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4500 years of morphological diversification in Western Europe wild boars (*Sus scrofa*) and the consequences of the Neolithic transition

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ABSTRACT

Evolutionary biologists have recently solicited archaeologists to help document and understand the morphological evolution of animals in response to human activities and, more generally, to help reconstruct the history and significance of the anthropogenic impact on worldwide ecosystems. Artificial selection associated with domestication is the best-known example of a major anthropogenic morphological evolution preserved in the archaeological record. However, the impact of the domestication process and dispersal on the morphological evolution of animals has been far less explored. To fill this gap, we focused on 4500 years of evolution in Western Europe *Sus scrofa*, covering the Neolithic transition – a major anthropogenic ecological disturbance involving landscape modification and the translocation of domestic mammals. Using geometric morphometrics on key phenotypic markers preserved in the archaeological record, associated with isotopic studies, we explored how, and in response to which cultural drivers, the Neolithic niche construction has influenced the morphological evolution of Western European wild boars (*Sus scrofa scrofa*). The decoupling of size and shape components from bone morphological variation has facilitated the identification of several processes of phenotypic diversification of *Sus s. scrofa* in response to human behaviour during the Neolithic transition in Western Europe.

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1. Introduction

Over the last few centuries, the human niche construction (Odling-Smee et al., 2003) has become "the world's greatest evolutionary force" (Palumbi, 2001), generating a change in the ecological and evolutionary dynamics of species on a global scale (Hendry et al., 2017). The human engineering of ecosystems with habitat fragmentation (Cheptou et al., 2017), urbanisation (Alberti et al., 2017; McDonnell and Hahs, 2015) and the disruption of natural dynamics (Colautti et al., 2017) has induced rapid micro-evolutionary changes through strong directional selection, resulting in rapid diversification (Hendry et al., 2007, 2008, 2017). With the emergence of agriculture and, more generally speaking, the

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Neolithic transition, the human niche construction caused a major ecological disturbance, with the opening and fragmentation of the landscape, the emergence and spread of domesticated animals and plants from several independent centres across Eurasia, the protection of livestock from predators and competitors, and the dispersal of invasive species and pathogens (Ellis et al., 2021; Sullivan et al., 2017). To date, the influence of the Neolithic niche construction has been mainly explored through human-induced species distribution (Boivin et al., 2016; Cucchi et al., 2020; Vigne, 1999), and over the temporal depth of the direct human influence over species during the process of animal domestication (Ameen et al., 2019; Brassard et al., 2022; Clutton-Brock, 1992; Cucchi et al., 2021; Fages et al., 2019; Frantz et al., 2020; Larson and Fuller, 2014; Zeder, 2015). Yet, its consequences on non-domestic species evolution remain to be fully documented and understood (Erlandson et al., 2016; Sarrazin and Lecomte, 2016).

To contribute to this research avenue, this study explores the influence of the Neolithic transition in Western Europe on the phenotypic diversification of an indigenous species: the wild boar (*Sus scrofa*). Emerging in the Near East around 9500 BCE, the Neolithic dispersal reached central-western Europe by 5850 BCE through demic and cultural diffusion via the Danube River and the northern Mediterranean coasts, with the adaptation of technoeconomic strategies to different ecological conditions along the way (Manen et al., 2018, 2019). *Sus s. scrofa* was present in North Western Europe since the Middle Pleistocene, and was evidenced in MIS 7 by 250 ka BCE (Auguste, 2009). These animals were common and widespread from France to Belarus from the early Holocene onwards, varying in body size according to Bergman's rule, with northern individuals from north-eastern Germany being larger than southern ones from Spain and Italy (Albarella et al., 2009). Despite the recent intensification or reintroduction and introgression with domestic pigs on the genetic make-up of wild boar populations in Europe (Goedbloed et al., 2013), their deep genetic structure across Europe remains mainly determined by the post glacial dispersal from southern refuges located in Spain, Italy for Western Europe, and the Balkans for Central Europe (de Jong et al., 2023; Niedziałkowska et al., 2021), with a loss of genetic diversity towards the northern range of the species (Vilaça et al., 2014).

The earliest anthropogenic influence over the genetic diversity of European *Sus scrofa* has been documented by paleogenetics with the introduction of domestic pigs of Near East ancestry by Neolithic stock-herders along the two dispersal waves mentioned previously (Larson et al., 2007). These pigs stemmed from the long domestication process of Near Eastern *Sus scrofa* populations between 9500 and 8000 BCE (Price and Hongo, 2019), from intensive hunting to first evidence of body size reduction compared to their wild relatives by 8000 BCE (Price and Evin, 2019). These small pigs, entered Europe by 6500 BCE, arriving in Central Western Europe around 5400 BCE (Evin et al., 2015; Larson et al., 2007; Ottoni et al., 2013). By 5000 BCE, the Near Eastern lineage no longer existed in the European pig genome, which, after this date, had 96% of its genetic variants coming from European wild boars. The extent of this genomic replacement is considered to have stemmed from introgressive hybridization facilitated by the small population size of Near Eastern pigs and a lack of barrier between them and the local wild boar populations (Frantz et al., 2019).

The introduction of domestic pigs into Europe by successive waves of newcomers from the Near East induced the co-occurrence of several lineages of *Sus scrofa* during part of the Neolithic period: the indigenous wild boar populations in their natural habitat, the domestic pig populations of Near Eastern origin reared by Neolithic people and their feralized populations. Indeed, thanks to paleogenetics, we know that hybridization and gene flow between wild, domestic and feral *Sus scrofa* populations, occurred all along the Neolithic (Frantz et al., 2019). This gene flow can be highlighted by traditional pig husbandry still undertaken in Papua New Guinea, where interbreeding is part of the rearing practices, with sows being left to fray with wild male boars (Dwyer, 1996), or in Mediterranean Europe (Albarella et al., 2011; Hadjikoumis, 2012; Halstead and Isaakidou, 2011). This does not exclude likely presence of commensal wild boars for which there is no genetic evidence. This co-habitation of several lineages of *Sus scrofa* produced new hybrid communities, with different ranges of interactions between suids and humans societies in Neolithic Europe (Albarella et al., 2011; Balasse et al., 2019), where boundaries between wild and domestic populations were not as tight as those currently engraved in the industrial and zootechnical views on animal domestication (Bogaard et al., 2021; Stépanoff and Vigne, 2018).

