several zooarchaeological proxies (discard rate, taxonomic richness, skeletal profiles) demonstrate that the camps located at QM and PR were functionally distinct, despite their geographic proximity and presumed contemporaneity. QM32 and QM35d are interpreted as residential camps, while PR5 and PR7 align with special purpose/logistic camps. Taphonomic issues, however, limit a more precise interpretation of the faunal record from QM12c.

The distal floodplain environments of PR had more limited flora and fauna resources and scarce forest availability, which could have influenced the way people camped there for short periods to carry out specific tasks, not yet well identified. Alternatively, they could have served as transit camps for inland groups moving to or from the coast, other unknown camps in the PdT, and lithic sources, such as Chipana-1 and Quebrada Blanca. The consumption of rodents and the absence of guanaco characterize the assemblages in PR. As transient groups, it would have been much easier for them to focus on the capture and consumption of rodents, which were possibly handy in the vicinity of the campsites. Alternatively, the absence of guanacos could have been a consequence of people arriving there during the fall or winter, when these camelids were more dispersed and out of the calving season.

In contrast, at QM35 and QM32 campsites, a landscape with increased vegetation cover and water availability during the spring-summer season (September to March) favoured more permanent occupation. The surrounding wetlands and groves supported a rich and biodiverse space environment including access to guanaco during their calving season.

Archaeological findings and contexts (e.g., projectile point typologies and exotic materials) further suggest that these different settlement patterns and the diversified dietary modes were developed by at least two culturally distinct hunter-gatherer groups. PR sites were apparently inhabited by people with a lithic tradition (i.e., Punta Negra projectile point style) more related to the Salt Puna, whereas people camping in the QM area were linked to the Dry Puna (Las Cuevas and Escallonia-Patapatane projectile point styles) (del Castillo, 2019; Osorio et al., 2017a; Ugalde 2023).

In sum, the faunal evidence, combined with lithic and contextual information show that the PdT played a key role in the early peopling of the Atacama Desert, not merely serving as a transit route between the Pacific coast and highland ecosystems but functioning as a residential node and even a congregational area for several hunter-gatherer groups over hundreds of years. This is attributable to the postglacial development of pristine ecosystems with more moderate climates and the development of plant communities that included groves where people camped. Trees are rare in the Andes and absent on the Pacific coast, where, in addition, fresh water is also limited. Future research should focus on locating other contemporary sites in Quebrada Maní, as well as in nearby canyons, to gain a more comprehensive understanding of the early hunter-gatherers' socio-ecological systems, which adaptive processes to changeable ecosystems were part of the old history of humanity in South America.

### 6.5. *Human animal interaction*

For a general overview directed at non-specialist readers of the journal, the relevance of the results can be synthesised across three thematic axes. First, assuming a low human population density, we estimate that the procurement of long-distance raw materials and other goods, and the reproduction of particular tool forms and techniques over continental areas, should have involved both direct and indirect exchange relationships. These far-distant connections account for the introduction of pieces of *Ceiba* sp. wood to the PdT, among other exotic goods (Santoro et al., 2019). Conversely, we propose that these people were part of larger interregional social network of interaction and regional territoriality, as has been also suggested for the Levant Pleistocene-Holocene hunter-gatherers (Byrd et al., 2016). Thus, given that the different ecosystems of South America were just beginning to be populated, there may have been low possibilities of exchange with neighbouring groups, as occurred during the Holocene. Therefore, people must have been accustomed to walking several tens or even hundreds of kilometres, which would have required strategies for learning about the territories in terms of climate, geomorphology, and distribution of biological and geological resources, and for being able to return to attractive enclaves such as those of the Pampa del Tamarugal on a permanent basis. This behaviour can be observed today in migratory birds that fly from the northern hemisphere to the southern hemisphere, stopping at strategic points visited by countless generations, as should have been the case in the PdT.

