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RESEARCH

Origins and interactions of Neolithic populations from Liguria (NW Italy): a craniofacial morphometric study

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Abstract
The Neolithic transition in Europe, marked by the shift from foraging to farming, has traditionally been explained through models of either cultural or demic diffusion. However, emerging evidence suggests more complex, regionally specific interactions between incoming farmers and local foragers. In Liguria, a coastal region in northwestern Italy, the Neolithic adoption appears later than in southern regions, and the scarcity of Mesolithic sites raises questions about potential interactions, though this may be due to preservation bias. To investigate the biological origins and history of Neolithic populations in Liguria, this study applies craniofacial morphometric analysis to 27 adult individuals from Early, Middle and Late Neolithic contexts. Two datasets including comparative samples ranging from the Upper Paleolithic to recent periods were employed, one with 30 measurements ($n=629$) and one with 10 ($n=2178$). Morphometric relationships were analyzed using multiple multivariate techniques, including Principal Coordinate Analysis, Neighbor-Joining clustering, Principal Component Analysis, and Discriminant Function Analysis. The results indicate that while Ligurian Neolithic individuals are part of the broader European Neolithic variability, Early Neolithic individuals show a certain morphological affinity with Mesolithic hunter-gatherers, suggesting possible genetic admixture. In contrast, Middle Neolithic individuals appear more homogeneous and less influenced by forager ancestry, suggesting population continuity without further admixture. These findings differ from the broader European trend of increasing hunter-gatherer ancestry over time. Although paleogenomic data from Liguria are currently lacking, this morphometric study provides critical insight into regional population dynamics during the Neolithic and highlights the need for integrated genetic and archaeological approaches in future research.

Keywords Neolithization · Western Liguria · Craniometric analysis · Morphological variation · Mesolithic

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Introduction

The Neolithic Transition, i.e. the shift from hunting and gathering to a production-based economy rooted in the domestication of plants and animals, was described as *one of the fundamental structural processes of human history* due to the unprecedented demographic expansion it triggered (Bocquet-Appel 2011). This pivotal milestone in human evolutionary history (Larsen 2023) involved cultural and societal changes, and transformed several key aspects of human ecology, including diet, the prevalence of specific diseases, levels of gene flow, and reproductive fitness (Pinhasi and Stock 2011; Page et al. 2016). This was a widespread phenomenon involving nearly all temperate regions globally, albeit at different times and arising from several independent centers of plant and animal domestication (Diamond 2002; Diamond and Bellwood 2003).

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In Europe, research in various archeological and paleobiological disciplines – including osteoarchaeology, craniometrics, dental anthropology, stable isotope analysis, and paleogenetics – suggests that the shift from foraging to farming was a complex phenomenon. Historically, two contrasting models dominated the debate: the cultural diffusion model, proposing that knowledge of plant and animal domestication spread from early West Asian farmers to indigenous European hunter-gatherers (Dennell 1983, 1985; Price 2000; Whittle 1996, 1997; Whittle and Cummings 2007; Zvelebil 1986, 1989, 2000; Zvelebil and Rowley-Conwy 1984, 1986), and the demic diffusion model, which posits that early farmers migrated from West Asia, replacing or intermixing with native populations (Ammerman and Cavalli-Sforza 1971, 1973, 1984; Barbujani and Bertorelle 2001; Barbujani et al. 1998; Cavalli-Sforza 1996; Cavalli-Sforza et al. 1993, 1994; Pinhasi et al. 2005; Renfrew 1992, 1996; Haak et al. 2010). However, this binary framework is now considered overly simplistic. The spread of a Neolithic way of life likely involved diverse modes of interaction between biology and culture, varying across time and space. Even before the advent of extensive paleogenetic datasets, archaeological and anthropological evidence indicated the need to acknowledge multiple mechanisms, including mass migration, demic diffusion, infiltration, elite dominance, leapfrog colonization, frontier mobility, and cultural contact (Lemmen et al. 2011; Shennan 2017; Zilhão 1993, 2000, 2001; Zvelebil 2001). It is therefore essential to study this mosaic of human interactions and adaptations from a micro-regional perspective and with high diachronic resolution (Shennan 2017; Tringham 2000).

Recent research, including new radiocarbon dates, has highlighted the diversity of Neolithization processes across the broader western Mediterranean (Guilaine 2017; Perrin and Manen 2021; Shennan 2017). This has led to the development of more nuanced models of Neolithic spread, which challenge the idea of a uniform process. In the northwestern Mediterranean, archaeological and palaeoecological data suggest that a potential period of coexistence occurred in the first half of the 6th millennium cal BCE. Settlement patterns during this period show that Mesolithic communities were predominantly situated in highland and lowland areas, while Neolithic communities tended to cluster along the coast. These differences likely reflect subsistence strategies, with Mesolithic populations focused on hunting, fishing, and gathering, contrasting with the Neolithic emphasis on agro-pastoralism (Branch et al. 2014; Battentier et al. 2018). However, Perrin and Manen (2021) caution against oversimplifying the interactions between late hunter-gatherers and early farming communities. They emphasize the need for precise chronological mapping to avoid assumptions about direct interaction due to the varying population densities among Late Mesolithic groups in the Mediterranean. In this study, we will focus on the region of Liguria in the northwestern Mediterranean, where limited evidence of overlap between Mesolithic foragers and Neolithic farmers has led some scholars to propose an "avoidance strategy" (Battentier et al. 2018).

Italy holds a rich archaeological record of early Neolithic settlements, dating back to the late 7th millennium BCE, particularly in southern regions such as Apulia, Basilicata, Campania, Calabria, and Sicily (Binder 2013; Fugazzola Delpino et al. 2002; Pinhasi et al. 2005; Skeates 2003). These sites exhibit a comprehensive cultural package that includes agriculture, animal husbandry, sedentism, polished stone tool technology, and ceramics. A key question concerns the interactions between the last hunter-gatherers and the first farmers in Italy during the spread of the Neolithic. The Impresso-Cardial Complex (ICC) persisted from 6200−5300 cal BCE in the south and from 5800−5000 cal BCE in the north, in temporal and geographical partial overlap with the last Late Castelnovian Mesolithic sites (Fugazzola Delpino et al. 2002; Franco 2011; Collina et al. 2019; Lo Vetro et al. 2022; Discosti et al. 2023).

Liguria, a mountainous coastal region in northwestern Italy, has extensive archaeological documentation spanning from the Middle Pleistocene to the Middle Holocene. Numerous cave sites, especially in the Finalese area (Savona province), have yielded traces of occupation belonging to all Neolithic phases, beginning with the earliest ICC dates in northern Italy (5800−5000 cal BCE; Biagi and Starnini 2016; Binder et al. 2017; Bruschini et al. 2023; Maggi et al. 2023). The shift to the "Middle Neolithic" phase – i.e., the entrenching of the Neolithic production economy – is marked in Liguria and northern Italy by the emergence of the "Square Mouthed Pottery" culture (SMP) starting from the beginning of 5th millennium BCE (Del Lucchese and Starnini 2021), while in central and southern Italy it is characterized by the appearance of painted pottery around the mid-6th millennium BCE (Bagolini and Pedrotti 1998). Liguria is also rich in late Neolithic Chassey-Lagozza evidence, and later Copper, Bronze, and Iron Age sites (Biagi and Starnini 2016; Binder 2013; Binder and Maggi 2001; Binder et al. 2017; Maggi and Tiné 2023; Maggi and Pearce 2023; Del Lucchese et al. 2023; de Marinis and Melli 2023). Notably, the karstic caves in western Liguria (Finalese and Val Pennavaira) have yielded well-preserved Neolithic burials, providing insights into population biology (Canci et al. 1993; Formicola 1997; Galland et al. 2023; Messeri et al. 1977; Milanesi and Lombardi 1978; Parenti and Messeri 1962; Passarello 1974; Sparacello et al. 2019, 2020). However, since most excavations took place between the 1880s and the 1940s (Table 1), the chronology of several

