

## RESEARCH ARTICLE

# Resilience and livestock adaptations to demographic growth and technological change: A diachronic perspective from the Late Bronze Age to Late Antiquity in NE Iberia

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## Abstract

There are strong interactions between an economic system and its ecological context. In this sense, livestock have been an integral part of human economies since the Neolithic, contributing significantly to the creation and maintenance of agricultural anthropized landscapes. For this reason, in the frame of the ERC-StG project 'ZooMWest' we collected and analyzed thousands of zooarchaeological data from NE Iberia. By considering these data in comparison with ecological indicators (archaeobotanical remains) and archaeological evidence (settlement characteristics and their distribution) this paper seeks to characterize changes in animal production and the relationship between people, livestock, and their environment. These methods allow for an investigation of the topic at different scales (site, zone, territory) with a broad diachronic perspective, and for consideration of orography and cultural traditions alongside climatic factors. Through this integration of various streams of evidence, we aim to better understand the structure of ancient economic systems and the way they conditioned human decision-making on animal production. Results show a shifting relationship with the territory between the Bronze Age and Late Antiquity, in which market requirements and an economic model with a higher degree of integration increasingly influenced husbandry strategies. These processes are reflected in changes in land use and forms of territorial occupation, although along different rhythms and trajectories.

## 1. Introduction

Europe experienced significant economic and political changes between Late Prehistory and the Classical period [1–6]. Complex societies with a strong territorial component developed during the Late Bronze Age and the Early Iron Age in the north-west of the Mediterranean basin (northeastern Iberia and the area of the Gulf of Lion), which subsequently led to the

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formation of proto-statal structures during the Middle Iron Age [1,7–14]. In this area, the culturally and politically atomized landscape attested during the Iron Age was transformed following the Roman conquest, and further modified through its integration within the Roman Empire, which grouped many communities under a previously unseen level of large-scale economic connectivity [15–20]. This first ‘globalized system’ on a Mediterranean scale experienced a major crisis during the 6<sup>th</sup> c. AD, leading to its deconstruction and a re-localization of production, which retracted and became more autarchical during Late Antiquity [17,21–23].

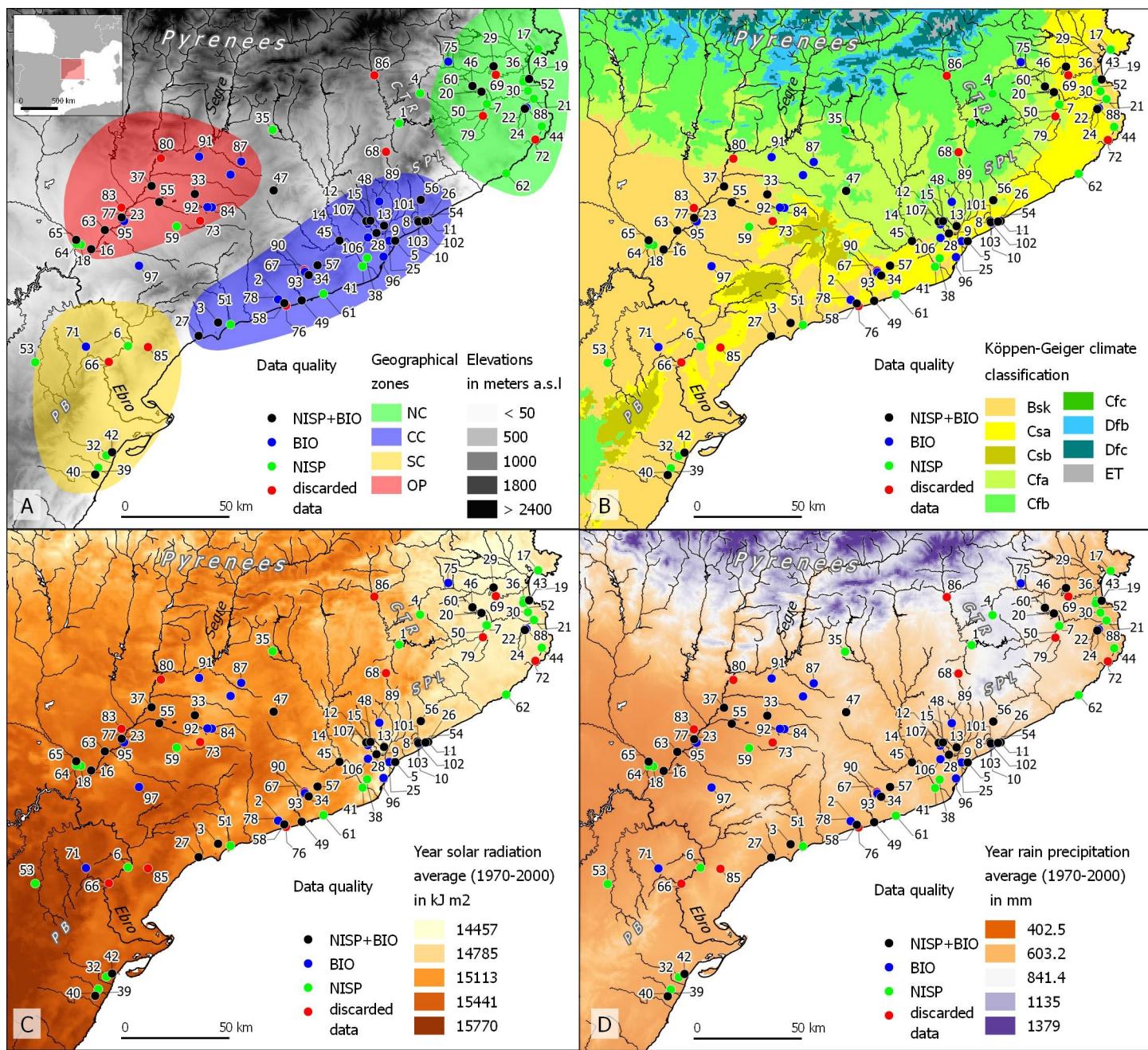
In the North-East (NE) of the Iberian Peninsula, the transition from the Bronze to the Iron Age marked a significant moment of change in settlement structure. In association with the spread of iron technology during the 8<sup>th</sup> c. BC, scattered huts made of perishable materials were replaced by stone-built settlements located on hilltops [24–26]. The spread of iron technology for tool production is thought to have promoted greater cereal production and a demographic increase, which subsequently led to increased pressure over resources, potentially inciting territorial conflicts, fortification and social stratification [25–28]. The impact of these phenomena on animal husbandry is not yet fully understood, but they appear to have had a significant influence on livestock body size, considering the general small size of animals attested during the Bronze and Iron Ages [29–31]. Animal size subsequently increased during the Roman period, as documented in many parts of Europe [31–46]. The factor(s) driving animal size changes through time are not clearly understood yet, but different models have been proposed to explain the size reduction during Late Prehistory including: the controlled selection of smaller individuals to produce more manageable animals [47], consequence of climatic changes [48], and an intensification of sub-adult breeding [49]. A further set of proposals has been advanced in relation to increases in livestock size during the Roman period, especially the introduction of new morphotypes [31]. Across time, factors for size change were probably influenced by the socio-political context in which animals were raised, and the different potentials and challenges provided by it [45,50–52]. Although increasingly recognized as a major determinant in shaping husbandry strategies, the interaction between animal management and the socio-political context in which these activities took place is rarely evaluated systematically. Previous synthetic works for the region have focused on smaller areas or time periods [53,54], but ours is the first study to combine species frequencies and detailed biometric analysis over protohistory and classical times, and to contextualize these data with larger scale environmental and archaeological evidence.

This paper aims to contribute to this debate by providing an integrated study that presents zooarchaeological data from the NE of the Iberian Peninsula from the Late Bronze Age to Late Antiquity. The zooarchaeological results are contextualized using other streams of archaeological evidence, i.e. settlement patterns, material culture, archaeobotanical data. The ultimate goal is to analyze to what extent ecology and / or socio-political factors may influence animal husbandry in terms of species selection and animal size.

## 2. Geographical setting

This study considers four areas within the NE Iberian Peninsula, present-day Catalonia (Fig 1): the North Coast (NC), Central Coast (CC), South Coast (SC), and Occidental Plain (OP) (Fig 1A). The region has several rivers connecting the Pyrenees with the Mediterranean shore. The biggest one is the Ebro River, which is partly navigable, and links the Occidental Plain (OP) to the South Coast (SC).

While present climate is not directly applicable to the past, especially over the millennia considered in this study, it nevertheless provides an indication of potential relative differences in temperature (Fig 1B), precipitation (Fig 1D), and solar radiation (Fig 1C). The shore of the



**Fig 1. Map of NE Iberia with locations of the studied sites.** A) Location of geographical areas (NC: North Coast, CC: Central Coast, SC: South Coast, OP: Occidental Plain) with sites colored depending of archaeozoological data availability (NISP: Counts by species, BIO: Biometrical data) with elevation map reprinted using open data from Geofabrik and the U.S. Geological Survey [55,56]; B) Köppen-Geiger climate classification reprinted from open data Zenodo [57]. The classification is based on threshold values and seasonality of monthly air temperature and precipitation. Considering vegetation as “crystallized, visible climate” C) Averages of year solar radiations between 1970–2000 [58]. D) Averages of rain precipitations between 1970–2000 [58] reprinted from WorldClim (CC-BY SA 4.0). List of sites: 1. Esquerda; 2. Alorda Park; 3. Antigons; 4. Aubert; 5. Baetulo; 6. Barranc de Gàfols; 7. Bosc del Congost; 8. Burriac; 9. Ca n'Oliver; 10. Can Bartomeu; 11. Can Cruzate; 12. Can Feu; 13. Turó de la Rovira; 14. Can Gambús 1; 14. Can Gambús 3; 15. Can Roqueta\_DIASA; 15. Can Roqueta CRV; 15. Can Roqueta TR; 16. Carretelà; 17. Ciutadella de Roses; 18. Cova Punta Farisa; 19. Empúries; 21. Fonollera; 22. Gou Battle; 23. Ilerda 1; 23. Ilerda; 23. Ilerda 2; 24. Illa d'en Reixac; 25. Puig Castellar; 26. Iluro\_VI\_VII; 27. La Llosa; 28. Mallols; 29. Mas Castellar rural; 29. Mas Castellar fortificat; 29. Mas Castellar; 30. Mas Gusó; 32. Moleta del Remei 1\_1; 33. Molí d'Espígol; 34. Olèrdola; 35. Olius; 36. Olivet d'en Pujol; 37. La Pedrera; 38. Penya del Moro; 39. Puig de la Misericordia; 40. Puig de la Nau; 41. Sant Boi\_Pl Constitució; 42. Sant Jaume Mas d'en Serrà; 43. Sant Martí Empúries; 44. Sant Sebastià de la Guarda; 45. Santa Margarida; 46. Saus; 47. Sigarra; 48. Sitges UAB; 49. Solana; 50. St. Julià de Ramis; 51. Tarraco; 52. Tolegassos; 53. Torre Cremada; 54. Torre Llauder; 55. Tossal Molinet; 56. Turó del Vent; 57. Turó Font de la Canya; 58. Vilarenc; 59. Vilars; 60. Vilauba; 61. Vil-la Vinyet; 62. Vil-la dels Ametllers; 63. Vilot de Montagut; 64. Vincamet; 65. Zafranales; 68. Camp de les Lloses; 69. Camp Gran-Camp d'en Pitu Porrusia; 70. Can Cruzate; 71. Coll del Moro; 72. Collet de Sant Antoni; 73. Estincells; 74. Fonollera; 76. Les Guardies; 77. Lleida\_Carrer Bafart; 78. Mas d'en Gual; 79. Mas Xirgù; 80. Monterò; 82. Puig de la Misericordia; 84. Rosella; 83.

Roques del Sarrò; 85. Tossal del Moro de Pinyeres; 86. Turo del Calvari; 87. Puig Castellar Biosca; 88. Puig de Sant Andreu; 89. Torre Roja; 91. Hereuet; 92. Missatges; 94. Iesso; 95. Vil·la Torre Andreu; 97. Vilans de Reig; 101. Can Mateu; 102. Can Bernat; 103. Can Rodon; 106. Can Sant Joan; 107. Mas Duran.

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**North Coast (NC)** is described as an arid cold steppe (Bsk) in the Köppen-Geiger climate classification [55]. Its hinterland, about 20 km from the coastline, is temperate, with a dry and hot summer (Csa). The Catalan Transversal Range (ca. 500–900 m.a.s.l.), located in the hinterland of the NC, is the wettest and most cloudy of the areas considered, with a relatively annual high rate of rainfall (841–1135 mm) (Fig 1D), and a relatively low solar radiation (14457–14785 kJ m<sup>2</sup>) (Fig 1C). The rivers of La Muga, Fluvia and Ter connect the Catalan Transversal Range to the coast. The **Central Coast (CC)** has a warmer climate on average compared with the NC, with dry and hot summers (Csa) in the coastal valleys, and a temperate climate, with no dry season and a hot summer (Cfa), in the neighboring mountain range (Serralada Prelitoral, 500–1000 m.a.s.l.). In addition, an arid cold steppe climate area (Bsk) is located in the southern part of CC (Fig 1C). The **South Coast (SC)** area is mostly composed of a semi-arid cold steppe climate (Bsk) (Fig 1B). A small part of this zone shows a temperate climate with dry and hot summers (Csa). Only in the Ports de Beseit mountain range (ca. 1000–1200 m.a.s.l.) is a dry and warm summer found (Csb). The SC has the highest annual average of solar radiation of the four zones studied (above 15441 kJ m<sup>2</sup>) (Fig 1C), and the annual rainfall is similar to the North and Central Coast (Fig 1D). Finally, the **Occidental Plain (OP)** shows mostly a semi-arid and cold steppe climate (Bsk) in the lower part of the Segre river (Fig 1B), and a temperate hot summer (Cfa) in the middle Pre-Pyrenees mountain range (ca 400–600 m.a.s.l.). This area is the driest of the four studied, with ca. 420 mm of annual rainfall (Fig 1C and 1D).

### 3. Archaeological context: Changes in settlement patterns and the political organization in NE Iberia

A detailed analysis of settlement dynamics in the North-East of the Iberian Peninsula during Late Prehistory and early historical times (Table 1) is beyond the scope of this paper, but a general overview is necessary to contextualize the zooarchaeological data. The following paragraphs present the main changes in settlement dynamics and site types according to synthetic works and the accepted terminology for the region (Table 2).

The **Late Bronze Age (LBA)** (13<sup>th</sup>–9<sup>th</sup> c. BC) shows a clear duality in the settlement pattern between coastal areas (CC and NC) and the interior plain (OP). These two models probably reflect different social and economic scenarios. On the coastal areas, the continuity of the previous models of habitation from the Middle Bronze Age is well attested (i.e. open-air villages with isolated huts and storage pits, also called *silos* [63]). This is thought to reflect a family residence model, characterized by small autonomous farms scattered through the territory

Table 1. Diachrony considered.

Periods	Subperiods	Abb.	Chronology
Bronze Age	Late Bronze Age	LBA	13th– 9 <sup>th</sup> c. BC
Iron Age	Early Iron Age	EIA	8th– 7 <sup>th</sup> c. BC
	Middle Iron Age 1	MIA1	6th– 5 <sup>th</sup> c. BC
	Middle Iron Age 2	MIA2	4th– 3 <sup>rd</sup> c. BC
Roman period	Roman Republic	RR	2nd– 1 <sup>st</sup> c. BC
	Early Roman Empire	ERE	1 <sup>st</sup> – 3 <sup>rd</sup> c. AD
	Late Roman Empire	LRE	4th– 5 <sup>th</sup> c. AD
Late Antiquity	Late Antiquity	LA	5th– 6 <sup>th</sup> c. AD

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**Table 2.** Description of the types of site. For details see [27,28,59–62].