Second, radiocarbon dating shows that the PR and QM camps were occupied synchronously during the intervals between ~ 12.4 and 11.2 ka, which means that both groups could have coincided during their stays at PdT. If this was the case, given that the PR and QM camps were separated by about seven kilometres (Fig. 1), face-to-face contact between the two groups was not automatic. However, given that the distance between the camps was shorter, this prevented them from living in total social isolation, which would have limited their opportunities to participate in the active local and regional collaboration and exchange networks of which they were supposedly part (Seong and Kim, 2022). Furthermore, even if the two groups did not coincide in the same season, we dare to suggest that the proximity of their camps would have been sufficient to learn whether the other group had recently been in the area. This was key information in verifying that the people of the other group were still moving towards the PdT and that the mobility circuits remained viable.

A third line of interpretation arising from the data indicates that regional sociocultural dynamics likely began earlier than previously recognized. The difference with the regionalization processes that began in the Holocene lies in the territorial scope of these processes. For example, the late Pleistocene or post-Ice Age hunter-gatherers in the PdT established much wider mobility circuits than their descendants. These groups, like migratory birds, undertook journeys that stretched from the Pacific coast to the rainforest, covering more than 800 km in a straight line, crossing the current borders of several South American countries. Furthermore, the cultural roots or origins of the two social groups recognized in the PdT came from different parts of South America. The first group, at Quebrada Maní, possibly came from the Andean northeast, given that the shapes and manufacturing techniques of their hunting tools (i.e., Las Cuevas and Escallonia-Patapatane style projectile points are common and distinctive to that area. In contrast, the second group, in Pampa Ramaditas, appears to have its roots in the territories and populations of the southeastern Andes, where the shapes and techniques of their hunting tools (Punta Negra style projectile point) distinguish that area as a distinct cultural region.

## 7. Conclusions

In summary, given its richness and diversity of resources, the PdT ecosystem was able to function as an ecological refuge where plants, animals, and humans converged and reproduced for some 1,600 years. This refuge became depopulated when surface and underground water sources ceased to sustain the vegetation cover that maintained the complex trophic structure and the ways of life of at least two sociocultural groups that colonized this pampa. As many of the animals that sustained their diet were extirpated, the PdT ceased to be a place of convergence and was abandoned some 11,200 years ago. The exodus led them to different environments in the Andes. In this ecological transformation of the PdT, it remains to be determined whether human interference was an influential factor in these changes, along with climatic factors. Our study also has implications for discussions regarding the consequences of early peopling of the Americas for the extinction of megafauna (Grayson, 2001; Barnosky and Lindsey, 2010; Politis et al., 2019; Prates et al., 2025). Although wetland development during the CAPE I did favour the occurrence of sloths, horses, dire wolves, and other extinct megafauna, it appears that the aridification that the PdT experienced ~ 14.5–13 ka might have catalysed their regional extirpation and eventual extinction by the time humans arrived in the region during the CAPE II (Caro et al., 2023; Straulino Mainou et al., 2025; Ugalde et al., 2024a). The zooarchaeological evidence from the five Late Pleistocene sites studied here points to an absence of human-megafaunal interaction. More importantly, our data verifies that when the first humans arrived in the PdT, they did not directly prey on megafauna and focused instead on hunting large mammals, such as guanaco, but also on smaller prey such as rodents and birds. While these results do not conclusively reject the possible participation of humans in the extinction of South American megafauna, they do highlight the significance of the procurement of alternative prey as part of the adaptive strategies of these early foragers.

## CRediT authorship contribution statement

**Rafael Labarca:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Paula C. Ugalde:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **José M. Capriles:** Writing – review & editing, Investigation, Conceptualization. **Eugenia M. Gayo:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Thomas A. Püschel:** Writing – original draft, Methodology. **Francisco Caro:** Formal analysis. **Gabriela Jarpa:** Data curation. **Natalia Villavicencio:** Writing – review & editing, Investigation, Data curation. **Claudio Latorre:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Calogero M. Santoro:** Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, 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 material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jaa.2025.101742.

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