Table 1 Details of the Neolithic craniofacial specimens from Liguria

Individual	Abbreviation	First source of craniometric data[1]	Sex	Excavator	Date ^{14}C BP	Calibrated age BCE	Chrono-cultural attribution	Museum repository[2]
Arene Candide 1 Tinè	AC1T	Canci et al. 1993	M	Tiné 1973-76	5700 ± 60	4704 − 4374	SMP	MAF
Arene Candide 2 Tinè	AC2T	Canci et al. 1993	M	Tiné 1973-76	6145 ± 25	5209 − 5011	ICC	MAF
Arene Candide 7PE	AC7PE	Parenti and Messeri 1962	M	Morelli 1884–1887	5815 ± 25	4767 − 4586	SMP	MAL
Arene Candide 8PE	AC8PE	Parenti and Messeri 1962	M	Morelli 1884–1887	5786 ± 25	4708 − 4555	SMP	MAL
Arene Candide I Issel (3407–3408 Ge)	AC3407GE	Parenti and Messeri 1962	M	Morelli-Issel 1884–1887	N/A	N/A	SMP (stone cist)	MSNG
Arene Candide III	ACIII	Parenti and Messeri 1962	M	Bernabò Brea 1940–1950	5860 ± 30	4800 − 4619	SMP	MAF
Arene Candide III Issel (5700 Pig)	AC5700P	Parenti and Messeri 1962	M	Morelli-Issel 1884–1887	N/A	N/A	SMP (stone cist)	MUCIV
Arene Candide IV	ACIV	Parenti and Messeri 1962	F	Bernabò Brea 1940–1950	5813 ± 25	4766 − 4558	SMP	MAL
Arene Candide IV Issel (5690 Pig)	AC5690P	Parenti and Messeri 1962	M	Morelli-Issel 1884–1887	N/A	N/A	SMP (stone cist)	MUCIV
Arene Candide IX	ACIX	Parenti and Messeri 1962	F	Bernabò Brea 1940–1950	5830 ± 25	4779 − 4611	SMP	MAF
Arene Candide V Issel (5733 Pig)	AC5733P	Parenti and Messeri 1962	M	Morelli-Issel 1884–1887	N/A	N/A	NEOL	MUCIV
Arene Candide VI	ACVI	Parenti and Messeri 1962	M	Bernabò Brea 1940–1950	5685 ± 25	4581 − 4457	SMP	MAL
Arene Candide VII	ACVII	Parenti and Messeri 1962	F	Bernabò Brea 1940–1950	5825 ± 25	4778 − 4603	SMP	MAF
Arma del Morto 252	AM252	Parenti and Messeri 1962	F	Amerano 1890s	6230 ± 25[3]	5301 − 5073	ICC	MAL
Arma dell'Aquila R1	AA1R	Parenti and Messeri 1962	M	Richard 1938, 1942	6318 ± 33	5361 − 5221	ICC	MAF
Arma dell'Aquila R2	AA2R	Parenti and Messeri 1962	M	Richard 1938, 1942	6155 ± 34	5213 − 5010	ICC	MAF
Arma dell'Aquila R5	AA5R	Parenti and Messeri 1962	F	Richard 1938, 1942	6118 ± 33	5208 − 4956	ICC	MAF
Arma di Nasino 1	AN1	Milanesi e Lombardi 1978	M	Anfossi 1961-74	5285 ± 30	4232 − 4000	Chassey-Lagozza	MNA
Bergeggi 2	BE2	Parenti and Messeri 1962	M	Modigliani 1880	5725 ± 25	4680 − 4494	SMP	MAL
Matta-Sanguineto 01083	MS01083	Parenti and Messeri 1962	N/A	Perrando 1872	6165 ± 35, 6130 ± 30[4]	ca. 5200-5000	ICC?	MAL
Matta-Sanguineto 01085	MS01085	Parenti and Messeri 1962	M	Perrando 1872	6165 ± 35, 6130 ± 30[4]	ca. 5200-5000	ICC?	MAL
Pollera 1 Tinè	PO1T	Messeri et al. 1977	F	Tiné 1972	5790 ± 30	4712 − 4552	SMP	MAL
Pollera 12	PO12	Parenti and Messeri 1962	F	Rossi (?) 1885–1892	5860 ± 25	4794 − 4687	SMP	MAL
Pollera 13	PO13	Parenti and Messeri 1962	M	Morelli 1885–1886	5745 ± 25	4686 − 4527	SMP	MAL
Pollera 30	PO30	Parenti and Messeri 1962	M	Rossi 1885–1892	5760 ± 25	4689 − 4543	SMP	MAL

Table 1 (continued)

Individual	Abbreviation	First source of craniometric data[1]	Sex	Excavator	Date ^{14}C BP	Calibrated age BCE	Chrono-cultural attribution	Museum repository[2]
Pollera 33	PO33	Parenti and Messeri 1962	F	Rossi 1885–1892	5790±25	4711−4555	SMP	MAL
Pollera 6246	PO6246	Parenti and Messeri 1962	F	Amerano 1890s	5710±25	4650−4462	SMP	MAL

[1]Parenti and Messeri (1962) named many specimens differently from here, see Sparacello et al. 2020 for disambiguation. *M* Male, *F* Female, *ICC* Impresso-Cardial Complex, *SMP* Square Mouthed Pottery, *NEOL* Neolithic

[2]*MAL* Museo di Archeologia Ligure, Genova Pegli, *MAF* Museo Archeologico del Finale, Finale Ligure, Savona, *MNA* Museo Navale Romano di Albenga, Albenga, Savona, *MUCIV* Museo delle Civiltà, Roma; *MSNG* Museo Civico Storia Naturale Genova Giacomo Doria, Genova

[3]Date obtained from associated postcranium of nearby burial 253

[4]Date obtained from associated postcranium of individuals Matta 01081 and 01088

burials remained uncertain until a recent radiocarbon dating program that attributed more than 130 individuals to the early (ca. 5700−5000 BCE), middle (ca. 5000−4300 BCE), and late (4300−3700 BCE) Neolithic phases (Sparacello et al. 2019, 2020, 2023a).

Our knowledge of the Ligurian Mesolithic is still very fragmentary, having derived for decades from surface collections from contexts subject to erosion (Biagi et al. 1988; Negrino et al. 2023). Stratified deposits in caves are very rare, and human remains are few and date only to the earliest phase of the Mesolithic. These include the burial of a newborn baby at Arma Veirana (Hodgkins et al. 2021) and two adults as well as several fragmentary remains from Arma di Nasino (Sparacello et al. 2023b). Regarding the cultural phases of the Mesolithic that may have overlapped with the Neolithic during the sixth millennium BCE, i.e. the Late Castelnovian, evidence derives mainly from surface collections of lithic artefacts from open-air sites in eastern Liguria, and only one in western Liguria (Maggi and Tiné 2023). However, none of these sites present a chronostratigraphic reference or is directly dated, and distinguishing between early and late Mesolithic lithic assemblages based solely on the morphology of the armatures is challenging (Negrino et al. 2023). Apparently, the initial Neolithic colonization of Liguria occurred in the western portion of the region, which appears to have been sparsely inhabited by Mesolithic foragers based on archaeological evidence (Binder et al. 2008; Maggi and Negrino 2016), leading to the hypothesis that the two ways of life coexisted for a period in the region but avoided each other (Battentier et al. 2018). However, this scenario may be biased by the fact that Neolithic sites are preserved almost exclusively in caves – which are numerous in the karstic areas of western Liguria and comparatively rare in the east – by erosion of open-air sites, and by the constant accumulation of sediments in the river mouth areas, as demonstrated by information from deep excavations for underground constructions (Arobba et al. 2018; Del Lucchese and Melli 2010).

The presence of microcharcoals dated to around 6100−6000 BCE, alongside *Plantago* pollen in core samples from Rapallo and Sestri Levante (eastern Liguria), has been interpreted as early evidence of agriculture – either from the initial presence of southern farmers or early contacts between Mesolithic foragers and incoming agriculturalists (Negrino 2022; Maggi and Tiné 2023). However, the *Plantago* genus includes over 100 species with cosmopolitan distributions (Pignatti 1982; Hassemer 2019), making its link to agriculture tenuous. Microcharcoals, meanwhile, are present in sediments since the Paleolithic (Marquer 2010), and evidence suggests that early humans did not use fire intensively for land management (Daniau 2008). Moreover, taphonomic processes affecting charcoal are less well understood than those for pollen, complicating interpretations of vegetation-fire dynamics (Patterson et al. 1987). In sum, clear evidence of Neolithic farmer-forager interactions in Liguria remains elusive, and genetic data – direct or via morphological proxies – may provide the only reliable trace of such early contacts.