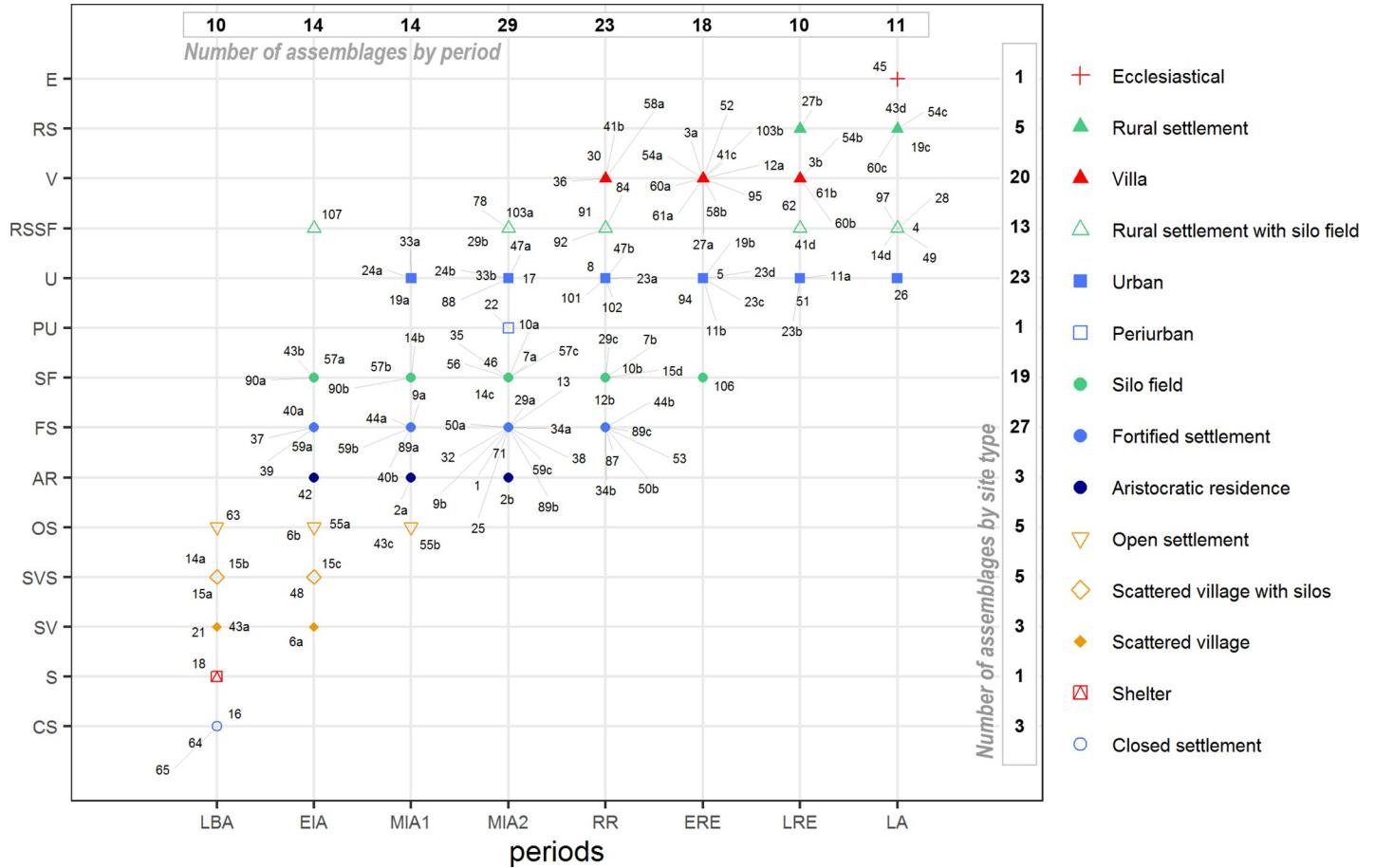
Categories	Abb.	Description
Aristocratic residence	AR	Small nuclei with solid and complex fortifications
Closed settlement	CS	Semi-detached houses with perimeter wall and central space for community use
Ecclesiastical	E	Rural churches without direct links with a known village, but which bring together a scattered population
Fortified settlement	FS	Houses surrounded by a wall and / or other defensive elements (towers, ditch, etc.), with a total surface varying from c. 0.5 Ha to c. 2 Ha
Open settlement	OS	Houses built with perishable materials and without fortifications
Periurban	PU	Houses or neighborhoods located on the outskirts of the wall of an urban nucleus
Rural settlement	RS	Detached houses with productive facilities and without fortification
Rural settlement with silo field	RSSF	Rural settlement with an associated extension of storage pits (silos). See 'Rural settlement'
Scattered village	SV	Settlement with a high scattering of dwellings, no complexity with regard to space, and an expansive use of the space. Each productive units possesses a certain degree of autonomy
Scattered village with silos field	SVSF	Scattered village with an associated extension of storage pits (silos). See 'Scattered village'
Shelter	S	Natural cover with a seasonal or permanent occupation
Silo field	SF	Wide extension of storage pits (silos) in which no habitation structures have been found
Urban	U	Settlements with a complex plot (domestic/public buildings, streets, etc.) and activities (high density/diversity of social interactions, economic production, etc.), larger than 2 Ha—first level sites
Villa	V	Roman country house for wealthy people with associated productive facilities built during the Roman Republic and the Roman Empire

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[8,13,25,27]. These sites were established in the vicinity of the crop fields and can contain a large number of *silos*, as is the case of Can Roqueta (15) in the CC area [64]. In contrast, in the occidental plain (OP) a proliferation of elevated sites with more stable stone structures is attested from the 10th c. BC, constituting the first closed settlements in the area (Fig 2) (e.g. Genó, Vincamet (64), Carretelà (16) and Zafranales (65); [28,65–68]). These villages are thought to represent a concentration of several families [28,68]. In the coastal areas, only one site—La Fonollera (21, NC)—includes several huts and can be considered as a small village [69,70]. Archaeobotanical data suggest that Late Bronze Age economy was mainly based on cereal production, most notably barley (*Hordeum vulgare*) and common wheat (*Triticum aestivum*) [71]. In the occidental plain (OP), agriculture probably involved ploughing, fallowing, and the use of manure as fertilizer [71]. In contrast, in the coastal areas a system of grazing and fire-based deforestation has been proposed [72,73], which would justify less stable settlements.

The absence of strong differences in the funerary record and within the settlements suggests that these societies were relatively egalitarian compared with those of later periods [74]. The end of the Bronze Age is marked by the collapse of complex long-distance exchange networks for the bronze industry (tin and copper [75,76]).

The **Early Iron Age (EIA)** (8<sup>th</sup>–7<sup>th</sup> c. BC) is characterized by the presence of the first occurrences of iron objects, and the expansion of open settlements due to population concentration processes [27,28,77–79]. Archaeobotanical data suggest that during the EIA the farming strategies were similar to previous periods. Even so, the introduction of viticulture (mainly in eastern Catalonia) was a novelty with respect to the previous period. At this time, the agricultural rhythm based on the immediate obtaining of yields was broken. This means that the surplus agricultural production became more archaeologically visible, suggesting a change in farming strategies [67]. The palaeoenvironmental data available for the four study regions are very



**Fig 2. Chrono-typology seriation of the 127 studied assemblages from Late Bronze Age to Late Antiquity.** (LBA: Late Bronze Age, EIA: Early Iron Age, MIA1: Middle Iron Age 1, MIA2: Middle Iron Age 2, RR: Roman Republic, ERE: Early Roman Empire, LRE: Late Roman Empire, LA: Late Antiquity). The x-axis represents the assemblages by periods and the y-axis represented the type of sites. List of assemblage numbers: 1. Esquerda; 2a. Alorda Park 2a; 2b. Alorda Park 2b; 3a. Antigons\_waste dump; 3b. Antigons\_Nymphaeum; 4. Aubert; 5. Baetulo; 6a. Barranc de Gàfols\_1; 6b. Barranc de Gàfols\_2; 7a. Bosc del Congost; 7b. Bosc del Congost; 8. Burriac; 9a. Ca n'Oliver 1; 9b. Ca n'Oliver 2\_3; 10a. Can Bartomeu; 10b. Can Bartomeu; 11a. Can Cruzate; 11b. Can Cruzate; 12a. Can Feu; 12b. Can Feu; 13. Turó de la Rovira; 14a. Can Gambús 3; 14b. Can Gambús 3; 14c. Can Gambús 1; 14d. Can Gambús 1; 15a. Can Roqueta CRV; 15b. Can Roqueta TR; 15c. Can Roqueta DIASA; 15d. Can Roqueta TR; 16. Carretelà; 17. Ciutadella de Roses; 18. Cova Punta Farisa; 19a. Empúries; 19b. Empúries; 19c. Empúries; 21. Fonollera; 22. Gou Battle; 23a. Ilerda; 23c. Ilerda1\_Carrer Magdalena 4; 23d. Ilerda2\_Carrer Bafart 46; 24a. Illa d'en Reixach 2\_3; 24b. Illa d'en Reixach 4\_5\_6; 25. Puig Castellar; 26. Iluro\_VI\_VII; 27a. La Llosa; 27b. La Llosa; 28. Mallols; 29a. Mas Castellar\_fortified; 29b. Mas Castellar\_rural; 29c. Mas Castellar; 30. Mas Gusó; 32. Moleta del Remei 1\_2; 33a. Molí d'Espíglol; 33b. Molí d'Espíglol; 34a. Olèrdola 1; 34b. Olèrdola 2; 35. Olius; 36. Olivet d'en Pujol; 37. La Pedrera IV-VII; 38. Penya del Moro; 39. Puig de la Misericordia; 40a. Puig de la Nau; 40b. Puig de la Nau; 41b. Sant Boi\_Pl. Constitució; 41c. Sant Boi\_Pl. Constitució; 41d. Sant Boi\_Pl. Constitució; 42. Sant Jaume Mas d'en Serrà\_sect; 1; 43a. Sant Martí d'Empúries; 43b. Sant Martí d'Empúries; 43c. Sant Martí d'Empúries; 43d. Sant Martí d'Empúries; 44a. Sant Sebastià de la Guarda; 44b. Sant Sebastià de la Guarda; 45. Santa Margarida; 46. Saus; 47a. Sigarra; 47b. Sigarra; 48. Sitges UAB; 49. Solana; 50a. St. Julià de Ramis; 50b. St. Julià de Ramis; 51. Tarraco; 52. Tolegassos; 53. Torre Cremada; 54a. Torre Llauder; 54b. Torre Llauder; 54c. Torre Llauder; 55a. Tossal Molinet I-II; 55b. Tossal Molinet III; 56. Turó del Vent 1-2; 57a. Turó Font de la Canya 0; 57b. Turó Font de la Canya 1; 57c. Turó Font de la Canya 2\_3; 58a. Vilarenc; 58b. Vilarenc; 59a. Vilars 0\_I; 59b. Vilars II; 59c. Vilars III\_IV; 60a. Vilauba; 60b. Vilauba; 60c. Vilauba; 61a. Vil-la Vinyet; 61b. Vil-la del Vinyet; 62. Vil-la dels Ametllers; 63. Vilot de Montagut 0-III; 64. Vincamet; 65. Zafrañales; 71. Coll del Moro; 78. Mas d'en Gual; 84. Rosella; 87. Puig Castellar Biosca; 88. Puig de Sant Andreu; 89a. Torre Roja; 89b. Torre Roja; 89c. Torre Roja; 90a. Mas d'en Boixos; 90b. Mas d'en Boixos; 91. Hereuet; 92. Missatges; 94. Iesso; 95. Vil-la Torre Andreu; 97. Vilans de Reig; 101. Can Mateu; 102. Can Bernat; 103a. Can Rodon; 103b. Can Rodon; 106. Can Sant Joan; 107. Mas Duran.

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heterogeneous. Although both the LBA and the EIA have shown recurrent signs of anthropization of the landscape, the indicators still do not show excessive disturbances [80–82].

During the EIA important differences between the interior and the coastal areas are visible at the funerary level in different tumular traditions, and in the settlement pattern. This duality is thought to reflect two distinct economic systems [13,67,71]. The first, located in the Occidental Plain (OP), represented a centralized economy based on the large-scale production of

one or several basic subsistence products. In this area, there is a low presence of imported products from the Mediterranean colonial trade [83]. The appearance of fortified sites, mostly located on elevated positions but also on the plain (e.g. Els Vilars (59), Molí d'Espígl (33), La Pedrera (37)), and 'warrior tombs' (e.g. Necropolis of La Pedrera) have been used to suggest that coercion was an important factor for power consolidation and for exercising effective control over the territory [13,28,84]. The second socio-economic model attested in coastal areas (CN, CC, SC), is thought to have been developed from an economy of prestigious goods. In this model, small group of individuals would control both the mechanisms of exchange of colonial trade and the redistribution of prestigious import objects [6,13,25,85,86]. In both zones (interior and coastal), a process of aristocratic emergence probably occurred, in which the exchange of prestigious goods acted as an element of social cohesion [13,25,27,67,87–93]. Some elements suggest that there were also important internal conflicts. In this regard, most sites in the SC were destroyed by fire in the 7<sup>th</sup> c. BC, which prevented these centers of power from fully consolidating until the 6<sup>th</sup> c. BC [13,92,94,95].

The **Middle Iron Age (MIA1)** (6<sup>th</sup>–5<sup>th</sup> c. BC) was characterized by the emergence of what has been called 'Iberian Culture' [27,96,97]. Emerging chiefs and aristocratic groups consolidated both in the OP [28,84,98] and the coastal areas [91,99,100]. A hierarchical system of occupation was implemented, organized into several centralized political units. There was a greater diversification in settlement types: central places with fortifications (more than 3 ha in size), peripheral mid-rank settlements (3 to 1.5 ha), and small-sized scattered settlements [11,27]. At this point, coercion would be used as a means of control in a strongly territorialized context. Protection became central, as evidenced by the spread of stone architecture, the presence of defensive elements in most sites and the generalization of weapons in the tombs [27,101,102]. In this period, the use of iron is mainly attested in the manufacture of weapons, and no major changes in the production model have been identified [30,67,71].

In the **Middle Iron Age 2 (MIA2)** (4<sup>th</sup>–3<sup>rd</sup> c. BC), there was significant growth of some settlements that became large urban centers (over 10 ha in size). In addition, other smaller nuclei with concentrated populations were created, and the number of dispersed farms and rural establishments generally increased, especially in NC and CC [11,25]. This settlement pattern is thought to reflect a greater integration of productive models, where agriculture experienced significant intensification, visible in the generalization of iron-made agricultural tools and the growing size of cereal storage structures [27,102–105]. In addition, fortification structures became increasingly complex (ditches, concealed entrances, towers, etc.). The development of more intensified production systems is thought to respond to both a growing internal (demographic increase) and external demand (colonial trade) [103]. The intensification processes promoted the consolidation of an administrative system managed by political entities with a larger territorial influence during the 3<sup>rd</sup> c. BC. The estimated areas covered by these territories vary between 2000–2800 km<sup>2</sup> for the smallest entities located in CC and NC [27], up to the 9500 km<sup>2</sup> of the largest entities in the OP [106]. This new scenario was characterized by a higher degree of specialization and hierarchization of settlements, and the existence of an Iberian coinage, weight system, and writing, all of which is thought to correspond to a proto-state political structure comprising different ethnic entities [25,99,107].

The 2<sup>nd</sup> Punic War (218–201 BC) and the Roman conquest of Iberia starting in 218 BC brought about profound transformations in the socio-political and economic system of the indigenous communities throughout NE Iberia. The Roman victory over Carthaginians marked the progressive incorporation of the whole area into the Roman economic and cultural system during **Republican period (RR)** (218–37 BC) [108–114]. During the first half of the 2<sup>nd</sup> c. BC (200–150 BC) an extraction model was imposed on the allies, which were still attached to the *oppida* as territorial administrative centers. But from 150 BC onwards, there was a

progressive transformation of the settlement pattern, first in the coastal areas and later in the Occidental Plain [108,115–119]. A new type of small rural sites located in the plains, without defensive systems and specialized in cereal production, spread in most areas (except in the SC [112]). The material culture and building practices were mainly of indigenous tradition, and a low degree of Roman acculturation has been proposed according to material culture and the presence of new construction techniques and structures (e.g. La Rosella (84) [120], Serrat dels Espinyers [121,122]). During the 1<sup>st</sup> c. BC, newly built *villae* were erected over many of these small rural sites, thus suggesting that the territory was then fully integrated into the economic and political Roman system [108,110,123].

The **Early Roman Empire (ERE)** (37 BC–AD 250) is associated with the end of the conflicts in the Iberian Peninsula and the creation of the new provinces by Caesar Augustus, who founded cities and reorganized the road network [114]. In the case of the *provincia Tarragonensis*, it was a time of territorial expansion with a high degree of economic integration. The changes related to the territorial reorganization of Augustus are the culmination of a new model of settlement and occupation of the territory. In the rural areas, an important nuclearization of dispersed sites is attested, due to the spread of the *villae* system [114]. The *villae* managed large *latifundia* (Latin: *latus* 'spacious' and *fundus* 'farm, estate') with a production system specialized in cereals and olive trees for the *villa*, and grapes for wine production and export [15,16,124]. The large territorial extension managed by the *villae*, allowed large areas to be exploited for crop fields, to have grazing areas for the flocks, and to have a large variety of natural resources from forested areas. The *villae* also had buildings for artisanal production (e.g. large ceramic ovens) and for the storage of agricultural surplus. All this made the *villae* self-sufficient in terms of food and supply of basic products, forming self-managed production units, although within a productive system clearly devoted to the imperial market [16,111,124,125]. On the other hand, cities occupied large areas (c. 80 ha in the case of *Tarraco*), and were densely populated [114,126]. Cities also concentrated the political and administrative power in the provinces, and articulated the territory together with large consumer and redistribution centers of surpluses sourced from rural areas [127–129]. The larger regional administrative units of the empire (compared to the pre-Roman periods) and the large road network were key elements in facilitating long distance trade and the circulation of products, livestock and people. The high degree of connectivity allowed this system to maintain a new large-scale production system, balancing the growing supply and demand [18,19].

During the **Late Roman Empire (LRE)** (AD 250–472), the pattern of rural settlements in the *provincia Tarraconensis* underwent important changes [129–131]. After the crisis of the 3<sup>rd</sup> c. AD, wine production in the *Tarraconensis* significantly decreased and some *villae* were partially or totally abandoned, or their facilities reduced [59,60,114,132]. Subsequently, some remaining *villae* experienced refurbishments and the monumentalization of some of their buildings during the 4<sup>th</sup> c. and the first decades of the 5<sup>th</sup> c. AD [129]. There were important changes in the relationships between the urban and rural worlds, which appear less interconnected and integrated compared with the Imperial period. These territorial changes are thought to reflect a progressive concentration of the land in the hands of fewer (and richer) owners [114]. From circa AD 450, small peasant houses are attested across the *provincia*, together with a progressive concentration of rural population in small rural hamlets and a significant reduction in the number of sites [129]. This period is often referred to as one of economic, demographic and urban recession, as evidenced by the decrease, and abandonment of some buildings, as attested in cities such as *Ilerda* (23, in the OP), *Tarraco* and *Iluro* (51 and 26, in the CC) among others [133,134].