Considering the new ecological and evolutionary forces introduced into Europe by the Neolithic transition, we wanted to explore the extent of its influence on the morphological diversification of *Sus s. scrofa* in Western Europe, over 4500 years of archaeological record. The remains are dated from the Middle Mesolithic, by 7500 BCE, i.e. before the spread of farmers and their domestic pigs, until the Late Neolithic 3000 BCE, when the new social and economic organization of the Bronze Age emerged. During this timeframe, we attempt to (1) understand whether the Neolithic transition influenced the phenotypic evolution of the autochtonous wild boars, (2) define the phenotypic diversity of the several lineages of *Sus scrofa* present in Europe at that period and (3) determine to what extent Neolithic societies of Europe have intentionally altered the phenotypic traits of domestic *Sus scrofa*. To track these intraspecific changes in bone morphology, we had to comprehensively capture enough organismal complexity using high resolution phenotypic data with three dimensional coordinate points analyzed via geometric morphometrics (Bardua et al., 2019; Goswami et al., 2019) and morphometric mapping (Bondioli et al., 2010a; Morimoto et al., 2011). To track the morphological evolution across the archaeological record, we relied on three skeleton bones (calcaneus, humerus and mandible) chosen for their good preservation in the archaeological record, following an experimental research program on the effects of captivity over skeletal development in European wild boars (http://anr-domexp.cnrs.fr/). This experimental research showed that functional changes due to mobility reduction and changes due to directional selection induced different morphological trajectories from the wild norm of variation, in both the calcaneus form (Harbers et al., 2020a) and the humerus shaft microanatomy (Harbers et al., 2020b). Likewise, the change in feeding behaviour with captivity induced functional responses in the skull and mandible, different from morphological changes induced by the last 200 years of selective breeding (Neaux et al., 2020, 2021, 2022). All this evidence supports the use of these phenotypic markers to disentangle, functional changes due to a cultural control of the individual's environment (Hecker, 1982), from selective breeding at a population scale, during the Neolithic transition. Such approach has already proven useful to identify the local domestication of the feral populations of wild boars by PPNB Neolithic people of Cyprus (Cucchi et al., 2021).

For this study, *Sus scrofa* from Mesolithic contexts will provide the baseline (T0) for the variation norm of *Sus scrofa* prior to the Neolithic transition in Europe. The *Sus scrofa* bones from Neolithic contexts were not divided beforehand into a wild or domestic category using a bone size criterion, as is usually done in zooarchaeological and paleogenetic studies, for three main reasons. First, as previously said, the wild and domestic boundaries might not be a relevant concept to approach these interactions during the Neolithic. Then, these preliminary categories based on bone size differences are too subjective and might introduce interpretation biases. Third, size changes in wild boars are not easily related to any

clear biotic or abiotic factors (Albarella et al., 2009). We have therefore chosen to assess the extent of Neolithic anthropogenic influence over *Sus scrofa* morphological diversity by confronting the archaeological specimen to a gradient of phenotypic variation representing (1) the reaction norms of *Sus scrofa* populations (Mesolithic and current) living in their natural habitat or (2) in contexts of controlled locomotion and feeding behaviours and (3) the phenotypic divergence induced by selective breeding over the last centuries. The relatedness of the Neolithic specimens to this anthropogenic gradient of phenotypic diversification in *Sus scrofa* was assessed using predictive and machine learning approaches. We also investigated the relationship between Neolithic suids and humans using stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios in bone collagen, as a greater proximity to humans may have induced changes in the feeding environment and diet of suids (Balasse et al., 2016, 2019; Brusgaard et al., 2022; Cucchi et al., 2016; Maring and Riede, 2019).

2. Material

From 101 archaeological *Sus scrofa* bones collected, we could analyze 73: calcanei (41), humeri (19) and mandibles (13) from adults and sub-adults (Supplementary Table S1). We analyzed calcanea with epiphysis known to fuse around 2 years in wild boars (Bridault et al., 2000). The humeri all had a complete distal shaft with a fused distal epiphysis, occurring in wild boar by 19–23 months (Bull and Payne, 1982). The mandibles belonged to specimens between 12 and 60 months old, according to both the tooth eruption (Legge, 2013) and wear stages (Horard-Herbin, 1997) of the premolars and molars.

These bones were collected from 13 archaeological sites in France, Switzerland and Germany (Fig. 1). Within the *Sus scrofa* specimens, 28 came from five hunter-gatherer contexts dated from the Middle and Late Mesolithic between 8700 and 5000 BCE, and 45 specimens from eight Neolithic settlements between 5500 and 3000 BCE (Supplementary Table S1 and Text S2). The latter includes 30 specimens of *Sus scrofa* (25 calcanei and 5 humeri) from the Neolithic site of Chalain, on which stable isotope analysis was performed and compared with the stable isotope analyses on large wild and domestic herbivores found at the same site, including 14 deer (*Cervus elaphus*), 5 aurochs (*Bos primigenius*) and 9 cattle (*Bos taurus*) (Supplementary Table S2). All Mesolithic specimens were considered as hunted wild boars, representative of the phenotypic variation of wild boars before the Neolithic transition. To assess the amount of anthropogenic diversification in Neolithic *Sus scrofa*, we used a comparative approach from a collection of *Sus scrofa* covering the phenotypic continuum from wild boars hunted in their natural habitat to highly selected domestic breeds, whose environment and reproduction was fully controlled by humans (Supplementary Table S3). The hunted wild boars included a sample of 28 Mesolithic specimens from Western Europe contexts (Fig. 1) and a sample of 32 specimens from current populations hunted in France and Switzerland. We have also included 24 captive wild boars from an experiment undertaken at a zoological reserve of the Natural History Museum of Paris (see details of the experiment in (Harbers et al., 2020a)). They were collected from a control population of wild boars (sampled by 8 specimens) and raised in captivity from the age of 6 months to 2 years. These 24 specimens were randomly split into two groups with the same male to female sex ratio. One group was raised in a 3000 m^2 pen and the second in a 100 m^2 stall where males and females were separated. Modern pig samples included 23 specimens from traditional European landraces including 5 free-ranging Corsican landrace pigs and 9 specimens of industrial breeds. A sample of five hybrids (crossed between wild boars and pigs of different breeds) is also included.

3. Methods

3.1. Geometric morphometrics

The morphometric study associate the 3D surface semilandmarks geometric morphometrics (3D GM) of the calcaneus and mandible (Bardua et al., 2019; Mitteroecker et al., 2013) and the 3D morphometric mapping of the humerus shaft cortical thickness (Bondioli et al., 2010a, 2010b). The 3D models of the calcaneus were reconstructed from medical CT scans and photogrammetry after segmentation in Avizo v.8.0 or reconstruction using Agisoft Photoscan 1.2.6.2834. Mandible 3D models were reconstructed from medical CT and laser scanning using an ARTEC Space Spider. All three acquisitions methods were compared using a common 3D GM framework without statistical biases (Waltenberger et al., 2021). The humeri were scanned using a medical CT and reconstructed to generate the external (periosteum) and internal (endosteum) 3D surfaces of the bone used to compute cortical thickness.