To date, no paleogenetic analysis on Ligurian Neolithic skeletal material has been published. Thus, this study aims to explore the origins and evolutionary trajectories of Ligurian Neolithic populations through craniofacial morphometrics, a robust proxy for assessing population affinities (Relethford and Harpending 1994; von Cramon-Taubadel 2011; Galland and Friess 2016; Galland et al. 2016). This approach relies on the principle that craniofacial morphology is widely recognized and utilized as a reliable proxy for neutral genetic affinities to reconstruct past population history, particularly in contexts lacking accessible ancient DNA. Numerous studies (e.g., Roseman 2004; Manica et al. 2007; Relethford and Smith 2018) demonstrate that human cranial variation is largely consistent with neutral microevolutionary models (based on genetic drift, dispersal, and gene flow) and has advantages over methods such as dental phenetics, due to a more global integration of the craniofacial complex, which is demonstrably less susceptible to random genetic drift.

While this neutral pattern is dominant, it is modulated by additional factors (von Cramon-Taubadel 2014): climatic selection (chiefly in extreme cold climates, Roseman 2004; Katz et al. 2016) and dietary changes (e.g., with the agricultural transition, Katz et al. 2017). Furthermore, different cranial regions exhibit differential susceptibility to non-neutral forces (Harvati and Weaver 2006; von Cramon-Taubadel 2014).

Despite these complexities, the strong empirical correlation between overall craniometric and neutral genetic variation allows us to confidently employ this morphological relationship to test alternative hypotheses regarding population change, such as those associated with the agricultural transition in Liguria. This may illuminate potential scenarios of population interaction and migration throughout the Neolithic. Through comparative morphometric analyses of craniofacial features, we seek to contribute to a deeper understanding of the demographic processes that shaped ancient communities in the region.

A key objective is to assess whether the Neolithic population of Liguria, as represented by the analyzed cranial remains and in the absence of genetic data, experienced genetic admixture with local hunter-gatherer (HG) groups across different chronological and cultural phases (Early, Middle, and Late Neolithic: EN, MN, LN). To this end, we will examine whether morphometric patterns of craniofacial variation align with known genetic relationships between Upper Paleolithic and Mesolithic hunter-gatherers (HG) and Neolithic early farmers (EF). The presence or absence of a correspondence between genetic and morphometric patterns will be assessed through comparative analyses of samples from different chronological periods and geographic locations in Western Eurasia.

We will explore three possible scenarios to explain variations in morphometric distances and their implications for Neolithic population dynamics in Liguria:

(1) Exclusive EF ancestry: the Neolithic populations of Liguria descended solely from early farmer groups who migrated into the region without genetic admixture with local HG groups.
(2) HG continuity: the Neolithic populations directly descended from local HG groups with no significant genetic input from EF migrants.
(3) EF-HG admixture: the Neolithic populations originated from EF groups who migrated to Liguria and interbred with HG groups, either locally or elsewhere in the Italian peninsula prior to their arrival.

Rather than employing formal hypothesis testing or statistical probability assessments, we will infer the plausibility of these scenarios based on direct observations of relationship patterns among groups.

Materials and methods

Materials

We collected morphometric data from 27 Neolithic craniofacial specimens excavated in Liguria. These specimens belonged to adult individuals recovered from well-known cave sites, including Caverna delle Arene Candide, Arma dell'Aquila, Arma di Nasino, Grotta Marina di Bergeggi, and Arma della Pollera ("Arma" meaning "cave" in the local dialect), as well as lesser-known sites such as Arma del Morto and Arma del Sanguineto or "della Matta" (Fig. 1; Table 1). Sex and adult age status were determined using standard anthropological criteria detailed elsewhere (Varalli et al. 2020). Direct AMS radiocarbon dates (Sparacello et al. 2019, 2020, 2023a) are available for 24 individuals (Table 1). For other specimens, chronological attributions were based on archaeological context from excavation reports, allowing identification of some individuals as belonging to the SMP culture through their characteristic stone cist burials (Bernabò Brea 1946, 1956; Del Lucchese 1997; Sparacello et al. 2020). All individuals exhibited no pathological alterations or taphonomic deformations that could have affected craniofacial morphology.

The sample was categorized into two chrono-cultural groups: the Early Neolithic (EN) associated with the ICC cultural complex and the Middle Neolithic (MN) associated with the SMP culture. A Late Neolithic (LN) group could not be established due to the presence of only a single individual from Arma di Nasino, contemporaneous with the Chassey culture. Consequently, this individual was analyzed separately or grouped with LN/Chassey samples from southern France.

The comparative dataset included cranial specimens spanning from the Early Upper Paleolithic (EUP) (Late Pleistocene MIS 3b) to recent historical periods (the last millennium CE). Data were collected through direct measurements, bibliographic sources, 3D virtual models, cranial contour drawings, and scaled 2D images.

For comparative purposes, a broader dataset was assembled, including adult cranial specimens spanning from the Early Upper Paleolithic (EUP, Late Pleistocene MIS 3b) to the recent historical period (i.e. the last millennium CE, encompassing the late Middle Ages through the modern era). All specimens showed no morphological alterations or pathologies that might affect cranial morphology.

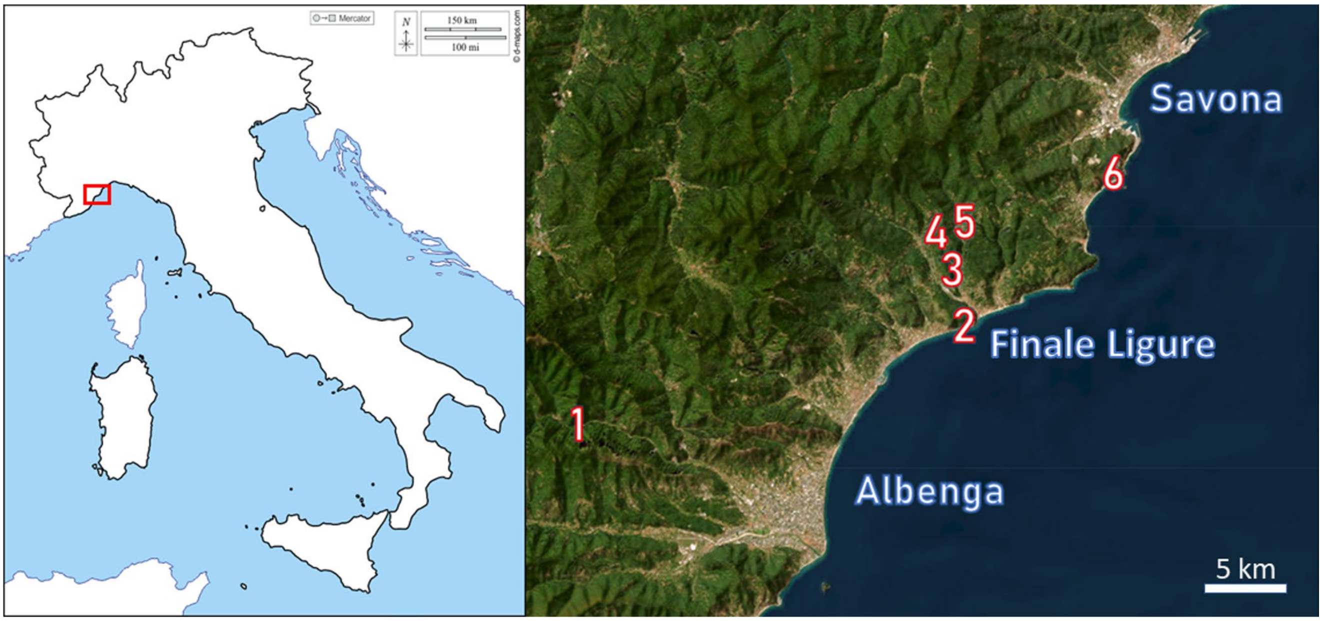

Fig. 1 Geographic locations of Neolithic sites in western Liguria analyzed in this study; 1 Arma di Nasino; 2 Caverna delle Arene Candide; 3 Arma del Sanguineto (o "della Matta") and Arma del Morto; 4 Arma della Pollera; 5 Arma dell'Aquila; 6 Grotta Marina di Bergeggi. Map created using: https://d-maps.com/carte.php?num_car=2322&lang=it and https://srvcarto.regione.liguria.it/geoviewer2/pages/apps/geoportale/index.html; copyright 2025 Maxar technologies

Methods

Data collection

Morphometric data for the comparative dataset were obtained from a variety of sources, including: direct measurements of original fossil specimens conducted by the authors; published literature and personal communications; virtual 3D models; cranial contour drawings and scaled 2D images.