During **Late Antiquity (LA)** (AD 470–572), Visigoth groups from Aquitaine gained control of the area. Between 470 and 475 AD, Euric conquered Roman Hispania and occupied

*Tarragonensis* [135]. Despite the resistance of the local nobles, Visigoths conquered the whole territory very quickly [136]. In 507 AD, the kingdom of Toulouse disappeared. The Visigothic court initially moved from Narbonne to Barcelona (between 531 and 572 AD), although it later moved the capital to Toledo. From the second half of the 5<sup>th</sup> c. AD, and throughout the 6<sup>th</sup> c. AD, the settlement pattern was reconfigured with a certain continuity of the pre-existing sites, although very transformed [59,114,129,137–146]. There was a gradual disappearance of the *villae* and archaeological evidence indicates important changes in their functionality and in the ways of rural life [132,142,147,148]. The drastic reduction of imports and the size of production facilities (e.g. wine and olive presses, warehouses, silos) suggest a decrease of production, adapted to the demand of more local/regional markets [149]. Some authors highlight the decline of long-distance Mediterranean trade as a result of the Byzantine conquest of North Africa, Italy, Sicily, Balearic Islands and South-eastern Hispania [150]. The monumental structures of the *villae* (e.g. baths, spaces of representation) were abandoned or re-used for productive activities, and building materials were extensively recycled to erect new and smaller habitation and productive units. New rural settlements also spread in the territory in the form of small agricultural villages with huts built with perishable materials (wood and other plant materials, [142,144,148]), which are thought to be inhabited by small family groups [151]. The period has been described as a time of self-reliance as a basic strategy, and of technological and architectural modesty. Although at this time the arrival of imports from other places of the Mediterranean is still attested in the *Tarragonensis*, this was mainly limited to coastal areas and cities located at main communication axes. These transformations are thought to reflect an increasingly autarkic and independent system of rural areas with respect to cities [152].

## 4. Materials and methods

### 4.1 Archaeological sites and zooarchaeological assemblages

[Fig 1A](#) shows the location of the 101 archaeological sites considered in this study, among which 28 have NISP data (number of identified specimens, green points), 23 have biometry data (blue points), and 34 have both data (black points). The complete dataset and related references are detailed in supplementary materials S1 in [S1 File](#). A total of 16 settlements (red points) were excluded from the analyses due to contextualization problems or to a low number of remains (< 110 NISP of main domesticates). As stated above, the studied area was divided into four zones ([Fig 1A](#)). To guarantee greater precision in the location of the sites and the study areas, all data were integrated into an open access geographic information system (QGIS). The criteria for defining the different areas of study considered their geographical, ecological and material culture coherence. The chrono-cultural framework ([Table 1](#)) was chosen to follow a broadly accepted periodisation [27,28,62,149,153]. The time-span was divided in eight different periods covering *circa* two centuries each, except for the Late Bronze Age (LBA, three centuries) and Late Antiquity (LA, three centuries). These time intervals allowed us to have a sufficient number of sites and data for each period.

In order to look for correlations based on their characteristics, the sites were classified into 14 categories based on their typology, functionality and surface extension following previous works on the topic ([Table 2](#) and [Fig 2](#)). Each site was given a number, and different phases / periods of occupation were distinguished with different letters of the alphabet (e.g. 1a; 1b; 1c, etc. See S1 and S2 in supplementary materials in [S1 File](#)). Contexts with a broad chronological attribution (e.g. 'Iron Age'), or including residual or intrusive materials were also excluded. In total, 127 contexts have been studied.

The corpus of zooarchaeological data for this meta-analysis—82,774 identified remains (see S1 in supplementary materials in [S1 File](#)) and 2,354 unique measurements (see S4 in

supplementary materials in [S4 File](#))—originates both from published works and unpublished reports (grey literature) written more than 10 years ago (2009 or before). New zooarchaeological analyses were also undertaken during the ERC-StG ZooMWest project (ERC-StG 716298) in order to increase the dataset for the periods with less available data (e.g. Late Antiquity). All the assemblages originate only from deposits found in habitat contexts, or non-specialized waste deposits, to reflect specifically the daily use of animal husbandry. Therefore, assemblages from ritual contexts (i.e. sanctuaries, necropolises, temples), animal bone groups (ABGs, special faunal depositions), military settlements, and sites with a seasonal occupation were excluded. In addition, we considered the contextual information available (e.g. taphonomical characteristics) and, as stated above, only the assemblages numbering more than 110 identified main domesticates specimens (cattle, pig, sheep and goat) were included in the analyses.

## 4.2 Quantification units and statistical analyses

The meta-analysis focused on the main domesticates because they constituted, by and large, the main meat source for all analyzed areas and periods according to zooarchaeological data [53]. The units of comparison used were relative frequencies calculated using the number of identified specimens (NISP) of the main domesticates—cattle, sheep, goat, and pig—, and log ratios calculated from biometric data. In order to explore the relations between site typology, site location, and changes in animal husbandry (NISP and biometry) over time, we performed various data visualizations and statistical analyses based on these variables: type of sites, geographical areas, and chronological periods.

NISP was selected as it is generally present in the reports and is more stable than other quantification units such as MNI or MNE [154,155]. The kill-of-patterns provide key information to characterize animal husbandry practices and assess changes through time. Unfortunately, the absence of a standardized way of recording and displaying the information made it impossible to compare and systematize the mortality profiles between different works.

Correspondence analyses (CA) were used to explore i) correlation between site's livestock frequencies, site's types and geographical areas; and ii) similarities between contemporaneous sites (intra-period comparisons). A hierarchical clustering analysis (HCA) based on these results allowed grouping of sites with similar animal consumption profiles. Significance in the observed differences between sites were assessed using Chi-square tests with the 'chisq.test' R native function. The CA algorithm comes from the R package 'FactoMineR' [156]. To avoid size effects, measurement of differences between sites were performed on the normalized values of cattle, pig and sheep/goat (main domesticates) with the 'dist' function of the basic package of R [157]. The HCA agglomeration method was complete (complete-linkage clustering) and performed with the 'hclust' R native function. On these figures, CA and HCA, site types and geographical areas are displayed using different shapes and colors in the symbols, but these variables did not have any effect on the clustering statistics.

Biometric analyses considered osteological size changes of postcranial elements from the main domestic species (sheep/goat, cattle and pig). Biometric data from actual domestic and wild species were also included in the graphs for comparative purposes, particularly to help assess the potential presence of wild individuals (or hybrids) in the archaeological samples. In order to establish the differences and limits between domestic and wild individuals, archaeological wild boars from different sites and periods and biometric data of actual *Capra pyrenaica hispanica* and *Capra pyrenaica pyrenaica* (extinct in January 2000) [158] were included in the graphs (Figs 7 and 8). Modern specimens of *Capra pyrenaica* were used as a comparative reference for zooarchaeological individuals. Consequently, they were both included in the "actual" category. The purpose of including wild goats was to identify if the observed size increase in

the domestic sheep/goats was due to the presence of wild animals in the dataset. In addition, data from individuals from two actual local breeds of sheep and goats—Xisqueta breed sheep and Catalan goat breed—were also included as reference measurements of present-day domestic individuals adapted to the ecology of the areas studied (Figs 7 and 8).

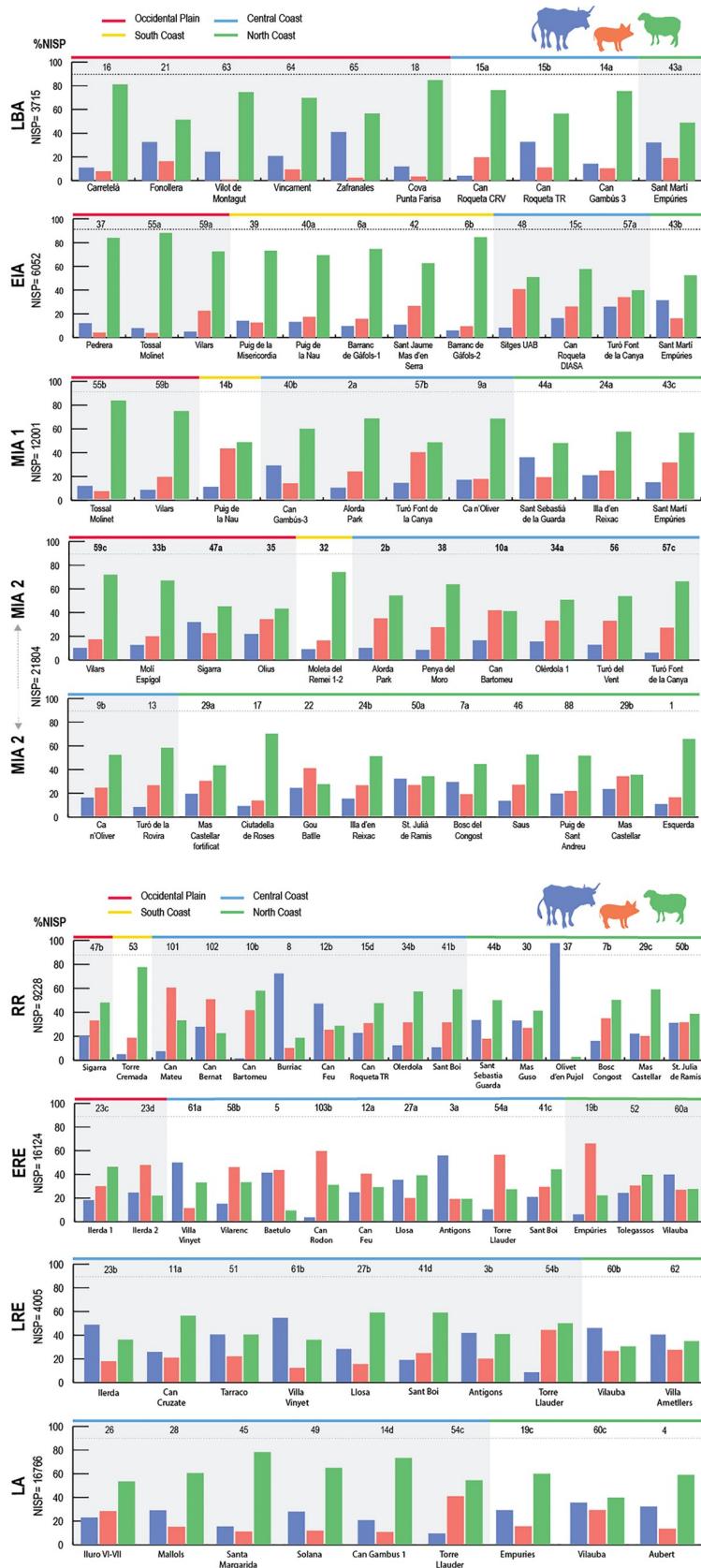
Changes in animal size were assessed using size-index scaled Log standard index values (LSI) [159]. Widely available standards were used for cattle [160], sheep and goats [161], and pigs [162]. The analysis follows the methodology described in Table 1 of [51]. However, in this case the SLC (smallest length of the collum scapulae [163]) was also used as a last option when no other width measurement was available. Differences between osteometrical distributions were assessed using Mann-U tests, with the R native function ‘wilcox.test’ [164], at different levels for each species (cattle, pig, sheep/goat) through periods and between areas.

## 5. Results

### 5.1 Site patterns in livestock ratios through time

During the Late Bronze Age (LBA, 13<sup>th</sup>–9<sup>th</sup> c. BC; Fig 3.1 top), the sites located in the Occidental Plain (OP) display a high frequency of sheep and goat remains (between 57 and 85% of the main domesticates). This is attested in different site types: Open settlements (OS), Closed settlements (CS) and shelters (S). In the Central Coast (CC) and the North Coast (NC) sheep and goats are also predominant (67,8%) but with higher proportions of pig (14,6%) and cattle (17,6%) (Fig 5). Although some sites have profiles that stand from the other sites in their area—e.g. Zafranales (65) from the OP, or Can Gambús 3 (14a) and Can Roqueta CRV (15a) from the CC—, the general trend is a high correlation between area and percentages of species consumed (as shown in Fig 4). The NISP results suggest that in this period the composition of the livestock frequencies are closely related to the location of the site (zone) and not to the settlement type.

During the Early Iron Age (EIA, 8<sup>th</sup>–7<sup>th</sup> c. BC; Fig 3.1) the two fortified stone-built settlements (FS) with NISP data in the OP, La Pedrera (37) and Vilars 0-I (59a), display lower frequencies of cattle remains (12–4,9%) and higher frequencies of sheep and goats (84–72,6%) compared with the LBA sites in the same region. The site of Vilars, the first in which a complex fortification (other than a closing wall) is attested, had a higher frequency of pig remains (22,5%) compared with the two other OP sites. This NISP profile, in which sheep and goats are the most common species, followed by pigs, and then cattle, is also attested at all the fortified stone-built settlements with zooarchaeological data located in the South Coast (SC) as Puig de la Misericordia (39) and Puig de la Nau (40a). The silos (SF) of Sant Martí d'Empúries (43b), in the NC, display a notable continuity with the NISP profiles attested in LBA assemblages of this area. Exploratory analysis showed a significant clustering according to settlement type and livestock ratios, in a moment when there was a greater diversification of the typology of sites (Fig 4). The six different types of settlements with NISP data are associated with different livestock profiles (Fig 4). The scattered villages with *silos*—e.g. Can Roqueta DIASA (15c) and Sitges UAB (48)—and the Aristocratic Residence—Sant Jaume Mas d'en Serrà \_sect. 1 (42)—are strongly correlated with high frequencies of pigs (26–41%) (Fig 3.1). These sites have also in common the important concentrations of colonial imported products from the Mediterranean. Another subgroup within the previous one (see Fig 4), are the silo fields—Turó Font de la Canya 0 (57a) and Sant Martí d'Empúries (43b)—, which are strongly correlated with cattle (26–33,3%) (Fig 3.1). Another big group aggregates the open settlements—e.g. Tossal del Molinet I-II (55a) and Barranc de Gàfols 2 (6b)—which have a great continuity with the previous period, with higher proportions of sheep/goats (88,2–83,3%) (Fig 3.1). Finally, the fortified settlements (with more complex urbanism) have pig frequencies between 10–20%—e.g. Puig de la Misericordia (39), Puig de la Nau (40a), and Vilars 0-I (59a).



**Fig 3. 3.1. NISP percentages histograms of main domesticates** (cattle, pig and sheep/goat) by site and periods (LBA: Late Bronze Age, EIA: Early Iron Age, MIA1: Middle Iron Age 1, MIA2: Middle Iron Age 2). Numbers of sites refer to [Fig 2. 3.2 NISP percentages histograms of main domesticates](#) (cattle, pig and sheep/goat) grouped by sites and ordered by periods (RR: Roman Republic, ERE: Early Roman Empire, LRE: Late Roman Empire, LA: Late Antiquity). Numbers of sites refer to [Fig 2](#).

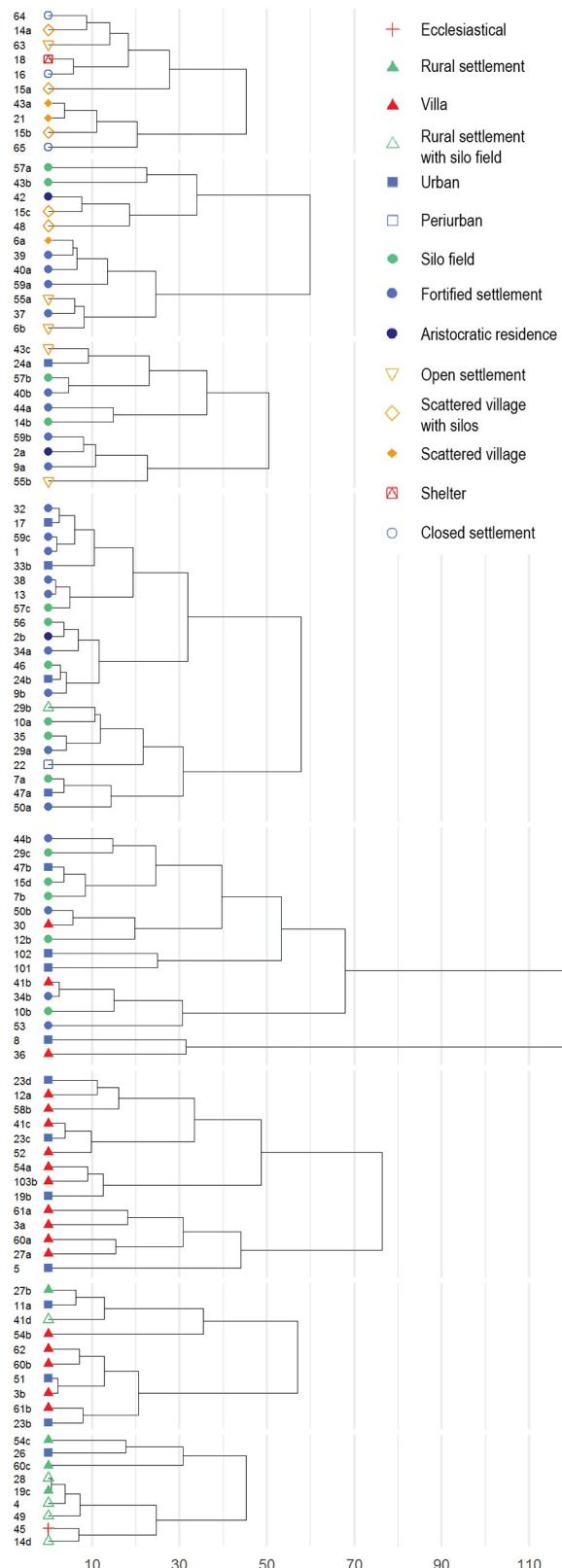
<https://doi.org/10.1371/journal.pone.0246201.g003>

In the **Middle Iron Age 1** (MIA 1, 6<sup>th</sup>–5<sup>th</sup> c. BC), the two sites—Tossal del Molinet (55b) and Vilars 59b—available for the OP continued with the same NISP distribution they had in EIA levels ([Fig 3.1](#)). Puig de la Nau (40b), the only site with NISP data in the SC, also has a profile where sheep and goats predominate (48%) followed by pigs (42%) and then cattle (10%). This 'staircase' pattern is also attested at most stone-built sites located in the OP and CC—fortified settlements like Ca n'Oliver (9a) and Vilars II (59b), and aristocratic residences like Alorda Park 2a (2a)—, with the exception of Can Gambús 3 (14b) ([Fig 3.1](#)). In the NC, the fortified settlement of St. Sebastià de la Guarda (44a) displays the 'U-shaped' pattern characteristic of the LBA assemblages in the area, with abundant cattle and sheep/goats (49,6%) and few pigs (17,4%), while the other two fortified settlements have 'staircase' pattern NISP distributions, in which sheep/goats are followed by pigs and then cattle. We recall here that this was the time when a real hierarchy between settlements is attested in the region. Unlike the previous period, no correlation between the livestock ratios and the ecological zones or site typology could be identified ([Fig 4](#)). At the same time, the differences in livestock ratios between sites are less apparent, thus suggesting a slight process of homogenization of the zooarchaeological records.