3D GM analyses were performed on 3D models using landmark and semilandmark protocols on curves and surfaces previously detailed for the calcaneus (Harbers et al., 2020a) and the mandible (Neaux et al., 2020). For the mandibles, the protocol was adapted to the symphysis and ramus, which are the most common anatomical parts of the mandibles in the archaeological record. The acquisition and standardisation protocol for 3D morphometric mapping of the humeral shaft cortical thickness follows (Harbers et al., 2020b). We adjusted the protocol to ensure its applicability to archaeological humeri missing the proximal end of the diaphysis by mapping only the distal half of the shaft (3–50%). Despite this reduction, all the entheses distinguishing free-ranging wild boars, captive wild boars and pigs are observable (Fig. 1, Harbers et al., 2020b). We used the cross-sectional area (CSA) at the distal end of the diaphysis (Fig. 1c) as a proxy of the humerus size. The Pearson correlation coefficient showed that this variable was almost perfectly correlated ($\rho = 0.965$) with the bone volume. Since the latter is also strongly correlated to body mass (Campione and Evans, 2020; Harbers et al., 2020b), we used the cross-sectional area as a body mass proxy of archaeological *Sus scrofa*.

Size variation differences between the nine subgroups of wild boars and domestic pigs, in the humeral CSA and calcaneus and mandible centroid sizes, were tested using a factorial ANOVA and visualised with boxplots. To assess the structuration of size variation and identify the occurrence of several populations within Neolithic *Sus scrofa,* we performed model-based Gaussian mixture analyses using density estimation on size variables.

The differences in humeral cortical thickness topography and calcaneus shape variation between the nine subgroups of wild boars and domestic pigs were tested with factorial MANOVAs. Patterns of morphological differentiation (in a morphospace) among wild boars and pig samples were visualised using canonical variate analyses (CVA). CVA morphospaces were performed after principal component analysis (PCA) computed on Procrustes coordinates in Mesolithic and modern *Sus scrofa,* retaining 95% of variance for data dimensionality reduction to prevent artificial group discrimination (Mitteroecker and Bookstein, 2011). Neolithic *Sus scrofa* are projected into this canonical morphospace, using a generic function (predict) which will get fitted values according to the multiple linear model computed for the Mesolithic and modern data. To assess the interaction mode (hunting, control or reproductive isolation) with human Neolithic societies for each Neolithic

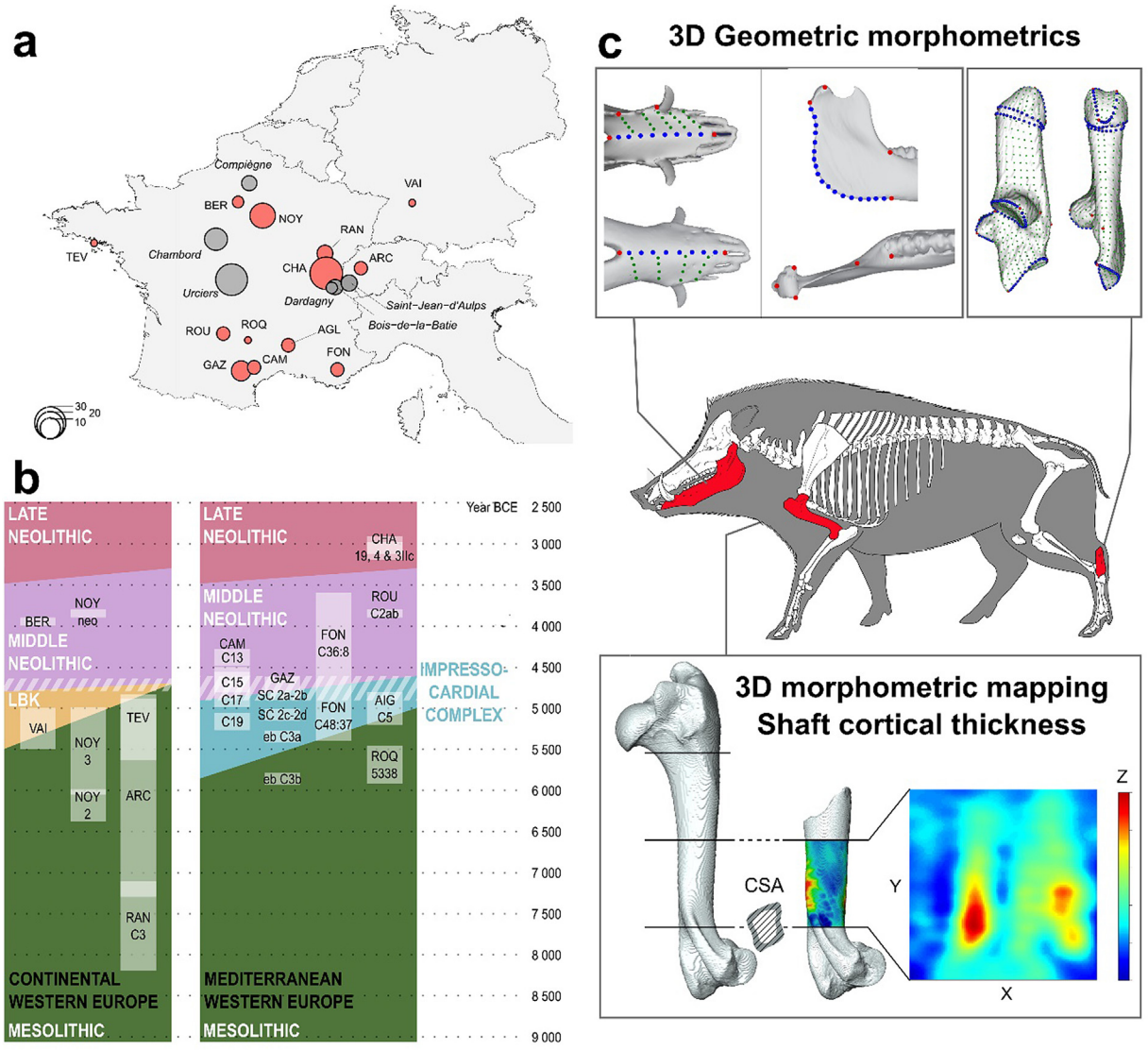

Fig. 1. **a.** Geographical location of the modern wild boars (grey filled circles) and archaeological *Sus crofa* (red filled circles) samples in western Europe: Ranchot (RAN), Arconciel (ARC), Gazel (GAZ), Chalain (CHA), Fontbrégoua (FON), Roquemissou (ROQ), Grotte de l'Aigle (AIG), Camprafaud (CAM), Roucadour (ROU) Téviec (TEV), Noyen (NOY), Vaihingen (VAI) and Bercy (BER). **b.** Chronological and cultural contexts of the *Sus scrofa* archaeological samples. **c.** Position of the phenotypic markers selected for the study of the *Sus scrofa* skeleton with their respective protocol of morphometric digitization: 3D surface and curve landmarks and semilandmarks respectively of mandible's symphysis and ramus (see Neaux et al., 2020 for methodological details), 3D surface semilandmarks of the calcaneus (see Harbers et al., 2020a for methodological details) and the 3D morphometric mapping and Cross Section Area (CSA) of the humeral shaft (See Harbers et al., 2020b for methodological details). The topography of the shaft cortical thickness is rendered by a standardized morphometric map with chromatic scale from thinnest (dark blue) to thickest (red). Red areas represent area of muscular insertions (see Harbers et al., 2020b for further methodological details).