To accommodate varying states of preservation and to enhance analytical scope, two datasets were constructed:

1) Analysis 1 comprised 30 craniofacial measurements and required nearly complete skulls for inclusion. This dataset included 629 crania, incorporating the 27 Ligurian Neolithic specimens. Measurements followed the protocol established by Howells (1973, 1989) and encompassed multiple craniofacial regions to facilitate comprehensive morphological analysis.
2) Analysis 2 included a reduced set of 10 measurements – six overlapping and four alternative variables compared to Analysis 1 – aimed at increasing sample size and improving representativeness. This dataset encompassed 2178 crania, including the same 27 Ligurian Neolithic specimens, with variables selected based on Martin and Saller (1957) and Bräuer (1988).

Specimens were grouped into 23 and 36 analytical units for Analyses 1 and 2, respectively, based on geographic, chronological, and cultural criteria (see Table 2). The complete list of measurements used in Analyses 1 and 2 is provided in Table 3a and 3b, respectively.

Stringent validation steps ensured accuracy:

- Multiple sources were cross-checked for consistency.
- 3D models were used to reconstruct missing data.
- Observer training and repeated measurements minimized error.
- The Perfect Screen Ruler 3.0 tool was used for digital measurements, ensuring intra-observer consistency.
- Cross-referencing of published datasets helped identify and correct errors. A detailed account of data collection and sources is provided in Supplementary Information (SI Text and SI Tables S1a-b)

Missing data estimation and standardization

Missing observations were estimated using multiple regression, stratified by sex and chrono-cultural classification. No more than 30% of data per individual was estimated. Additional measurements from Martin and Saller (1957) and Bräuer (1988) were used as strong correlates for estimation where applicable. The resulting complete datasets obtained after missing data estimation and used in the two analyses

Table 2 Comparative groups and classification criteria for analyses 1 and 2

Analysis 1: Group[1]	Macro-group[1]	Sample size	Approximate date range cal BCE	Geogr.location(s)	Possibly associated archeological cultures
EUP	HG	8	43,000 − 31,000	Czech Rep., Romania, Russia	Streletskian (Sungirian), Aurignacian (Kostenki)
MUP	HG	21	29,000 − 22,000	Czech Rep., France, Italy	Eastern Gravettian (Pavlovian), western Gravettian
LUP-w	HG	13	17,000 − 10,000	France, Switzerland, Germany, Slovakia	Magdalenian
LUP-s	HG	12	13,000 − 10,000	Italy	Late Epigravettian
Meso1	HG	21	9650 − 6500	Belgium, Denmark, England, France, Italy, Norway, Serbia, Spain	Azilian, Sauveterrian, Iron Gates, Maglemosian
Meso2	HG	32	6500 − 4700	Denmark, France, Germany, Italy, Portugal, Spain	Castelnovian, Teviecian, Kongemose, Erteboelle, Recent/Final Mesolithic
EN-Lig	LIG	7	5361 − 4956	Liguria (Italy)	ICC
MN-Lig	LIG	19	4800 − 4374	Liguria (Italy)	SMP
EN-e	EF/EN	8	6500 − 5500	Hungary, Serbia, Romania	Starčevo, Körös, Criș
EN-s	EF/EN	11	6100 − 4500	France (south), Italy	ICC, Epicardial
EN-w	EF/EN	18	5500 − 5000	Germany	LBK
MN-e	EF/MN	10	5700 − 5000	Austria, Slovakia, Hungary	eastern LBK, AVK (Bukk, Szakálhát), Sopot-Bicske
MN-s	EF/MN	8	5500 − 3500	Italy (south), Spain, Greece	Catignano, Ripoli (Painted Pottery), Sepulcros de Fosa, Greek Middle Neolithic (Painted Pottery)
MN-s(a)	EF/MN	11	4800 − 4200	Italy (north)	Chamblandes? (Villeneuve), SMP
MN-w	EF/MN	8	5000 − 4000	Germany, Switzerland	Stroke-Ornamented Pottery, Chamblandes
LN/CA-e	EF/LN/C	13	5200 − 2700	Romania, Hungary, Poland	Boian, Lengyel, Tisza, Globular Amphora, Baden
LN/CA-s	EF/LN/C	16	4000 − 2500	Italy, France (south), Spain, Portugal	Diana-Bellavista, Ozieri, Almeria, Néolithique récent/Calcolithique, Neolitico Finàl/Eneolitico, Vila Nova de São Pedro
LN/CA-w	EF/LN/C	18	4400 − 2500	France, Belgium, Switzerland, Denmark	Michelsberg, Cortaillod, Funnel Beaker, Atlantic Late Neolithic, Seine-Oise-Marne
CA	MA	38	3500 − 2200	Italy	Remedello, Vecchiano, Rinaldone, Gaudo, Moarda
BA	MA	20	2200 − 1000	Italy	Terramare, Apennine, Castelluccio, Pantalica.
Norse	REC	110	Medieval	Oslo (Norway)	Medieval Norsemen
Zalav	REC	98	9th-11th cen CE	Zalavar (Hungary)	Medieval Hungarian
Berg	REC	109	19th cen CE	Berg (Austria, Carinthia)	Modern
Analysis 2: Group[1]	Macro-group[1]	Sample size	Approximate date range cal BCE	Geographical location(s)	Possibly associated archeological cultures
EUP	HG	8	43,000 − 31,000	Czech Rep., Romania, Russia	Streletskian (Sungirian), Aurignacian (Kostenki 14)
MUP-e	HG	12	29,000 − 26,000	Czech Rep.	Eastern Gravettian (Pavlovian)
MUP-sw	HG	13	29,000 − 22,000	France, Italy, Spain	Gravettian, Solutrean
LUP-w	HG	14	17,000 − 10,000	France, Switzerland, Germany, Slovakia	Magdalenian
LUP-s	HG	19	13,000 − 10,000	Italy	Late Epigravettian
Meso1	HG	52	9650 − 6500	Belgium, Denmark, France, Germany, Great Britain, Greece, Italy, Norway, Serbia, Spain, Sweden	Azilian, Sauveterrian, Iron Gates, Maglemose
Meso2	HG	78	6500 − 4700	Denmark, France, Germany, Italy, Luxembourg, Portugal, Spain, Sweden, Switzerland	Teviecian, Kongemose, Erteboelle, Recent/Final Mesolithic
EN-Lig	LIG	7	5361 − 4956	Liguria (Italy)	ICC
MN-Lig	LIG	19	4800 − 4374	Liguria (Italy)	SMP
EN-e	EF/EN	47	6500 − 5500	Greece, Bulgaria, Romania, Hungary, Serbia	Proto-Sesklo, Karanovo I-III, Starčevo, Körös, Criș

Table 2 (continued)

Analysis 1: Group[1]	Macro-group[1]	Sample size	Approximate date range cal BCE	Geogr.location(s)	Possibly associated archeological cultures
EN-s	EF/EN	15	6100 − 4500	France (south), Italy	ICC, Epicardial
EN-w	EF/EN	76	5500 − 5000	France (north), Germany	LBK
MN-e	EF/MN	27	5700 − 5000	Hungary, Czech Rep., Slovakia, Austria	Eastern LBK, AVK (Bukk, Szakáhát), Sopot-Bicske
MN-s	EF/MN	15	5200 − 4200	Italy (central-south)	Catignano, Passo di Corvo, Ripoli, Serra d'Alto (Painted Pottery)
MN-s(a)	EF/MN	17	4800 − 4200	Italy (north), France (south)	Chamblandes (Villeneuve), SMP, pre-Chassey
MN-w	EF/MN	65	5000 − 4000	France (north), Germany, Switzerland	Rossen, Stroke-Ornamented Pottery, Chamblandes, Egolzwil
MLN-e	EF/MN	11	5500 − 3000	Greece	Sesklo, Tsangli, Dimini
MLN-n	EF/MN	38	4300 − 2800	Denmark, Germany, Poland	Funnelbeaker
MLN-s	EF/MN	10	4500 − 3500	France (south), Italy	Chasséen
MLN-sw	EF/MN	9	4200 − 3100	Spain	Sepulcros de Fossa
MLN-w	EF/MN	44	4000 − 2500	France (north), Great Britain, Ireland	Atlantic LN, British Isl. MN & LN
LN-e	EF/LN	59	5200 − 4000	Romania, Hungary, Serbia, Poland	Boian, Lengyel, Tisza, Vinča-Pločnik
LN-s	EF/LN	24	4000 − 3000	Italy, France (south), Spain, Portugal	Diana-Bellavista, Ozieri, Almeria, Neolitico tardìo
LN-w	EF/LN	37	4400 − 2800	France (n), Belgium, Germany, Switzerland	Michelsberg, Tiefstichkeramik, Walternienburg, Cortaillod, Pfyn
FN/CA-e	FN/CA	32	4600 − 2800	Hungary, Poland, Romania	Tiszapolgar, Globular Amphora
FN/CA-s	FN/CA	134	3500 − 2500	Spain, Portugal	Neolitico Finàl/Eneolitico
FN/CA-w	FN/CA	169	3000 − 2200	France (north), Belgium	Seine-Oise-Marne
CA-e	MA	120	4500 − 3000	Bulgaria, Romania, Hungary, Poland	Karanovo VI, Baden, Bodrogkeresztúr, Sopot-Bicske, Zlota, Cernavoda, Gumelnita
CA-s	MA	114	3500 − 2200	Italy, France (south), Spain, Portugal	Remedello, Rinaldone, Gaudo, Moarda, Los Millares, Vila Nova de São Pedro
CA-s(a)	MA	10	3500 − 2500	Italy (east Liguria, north Tuscany)	Vecchiano
BA-ce	MA	311	2500 − 1000	Hungary, Poland, Romania, Serbia, Austria, Czech Rep., Germany	Únětice, other EBA and MBA
BA-se	MA	146	3000 − 1100	Greece	Early, Middle & Late Helladic, Minoan, Mycenean
BA-sw	MA	239	2200 − 1000	Italy, France, Spain	Terramare, Apennine, Castellucian, Pantalica, Nuragic, Polada, El Argar
Tusc	REC	100	19th cen CE	Tuscany (Italy)	Modern
Sicily	REC	44	20th cen CE	Sicily (Italy)	Modern
Sard	REC	43	18th-19th cen CE	Sardinia (Italy)	Modern