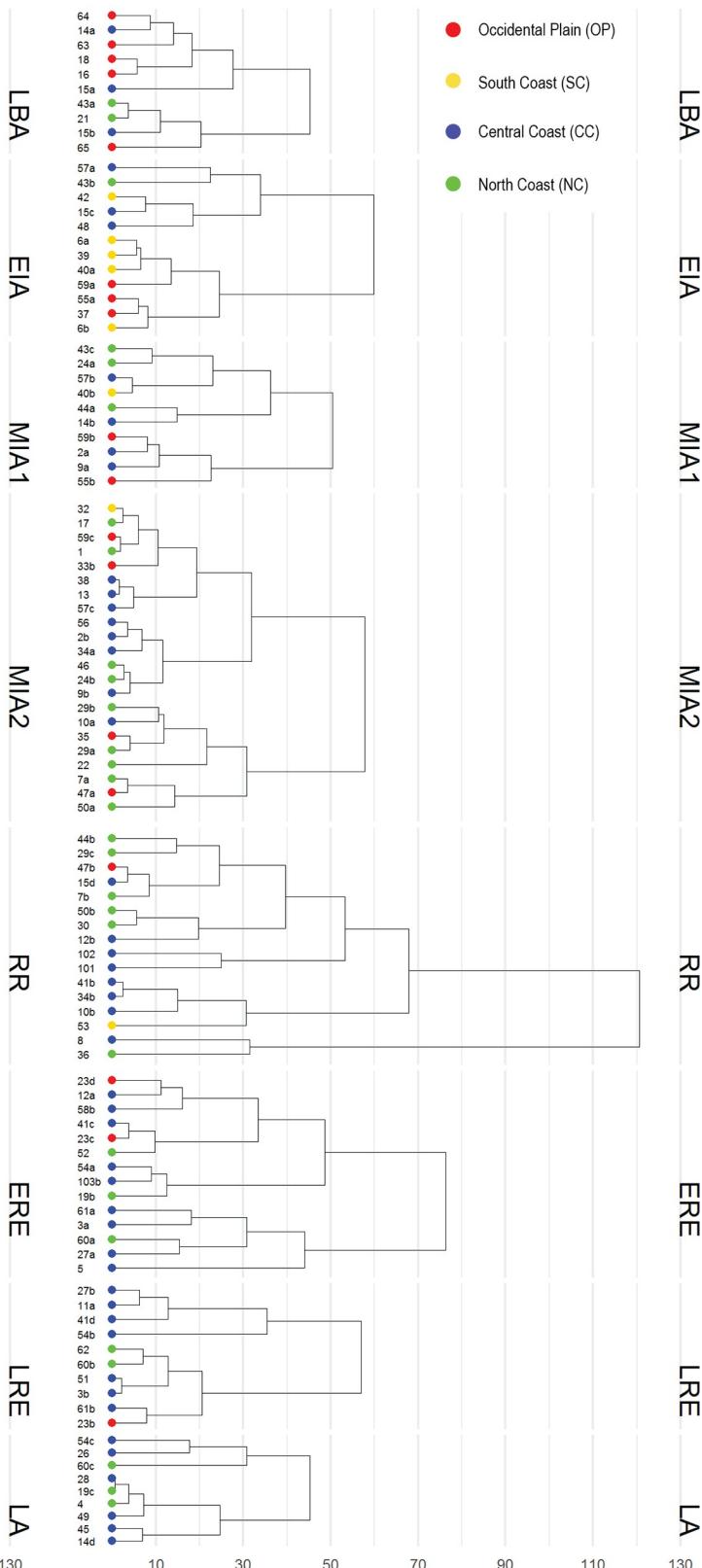
During the **Middle Iron Age 2** (MIA 2, 4<sup>th</sup>–3<sup>rd</sup> c. BC) two sites in the east of the OP—Olius (35) and Sigarra (47a)—display cattle frequencies over 20%, in contrast with the other two sites available further west in this area—Molí d'Espígol (33b), Vilars III-IV (59c)—, which display the 'staircase' pattern ([Fig 3.1](#)). This NISP 'staircase' pattern is also found in the two sites available in the SC—Penya del Moro (38), Moleta del Remei (32)—and across most sites in the Central Coast, no matter their extent or characteristics. Only the assemblages coming from some *silos* in Can Bartomeu (10a) ([Fig 3.1](#), penultimate row) have NISP profiles that slightly differ from the rest. In the NC, the faunal assemblages have a higher degree of diversity. The peri-urban houses of Gou Batle (22) stand because of the predominance of pig remains (44,3%). Several sites display the 'staircase' pattern while two sites—the fortified settlement of Sant Julià de Ramis (50a) and the *silos* of Bosc del Congost (7a)—had the 'U-shaped' pattern commonly found during the LBA. In this area, cattle frequencies are generally higher (over 20%) compared with the sites located in the CC and the SC. The NISP profiles of first-order cities—like Molí d'Espígol (33b), Illa d'En Reixach (24b) or Puig de Sant Andreu (88)—are not correlated one to another, but are similar to silo fields and other fortified settlements ([Fig 4](#)). From the end of the 4<sup>th</sup> c. BC there was a greater diversification and hierarchization between sites, and this contrasts with the homogeneity and the predominance of the 'staircase' pattern at most sites ([Fig 3.1](#) final two rows). The short length of the dendrogram's branches ([Fig 4](#)) shows that the differences between sites are very small, and suggests a process of homogeneity or generalization of similar dietary practices.

The **Roman Republican** period (RR, 218–27 BC) displays a different and much more diversified picture ([Fig 3.2](#), top). Many changes took place between the middle of the 2<sup>nd</sup> c. BC and the 1<sup>st</sup> c. BC, as it coincided with the Roman conquest (RR) and the progressive disappearance of the Iberian system of *oppida*, that was replaced by the Roman system of the *villae* (V). The long length of the dendrogram's branches, the widest of all the periods, shows that the differences in livestock patterns between sites were very high ([Fig 4](#)). Several sites from the OP, the SC and the CC have the 'staircase' pattern characteristic of the Middle Iron Age. They include newly built sites—e.g. Torre Cremada (53), Sant Boi\_Pl. Constitució (41b)—and others

## Type of sites



## Ecological zones



**Fig 4. Hierarchical clustering analysis (HCA) of sites' NISP profiles ordered by periods.** (LBA: Late Bronze Age, EIA: Early Iron Age, MIA1: Middle Iron Age 1, MIA2: Middle Iron Age 2, RR: Roman Republic, ERE: Early Roman Empire, LRE: Late Roman Empire, LA: Late Antiquity). Numbers of sites refer to Fig 2. Dendograms are identical except for site labelling: HCA left aligned shows symbols of sites' types (see Fig 2). HCA right aligned shows symbols of sites' geographical zones (see Fig 1).

<https://doi.org/10.1371/journal.pone.0246201.g004>

previously inhabited—e.g. Sigarra (47b), Olèrdola (34b), Can Roqueta TR (15d). In contrast, cattle remains predominate on two sites in the CC with a previous occupation—Can Feu (12b) (46,7%) and Burriac (8) (72%)—, and pig is the most represented species at two newly built sites in the same area—Can Bernat (102) (50,5%) and Can Mateu (101) (60,2%). In the NC, cattle frequencies are generally over 20%, and some sites display the 'U-shape' pattern in which caprines and cattle constitute the majority of faunal remains (Fig 3.2, top). The diversity in the NISP profiles shows an important heterogeneity between geographical areas and types of sites (Fig 4).

The assemblages dated from the **Early Roman Empire** (ERE, 27 BC–AD 250; Fig 3.2) also have a notable diversity. There is a hierarchical and differentiated NISP distribution according to site type, with an important dichotomy between the *villae* and urban sites.

A first large group is attested with three related subgroups within Fig 4. A first subgroup, formed by two assemblages—the city of *Ilerda 1\_Carrer Magdalena 47* (23c) in the OP, Sant Boi-Plaça Constitució (41c) in the CC and the *villa* of Tolegassos (52) in the NC—have NISP profiles similar to the 'staircase' pattern of the Iron Age, although with lower values of caprines (about 40%). A second one groups the *villae* of Vilarenc (58b) and Can Feu (12a) in the CC, and another set of the city of *Ilerda 2\_Carrer Bafart 46* (23d). This second subgroup is characterized by a higher percentage of pigs (about 40%) and lower frequencies of caprines (about 30%) compared with the first subgroup. The third subgroup counts the richer *villae* of Can Rodon (103b) and Torre Llauder (54a) in CC, and the city of Empúries (19b) in NC. This subgroup is also characterized by high percentages of pigs (60–70%) and very low percentages of cattle (below 10%).

A second large group is formed, firstly, by the *villae* of Vinyet (61a), Antigons waste dump (3a) and La Llosa (27a) in the CC, and Vilauba (60a) in NC. It is composed of two subgroups correlated with high percentages of cattle (between 40–60%). Finally, the city of Baetulo (5), the main urban site of the area, has a different profile characterized by lower percentages of sheep/goats (c. 10%), and a balance between pigs and cattle (c. 40%).

Although there seems to be quite a lot of diversity, there are some general patterns (Fig 3.2). The tendencies observed on NISP frequencies show that some *villae*—e.g. Can Rodon (103b), Vilarenc (58b), Can Feu (12a)—, cities—Empúries (19b)—, and the rich *domus* of Torre Llauder (54b) (also located in an urban context)—have high pig frequencies (c. 60–70%). The cities of Baetulo (5) and *Ilerda* (23c, 23d) also present high values of pig remains, although in smaller percentages (36–46%). Other *villae* have lower percentages of pig (10–28%) and are strongly correlated with cattle—e.g. La Llosa (27a), Vilauba (60a), Vinyet (61a), Antigons\_waste dump (3a), and Tolegassos (52).

The picture changed again during **Late Roman period** (LRE, AD 250–472). Three groups are observed according to livestock frequencies during this period. A first subgroup presents very homogeneous profiles, with six out of the ten assemblages displaying a 'U-shape' pattern in which cattle remains predominate over caprines or have similar frequencies (Fig 3.2, center-bottom). This is the case of the urban sites of Ilerda (23b) in OP and Tarraco (51) in CC, as well as the *villae* of Antigons\_Nymphaeum (3b), Vinyet (61b), Vilauba (60b) and Ametllers (62). Other two *villae*—Can Cruzate (11a) and La Llosa (27b)—also have a 'U-shape' profile but with a greater predominance of caprine remains (55–57,7%). The rural settlement of Sant Boi (41c) displays the 'staircase' profile. Finally, the *villa* of Torre Llauder (54b) preserved a high

frequency of pig remains (over 40% NISP), although surpassed by caprines, which significantly differentiates its profile from the rest of the sites. For the first time, some *villae* and urban contexts had profiles where sheep/goats are clearly the most frequent species (between 40–60%), and there was a drastic decline of pigs in all of them.

The assemblages available from **Late Antiquity** (LA, AD 472–711) are all located in the CC and the NC ([Fig 3.2](#), bottom). New rural settlements appear at this time, which coexist with the last Roman cities and *villae*. These newly created settlements have a totally different architecture and are characterized by NISP profiles with a higher predominance of sheep/goats (40–70%) followed by cattle (14–27%). Most sites—six out of nine, sites 28 to 14d in [Fig 4](#)—form a subgroup with very homogeneous NISP profiles, characterized by the predominance of caprine remains (57,9–70,2%), followed by cattle (10,1–27,7%) and then pigs (10,1–14,4%) ([Fig 4](#)). These sites have livestock ratios similar to those attested in LBA and EIA assemblages. On the other hand, the ancient *villae* of Torre Llauder (54c) in CC and Vilauba (60c) in NC display similar profiles compared to their Late Roman levels, but with an increase of caprine remains (38–52%) in both cases. In this sense, these *villae* and the city of Iluro VI–VII (26) display a pattern of consumption similar to Roman times, with high percentages of pig remains (27,1%) ([Fig 3.2](#), bottom).

## 5.2 Regional patterns in livestock ratios through time

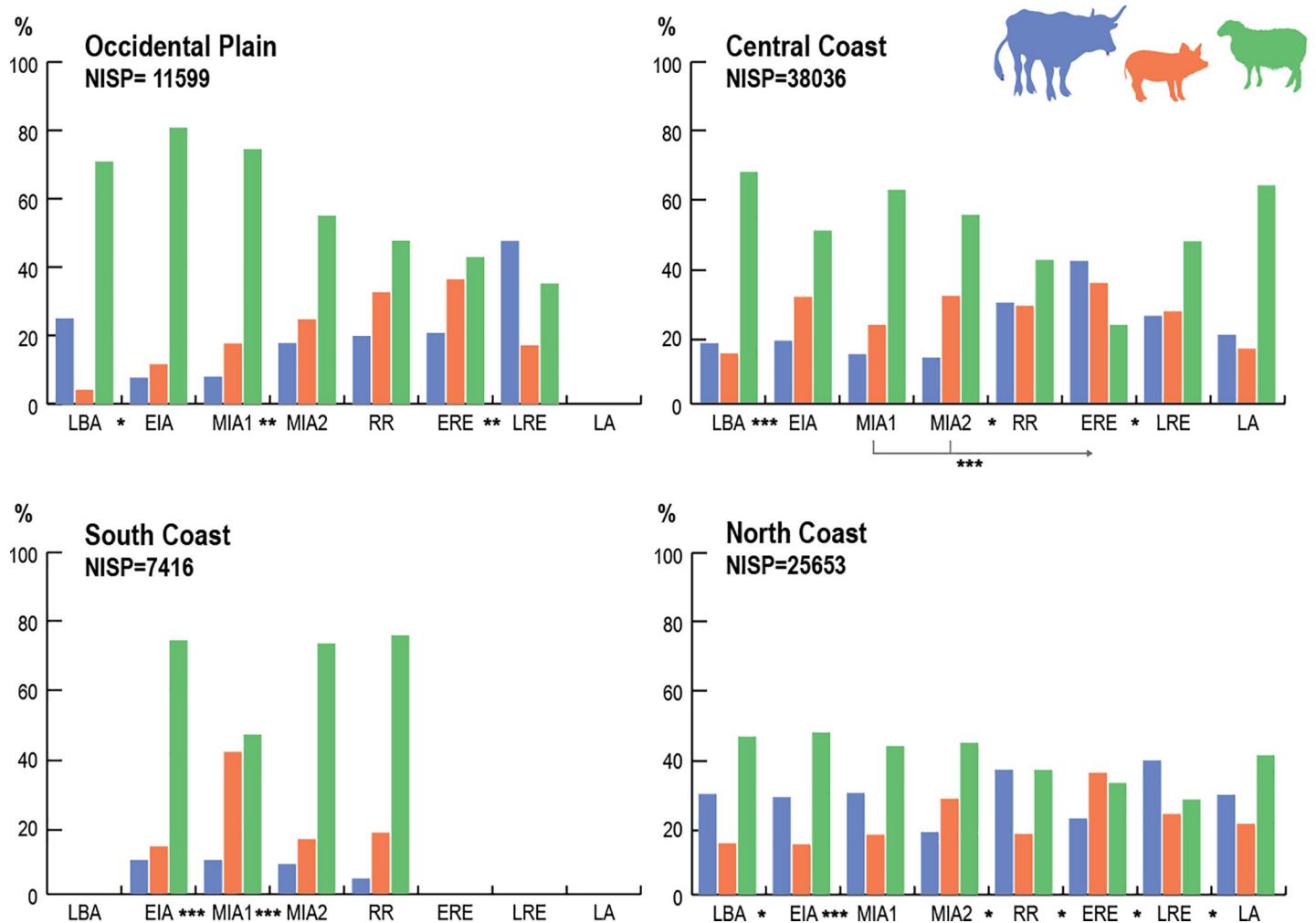
Meta-analysis of NISP data for taxon abundance of the main domesticates ([S3 File](#)) suggests that livestock representation varied significantly between regions and time periods. [Fig 5](#) displays the trends obtained from aggregating the different sites available in each area and period.