Sus scrofa, we used a k-nearest neighbor (kNN) classification in the two first canonical axes of the morphospace via a training model of three groups representing each of these interaction modes: (1) modern and Mesolithic wild-caught wild boars, (2) modern captive wild boars, and (3) modern pigs including industrial breeds and landraces. The value of "k" was chosen as the square root of the number of specimen's "n" in the comparative material following (Lall and Sharma, 1996); therefore, $k = 9$ for the humerus dataset ($n = 86$), $k = 10$ for the calcaneus dataset ($n = 95$) and $k = 7$ for the mandible dataset ($n = 43$). To check for the reliability of the kNN classification we assessed its congruence with the prediction obtained by fitting their values with the multiple linear discriminant model (CVA) performed for the three groups described previously (Supplementary Figure S4).

To visualise calcaneus and mandible shape deformations along the canonical axes, we calculated the theoretical minimum and maximum shapes for each axis, then associated them, using a heatmap, on the landmarks corresponding to the distance between the minimum and maximum values along the first two canonical axes. To visualise variations in humerus cortical thickness topography along the canonical axes, we calculated the theoretical minimum and maximum morphometric map for each axis.

All the statistics were performed using R (R Core Team, 2017). ANOVA and PCA were performed using the R package "stat" (R Core Team, 2017). Model based Gaussian mixture analyses of size univariates were performed with "Mclust 5" (Scrucca et al., 2016). LDA prediction using the package "MASS" (Venables et al., 2002) and visualisations were performed using "geomorph" (Adams and Otárola-Castillo, 2013) and "rgl" (Adler and Murdoch, 2017). The kNN algorithm was performed using the package 'class'(Torgo, 2011).

3.1.1. Stable isotope study

A piece of bone was cut from the diaphysis of the *Sus scrofa* calcaneus or humerus. Bone surfaces were cleaned by abrasion and reduced to powder. A fraction comprised between 355 and 710 μm was used for collagen extraction. The extraction used approximately 150–250 mg of powder and followed the procedure described in (Bocherens et al., 1991). Coupled measurements of $\delta^{15}N$ and $\delta^{13}C$ were conducted on 300–400 μg of collagen on an elemental analyser Thermo Flash 2000 interfaced with a Thermo DeltaVAdvantage IRMS. The analytical precision, estimated from the repeated analysis (N = 8 to 12 within each run) of our laboratory standard (alanine normalised to the IAEA-600 caffeine international standard), was 0.1‰ for $\delta^{13}C$ and $\delta^{15}N$ values. Over the course of these analyses, the alanine standard gave mean values of 0.58‰ for $\delta^{15}N$ (expected value: 0.60‰), −22.08‰ for $\delta^{13}C$ (expected value: −22.17‰), 40,4% for C content (expected value: 40.4%) and 15.6% for N content (expected value: 15.7%). The aurochs, deer and cattle bone collagen were extracted within the framework of a previous study, following the same procedure. The $\delta^{13}C$ were published (Drucker and Bocherens, 2009) but the $\delta^{15}N$ values remain unpublished.

4. Results

4.1. Bone size variation in modern and ancient Sus scrofa

All four phenotypic markers displayed a common pattern of size variation (Fig. 2), with overall significant differences among the samples of wild, captive and domestic *Sus scrofa* for the humerus cross section (ANOVA = F:10.81, $p < 0.0001$), the centroid sizes of calcaneus (ANOVA = F:9.302, $p < 0.0001$), the mandible symphysis (ANOVA = F:2.635, $p = 0.0463$) and the ramus (ANOVA = F:3.428, $p = 0.0251$). All four markers displayed (1) an important size decrease between Mesolithic and extant wild boar populations of Western Europe (−16% for the calcaneus) and (2) an increase in bone size (+15% for the calcaneus) in traditional and industrial pig breeds compared to modern hunted or captive wild boars, or even Mesolithic wild boars. Captivity in wild boars does not induce any significant size changes in calcaneum and mandible but it does show an increase in the CSA of the humerus compared to free ranging wild boars (Fig. 2), suggesting that captivity induce an increase in wild boar body mass but not of their body size.

Size variation in Neolithic *Sus scrofa* calcaneus covers the whole size range from the smallest wild boars to some of the largest industrial pig breeds. Regarding the body mass proxy (humeral shaft cross section area), Neolithic *Sus scrofa* are within the range of Mesolithic and modern wild boars. According to model-based density estimations, calcaneus size variation is clustered into two groups: a small one, similar in size to current wild boars, and a large one, similar in size to current pigs and Mesolithic wild boars. Current pigs, from landraces to industrial breeds have a larger CSA than extant and Mesolithic wild boars. Density estimations found three components of variation in the humeral CSA of Neolithic *Sus scrofa*: (1) a small one, similar to small extant wild boars, (2) a medium one, similar to large extant wild boars, and (3) a large one, similar to current-day pigs or Mesolithic wild boars.