[1]Abbreviations: *EUP* Early Upper Paleolithic, *MUP* Middle Upper Paleolithic, *LUP* Late Upper Paleolithic, *Meso* Mesolithic; Meso1: First (=Early) Mesolithic; Meso2: Second (=Late) Mesolithic; *EN* Early Neolithic, *MN* Middle Neolithic, *LN* Late Neolithic, *MLN* Middle-Late Neolithic, *LN/CA* Late Neolithic/Copper Age (Macro-group), *FN/CA* Final Neolithic/Copper Age (Macro-group), *LN/CA* Late Neolithic/Copper Age, *CA* Copper Age, *BA* Bronze Age, *HG* Hunter-gatherers, *EF* Early Farmers, *MA* Metal Ages, *REC*: Recent (the last millennium CE, encompassing the late Middle Ages and modern era); *Lig*: Liguria; e: Eastern; s: Southern; w: Western; c: Central; (a): distinguishes a group from another with the same name; e.g. *MN*-s(a): Middle Neolithic southern Europe, southern Alpine region; *CA*-s(a): Copper Age southern Europe, Apuan Alps region, *ICC* Impresso-Cardial Complex, *SMP* Square Mouthed Pottery, *AVK* Alföldi Vonaldíszes Kerámia, *LBK* Linearbandkeramische Kultur

are reported in SI Table S1c for Analysis 1 and Table S1d for Analysis 2, respectively.

Standardization of datasets followed the Q-mode method (Darroch and Mosimann 1985; Jungers et al. 1995), where each measurement was divided by the geometric mean of all individual values to optimize shape analysis. This step addresses the challenges of determining the sex of prehistoric individuals, which can be complicated by a diachronic trend toward gracilization that varies between males and females. Additionally, sexual dimorphism in shape should only impact within-population variation, and any variation due to shape sexual dimorphism should be minimal among different populations (D'Amore et al. 2010).

Table 3 Measurements used in (a) Analysis 1 (30 variables) and (b) Analysis 2 (10 variables)

a) Analysis 1									b) Analysis 2		
#	Code	Name	#	Code	Name	#	Code	Name	#	Code	Name
1	GOL	glabello-occipital length	11	NLH	nasal height	21	WMH	cheek height	1	M1	glabello-occipital length
2	BNL	basion-nasion length	12	OBH	orbit height (left)	22	FRC	nasion-bregma chord	2	M8	maximum cranial breadth
3	BBH	basion-bregma height	13	OBB	orbit breadth (left)	23	FRS	nasion-bregma subtense	3	M9	minimum frontal breadth
4	XCB	maximum cranial breadth	14	NLB	nasal breadth	24	FRF	nasion-subtense fraction	4	M17	basion-bregma height
5	XFB	maximum frontal breadth	15	MAB	palate breadth	25	PAC	bregma-lambda chord	5	M45	bizygomatic breadth
6	ZYB	bizygomatic breadth	16	MDH	mastoid height	26	PAS	bregma-lambda subtense	6	M48	nasion-prosthion height
7	AUB	biauricular breadth	17	ZMB	bimaxillary breadth	27	PAF	bregma-subtense fraction	7	M51	orbit breadth (left)
8	ASB	biasterionic breadth	18	FMB	bifrontal breadth	28	OCC	lambda-opisthion chord	8	M52	orbit height (left)
9	BPL	basion-prosthion length	19	EKB	biorbital breadth	29	OCS	lambda-opisthion subtense	9	M54	nasal breadth
10	NPH	nasion-prosthion height	20	DKB	interorbital breadth	30	OCF	lambda-subtense fraction	10	M55	nasal height

Morphometric analysis

Morphometric biodistances were assessed using multiple quantitative approaches:

- R-matrix analysis: Used to calculate Mahalanobis generalized distances (D^2), assuming phenotypic variance is proportional to genetic variance (Harpending and Jenkins 1973; Relethford and Blangero 1990). Since sampling effects can significantly impact results, standard errors and sample size were adjusted to account for potential biases. In case of small sample sizes in respect to the number of variables, there is a concrete risk of loss of diagnostic power, biased outcomes, and misinterpretations (see D'Amore et al. 2010 and references therein). To address this potential bias, we employed the methods described by Relethford et al. (1997). The resulting distance values were scrutinized to identify patterns of relationships among Ligurian Neolithic groups and between them and the other groups, both HGs and EFs.
- Principal Coordinate Analysis (PCoA) and Neighbor-Joining (NJ) tree clustering: Employed to visualize morphological relationships among groups and infer their phylogenetic relationships.
- Principal Component Analysis (PCA): Conducted as an exploratory tool to examine individual variation and identify key contributing measurements.
- Discriminant Function Analysis (DFA) or Canonical Variate Analysis (CVA): Ligurian Neolithic specimens were analyzed as "unclassified" cases and compared against predefined macrogroups (Table 2) to assess their morphological affinities.

Software Used.

- R-matrix and PCoA: RMET Version 5.0 (J. Relethford, freely available at http://konig.la.utk.edu/relethsoft.html).
- Multiple regression for MDE, PCA, and DFA: STATISTICA Version 12 (StatSoft Inc. 2014; www.statsoft.com).
- NJ trees: Phylip Version 3.69 (Felsenstein 2004) and TreeView (Win32) Version 1.6.6 (Page 2001; freely available at http://taxonomy.zoology.gla.ac.uk/rod/rod.html).

This methodological approach ensures robust and comprehensive morphometric analyses to explore the biological affinities of Neolithic Ligurian populations in a broader comparative framework.

Results

Summary descriptive statistics for craniometric measurements (sample size, mean, and standard deviation) are summarized by sex and group in Table 4 (Analysis 1) and Table 5 (Analysis 2). Note that the sample sizes in Table 5 are slightly smaller, both per group and overall (N total), compared to Table 2 because $n=59$ crania lacking a sex estimate were necessarily excluded from the sex-specific descriptive statistics reported in Table 5.