Sheep/goats generally predominate in all areas and periods, but significant differences across time and space exist. The sites located in the **Occidental Plain (OP)** and **South Coast (SC)** are strongly correlated with sheep and goats compared with the other areas ([Fig 6](#)). In the OP, changes in the livestock ratios occurred more progressively compared to coastal zones. Correspondence analysis ([Fig 6](#)) indicates that the **Central Coast (CC)** mostly correlates with pig and sheep and goat remains. The most pronounced diachronic changes occur in this area. Conversely, the **North Coast (NC)** displays the most stable trend through time ([Fig 5](#)). This last area shows a strong correlation with cattle, except for the Middle Iron Age (MIA) and Early Roman Empire (ERE), when it had a higher percentage of pigs, like the other areas.

This inter-regional comparison ([Fig 6](#)) showed that each area kept these peculiarities during most periods, showing significant differences between them. Only during MIA2 did these differences seem to disappear or soften (see also [Fig 4](#)). In Roman times, and despite local differences, all areas display a greater proportion of pigs and a drastic decrease in sheep/goat frequencies.

## 5.3 Variables of homogeneity/diversity in livestock ratios

Exploratory and descriptive statistics ([Fig 4](#)) on NISP over these periods show two main husbandry systems (Iron Age and Roman) framed by transitional stages (LBA, RR, LA). The whole Iron Age showed a strong correlation with sheep and goats, while all areas are strongly correlated with pigs and cattle during the Roman period ([Fig 5](#)). At the site level, the initial diversity between sites observed in LBA and EIA assemblages was progressively reduced during the MIA ([Figs 3 and 6](#)). In Roman times, there was a higher diversity between sites, coherent with the greater diversity and specialization of settlement types (i.e. urban contexts vs. *villae*). Interestingly, the transitional period between these two different socio-political systems (RR), marked by the Roman conquest, displays the highest degree of diversity between zones and sites.



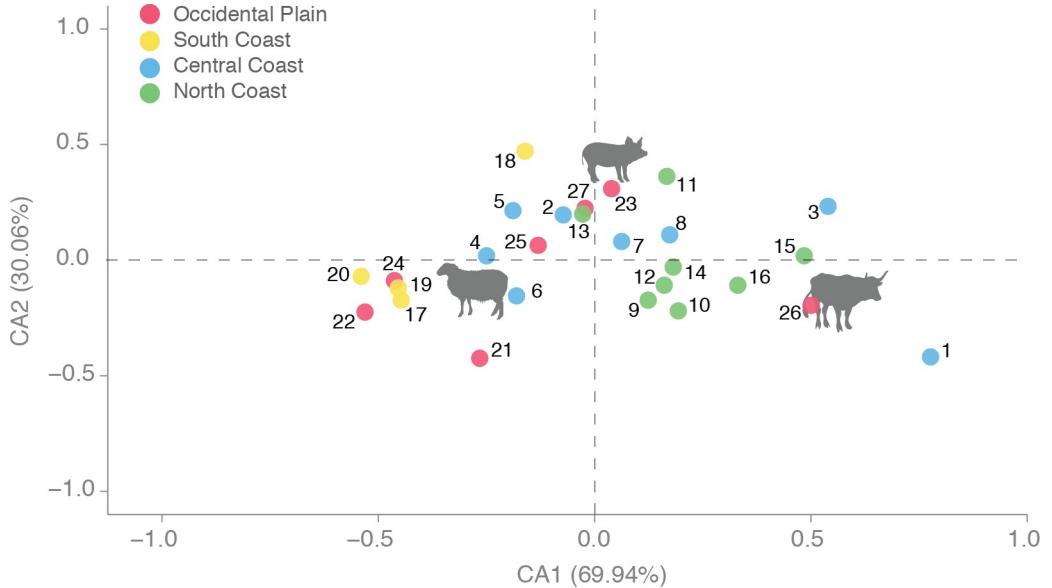
**Fig 5.** NISP percents of main domesticates (cattle, pig and sheep/goat) grouped by zones and ordered by periods. (LBA: Late Bronze Age, EIA: Early Iron Age, MIA1: Middle Iron Age 1, MIA2: Middle Iron Age 2, RR: Roman Republic, ERE: Early Roman Empire, LRE: Late Roman Empire, LA: Late Antiquity). Chi-square results showing significant changes between periods are displayed with their *p*-value: \*\*\*: highly significant (< 0.01); \*\*: significant (< 0.05); \* less significant (< 0.1).

<https://doi.org/10.1371/journal.pone.0246201.g005>

#### 5.4 Changes in animal size through time

Analysis of livestock biometry was based on 2354 (557 lengths and 1797 widths) unique post-cranial measurements (see S4 File). Figs 7 and 8 present LSI values by species, region and period, and Figs 9–11 show LSI values for each species at site level and period. Sheep and goat measurements were considered separately, plotted with different colors as similar trends, both on lengths and widths, and no significant differences were found between these two species (see S5 File). Full statistical results on the temporal variation of size are available in S6 File (table Mann-Whitney). In general terms, the number of available length measurements was very uneven between areas and periods, especially for CS and NC. Even so, our data were sufficient to highlight some general trends, which are presented below.

**5.4.1 Availability of biometric data and regional patterns.** In some cases, the availability of biometric data is uneven depending on the type of measurement, the area, or the species. There were a lower number of effective lengths with respect to widths in all species. The pig was the most underrepresented species with regard to biometric data, especially in the area of OP and SC. Few studies have been done in the SC so far, which affected all main domestic



**Fig 6. Correspondence Analysis (CA) on main domesticates NISP (cattle, pig and sheep/goat) grouped by periods and zones (i.e. statistical individuals).** Symbol colors refer to the geographical zones (see Fig 1): Occidental Plain (red points), South Coast (yellow points), Central Coast (blue points), North Coast (green points). Main domestic species (i.e. statistical variables) are represented by their animal shape. Numbers refer to zones and periods: 1. CC-LBA; 2. CC-EIA; 3. CC-ERE; 4. CC-MIA1; 5. CC-MIA2; 6. CC-LA; 7. CC-ERE; 8. CC-RR; 9. NC-LBA; 10. NC-EIA; 11. NC-ERE; 12. NC-MIA1; 13. NC-MIA2; 14. NC-LA; 15. NC-LRE; 16. NC-RR; 17. SC-EIA; 18. SC-MIA1; 19. SC-MIA2; 20. SC-RR; 21. OP-LBA; 22. OP-EIA; 23. OP-ERE; 24. OP-MIA1; 25. OP-MIA2; 26. OP-LRE; 27. PO-RR.

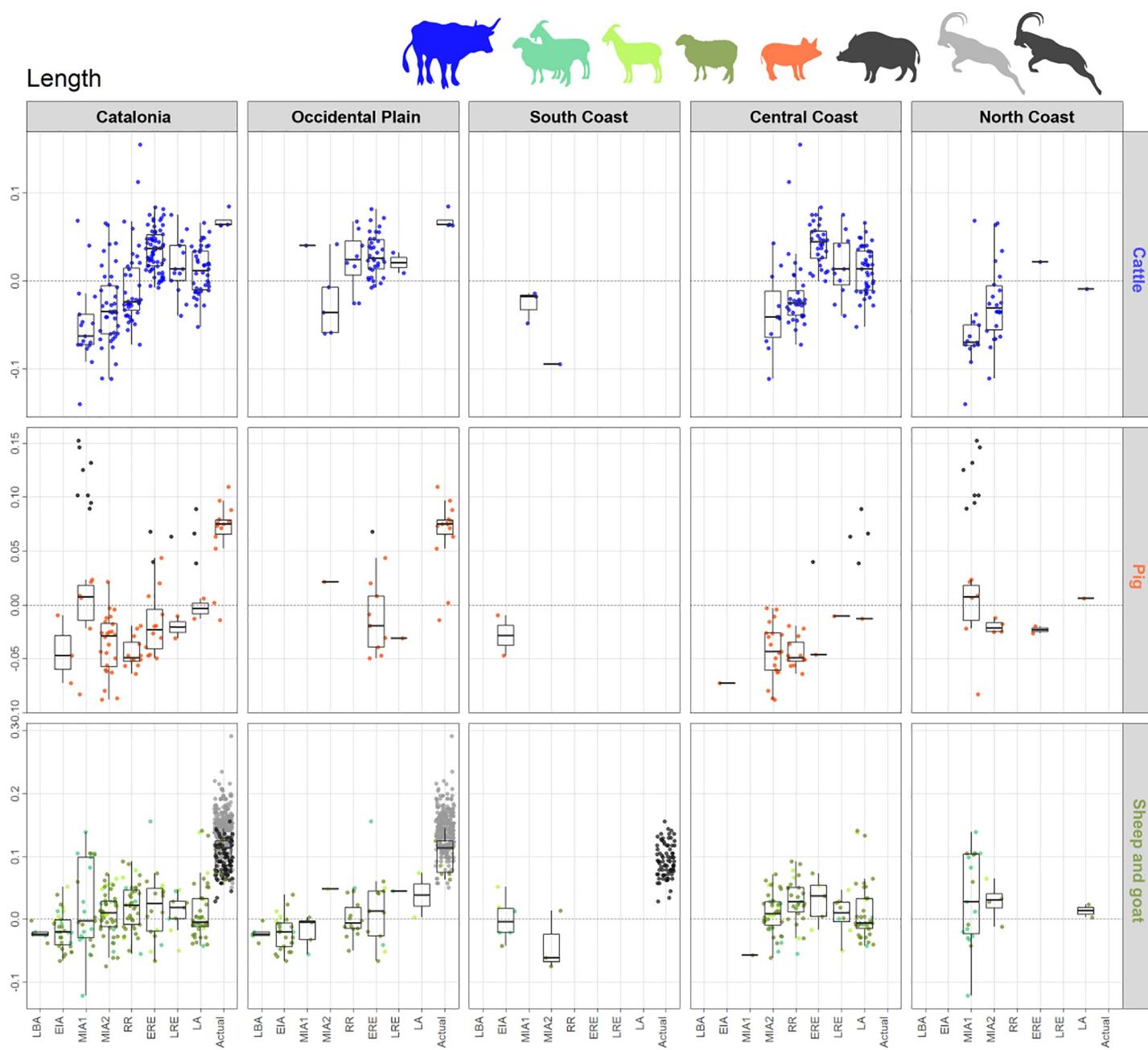
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species; here we simply included the currently accessible data so that it is recorded. Also for pigs, the protohistoric periods have many more gaps, in all areas, compared to the Roman periods (Figs 7 and 8): a fact which is due to the greater availability of pig remains in this moment. For cattle we have few lengths and widths in the case of the NC, and some small gaps in the case of the OP and the CC. Regarding sheep/goats there are some similar limitations to those of cattle, with large gaps for lengths in the NC, as well as for protohistoric periods in CC. However, a large set of width measurements helps to counteract these gaps.

Comparisons between zones show the first significant differences in **cattle** LSI values (for all statistical results see S7 in supplementary materials [S7 File](#)) occurring in the RR period, for both widths ( $p = 0.000$ ) and lengths ( $p = 0.005$ ). This difference is due to the presence of larger individuals in OP (see Figs 7 and 8). The same trend is observed in cattle width LSI values during LRE ( $p = 0.043$ ).

On the other hand, intra-period analysis shows significant differences in LSI values from **sheep/goats** bone widths between OP and CC during EIA ( $p = 0.041$ , higher medians in CC), NC and CC in MIA1 ( $p = 0.004$ , higher medians in NC), SC and all other areas in MIA2. This latter difference is due to the low median in SC (Fig 8). During RR the sheep/goat biometric analysis shows a substantial difference between OP and CC in lengths ( $p = 0.017$ ) due to the presence of larger individuals in CC (Fig 7). It should be noted the largest sheep/goat that appeared in NC during MIA1, with lengths equivalent to those of wild goats and domestic sheep and goats from the same area (Fig 7). The LSI values from **pig** bone widths only showed significant differences between OP and NC during MIA2 ( $p = 0.016$ ); in this latter case, the difference can be related to the lack of biometric data for this species.

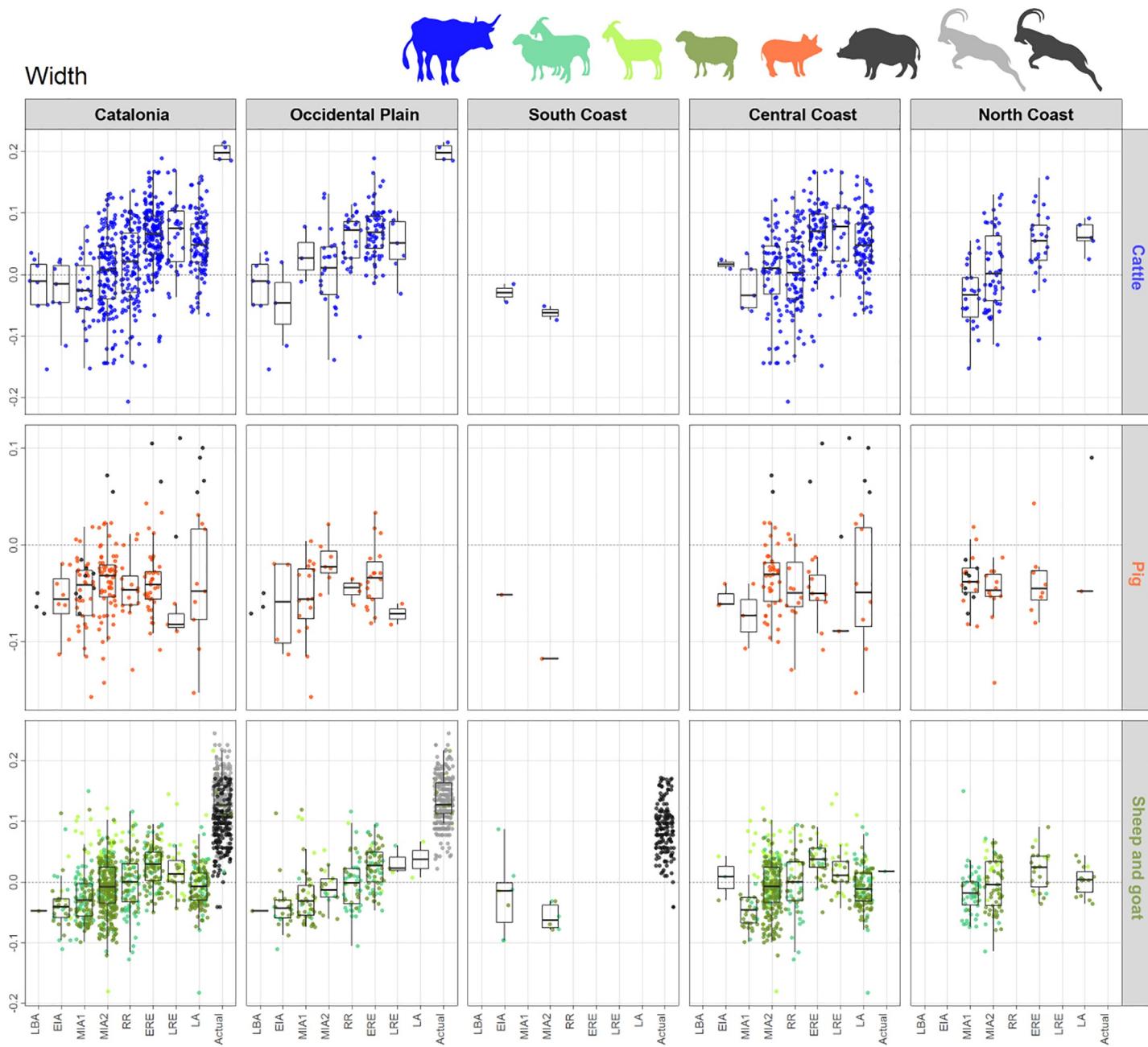
**5.4.2 Diachronic change by zone.** *Cattle.* At a regional scale, cattle LSI values indicate a general cattle size increase from MIA1 up to ERE, followed by a size decrease during the Late



**Fig 7. Length LSI values distribution diagram of cattle, pig and sheep/goat bones, by species (in rows) and geographical areas (in columns).** Sheep and goats were considered together (see text for details). For each cell of the diagram, LSI values are displayed on the y-axis and chronological periods on the x-axis: LBA: Late Bronze Age, EIA: Early Iron Age, MIA1: Middle Iron Age 1, MIA2: Middle Iron Age 2, RR: Roman Republic, ERE: Early Roman Empire, LRE: Late Roman Empire, LA: Late Antiquity. Box plots quartiles measures only represent statistics on main domesticates, i.e. wild individuals values are displayed but excluded from statistics. Wild individuals: wild boar (black points), actual *Capra pyrenaica hispanica* (black points), modern *Capra pyrenaica pyrenaica* (grey points) [15]; actual Xisqueta breed sheep and Catalan goat breed.