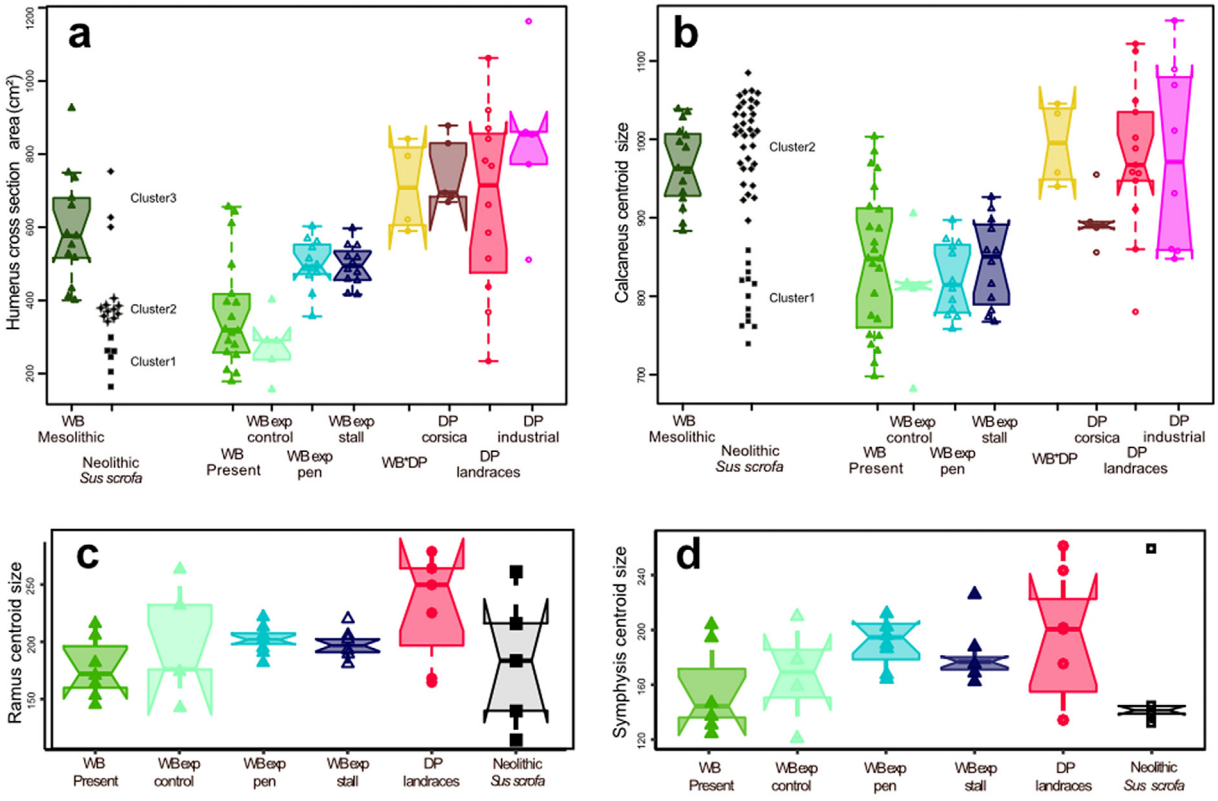

Fig. 2. Size variation in modern and archaeological *Sus scrofa* of Western Europe: (a) humerus shaft cross-section area (CSA), centroid size of (b) calcaneus (c) mandible's ramus, (d) mandible's symphysis. Modern samples are presented with notched boxplots. Model-based Gaussian mixture of size variation in archaeological *Sus scrofa* were performed for humerus shaft CSA (a) and calcaneus centroid size (b) with model-based clustering results displayed by different symbols and named accordingly. Abbreviations: WB = wild boars, WB exp = experimental wild boars, DP = domestic pigs.

4.2. External and structural bone variation in modern and ancient *Sus scrofa*

The variation in bone shape and humeral cortical thickness in Mesolithic and modern wild and domestic *Sus scrofa* displayed congruent patterns of diversification in the CVA morphospace, albeit with slight discrepancies (Fig. 3). This variation is mainly influenced by human-driven selection between modern wild boars and modern pig breeds (CV1), while a plastic response to the human-driven control of mobility in wild boars is aligned with the second canonical axis (CV2), showing the prevalence of artificial selection over anthropogenic behavioural control in the phenotypic diversification of this species. It is worth noting that hybrids between wild boars and pigs (which were only available for the calcaneus and humerus) show a different diversification pattern: closer to hunted wild boars for the calcaneal shape variation (Fig. 3a) and closer to landrace and industrial pig breeds for the topography humeral shaft cortical thickness, showing the greater influence of heredity in the former (Fig. 3b). Finally, one can also note that Mesolithic and extant wild boars display similar humeral cortical topography (Fig. 3b) but clear phenotypic divergence in their calcaneal shape variation (Fig. 3a). For the mandibular-ramus (Fig. 3c) and symphysis (Fig. 3d), the divergence due to selection and plasticity is found along both the CV1 and CV2, but also

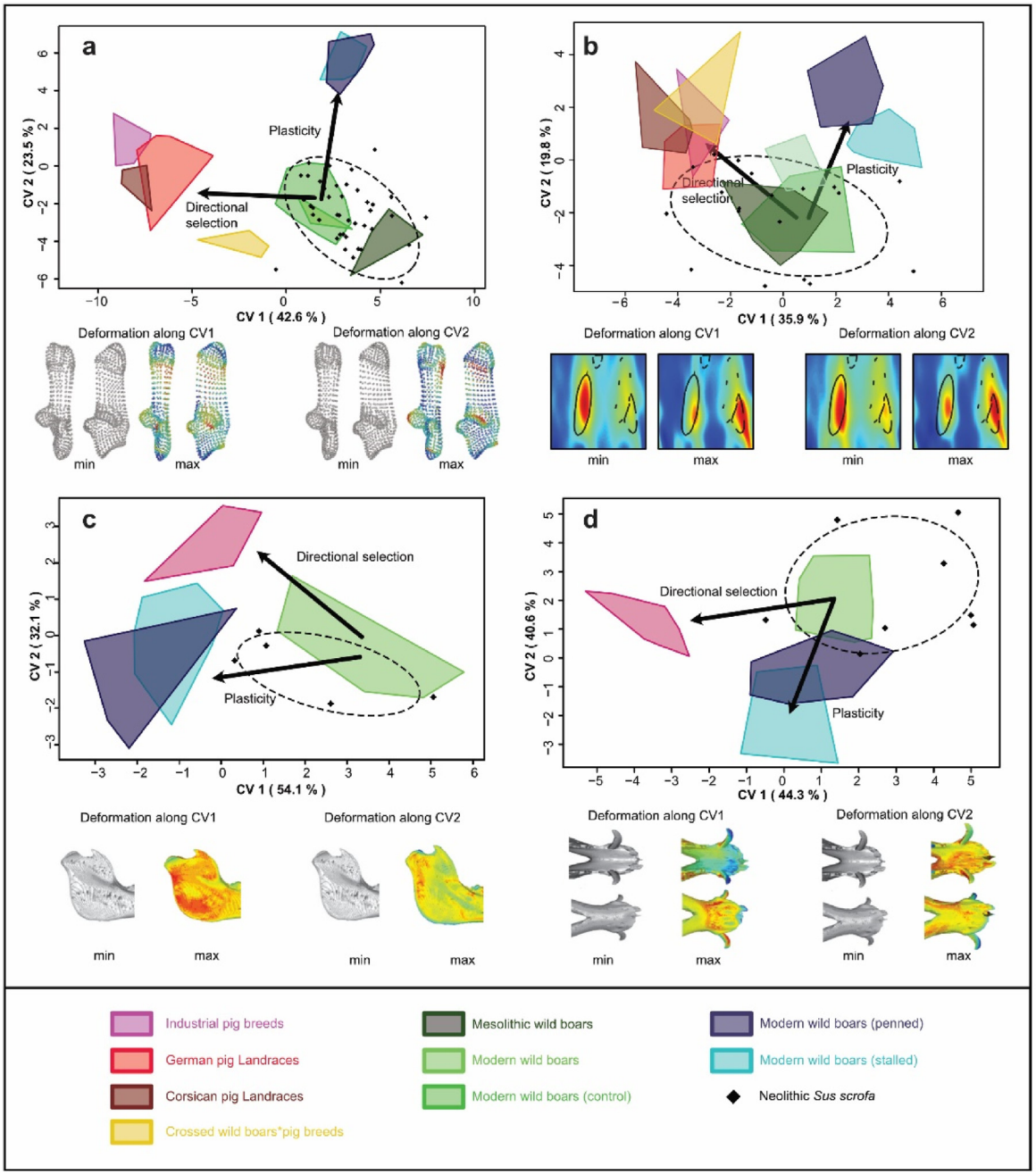

Fig. 3. Phenotypic variation of Neolithic *Sus scrofa* compared to Mesolithic, modern wild captive and domestic *Sus scrofa* from Western Europe. Morphospaces and shape deformations from first and second CVA axes were computed from the shape variation of the calcaneus (a), the morphometric mapping of the humeral shaft cortical thickness with the four muscle attachment displayed (b), the mandible-ramus (c) and the mandible's symphysis (d).

resembles the pattern observed for post-cranial bones (even though the morphospace is rotated).