PCoA

The R-matrix obtained using 30 measurements for the overall sample of 629 individuals, divided into 23 groups (including the two groups from Liguria), was used to

Table 4 Summary descriptive statistics for Analysis 1 complete dataset. Mean, standard deviation (S.D.), and sample size of craniometric measurements are presented, stratified by sex and group. Abbreviations for groups follow Table 2; abbreviations for craniometric variables follow Table 3

Male means															
Group	N	GOL	BNL	XCB	XFB	AUB	ASB	BBH	MDH	FRC	FRS	FRF	PAC	PAS	PAF
BA	10	186.20	103.50	143.50	122.75	121.50	110.70	140.00	30.21	114.50	27.55	51.80	118.75	26.45	57.40
Berg	56	180.32	98.59	147.61	124.63	127.52	113.61	130.25	28.34	111.05	27.05	50.21	110.09	24.09	58.50
CA	26	184.69	101.89	142.46	120.77	122.16	111.19	136.80	29.36	112.08	26.28	51.90	114.65	25.57	57.70
EN-e	1	190.00	110.51	122.00	108.44	107.50	99.65	150.00	28.76	113.42	21.97	51.05	116.65	22.30	66.24
EN-Lig	5	194.40	104.98	140.00	116.36	118.62	112.22	141.05	30.14	116.82	26.98	53.29	118.82	24.44	63.29
EN-s	6	189.59	107.17	138.40	120.37	115.41	111.06	140.03	31.10	119.79	29.42	58.90	120.87	28.34	66.78
EN-w	10	186.40	102.52	137.50	118.30	116.81	109.08	139.60	33.08	117.61	28.26	52.22	121.29	26.77	65.41
EUP	3	194.00	98.05	141.33	120.63	127.14	110.83	135.67	28.83	116.90	27.40	52.10	119.83	24.97	65.17
LN-e	6	187.67	103.15	138.83	118.83	113.17	109.11	139.25	32.68	116.04	26.62	55.27	117.80	23.68	63.11
LN-s	12	184.92	101.84	137.67	118.83	114.89	109.23	136.04	30.55	113.86	26.68	51.33	117.87	26.13	63.30
LN-w	11	183.82	102.05	142.09	120.73	120.36	109.96	137.55	29.85	117.28	28.24	51.13	116.88	26.21	65.87
LUP-s	8	191.51	98.75	140.56	116.22	128.55	114.14	139.19	31.82	112.88	27.78	52.09	124.54	28.07	65.44
LUP-w	6	194.42	104.33	141.50	118.47	128.03	114.42	137.14	32.34	114.90	28.37	53.10	120.07	25.79	64.43
Meso1	12	189.96	103.22	142.42	117.38	126.09	115.78	141.42	31.47	113.08	28.14	54.33	119.48	26.02	63.07
Meso2	16	187.66	102.38	137.97	116.28	122.53	111.93	139.91	31.05	112.52	27.22	52.03	118.37	25.64	62.44
MN-e	9	184.67	106.01	140.06	121.33	120.33	107.78	140.73	30.49	116.48	27.21	51.98	115.43	24.94	61.24
MN-Lig	14	188.57	103.74	137.25	117.71	114.85	108.35	140.19	30.12	113.25	25.61	52.77	117.68	25.29	61.15
MN-s	4	185.50	100.25	137.25	111.75	119.00	111.34	135.75	29.20	111.00	26.10	49.90	117.00	26.03	63.15
MN-s(a)	7	186.16	104.07	139.86	121.93	117.87	110.84	139.45	30.20	114.00	28.65	53.32	117.93	25.23	59.34
MN-w	5	185.20	100.83	140.80	118.00	119.60	110.26	138.60	33.30	112.54	26.54	55.09	124.60	28.43	70.41
MUP	13	196.97	104.73	141.42	123.80	125.66	110.30	136.21	30.50	117.06	28.58	55.72	123.06	25.69	64.99
Norse	55	188.47	101.80	141.87	119.13	124.67	111.89	131.73	29.55	113.13	25.11	51.67	114.44	24.69	61.02
Zalav	53	185.13	101.28	141.40	119.30	123.74	110.98	134.85	29.51	112.70	26.79	50.00	115.28	25.13	58.64
N total All Groups	348	186.39	101.78	141.85	120.14	122.93	111.51	135.61	29.96	113.44	26.86	51.81	116.09	25.32	61.04
Male S.D.															
Group	N	GOL	BNL	XCB	XFB	AUB	ASB	BBH	MDH	FRC	FRS	FRF	PAC	PAS	PAF
BA	10	4.87	4.10	5.46	4.54	5.01	4.27	4.38	1.46	3.93	1.77	4.04	6.29	2.37	2.96
Berg	56	7.35	4.52	5.52	5.17	5.42	4.34	4.31	2.79	3.99	2.56	3.23	4.71	2.85	4.49
CA	26	7.33	3.66	5.93	4.98	4.77	4.15	3.59	1.11	4.61	2.56	4.74	5.77	2.95	4.86
EN-e	1	\	\	\	\	\	\	\	\	\	\	\	\	\	\
EN-Lig	5	7.37	2.58	7.58	5.51	6.48	4.79	2.58	1.33	4.14	4.31	10.30	4.80	2.00	5.07
EN-s	6	5.83	6.43	10.14	8.43	7.38	7.59	6.61	2.47	3.90	2.77	4.77	6.94	1.67	5.17
EN-w	10	7.66	3.37	4.03	5.19	7.71	5.99	8.26	3.42	7.93	2.48	8.02	7.80	4.08	5.88
EUP	3	6.00	8.75	3.06	9.13	1.42	3.25	4.93	2.84	3.29	5.39	7.02	3.01	4.34	3.69
LN-e	6	5.39	4.94	7.49	5.04	5.85	5.19	3.95	2.94	2.52	2.87	5.71	5.15	1.89	4.70
LN-s	12	5.90	3.24	7.13	6.18	7.23	4.40	3.92	3.68	3.88	2.25	4.03	5.47	2.44	3.15
LN-w	11	7.73	3.04	7.16	5.50	4.98	2.88	6.23	3.55	6.15	3.64	5.79	6.77	3.94	6.07
LUP-s	8	7.93	5.50	5.07	5.23	5.62	4.20	9.03	2.45	4.47	1.99	3.15	6.81	3.33	4.70

Table 4 (continued)

LUP-w	6	3.93	8.39	3.39	4.13	4.58	2.69	9.33	1.48	4.88	3.09	3.98	6.25	4.65	6.03
Meso1	12	4.51	4.80	5.40	5.47	5.47	7.22	4.59	2.26	2.28	1.90	3.82	7.48	2.96	5.32
Meso2	16	6.97	6.05	6.80	5.97	7.08	4.75	7.44	2.90	5.70	2.69	4.93	6.07	2.16	4.73
MN-e	9	4.90	7.73	6.42	6.32	9.41	7.12	6.88	3.44	6.93	3.38	4.94	7.84	3.54	6.35
MN-Lig	14	6.51	4.38	3.68	4.21	3.78	3.30	4.80	1.30	7.49	3.16	4.52	7.91	3.46	4.24
MN-s	4	7.94	6.24	6.45	4.57	5.81	5.95	3.86	2.47	3.56	1.54	2.93	1.41	1.46	2.60
MN-s(a)	7	6.01	4.82	3.85	4.10	4.56	5.00	5.31	2.46	4.83	2.34	2.99	6.48	2.54	4.32
MN-w	5	7.12	6.09	3.03	3.94	3.36	1.95	5.59	2.59	5.96	1.90	9.26	4.87	3.61	5.16
MUP	13	6.03	5.46	6.39	6.94	8.07	4.94	6.43	3.14	3.84	3.11	4.88	8.66	2.53	4.94
Norse	55	5.25	3.55	4.72	5.59	4.04	3.56	5.13	3.49	4.78	2.59	3.97	5.35	2.76	3.17
Zalav	53	5.77	4.37	4.03	4.61	3.99	3.79	5.14	2.87	3.88	2.44	3.03	4.79	2.28	3.26
N total All Groups	348	7.33	4.92	6.08	5.84	6.59	4.65	6.40	2.99	5.02	2.79	4.64	6.81	2.94	5.10