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Roman and Late Antiquity phases (LRE and LA), both in lengths and widths (Figs 7 and 8). In the OP, the only length measurement available for MIA1 attests the presence of at least one large individual of a similar height to the ones recorded in Roman times, which contrasts with the three measurements available for MIA2, all notably smaller. The median value of the LSI lengths and widths increased significantly during RR compared to MIA2 (Figs 7 and 8). For all



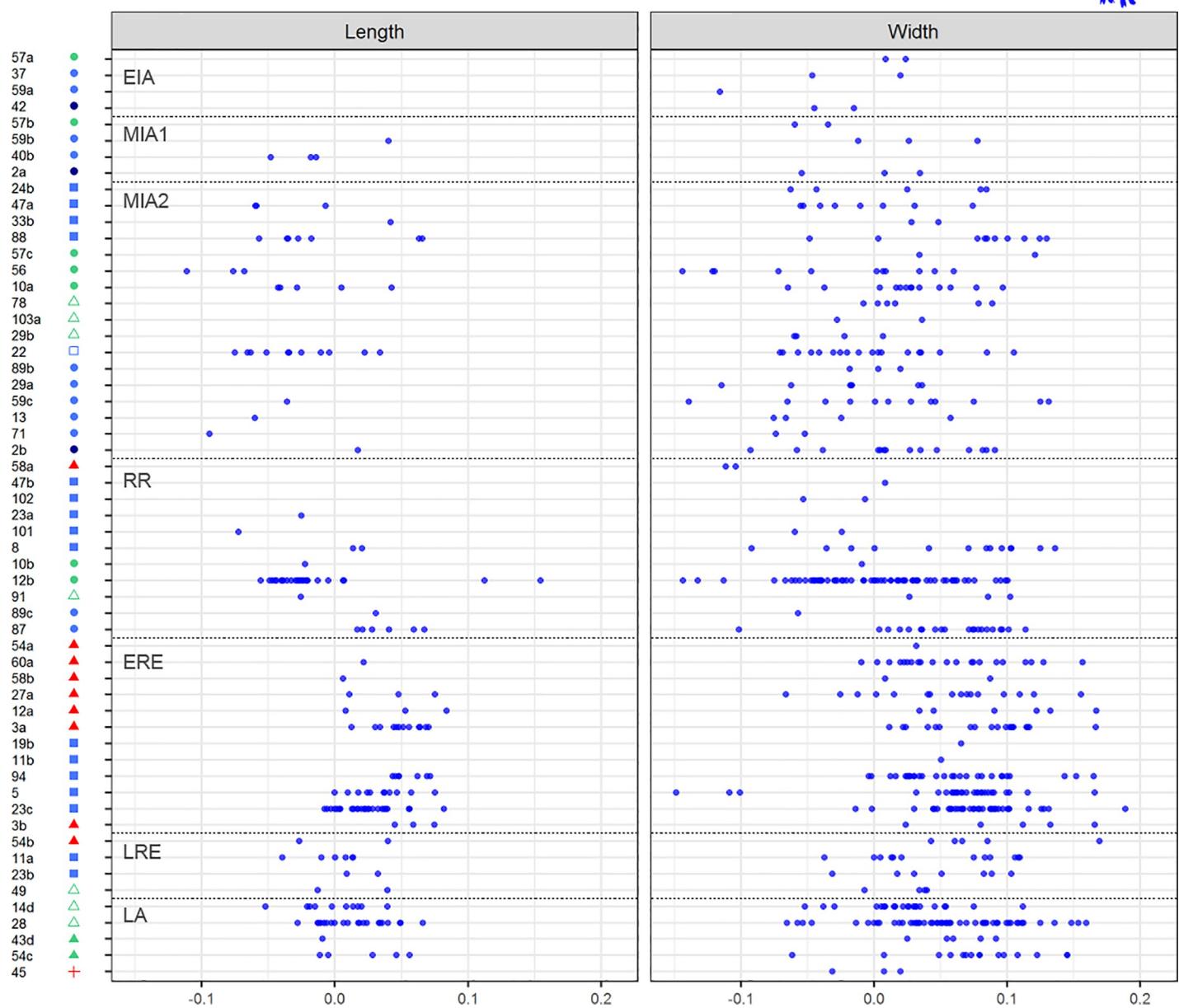
**Fig 8. Width LSI values distribution diagram of cattle, pig and sheep/goat bones, by species (in rows) and geographical areas (in columns).** Sheep and goats are considered together. For each cell of the diagram, LSI values are displayed on the y-axis and chronological periods on the x-axis: LBA: Late Bronze Age, EIA: Early Iron Age, MIA1: Middle Iron Age 1, MIA2: Middle Iron Age 2, RR: Roman Republic, ERE: Early Roman Empire, LRE: Late Roman Empire, LA: Late Antiquity. Boxplots quartiles measures only represent statistics on main domestic, i.e. wild individuals values are displayed but excluded from statistics. Wild individuals: wild boar (black points), actual *Capra pyrenaica hispanica* (black points), modern *Capra pyrenaica pyrenaica* (grey points) [15]; actual Xisqueta breed sheep and Catalan goat breed.

<https://doi.org/10.1371/journal.pone.0246201.g008>

statistical results see S5 in supplementary materials in [S5 File](#)). No significant changes were found between the different Roman periods in the OP. In the CC, no significant differences in width LSI values were found between MIA2–RR ( $p = 0.191$ ), but two extraordinarily large individuals in RR are attested. A greater diachronic variability was visible during Roman times in both lengths ( $p = 0.000$ ) and widths ( $p = 0.000$ ), together with a height increase between



## Cattle



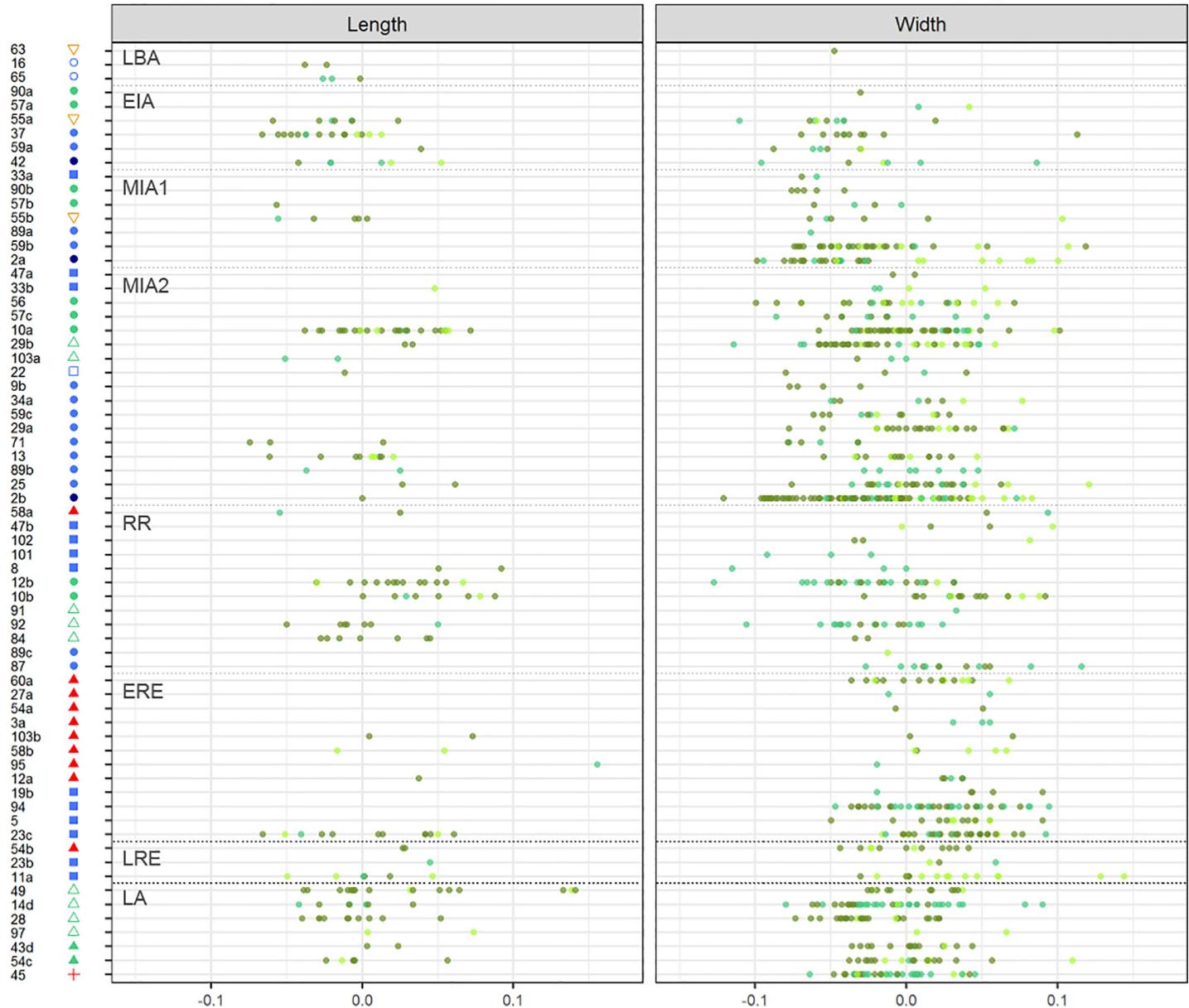
**Fig 9.** Cattle LSI length and width values by assemblages ordered by periods. (from top to bottom, EIA: Early Iron Age, MIA1: Middle Iron Age 1, MIA2: Middle Iron Age 2, RR: Roman Republic, ERE: Early Roman Empire, LRE: Late Roman Empire, LA: Late Antiquity). Left column shows length LSI values, right column shows width LSI values. Assemblages' symbols refer to their type (see Fig 2).

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RR–ERE. In contrast, the length values from LRE are significantly smaller than ERE ones ( $p = 0.034$ ). Subsequent size decrease in LA (not significant) is attested on width values ( $p = 0.119$ ). Published data for the NC are scarcer, but the available ones showed that there was a size increase between MIA1–MIA2, both in lengths ( $p = 0.005$ ) and widths ( $p = 0.01$ ), suggesting that during MIA2 there were some large individuals comparable to those from OP and CC during Roman times. The presence of large individuals contrasts with the short cattle attested in the other areas during MIA2.



## Sheep and goat



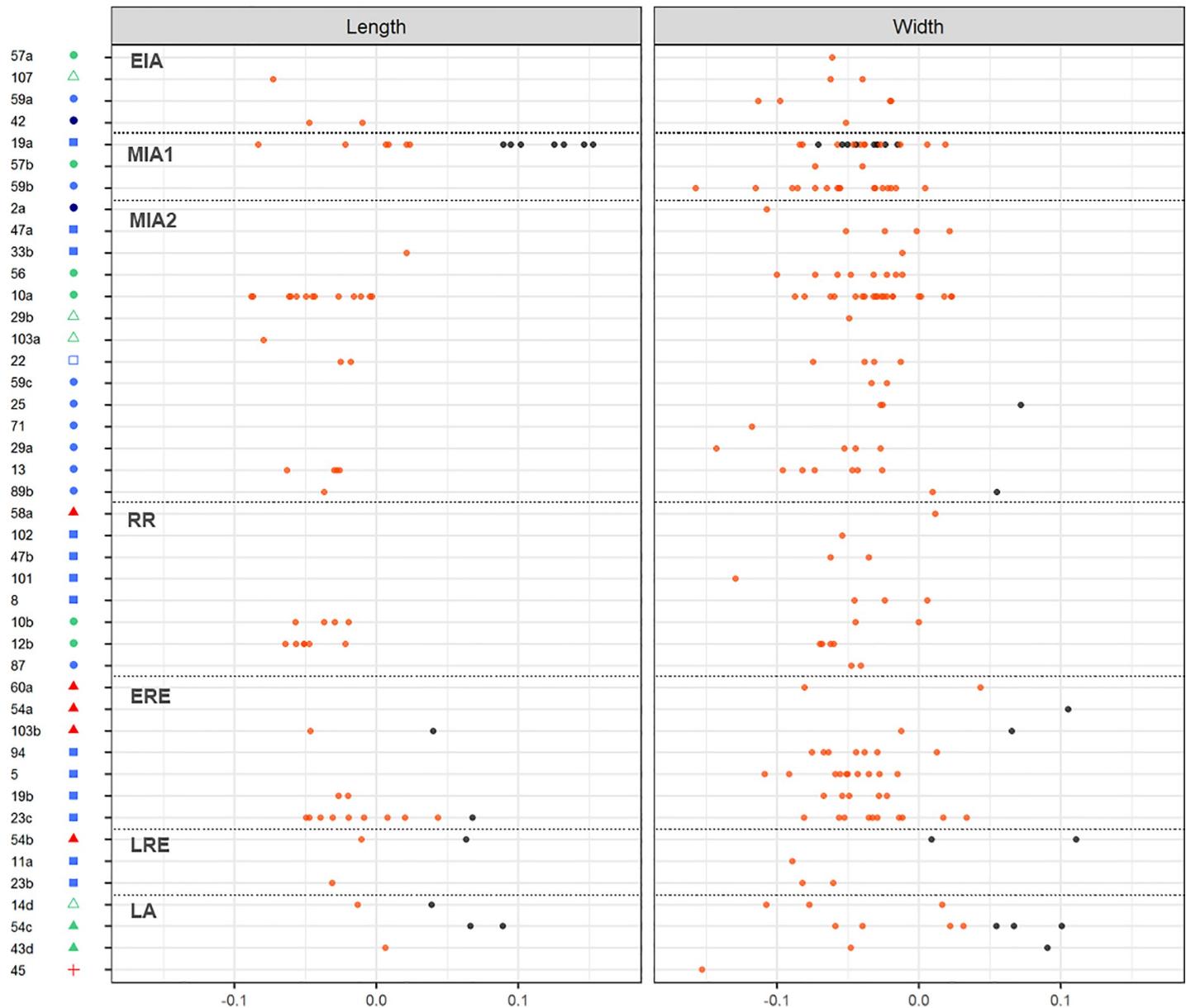
**Fig 10. Sheep and goats LSI length and width values by assemblages ordered by periods.** (from top to bottom, LBA: Late Bronze Age, EIA: Early Iron Age, MIA1: Middle Iron Age 1, MIA2: Middle Iron Age 2, RR: Roman Republic, ERE: Early Roman Empire, LRE: Late Roman Empire, LA: Late Antiquity). Left column shows length LSI values, right column shows width LSI values. Assemblages' symbols refer to their type (see Fig 2).

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**Sheep and goats.** Sheep and goats increased in size from the LBA to ERE, both in lengths and widths (Figs 7 and 8) followed by a size decrease during LA (Figs 7 and 8). For all statistical results see S5 in supplementary material in [S5 File](#). Considering the different areas, an increase in the animals' height is observed between MIA2–RR in the CC ( $p = 0.015$ ) followed by a progressive decrease in widths during Roman times, and even more in LA. Width values also reflected a rapid growth from MIA1 to MIA2 ( $p = 0.039$ ). The maximum median is



## Pig and Wild board



**Fig 11. Pigs LSI length and width values by assemblages ordered by periods.** (from top to bottom, EIA: Early Iron Age, MIA1: Middle Iron Age 1, MIA2: Middle Iron Age 2, RR: Roman Republic, ERE: Early Roman Empire, LRE: Late Roman Empire, LA: Late Antiquity). Left column shows length LSI values, right column shows width LSI values. Assemblages' symbols refer to their type (see Fig 2).

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attested during ERE, both on lengths and widths, and there was a subsequent size decrease from LRE to LA, most notably in widths ( $p = 0.001$ ). In the OP, the median values show a progressive increase since LBA with a statistically significant difference between EIA and ERE for both lengths ( $p = 0.032$ ) and widths ( $p = 0.000$ ) (Figs 7 and 8). There are fewer data from the NC, but the width results suggest that there were no major differences between MIA1 and MIA2. In ERE, sheep and goats were significantly larger (or more robust) compared to Iron

Age ones ( $p = 0.000$  for MIA 1,  $p = 0.02$  for MIA2). There is also evidence of a decrease in widths between ERE and LA (not significant,  $p = 0.11$ ).

*Pig.* The LSI values from pig bone lengths (Figs 7 and 8. For all statistical results see S5 in supplementary material [S5 File](#)) do not reveal diachronic differences in any area, possibly due to the scarcity of data. LSI values from bone widths reveal a significant increase in size between MIA1–MIA2 in both CC ( $p = 0.083$ ) and OP ( $p = 0.033$ ). Unlike the other areas, **the OP** shows a significant decrease in pigs width between MIA2–RR ( $p = 0.042$ ) that also occurred between ERE–LRE ( $p = 0.088$ , although there were few measures for LRE). In **the NC**, more data are necessary to draw any conclusion, but the data available for widths suggest that there were no significant changes in pig size between MIA and Roman times, as very stable median values are attested.

### 5.5 Changes in animal size by site type and period

The distribution of the LSI values from the main domesticates, according to the type of site in diachrony, shows that the general changes observed in the different zones (Figs 7 and 8) occurred in all the sites in a similar way, regardless of their typology (Figs 9–11). Only some sites stand out with some peculiarities, especially during the Iron Age (EIA and MIA) and Roman times (RR to LRE).

In MIA2, some sites of different typologies and located in different areas—i.e. Puig de Sant Andreu (88), Gou Batlle (22), Turó Font de la Canya (57c) and Vilars III-IV (59c)—stand out because of the presence of cattle individuals with large widths. Very large cattle lengths are also attested at Puig de Sant Andreu (88). Conversely, no differences in sheep/goats or pigs sizes are attested at those sites during MIA.

During the RR, some sites have LSI cattle bone lengths similar to those of the Iron Age, while others reveal the presence of much larger cattle—e.g. Burriac (8) in CC and Puig Castellar de Biosca (87) in OP. During ERE, a generalized cattle size increase is attested, and especially large cattle are recorded both in *villae* and in urban contexts (Fig 9).

The sheep and goat measurements dated to RR seem to be smaller in rural settlements with *silos* at OP–Rosella (84) and Missatges (92)—compared to other sites types close to them—e.g. Puig Castellar de Biosca (87)—and the coast silo fields at CC–Can Bartomeu (10b) and Can Feu (12b). On the other hand, LSI sheep/goat widths became larger in all sites during Roman Imperial times.