When projecting the variation of Neolithic *Sus scrofa* over the pattern of phenotypic diversification described previously, we observed that it was centred, albeit greater, within the phenotypic variation of Mesolithic and modern wild boars in their natural habitat; however, patterns differed according to the markers considered. Variability in humeral cortical topography stretches towards the directional selection trajectory of pig breeds and overlaps with the variation of landraces pigs (Fig. 3b). On the other hand, the calcaneus shape variation spreads towards captive wild boars without overlapping (Fig. 3a), the mandible-ramus displays a variation intermediate between hunted and captive wild boars (Fig. 3c), while the symphysis reaches the range of captive wild boars (Fig. 3d).

4.3. Neolithisation and phenotypic diversification in Sus scrofa

CVA prediction and kNN Classification of the Neolithic *Sus scrofa* according to the hunted, captive or domestic phenotypic comparative models computed separately for each morphospace (Fig. 4a, SI4) shows that 92% of the Neolithic *Sus scrofa* have a phenotypic variation aligned with the variability of wild boar living in a natural habitat, suggesting that they behaved like wild boar, in an environment without human ecological disturbance, apart from harvesting. The projection of these morphometric inferences along the timeline from Mesolithic to Late Neolithic (Fig. 4c) shows that by 5200 BCE, in Early Neolithic contexts of Southern France, and by 4000 BCE in Middle Neolithic France (Bercy) and Germany (Vaihingen), a new morphotype of small *Sus scrofa* can be observed. This small morphotype is on average 27% smaller than the large morphotype present since the Mesolithic and up to 29% smaller when compared with the large Neolithic *Sus scrofa* populations. Moreover, between the Mesolithic and the Late Neolithic, the large hunted *Sus scrofa* displays a 4% size increase.

CVA predictions and kNN algorithm identify only four Neolithic *Sus scrofa* with the phenotypic signature, for the humerus and mandible, of adult wild boars raised in captivity (Fig. 4a). These captive specimens are observed around 5200 BCE in Early Neolithic contexts of Fontbrégoua, circa 4750 BCE at Gazel (context of transition between Early and Middle Neolithic) and later, by 4000 BCE, in the Middle Neolithic contexts of Bercy in Northern France.

Finally, the first phenotype that could be considered under anthropogenic reproductive selection was observed in the middle Neolithic site of Noyen-sur-Seine around 3800 BCE and in the late Neolithic site of Chalain around 3000 BCE. These five domesticated phenotypes were only detected via the morphometric mapping of the humeral cortical thickness, in both small and large morphotypes (Fig. 4a).

4.4. Results from stable isotope analysis at Chalain

The collagen extraction yield averaged 136 mg/g (24–199 mg/g) and the collagen carbon and nitrogen contents averaged 42.3% (39.5–44.2%) and 15.2% (14.0–16.2%). The C:N atomic ratios varied from 3.24 to 3.31 in *Sus scrofa* and 3.17 to 3,25 in the remaining fauna (SI 2). These criteria testify to the high preservation of bone collagen at this site and support the suitability of all stable isotope data for interpretation.

The $\delta^{13}C$ values measured in *Sus scrofa* vary between −22.3‰ and −19.6‰ (Fig. 4b). These values are higher than those measured in aurochs (−24.6‰ to −23.6‰) and red deer (−24.3‰ to −22.6‰) and partly overlap with those measured in domestic cattle (−23.5‰ to −22.0‰) at the same site (Fig. 4). In *Sus scrofa*, the $\delta^{15}N$ values vary from 4.2‰ to 8.0‰ and are on average higher (6.4‰) than those measured in aurochs, red deer and cattle when considered together (mean = 5.8‰, from 4.9‰ to 6.8‰) (Supplementary Table S2 and Fig. 4). The δ13C and δ15N values of the four suids with a “wild caught” phenotype and a small size do not differ from the large size wild caught *Sus*. The three suids classified in the “domestic pig” phenotypic category have intermediate $\delta^{13}C$ values (−21.3‰ to −21.1‰), two of which have the lowest $\delta^{15}N$ values of this dataset for *Sus scrofa* (4.2‰ and 4.4‰).

5. Discussion

Using wild boars from the Mesolithic, as with the T0 for *Sus Scrofa* evolution during the Holocene, we first observed that current wild populations of *Sus scrofa* in the area under study have lost 16% of their body size compared to wild populations living in Western Europe some 2500 years before the Neolithic transition. This supports our current understanding of a global body mass reduction of large mammals by the end of the Pleistocene (Smith et al., 2018). Considering that body size in wild boars follows Bergman's rule Albarella et al., 2009, it has been argued that their body size reduction over the last 10 000 years was mainly due to adaptations to the global temperature increase during the Holocene (Albarella et al., 2009) However, human disturbance as the driver of the reduction in the body size of large mammals since the Late Pleistocene is also proposed (Pelletier and Coltman, 2018; Pigeon et al., 2017; Smith et al., 2018; Sullivan et al., 2017), with the unbalanced human harvesting of large prey as a key driver for body size reduction in large mammals (Darimont et al., 2009, 2015). Interestingly, we found a slight increase of wild boar body size during the Neolithic, in agreement with what has been found for wild boar populations during the Neolithic and Bronze Age in the Iberian Peninsula (Navarrete Belda and Saña Seguí, 2017). This suggests that the harvesting behaviour inducing size-selective harvesting of wild *Sus scrofa* populations occurred later, probably over the last two centuries, when harvesting pressure accelerated drastically (Coltman et al., 2003; Pigeon et al., 2017).

With the Neolithic transition in Western Europe by the 6th millennium BCE, we can observe the co-existence of a large and a small morphotype of *Sus scrofa*, with an almost 30% size difference during the whole Neolithic. The occurrence of small-sized *Sus scrofa* from the early Neolithic onward in Europe would be congruent with the well-documented arrival in Western Europe of small populations of *Sus scrofa* domesticated from a Near Eastern population (Evin et al., 2015; Krause-Kyora et al., 2013; Ottoni et al., 2013). The factors explaining this size difference compared to endemic European wild boar have not been fully investigated yet, but they might be inherited from both the wild ancestral populations in the Near East, considered as a smaller sub-species (*Sus scrofa lybicus*) (Groves, 2007), with their body size reduction being the process of domestication by 8000 BCE in this area (Price and Evin, 2019). Both genetic legacies have left a strong phenotypic imprint on this population which then dispersed throughout Europe (Evin et al., 2015; Ottoni et al., 2013). Despite their size difference, however, both the large and small Neolithic *Sus scrofa* in our dataset displayed a shape variability within the norm of reaction of wild boars behaving in their natural habitat, without any mobility control.