Male means																
Group	OCC	OCS	OCF	L	FMB	EKB	ZYB	ZMB	NPH	WMH	DKB	OBB	OBH	NLB	NLH	MAB
BA	100.23	26.47	46.88	99.76	99.90	97.59	131.89	94.13	68.85	24.80	23.61	40.53	32.30	25.09	51.29	64.65
Berg	94.00	28.50	48.34	93.75	99.59	98.70	135.55	93.29	67.89	23.14	22.88	40.14	33.75	25.46	51.71	63.88
CA	100.18	26.68	50.76	99.41	100.17	97.23	131.86	94.85	68.27	24.73	22.58	41.12	32.10	24.03	50.79	63.18
EN-e	100.17	33.61	60.75	98.88	107.33	108.73	122.00	104.55	65.00	25.44	22.30	39.00	32.00	22.00	57.00	64.12
EN-Lig	101.50	27.05	46.58	99.43	98.76	96.78	128.80	94.51	64.34	21.59	22.18	41.31	32.40	25.20	48.57	60.87
EN-s	98.34	24.00	46.04	102.93	98.97	92.04	128.04	93.01	64.49	22.89	24.85	39.36	31.58	24.83	51.17	62.60
EN-w	100.81	27.94	52.70	101.30	100.21	98.53	130.20	95.90	69.83	23.22	25.15	40.03	31.30	25.10	50.00	62.12
EUP	101.67	31.53	49.47	107.10	105.53	104.76	136.13	102.09	70.74	24.67	23.38	42.38	31.95	25.83	50.93	70.93
LN-e	101.14	28.57	50.23	101.54	101.59	99.62	132.41	100.26	68.38	22.96	23.65	39.88	32.50	25.65	52.33	64.82
LN-s	98.43	28.05	50.31	95.26	98.23	96.08	128.35	94.09	64.56	22.05	23.54	39.27	31.33	24.03	49.17	63.55
LN-w	98.03	26.44	49.48	95.18	100.86	99.97	129.05	95.68	67.69	22.73	22.96	40.21	32.52	25.24	51.18	62.83
LUP-s	98.75	26.35	41.93	95.84	103.10	101.83	143.88	101.77	65.23	22.79	22.12	41.40	30.65	24.61	49.67	64.57
LUP-w	98.21	28.82	48.06	102.65	105.51	102.62	143.42	100.88	69.57	25.44	25.12	42.17	29.63	24.07	51.50	64.60
Meso1	101.85	28.64	53.25	98.13	100.81	99.59	137.67	96.21	68.92	23.98	21.75	40.72	31.49	24.34	51.59	62.18
Meso2	100.26	27.83	49.37	98.38	100.02	99.68	135.56	98.05	67.59	24.25	22.15	40.99	30.31	25.61	50.26	64.21
MN-e	97.07	26.98	50.72	98.07	100.37	98.38	130.39	96.54	69.51	22.85	24.52	40.32	33.78	25.50	53.11	63.14
MN-Lig	103.61	28.03	48.48	101.03	99.42	97.76	128.82	96.16	65.60	21.82	22.66	40.01	33.29	25.21	50.67	60.83
MN-s	99.50	28.22	46.78	100.00	97.45	97.00	129.00	92.91	67.13	22.95	22.75	38.00	31.00	23.25	48.00	65.00
MN-s(a)	100.23	27.54	50.29	100.08	99.94	96.80	131.64	94.30	66.85	23.23	23.56	39.26	30.21	23.65	50.03	62.32
MN-w	98.37	26.04	47.73	99.87	102.08	100.23	130.60	102.27	67.51	23.82	24.66	39.52	30.60	24.00	46.80	64.13
MUP	98.96	29.73	48.24	104.95	105.11	105.05	138.40	99.57	64.55	24.62	25.75	42.47	29.83	26.49	50.85	65.61
Norse	97.25	30.82	47.40	96.96	99.02	98.89	134.44	94.02	68.93	24.20	22.35	40.38	33.75	25.42	51.96	63.62
Zalav	96.17	29.64	47.51	97.06	98.06	97.70	133.00	94.75	68.45	23.23	21.42	39.96	32.68	25.36	51.43	64.15
N total All Groups	97.99	28.54	48.55	97.85	99.88	98.68	133.59	95.39	67.83	23.54	22.83	40.38	32.44	25.12	51.12	63.66
Male S.D.																
Group	OCC	OCS	OCF	BPL	FMB	EKB	ZYB	ZMB	NPH	WMH	DKB	OBB	OBH	NLB	NLH	MAB
BA	5.25	2.25	8.63	4.40	1.92	3.24	4.40	4.15	3.08	1.92	2.17	1.32	2.18	2.04	3.06	2.26

Table 4 (continued)

Berg	5.22	3.38	6.27	5.70	3.33	3.20	4.89	4.31	4.17	2.46	2.50	1.45	1.83	1.98	2.94	3.25
CA	5.54	4.49	7.50	4.64	2.38	2.84	4.71	3.45	3.38	1.80	2.46	1.34	2.11	1.73	1.78	2.81
EN-e	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\	\
EN-Lig	5.00	2.01	10.10	3.49	3.40	3.65	7.40	1.92	2.92	1.48	2.17	3.02	1.95	1.64	1.75	4.47
EN-s	6.39	3.35	10.54	9.39	5.07	7.54	14.49	5.72	6.18	2.56	2.55	1.61	1.63	2.93	1.17	3.89
EN-w	6.01	4.19	7.27	4.17	4.51	4.12	6.80	6.47	3.21	2.80	2.25	2.08	2.21	1.20	3.74	3.71
EUP	7.51	5.22	2.34	4.63	3.08	3.03	5.14	1.14	3.91	2.31	1.51	1.61	1.93	1.04	3.27	2.61
LN-e	7.25	4.70	8.36	6.25	7.27	6.44	7.61	5.75	3.22	1.03	1.66	1.98	1.97	2.59	1.21	3.00
LN-s	7.41	5.11	6.33	2.93	5.63	4.46	7.42	6.54	4.64	2.64	2.01	2.16	2.61	1.65	3.21	4.10
LN-w	4.36	2.78	5.96	4.68	3.82	3.49	6.76	3.35	3.15	1.39	2.49	1.69	2.14	1.77	3.74	3.19
LUP-s	9.17	5.16	4.41	4.93	4.94	5.49	6.17	6.71	3.75	1.56	4.17	2.24	2.38	1.92	2.36	1.56
LUP-w	4.47	2.25	8.84	4.87	3.17	4.47	4.57	3.71	6.48	2.26	5.08	2.67	1.79	1.77	5.38	3.52
Meso1	4.08	3.05	5.73	5.02	3.81	2.89	6.22	4.20	5.06	2.54	4.28	2.25	2.75	3.13	2.51	1.35
Meso2	4.24	3.62	8.45	6.58	5.46	4.91	8.49	6.88	5.20	2.73	2.30	2.57	2.50	1.94	3.75	3.85
MN-e	6.07	4.77	6.26	8.76	4.64	3.87	5.96	5.25	4.21	2.74	1.03	2.46	1.66	2.06	2.37	2.83
MN-Lig	6.65	3.45	3.41	4.34	4.42	3.36	4.40	1.98	3.96	1.08	1.94	1.82	2.81	1.52	2.65	3.28
MN-s	3.70	1.02	2.62	2.71	2.92	6.58	8.68	5.52	2.46	1.59	3.59	2.16	0.82	1.50	2.83	2.94
MN-s(a)	6.76	2.12	6.81	2.93	4.87	2.23	4.06	3.54	5.62	2.59	2.59	1.28	1.63	0.58	3.38	3.50
MN-w	4.96	2.58	5.02	4.07	7.95	7.68	5.13	5.31	7.19	3.42	3.35	2.22	1.52	1.22	5.40	2.72
MUP	4.04	5.00	6.53	6.62	5.80	4.49	8.95	7.01	5.07	2.28	2.62	2.53	3.52	2.17	3.51	4.69
Norse	3.96	3.26	5.44	5.15	2.88	2.88	3.87	5.02	3.37	2.02	2.48	1.43	2.21	1.45	2.65	3.21
Zalav	5.11	3.03	5.10	4.94	2.73	2.72	3.54	4.14	4.23	2.31	2.38	1.16	1.99	1.52	2.91	2.81
N total All Groups	5.75	3.81	6.45	5.91	4.14	4.10	6.44	5.19	4.31	2.33	2.75	1.85	2.48	1.87	3.05	3.33