Pig width values seem to be decreasing during RR in most of the analyzed sites, with the exception of Burriac (8)—an indigenous site quickly romanized—and the *villa* of Vilarenc (58a) that had more robust individuals (Fig 11). During ERE width values are still low in most sites compared to the previous period. But there are some sites with more robust pigs, as in the urban contexts of *Ilerda\_Carrer Magdalena* (23c) and *Iesso*—in the OP—, as well as in the rural site of *Vilauba* (60a) in the NC. On the other hand, lengths seem very stable throughout all periods, with the outstanding case of the urban context of *Ilerda* (23c), with larger-sized individuals during ERE. In all cases, these larger animals do not fall within the range of wild boars (Fig 11, black points), which suggests that they are larger domestic pigs.

Finally, during LA, all site typologies (both newly created and those with Roman levels), present smaller LSI lengths and **widths** for the main domesticates.

## 6. Discussion

The settlement patterns reflect human social organization and their impact over the landscape [8,165–168], and the study of the animal husbandry allows us to characterize the human subsistence strategies [169–171]. In the following paragraphs we will discuss the ecological and

socio-economic reasons that probably influenced and conditioned livestock strategies, integrating the zooarchaeological data with those of other archaeological disciplines. For this purpose, a multiscale and diachronic analysis will be implemented, to be able to observe the nature and impact of changes at both a micro-spatial (site scale) and macro-spatial level (territory scale).

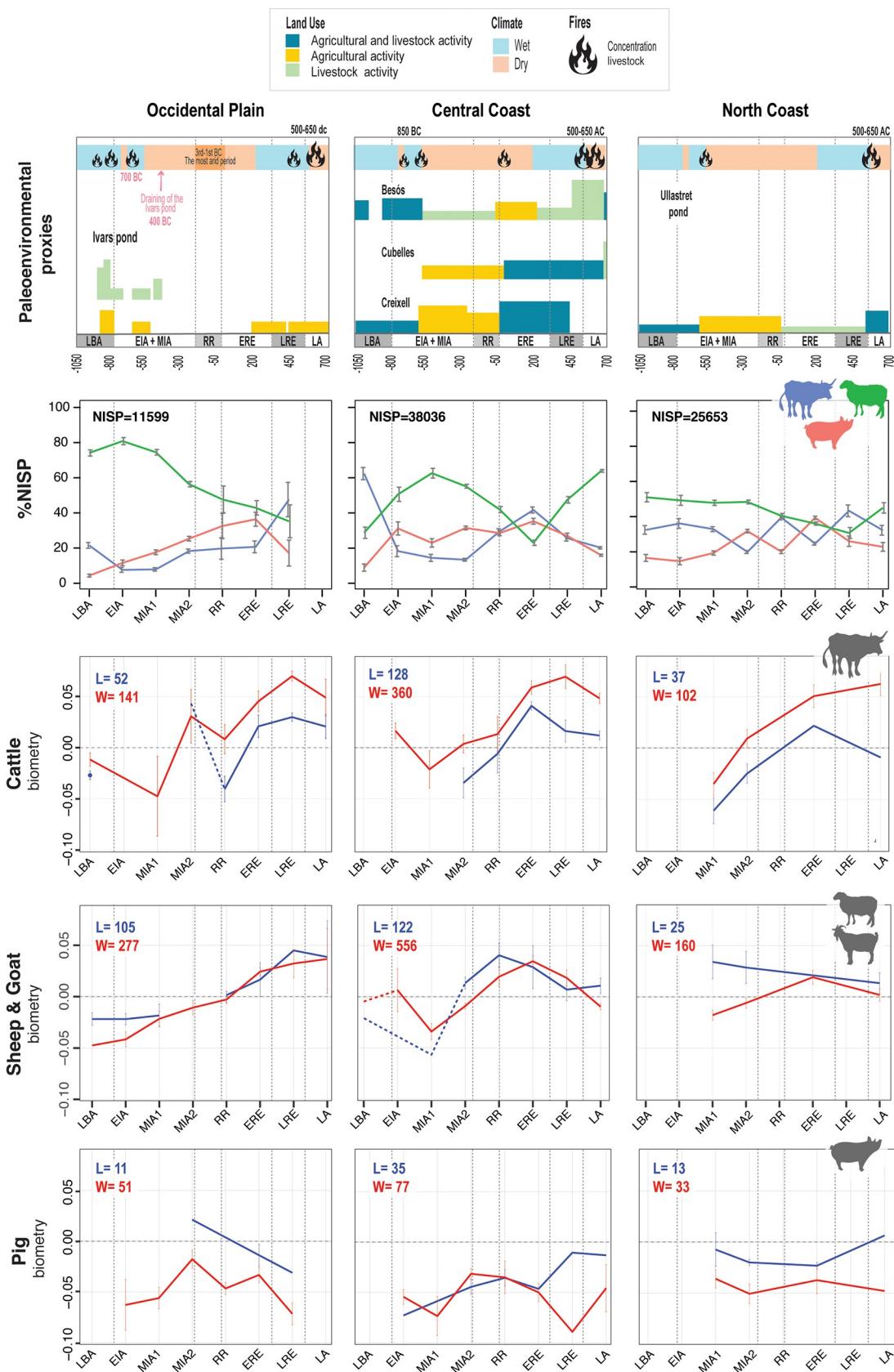
### 6.1. Impact of ecology on livestock patterns in the NE of the Iberian Peninsula

Factors contributing to the degree of heat stress and seasonal effects on reproduction experienced by animals include environmental temperature, and landscapes less conducive to grazing (Fig 1B), solar radiation (Fig 1C), relative humidity (Fig 1D), and wind speed. These environmental factors produce changes in animal conformation, including the increase or decrease of their size and robustness (e.g. [172,173]). To complement the different ecological information of the studied areas provided by Figs 1 and 12 summarizes the ecological information available on fire incidence and landscape use based on palynological and sedimentological information on the region [81,82,174–179]. The integration of these different ecological data has made it possible to characterize which areas are potentially more or less suitable for grazing, taking into account the ethology of the different livestock species. This can be contrasted with the summary of NISP frequencies and animal size through time in the three areas for which we have reliable data (OP, NC, CC); data from the South Coast (SC) have not been considered in detail in this synthesis on account of the relatively scarce data available for the region (see e.g. Figs 3.1 and 5). In combination with Fig 6, we will discuss how the zooarchaeological results correlate with ecological differences between the areas.

Exploratory statistics on **livestock ratios** (Fig 6) suggest that during LBA and EIA there was an important correlation between the location, and hence ecological conditions of each studied area, and NISP frequencies at each site. During these times, geography, watersheds, potential local landscapes, solar radiation and annual rainfall (Fig 1) seem to have been the main factors influencing NISP frequencies. The OP and NC, the two study areas with the most dissimilar ecologies, show clearly different trends. The OP consistently correlates with higher frequencies of sheep and goats, and the NC, which is the wettest and the cloudiest of the four zones analyzed here, had higher cattle frequencies (Fig 5, and also Fig 12).

Environmental factors, and notably heat stress, are key determinants in cattle production (e.g. [173,180–182]), and the environmental situation in NC was likely more favorable for cattle production than the other study areas. The NC area is characterized by a complementarity between two types of climates (Fig 1B): an area near the coast characterized by a type Csa (Hot-summer Mediterranean climate; coldest month averaging above 0°C, at least one month's average temperature above 22°C, and at least four months averaging above 10°C. At least three times as much precipitation in the wettest month of winter as in the driest month of summer, and driest month of summer receives less than 30 mm) and type Cfb (Temperate oceanic climate; coldest month averaging above 0°C, all months with average temperatures below 22°C, and at least four months averaging above 10°C; no significant precipitation difference between seasons). In addition, palynological and sedimentological studies show that the NC had large areas of wetlands until Roman times [175,177]. In this sense, the NC offers better conditions for cattle compared to the other areas, which are drier and warmer. The high percentages of cattle documented in the NC (between 30 and 40%) have also been attested in the neighboring area of Languedoc (France), which has an identical ecological setting [42,52,183].

In contrast, sheep and goats are better adapted to graze on the dry inland area, as they are more sensitive to humidity and bacteria, but are more resistant to solar radiation [184–186]. In



**Fig 12. Synthesis of NISP frequencies and animal size for the main domesticates between Late Bronze Age (LBA) and Late Antiquity (LA) in the Occidental Plain (OP), Central Coast (CC) and North Coast (NC) compared to paleoenvironmental proxies.** From top to bottom: paleoenvironmental proxies, main domestic NISP profiles (in percent), main domestic LSI lengths (in blue, Length) and widths (in red, Width) values with their total number of bones considered (see text for references).

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addition, they prefer pastures and forested areas with different types of vegetation [187–190]. This is consistent with the greater correlation of sheep and goats in the OP, which is the driest of the four areas (Fig 1), with a climate that has been classified as cold and semi-arid (Bsk). This climate type is typically found in continental interiors at some distance from large bodies of water, and it usually features warm-to-hot dry summers. It features major temperature swings between day and night, with dry summers, relatively wet winters, and even wetter springs and autumns (see Fig 1C). The CC, with greater solar radiation and lesser amount of rainfall than the NC, is strongly correlated with caprines and pigs. This area has a mixed ecology, with some regions closer to OP ecology (i.e. southwest zone, Bsk climate [57]) and others closer to NC (i.e. northeast zone, Csa and Cfb climate [57]). The general diversity of NISP profiles during LBA and EIA is consistent with the different ecological settings of the area.

These strong regional trends in livestock ratios, with statistically significant variations between ecological zones during LBA, EIA and MIA1, are also attested for LA assemblages (Figs 3.2 and 5). Interestingly, ecology does not seem to have the same influence in all periods. In this sense, during MIA2 there was a strong process of homogenization of livestock ratios in most sites, independent of the ecological zone or their typology (Fig 4, see also Fig 12). In addition, pig frequencies clearly increased during Roman times in all areas (Figs 5 and 12). This does not seem to be related to the ecological potentialities and/or limitations of each area, but rather reflects a global economic change driven by the well-known pig preference of Romans from central Italy [191–193]. This is mostly visible in urban contexts and the richest *villae*, which seem to be the most 'Romanized' contexts.

Together with NISP frequencies, animal size also attests major changes in animal husbandry and may reflect adaptations to particular ecological requirements. As presented above, the results of the **biometric analyses** at the inter-regional level show (with exception of samples containing very few measurements) that mean LSI values from **cattle** widths and lengths increased from MIA1 to MIA2, and subsequently up to ERE, when the largest animals are documented (Figs 9 and 10). Both lengths and widths increased in a quite linear way, which suggests that the size change relates either to a better nourishment of the animals, import of larger animals that have a similar body conformation, or both. In any case, detailed examination of the robustness of metacarpals [194] suggests that the increase of cattle size was not related to a different sex ratio or castration practices. At the sub-regional level, the increase of cattle size happened earlier in the OP compared to CC (see Figs 9 and 10, and S5 in supplementary material in [S5 File](#)). This cannot be related with better ecological conditions in the OP, which is the driest of the four zones analyzed (Fig 1). Size increase during RR in OP is not incidental either, as large cattle in OP have the same size as those recorded during ERE. Consequently, the OP provides a clear example that, in some periods, human decisions and technical capacities may have a larger impact on animal morphology than purely the ecological setting.

This is also visible in **sheep and goats**, which experienced a similar trend, with a general size increase from LBA to Roman times, and a later decrease of size during LA, visible in both lengths and widths. At the sub-regional level, the NC displays wide variation in sheep/goat size during MIA1 (Fig 7). This could be the consequence of the presence of wild animals identified as domestic sheep/goats, although the importation of animals cannot be completely excluded. The SC had smaller and slender caprines compared with the other areas (Figs 7 and 8). These size differences between zones cannot be solely explained by environmental conditions like

rainfall or solar radiation, as the same size increase process is attested in different ecological zones—OP and CC—early after the Roman conquest (RR).

Trends observed in **pigs** suggest a greater variability between zones. In OP the LSI values of widths decrease in two moments: from MIA2 to RR, and from ERE to LRE. Length data are scarce, but there are also hints—as happens with the other two species—that before the Roman conquest (MIA2) there were larger pigs in OP than in the other areas. It should also be noted that in OP during the RR there is also a significant decrease in the robustness of animals, as is also observed in sheep/goats and cattle. This trend, which is only observed in OP, could indicate a different impact of the first moments of Romanization with respect to the other areas. On the other hand, the CC shows a progressive increase in the size of the pigs from EIA to RR—ERE, with hints of large pigs during LRE and LA. The LSI values of widths show a progressive decrease in the robustness of the animals from MIA2 to LRE, with an important change during LA with individuals of greater robustness. In this regard, it should be noted that there is also a decrease in the robustness of pigs from ERE to LRE in the other areas. The scarce information for the NC only allows us to say that a very different trend is apparent, with a progressive and slight decrease of pig from MIA1 to ERE, and the presence of larger size pigs during LA.

Our results suggest that the size increase does not seem to be linked to those periods with more water availability or a more conducive climate. In this respect, in the OP, the LBA and MIA1 correspond to the wettest periods and with more deforestation activity, in relation to documented regional fires (Figs 12 top and 13 bottom) linked to the intensification in agriculture and animal herding (Fig 13 bottom) [82], and this is also documented in the pre-littoral plain (CC) [81]. Despite the potential for more arable land and water availability, cattle frequencies decreased over these time periods, together with animal size (Fig 12), following a tendency consistently observed from the LN and early Bronze Age [45,195]. Conversely, the transition from MIA1 to MIA2 suggests an increase in animal size before the Roman conquest (or at least the presence of some large animals), coinciding with a period of maximum drought (Fig 12 top), and evidence of an intensification of land use for agriculture (Fig 13 bottom) in most areas studied [82,176,178] (Fig 12 sup). As we will discuss below, this also coincided with the maximum territorial expansion of Iberian Archaic states (Fig 13 bottom) [12,27,99,106,107]. Another evidence suggesting that the increase in size does not appear to be solely linked to periods with a more favorable ecological context, is the divergent patterns of cattle and pig size change in the different areas during the same episode of maximum drought in Catalonia between the 3rd and the 2<sup>nd</sup> c. BC [176,178] (Figs 12 top and 13 bottom). While there was a significant increase in the cattle size in the OP (Figs 7 and 8), in CC no major changes are attested from MIA2 to RR based on the data currently available.

Overall, the evidence from NISP and biometry suggests that the changes in animal husbandry were only partially related with regional environmental and/or ecological factors. Beyond the particular inter-regional dynamics observed during protohistoric periods, the results show a general tendency for common diachronic change in all areas from MIA2. Some size change patterns occur in all sites, regardless of their typology, including both urban centers and small rural settlements with only some exceptions (see [results](#) section). Other works have previously documented the same processes of progressive augmentation of cattle size from the Iron Age to Roman times in other European countries with very different ecologies, and related to the development of market economies (e.g. [43,45,50,196,197] and references within). Consequently, size change and different livestock ratios did not result from a universal or external factor (e.g. a general climatic change) but seems closely related to cultural and economic decisions as discussed below.

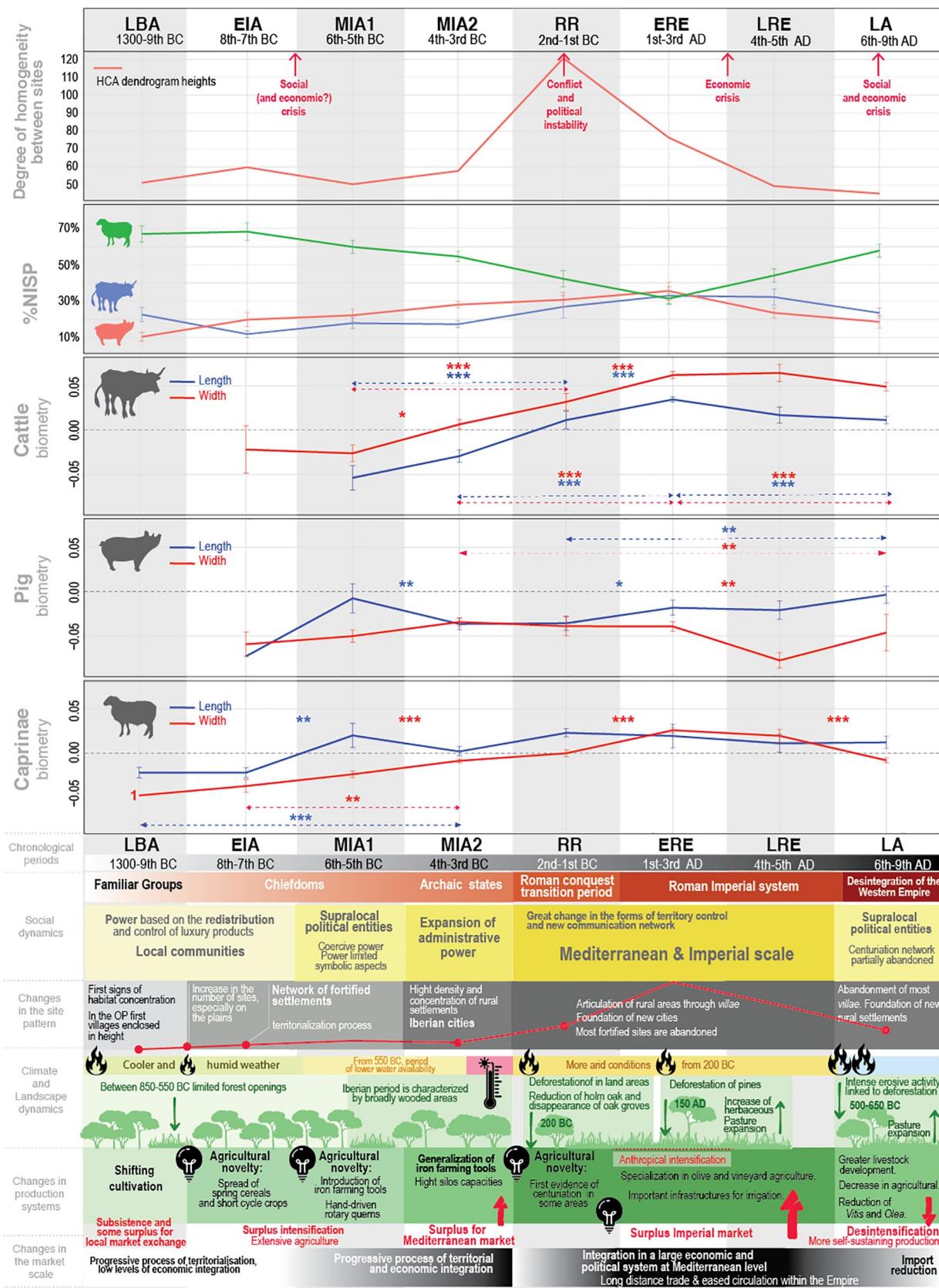
## 6.2 Changes in animal husbandry, demographic growth and technological innovation

[Fig 13](#) summarizes the main socio-political events attested for the NE of the Iberian Peninsula between the Late Bronze Age and Late Antiquity, together with a synthesis of the main zooarchaeological and ecological data available.