The wild behaviour suggested by their bone morphology is not contradicted by their feeding behaviour, assessed through the stable isotopic study of the 30 large and small *Sus scrofa* from the Late Neolithic site of Chalain (Fig. 4b). Here, the $\delta^{13}C$ values measured in aurochs and red deer reflect a forested habitat, where the canopy effect results in lower $\delta^{13}C$ values in plants (van der Merwe and Medina, 1991) and in the herbivores feeding on them (bone collagen $\delta^{13}C$ values in modern deer from deciduous forests

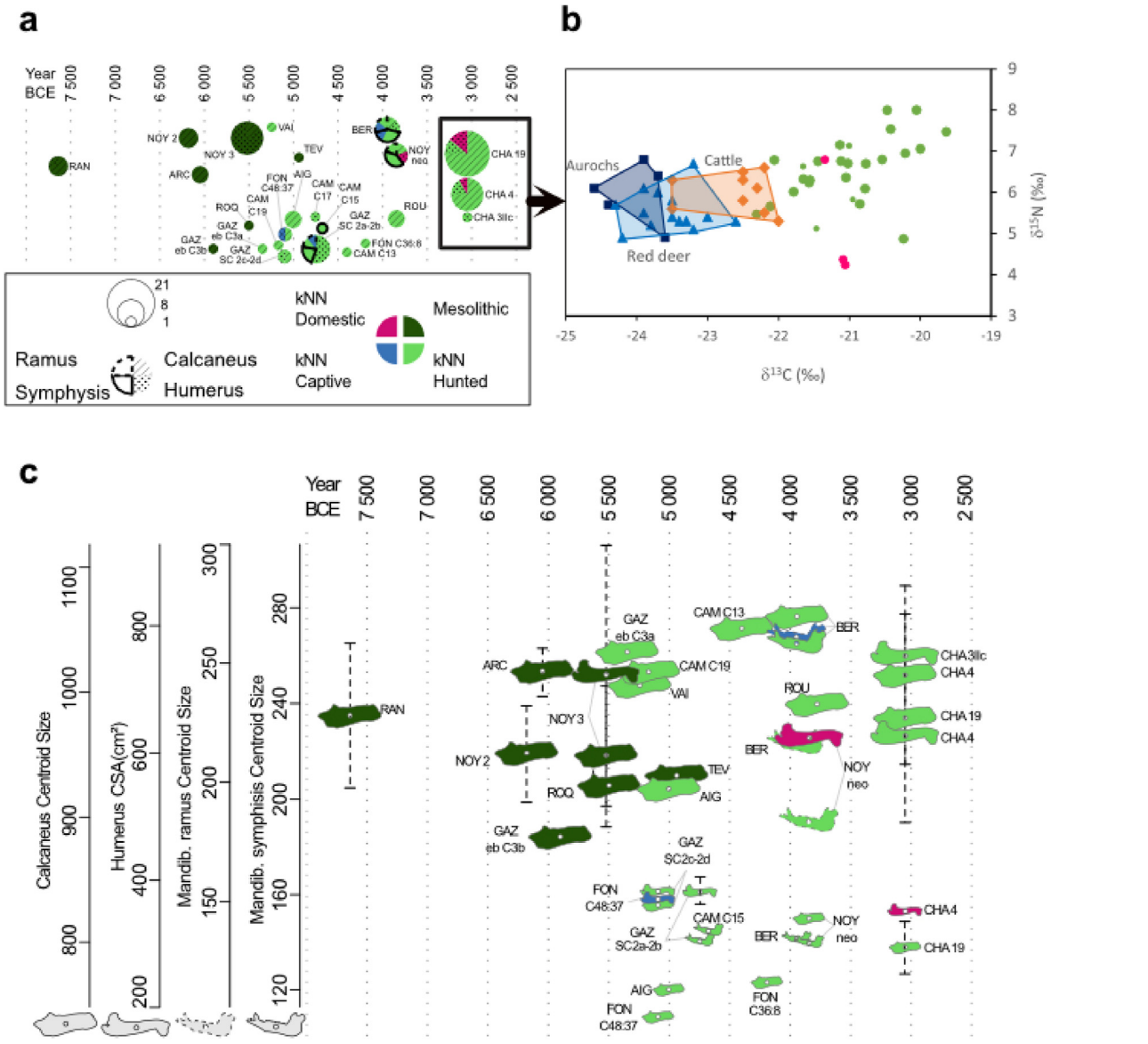

Fig. 4. **a.** Pie charts representing the classification of Neolithic specimens according to the kNN algorithms in the canonical morphospace of each bone marker (humerus, calcaneus, mandibular ramus and symphysis). The pie charts are spread horizontally along the chronology of the archaeological contexts and vertically according to their latitudinal positions. **b.** Diagram displaying the distribution of the $d^{13}C$ and $d^{15}N$ values obtained from the bone collagen of *Sus scrofa* specimens from Chalain 3, 4 and 19. Also included are the isotopic values for aurochs, red deer and cattle (Drucker and Bocherens, 2009). *Sus scrofa* individuals are displayed according to their kNN identification and their model-based size clustering (Small = small dot, Large = large dot) **c.** Phenotypic diversification of *Sus scrofa* from Mesolithic to Late Neolithic displayed by size variation and kNN identification of each bone (CSA=Cross Section Area). The large and small size of the bone pictograms correspond to their size cluster identified by model-based Gaussian Density estimations.

average −23.8‰ and are mostly ≤ −22.6‰; (Drucker et al., 2008), values corrected for the fossil fuel effect). The higher $\delta^{13}C$ values measured in *Sus scrofa* may not be directly comparable to those measured in herbivores because their diet may have included a significant proportion of fruits (Ballari and Barrios-García, 2014; Schley and Roper, 2003). Fruits have higher $\delta^{13}C$ values (by 1‰) compared to leaves in understory vegetation (Roberts et al., 2017), and this difference is inherited in frugivorous species compared to folivorous species (+1–1.5‰ (Krigbaum et al., 2013). Taking this into account, the *Sus scrofa* found at Chalain would have occupied a wide range of habitats from forests to open environments, while their $\delta^{15}N$ values suggest a low to moderate contribution of animal protein in their diet. Overall, these results are in agreement with the opportunistic omnivorous feeding behaviour and wide foraging habitat observed in modern wild boars (Ballari and Barrios-García, 2014), as well as in Mesolithic European wild boars which were alternatively found foraging in woodlands on a very low animal protein diet (in Denmark (Maring and Riede, 2019)), in a wider range of habitats with varying degree of openness (in the Netherlands (Brusgaard et al., 2022)) or in an open environment and with a greater animal protein component (in Belgium (Bocherens et al., 2007)).