The progressive increase of pig frequencies during **LBA** ([Fig 13](#)) is concurrent with the greater territorialization and evidence of a demographic increase, visible in, for example, the number of graves in the necropolises [27,85] and the colonization of new lands [13,28,67,71]. According to some authors, this demographic increase, together with the colonial stimulus, increased the pressure on the resources [27]. Such pressure promoted consolidation of territorial control to guarantee access to resources and probably led to a progressive decrease in the land directly accessible for each settlement. The diversity observed in the livestock ratios between sites and areas (Figs 3.1, 4 and 12) suggest that each site chose the most sustainable livestock model and prioritized the domestic species better adapted to its immediate environment. The small size of animals suggests a strategy based on community self-sufficiency but with a possible stock surplus complementary to that of surrounding regions, and it could also reflect the prioritization of more adaptable and less demanding animals on fresh pasture [194]. Consequently, our results are consistent with the population model and social organization suggested for this area, in which each village would constitute an economically self-sufficient population cell-to a notable extent—that would manage and operate on the surrounding territory according to the membership of a human group for kinship relationships [13,27,28,198–200].

Some authors have defined the **EIA** as a period of continuity (e.g. [13,28,68]), but livestock frequencies are significantly grouped by site type in this period. The fortified sites of the OP—with a greater urban complexity—had higher percentages of pigs, and the sites associated with silos fields in CC and NC—that attest of a significant presence of imported products—had notable percentages of pigs and cattle, constituting a fairly homogeneous group (Figs 4 top and 6). This pattern is also present at the aristocratic residence of Sant Jaume Mas d'En Serrà\_sect. 1 (42). Pigs and cattle are the two species with higher meat yield per animal. Considering the functionality of these sites—e.g: Vilars 0-I (59a), Can Roqueta (15c), Turó Font de la Canya 0 (57a), Sant Jaume Mas d'En Serrà\_sect. 1 (42)—and their significant quantities of colonial products such as amphorae, tableware related to wine consumption and other sumptuous objects, this NISP profile may be related to collective meat and wine consumption during feasting practices in order to reinforce social and territorial cohesion within and between groups [201–205]. This seems consistent with the evidence of territorial authorities, growing social hierarchy, and the impact of exchanges and redistribution of Mediterranean products on local communities. In addition, the higher frequency of pigs can also be related to the increased pressure on the landscape and the demographic increase, as pigs are prolific and efficient meat producers, and can feed in marginal forest areas and domestic refuse [206,207]. In addition, the demographic growth and grain farming may have reduced the pastures available for cattle and caprines (per animal/herd). Also in this period, the maximum storage capacity transcends, for the first time, the scale of domestic consumption in some sites, reaching profiles that are compatible with the production of a surplus for exchange [103,105]. The profiles of the domestic triad are consistent with a greater territorialization and competitive processes for the exploitation of the best resources and the control of pastures and/or routes of circulation of colonial products. It may also reflect the progressive integration of the area in larger Mediterranean markets.

From the middle of the 6<sup>th</sup> c. BC (**MIA1**) and up to the 3<sup>rd</sup> c. BC (**MIA2**) the evidence of social hierarchy was increasingly reflected both in the necropolises (the number of tombs is



**Fig 13. Synthesis of the NISP percentages and size change of the main domesticates (top) compared to other proxies (bottom) in Catalonia between Late Bronze Age (LBA) and Late Antiquity (LA), from left to right, LBA: Late Bronze Age, EIA: Early Iron Age, MIA1: Middle Iron Age 1, MIA2: Middle Iron Age 2, RR: Roman Republic, ERE: Early Roman Empire, LRE: Late Roman Empire, LA: Late Antiquity. Chi-square results showing significant changes between periods are displayed with their *p*-value: \*\*\*: highly significant (< 0.01); \*\*: significant (< 0.05); \* less significant (< 0.1).**

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reduced but the grave goods are richer) and in the settlement pattern (diversification of the sites types, and spread of the fortified settlements (FS) that constituted the centers of power [27,84,91,208]. This period has been described as a moment of transition from a regional system (MIA1: 6<sup>th</sup>–5<sup>th</sup> c. BC) and the expansion of an administrative system with the appearance of the first archaic states in the region (MIA2: 4<sup>th</sup>–3<sup>rd</sup> c. BC). The increase of animal size coincided with a period of maximum drought, the intensification of land use for agriculture in most areas studied [82,176] (Fig 12 top), and also with the moment of maximum territorial expansion of the Iberian states [28,99,106]. A homogenization of livestock ratios during this period is also well attested (Figs 3.1, 4 and 13 top), and some authors have linked this pattern to an increase in interdependence between sites and the influence of the aristocratic and military elites on animal production [29,30,53]. The decrease in the percentage of cattle and the increase in their size and robustness (Fig 13) is also consistent with a more intensified agricultural system where cattle are selected to obtain more efficient individuals for work. In parallel, technological innovations such as the generalization of iron tools for agricultural work, the appearance of rotary mills from 5<sup>th</sup> c. BC [27,71,102,209–211], and emergence of wheel-thrown pottery show an intensification in harvest production and post-harvest transformation/conservation. The spread of cereal farming with probable larger areas under cultivation [212]—observed also on pollen and anthracological analyses (e.g. [213–215])—, could have led to a reduction of forest resources with a limitation of the range of movement of pigs [206], and the opportunities for domestic pigs to interbreed with larger wild boar [51], contributing to their size reduction. These results are consistent with the introduction, from the end of the 4<sup>th</sup> c. BC, of an Eurasian model of agriculture, based on permanent land use and sectoral fallow land [71,216–218]. The existence of a centralized administrative power, of technological advances (which could include improvements in working animals) and the availability of local labor (demographic growth), would have favored a production increase, allowing a production surplus with speculative and commercial purposes (e.g. [27,103,105]).

The moment of maximum expansion of the Iberian states coincided with the beginning of the **Roman conquest (RR)** in the NE of the peninsula. The majority of faunal assemblages from this period date from the 2<sup>nd</sup> c. BC, when Romans imposed heavy taxes on the allies (e.g. [219,220]) in a period of strong instability due to the constant rebellions of the different Iberian peoples as the *Ilergetes* (in 206 and 205 BC: *Polybius*, 11, 32), *Sedetani* (200 BC: *Livy*, 31, 49, 7), *Indigetes* (195 BC: *Appian, Iberia*, 40). The indigenous territorial and political system was maintained at first and some *oppida* persisted—e.g. Sigarra (47b), Burriac (8)—but there was a general abandonment of the fortified settlements—e.g. Puig de Sant Andreu (88), Alorda Park (2), Penya del Moro (38), Puig Castellar (25). In addition, new open and small rural settlements devoted to agricultural production and with some associated silos were built—e.g. Missatges (92), Hereuet (91), la Rosella (84), Can Bartomeu (10b)—[108,109,112,116–121], perhaps to face the heavy taxes imposed by Rome and supply of the Roman army present in the area. The great diversity observed, both in the types of sites and in the frequencies of the main domesticates (Figs 3.2 and 4), seems to reflect this period of war and instability, in which each territory/site had different responses and adaptations to the invasion. In this context, there are divergent patterns of animal size in the different areas during the same episode of maximum drought between the 3<sup>rd</sup> and 2<sup>nd</sup> c. BC [176,178] (Fig 12). In CC and NC, there was an increase

of cattle and sheep/goat sizes from MIA2 to RR. This probably reflects the introduction of new animal morphotypes during the Romanization process, as previous works on the NC have suggested [221]. In the same period, the significant decrease in the width values of animals observed for cattle and pigs in OP and CC could indicate a higher degree of economic disruption, for example due to military conflicts in the area.

During Roman Imperial times (ERE) a new settlement pattern is attested in the region, seen in the concentration of dispersed settlements and the spread of the *villae* system. This new and specialized farming system had a fundamental role in territorial structuring [129]. In addition, large urban centers appeared with high population densities, and they concentrated the political and administrative powers of the provinces [114,222]. The drastic reduction of sheep/goat frequencies and the rise of pig (meat producers that could feed in forests or court-yards)—is concurrent with a time of greater specialization and intensification of food production, as observed on pollen analyses (e.g. [82,176,178,223]). The high frequencies of pigs also could reflect the well-known dietary preference for pork of Roman populations from central Italy [191–193]. Interestingly, high pig frequencies are mainly attested in urban centers and the richest *villae* (Figs 3.2 and 4). This phenomenon has also been observed in Britain [191,224] and other European territories (e.g. [225] and references within). In addition, some *villae* display high cattle frequencies, perhaps related to their role as a working animal [226–229]. The increase of cattle size is well attested in all kinds of sites, irrespective of their typology (Fig 9). On the other hand, sheep/goats and pigs management show a different tendency, as their size stabilized and even decreased during Roman times (Fig 13). Further research is needed to explain this divergent phenomenon. Nonetheless, our results are consistent with the existence of a large-scale productive system with specialized livestock productions. The Roman economic system was sustained on a high index of connectivity and large-scale and long-distance road and commercial network that provided the supply and free movement of products and people within the limits of the empire (e.g. [17]). Strontium isotopic results on livestock suggest this also included animals [52,230,231].

During the LRE period there was a substantial reduction in the total number of settlements [129–131]. In addition, there was a significant change in the interactions between urban and rural sites. The drastic reduction in imports and the size of production facilities in many *villae* [61,129,142,147] is considered to reflect a time of economic crisis as a result of the decline of large-scale Mediterranean trade [114,152]. The zooarchaeological results are consistent with a decline of the Roman imperial system. First, there was a drastic decrease of pig frequencies compared to the previous period (Fig 13), most notably in the cities (Figs 3.2 and 4). Second, this was coupled with increased frequencies of caprines and cattle at most sites (Fig 13). The prioritization of these two taxa reflects more extensive livestock models, where the species best adapted to local landscapes are selected, but which are also those with the highest land costs (greatest need for pasture). In cities, the decline in pigs relates to changing urban supply systems, which became less concerned with surplus meat provisioning to the non-farming consumers that lived in cities, due to a decline urban population size and probably also living standards [193]. Therefore, these profiles provide the first indexes of de-intensification processes of agricultural production, consistent with a context of lower population density, as suggested by the reduction in the number of settlements. The livestock ratios are consistent with a strategy of greater self-sufficiency and perhaps a way back to more extensive livestock production, linked to the exploitation and use of local natural resources as suggested by the increase in caprines ratios. Palynological and micro-charcoal studies attest to a higher presence of fires, which probably aimed to create pasture areas during this period [176]. There was also a significant increase in the degree of homogeneity between sites, thus suggesting a decrease in specialized sites in addition to the general decline of production. This is also consistent with the reduction of animal size (Fig 13).

The **Late Antique period (LA)** marked a new structuring of settlement patterns, with the continuity of some sites—which underwent major transformations [144,146,148,149]—and the building of new settlements adapted to a new political and economic structure, as well as to new ideological needs [132]. In this context, the frequency of caprines increased compared to pigs and cattle, most notably in the CC area (Figs 5, 12 and 13). This suggests an expansion of more extensive livestock systems, more adapted to the ecology of the different environmental zones and better suited to exploitation of marginal areas. In this regard, most sites have livestock profiles that are reminiscent of those observed during the LBA and EIA (Figs 3.1, 3.2 and 4), when the economic system is thought to be significantly more self-sufficient and territorialized [129,142,149,152,232]. Cattle, which had already experienced a significant decline in size during late Roman times, decreased even further, and sheep and goats became less robust. Our results are consistent with a more sustainable and smaller-scale livestock model in a context of large-scale trade recession. Human communities focused on a strategy based on self-sufficiency, prioritizing the most resilient species for the region. Intense erosive activity and evidence of forest burning [178,223,233] also suggests the creation of pastures for extensive herding and, overall, an agricultural model adapted to a less intensified and more local economic system. This is consistent with a significant decrease in the interdependence between sites.

## 7. Conclusions

The archaeozoological meta-analysis presented here provides a general perspective on the evolution of animal husbandry over c. 1700 years in the NE of the Iberian Peninsula, taking into account the ecological characteristics of four different areas in present-day Catalonia. This broad diachronic perspective was necessary to elucidate whether animal husbandry practices were mainly related to the ecological characteristics and climatic changes in the region, or were the result of socio-economic processes. The zooarchaeological results suggest that, although the ecological character of the different zones played an important role, livestock frequencies and changes in animal size are mostly related to socio-economic choices. The impact of ecology on animal husbandry fluctuated over time in direct relation to the specific socio-economic circumstances of each cultural period. The periods with a lesser degree of economic integration—with a more fragmented political and territorial system, and with production more focused on supplying local markets (i.e. Late Bronze Age, Early Iron Age and Late Antiquity)—displayed husbandry strategies closely related to the ecological conditions of each area, thus maintaining a better balance between the carrying capacity of the local environment and the needs of the population. Their particular ecologies allowed them to generate some surplus—more fitting with their own environmental conditions—that could be traded with neighboring sites and/or in the local markets. During these periods, the sites located in the Occidental Plain (OP) and the south coast (SC) focused on the extensive grazing of sheep and goats, sites in the north coast (NC) display higher frequencies of cattle, and sites in the central coast (CC) balance between caprines and pigs. In contrast, this link between livestock exploitation and the environment is less apparent during periods when production turned towards an increasingly pan-Mediterranean market economy, which mainly happened during the 4<sup>th</sup>–3<sup>rd</sup> c. BC and Roman times. These two periods (Iron Age and Roman times) display two different models of animal production: the Iron Age strategy focused on sheep and goats, and the Roman model focused on pigs and cattle. This probably shows a cultural choice but also a radical change of demand and production, that was not conditioned any more by regional environmental differences but by a large Mediterranean market with access to a variety of productive environments.

The study also reveals that animal size significantly changed through time and, again, this was not linked to local ecological conditions but the degree of economic integration. In the Roman period, surplus production focused on specific local products (most notably wine). This, in combination with the important increase in the number and size of cities in the area, the increase in the non-productive sector of the population, and Roman colonial land distribution practices, facilitated the adoption of large-scale agricultural production linked to the expansion of first rural *fundi* and, later on, proper *villae*. This can be related to the significant increase in size and robustness of cattle. The influence of the political and economic context is also apparent during Late Antiquity, when smaller political units and more autarkic modes of production were put in place. This is consistent with the decrease in cattle size (i.e. small cattle are better suited to small-scale economic units/small scale-exploitation strategies) as well as the prioritization of more extensive, resilient livestock systems, as shown by the increase of sheep and goat frequencies.

This study contributes to the understanding of the dynamics of landscape exploitation between the Late Bronze Age and Late Antiquity in NE Iberia, and offers a valuable foundation to further explore the impact of socio-political systems on animal husbandry over time. Overall, our results show that human communities adapted animal husbandry to their social, political, and economic environment, as well as the physical landscape. Within each chronological period, the capacity of societies to implement the most productive and most intensive economic systems—which are not always the most sustainable in the long term—depended on context-specific factors. These include technical innovations, production and consumption needs, and market demands, which are shaped by the existing political system, availability of labor, and technology. In charting the impact of these factors on animal production, zooarchaeology proves to be a key discipline to explain and characterize socio-economic and political changes through time.

## Supporting information

**S1 Checklist. PRISMA 2009 flow diagram.**

(DOC)

**S1 File. Studied dataset, archaeological sites with periods, geographical areas, total of livestock NISP and associated references.**

(PDF)

**S2 File. Maps of the studied area by period with site locations by types and geographical areas [55].**

(PDF)

**S3 File.** Chi-squared results on livestock NISP by periods, type of site (left aligned) and geographical areas (right aligned).

(TIFF)

**S4 File. Summary table of the length and width measurements ordered by taxa with the geographical areas and periods.**

(XLSX)

**S5 File. Mann-Whitney pairwise results between periods for taxon's length and width measurements grouped by geographical areas.** P-values significant differences: \*\*\*: highly significant ( $< 0.01$ ); \*\*: significant ( $< 0.05$ ); \* less significant ( $< 0.1$ ).

(XLSX)

**S6 File. Mann-Whitney pairwise results between periods for taxon's length and width measurements for the whole studied area.**

(PDF)

**S7 File. Mann-Whitney pairwise results between geographical areas for taxon's length and width measurements grouped by periods.**

(PDF)

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