Both morphometric and isotopic signatures suggest that the evolutionary interaction between both large and small Neolithic *Sus scrofa* populations and the Neolithic societies of Western Europe was mainly driven by harvesting (hunting). This hypothesis is supported by the recent integrated study of Late Mesolithic-Neolithic human-suid interaction in Rhine-Meuse, which found no evidence of small suid management during the Neolithic occupation (Brusgaard et al., 2022). However, previous studies from

Eastern Europe in Late Neolithic Romania have considered small *Sus scrofa* as domestic livestock living in close proximity to the Neolithic settlements (Balasse et al., 2016, 2019; Evin et al., 2015), suggesting that suid interactions with Neolithic societies/villagers has differed at both ends of the Neolithic dispersal in Europe. Nevertheless, the co-occurrence of large and small wild morphotypes of *Sus scrofa* in Neolithic Western Europe raises several questions. Were these small *Sus scrofa* feral populations, stemming from the domestic *Sus scrofa* introduced by early Neolithic farmers, roaming free and independently from the care of Neolithic people and hunted throughout the period? If so, can we consider that events of admixture and gene flow between the small and large populations were limited in time and space, preventing the morphological homogenization of the two lineages? Were these small *Sus scrofa* under the care of Neolithic people and therefore "domestic" (Dwyer, 1996), albeit under an extensive management system as seen in the pre-industrial diversity of pig production in New Guinea (see synthesis and references in (Price and Hongo, 2019)) where they are considered as livestock but behave freely in a natural habitat, with occasional proximity to the settlement? In these extensive management systems, females are captured (along with the occasional male) and penned for several months for impregnating and then left free to roam in order to be harvested in the wild for pork (Dwyer, 1996). Their short period of captive life would not have left a strong enough imprint in their bone variation for our morphometric approach to detect. Whatever the answers, the emergence of this small, wild type of *Sus scrofa* has produced a new phenotypic and genetic diversity in the *Sus scrofa* populations of Western Europe.

Beyond the body-sized diversity of *Sus scrofa*, fostered by the translocation of domesticated pigs of Near Eastern ancestry, few anthropogenic morphological changes beyond the phenotypic variation of *Sus scrofa* living freely in its natural habitat can be observed during the Neolithic niche construction in Europe. The first phenotypic change observed during the Early and Middle Neolithic is a plastic response of tarsal and skull bones similar to the variation induced by a life in captivity (Harbers et al., 2020a; Neaux et al., 2020, 2021). The rare occurrence of this plastic response to captivity in the Neolithic *Sus scrofa* suggests that captivity was a rare practice in Neolithic Europe and that wild capture management (Dwyer and Minnegal, 2020), as described above, would have been the main interaction at that time. According to this management system, only a few females and occasionally castrated males were kept in captivity, which would explain why so few occurrences are observable in the archaeological record. The limitations of our study, aside from the finite number of individuals to cover such a long time period over such a large geographic area, are therefore double. First, our methodological approach relies on adult and sub-adult specimens, while husbandry practices could necessitate the culling of most males before the age of two. This means that the phenotypic variation of a large proportion of the population may not have been sampled in this study, reducing the possibility to capture phenotypic adaptations to Neolithic habitat transformations at a greater scale. Further age-free phenotypic markers, therefore, need to be developed. The second limitation is the reductionist character of a comparative approach relying on a modern referential, even with experimental conditions such as the one presented here. The complexity of the potential configuration encompassing the interaction between people and suids during the Neolithic can never be fully covered or deciphered.

Around 6000 years ago, by the Middle and especially the Late Neolithic, the 3D topography of the humeral shaft cortical thickness can pick rare but significant phenotypic changes along the selective trajectory towards modern pig breeds (Fig. 3b). To understand the human intention behind these changes, one need to consider first that differences in cortical topography between hunted wild boars and current pig breeds are due to functional changes driven by selection for fast growth and muscle production, altering the gait of the animal (Harbers et al., 2020b). Then, that humeral shaft topography in wild boars is mainly influenced by body mass variation (Harbers et al., 2020b). Accordingly, the similarity in the shaft cortical topography of some Middle and Late Neolithic *Sus scrofa* with current pig breeds suggests that they might have reached extreme body masses leading to a functional change in their humeral shaft anatomy. Was their diet controlled for extreme weight gain? Are we witnessing the early evidence of selection for fast body growth or greater fat production? It is impossible to answer this question yet; although, in the pre-industrial pig husbandry systems of New Guinea, there are ethnographic examples of captured wild boars fattened to the point that they cannot stand on their feet (Dwyer, 1996). The isotopic signature of Late Neolithic specimens of Chalain, where "domestic", "wild" and "captive" phenotypes are present, did not provide any evidence that these "domestic" pigs had a diet richer in animal protein compared to the others (Fig. 4b). However, if these special pigs had been fattened with a grain-rich diet, we would not have been able to observe it with these isotopic proxies, unless the grains were grown on manured fields (Price and Hongo, 2019).

6. Conclusion

This study has provided strong confirmation that the archaeological record can help track the impact of a millennia of human niche construction on the evolution of animals (Laland and O'Brien, 2011) and contribute to the documentation of their evolutionary trajectory (Sarrazin and Lecomte, 2016). We found that the Neolithic Niche Construction had inceptive but limited impact on the phenotypic evolution of *Sus scrofa* in Western Europe. In the 4500-year timeframe of our study we did not find any evidence of size-selective harvesting, though a strong size decline between Pre-Neolithic and modern wild boar populations was observed, suggesting that harvesting pressures on size in *Sus scrofa* populations did not happen during the Neolithic transition. The main impact was the translocation of allochthonous domestic populations of a smaller size, which increased the local phenotypic diversity of *Sus scrofa* in Western Europe. The feralisation of these alien populations did not seem to induce a novel selective pressure on local populations or a phenotypic homogenization among the local and feral populations. Nevertheless, the greater phenotypic diversity in Western Europe *Sus scrofa* produced by this introduction could have fostered the local domestication in Europe. A loose rearing model, which would have induced no observable traits for most of the Neolithic *Sus scrofa* in our dataset, might have been the most common husbandry practice for these animals during this period; nonetheless, rare evidence of phenotypic divergence from the variation seen in boars in a natural habitat was documented. The first is observed from the Early Neolithic onwards and is most likely due to major mobility constraints. Later in the Neolithic, phenotypic changes suggest new selective pressures on *Sus scrofa* populations cared for by Neolithic people, maybe as early evidence of selective breeding for fast growth or fat production. Further research is still required, therefore, including paleogenomic and metabolomic studies on relevant and well-dated samples from Mesolithic to modern times in order to document the rapid evolutionary pace of cultural processes.

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Authors contributions

TC conceptualized and funded the research, conducted the experimental research, supervised the research activity and wrote the initial draft and the review. HH and DN performed the formal Morphoemtric analysis, performed the visualisation of the results and contributed to write the mansucript. MB conducted and interprete the isotopic study and performed the visualisation of the results and contribute to write the paper. GL and FD performed formal isotopic analyses. HB and DD provided isotopic values and contributed to write the draft. CZ and RC provided computing resources and contribute to write the paper. RMA, SB, AB, LG, LG, CM, TP, AT, JDV provided contextualised remains of *Sus scrofa* and contributed to write the manuscript. AH conceptualized and supervised the research activity with TC and contribute to write the paper.

Declaration of competing interest

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

Data availability

I have share the link to my data/code in the data availability section at the end of the manuscript downloaded

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2023.108100.

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