Female means

Group	N	GOL	BNL	XCB	XFB	AUB	ASB	BBH	MDH	FRC	FRS	FRF	PAC	PAS	PAF
BA	10	179.50	99.30	139.04	118.01	117.94	107.40	133.55	27.48	109.25	27.20	47.90	110.85	23.75	56.50
Berg	53	170.53	92.92	140.36	118.74	120.32	108.19	124.47	25.58	106.23	26.51	46.85	105.21	23.32	54.66
CA	12	178.83	98.38	137.92	118.25	117.94	108.96	131.63	26.80	108.92	27.00	47.29	112.63	25.42	56.96
EN-e	7	174.29	97.07	134.93	115.43	109.30	107.20	131.08	26.27	109.38	26.97	49.38	110.69	23.88	60.37
EN-Lig	2	182.00	103.59	138.00	118.50	115.33	108.53	137.29	26.85	108.50	26.51	49.07	110.50	24.06	61.17
EN-s	5	184.90	103.10	136.70	118.60	114.93	110.03	137.42	30.16	113.76	25.90	54.08	119.38	25.67	64.37
EN-w	8	178.88	99.63	132.75	112.63	110.15	101.50	134.38	27.44	113.38	29.13	49.47	119.85	26.21	59.38
EUP	5	187.64	97.51	134.44	118.08	124.37	109.19	129.10	28.35	114.40	28.60	49.00	116.50	26.00	63.80
LN-e	7	177.14	99.47	136.14	116.14	110.50	107.95	135.53	26.60	110.08	27.19	52.21	116.95	27.05	61.80
LN-s	4	178.00	92.29	133.00	110.25	105.52	104.40	128.85	27.23	113.08	24.89	49.11	109.98	21.90	57.04
LN-w	7	183.00	102.19	135.86	117.71	112.40	109.10	134.57	27.36	111.36	26.02	49.90	115.37	25.34	61.42
LUP-s	4	191.00	100.38	140.88	114.75	123.78	114.00	136.25	28.65	111.75	28.30	48.05	122.25	26.13	64.75
LUP-w	7	183.00	98.36	136.86	112.54	122.67	111.67	132.14	28.31	108.04	26.50	49.19	121.31	27.36	64.81
Meso1	9	182.75	100.85	139.94	112.83	123.17	111.55	135.00	30.68	109.09	26.25	51.35	113.88	24.74	60.88
Meso2	16	179.08	93.76	135.44	111.95	117.58	110.96	130.51	26.75	105.76	26.30	48.37	113.06	24.47	59.59
MN-Lig	5	180.60	98.30	134.40	114.40	113.60	106.91	131.39	27.68	107.60	24.30	51.80	121.20	28.13	65.40
MN-s	4	177.75	98.56	130.50	113.63	110.75	105.35	130.61	26.00	109.82	27.08	50.61	109.94	23.87	60.20

Table 4 (continued)

MN-s(a)	4	177.66	95.54	134.75	117.75	115.57	106.52	130.36	26.74	112.13	28.47	48.67	112.25	24.95	59.43
MN-w	3	181.00	98.89	137.00	119.00	114.09	107.48	130.67	27.74	111.34	26.89	48.08	117.60	25.91	58.19
MUP	8	187.69	101.41	137.63	119.81	122.75	107.59	132.70	27.13	111.62	28.31	50.81	116.11	23.56	60.92
Norse	55	179.98	97.31	136.29	114.31	117.65	106.71	125.96	26.02	107.98	25.55	48.31	109.53	23.13	58.20
Zalav	45	176.44	96.51	136.89	115.67	118.62	107.78	128.76	26.31	107.47	26.53	46.98	110.64	23.67	56.60
N total All Groups	280	178.05	96.91	137.17	115.92	117.78	107.96	129.17	26.68	108.46	26.52	48.38	111.38	24.16	58.31
Female S.D.															
Group	N	GOL	BNL	XCB	XFB	AUB	ASB	BBH	MDH	FRC	FRS	FRF	PAC	PAS	PAF
BA	10	9.74	3.98	4.76	5.61	5.29	3.26	5.25	2.07	4.50	2.02	5.52	9.40	3.71	5.85
Berg	53	6.51	3.82	4.63	4.70	4.45	4.95	4.77	2.59	3.91	2.61	3.31	5.66	2.93	4.07
CA	12	5.28	5.21	5.38	5.19	5.49	3.05	5.86	1.62	3.84	2.64	3.22	4.34	2.51	3.48
EN-e	7	6.18	6.00	6.00	5.97	4.74	4.33	2.96	1.31	5.92	2.64	5.08	4.30	2.51	5.67
EN-Lig	2	1.41	2.25	1.41	0.71	2.69	0.66	0.41	0.89	2.12	1.27	1.03	2.12	0.48	2.73
EN-s	5	7.35	5.35	5.22	6.18	6.44	5.09	5.98	1.34	7.27	3.10	4.79	2.63	3.28	8.19
EN-w	8	5.72	4.41	4.56	7.76	5.20	3.34	6.35	2.17	6.39	2.38	5.34	4.49	2.36	4.96
EUP	5	8.35	4.00	5.30	4.53	4.89	7.05	5.98	2.89	12.78	2.70	7.97	6.58	3.32	1.79
LN-e	7	7.17	5.70	4.26	3.72	8.08	4.81	5.89	2.54	10.37	2.99	5.77	7.47	3.34	4.64
LN-s	4	8.08	3.41	5.42	6.65	8.11	5.65	4.51	1.09	3.18	2.09	5.20	9.60	2.50	7.97
LN-w	7	7.30	4.48	6.96	5.65	3.81	6.23	5.06	2.02	5.25	0.96	2.56	8.15	2.43	5.29
LUP-s	4	9.57	1.80	6.56	5.25	3.72	4.65	7.64	3.77	7.19	3.37	2.29	14.13	3.88	7.63
LUP-w	7	4.40	4.25	4.85	1.86	7.03	5.10	4.91	2.95	3.81	3.29	4.58	4.11	1.97	8.86
Meso1	9	3.91	6.06	8.26	5.68	8.36	8.44	4.20	2.29	4.08	1.85	4.78	6.02	3.51	6.06
Meso2	16	4.60	6.17	7.38	5.18	5.64	6.23	6.19	1.83	3.60	2.28	3.35	4.82	2.88	3.98
MN-Lig	5	4.93	5.00	2.30	1.95	3.15	5.41	4.32	1.11	8.71	3.65	4.03	8.79	5.28	10.62
MN-s	4	6.85	5.61	1.73	2.50	3.73	4.67	1.25	2.79	5.35	3.05	5.47	4.23	1.47	2.42
MN-s(a)	4	5.63	3.01	3.59	4.27	3.54	3.37	4.23	3.21	5.86	3.14	4.98	4.03	5.34	5.16
MN-w	3	7.55	6.12	4.58	3.61	2.75	1.03	5.86	2.01	3.69	5.15	0.52	10.36	3.11	12.38
MUP	8	5.75	5.46	5.37	3.18	6.09	3.27	2.63	4.26	3.58	1.75	3.56	7.58	2.58	4.77
Norse	55	4.66	3.58	4.31	4.35	3.76	4.11	4.10	2.51	3.75	2.25	2.96	5.18	2.37	3.26
Zalav	45	5.96	3.87	4.44	4.12	4.18	5.13	5.11	2.78	4.41	2.31	3.53	5.55	2.45	4.36
N total All Groups	280	7.48	5.04	5.32	5.13	6.01	5.10	6.03	2.68	5.18	2.56	4.04	7.33	3.00	5.47

Female means															
Group	OCC	OCS	OCF	BPL	FMB	EKB	ZYB	ZMB	NPH	WMH	DKB	OBB	OBH	NLB	NLH	MAB
BA	98.26	28.00	45.24	95.80	97.26	95.05	125.91	90.97	64.80	22.15	21.58	40.17	32.50	23.12	49.03	60.67
Berg	91.43	27.91	45.94	89.91	95.04	95.19	126.38	89.53	63.49	21.09	22.08	38.38	32.75	24.89	48.23	60.60
CA	96.08	26.75	47.67	96.66	98.94	95.17	124.22	89.41	62.92	21.75	20.88	40.66	32.38	23.44	48.22	59.76
EN-e	97.78	26.14	46.15	94.57	98.47	96.99	121.21	90.58	63.58	21.72	23.53	38.10	31.55	25.82	47.29	59.11
EN-Lig	98.00	28.01	52.43	99.44	98.13	96.00	123.50	94.31	59.77	20.59	22.63	40.09	31.00	24.00	49.18	57.35
EN-s	99.30	25.63	52.13	99.31	96.37	93.88	125.51	92.55	66.04	21.02	21.22	39.45	32.90	24.40	50.26	56.53
EN-w	95.58	24.21	45.33	96.69	94.51	92.75	118.75	90.96	63.40	19.98	22.03	38.32	31.25	24.25	46.13	60.38
EUP	96.00	30.00	43.40	98.69	105.01	105.61	135.59	94.80	60.39	22.30	25.65	41.96	31.37	25.83	46.50	62.44

Table 4 (continued)

LN-e	94.00	23.37	43.94	95.40	95.77	95.14	125.33	93.60	62.77	21.27	23.29	38.98	31.93	24.48	47.29	60.78
LN-s	97.96	28.58	46.97	88.75	94.95	91.77	116.66	88.02	61.38	21.11	21.79	36.57	33.25	21.38	46.25	58.07
LN-w	100.92	27.95	49.53	98.30	98.02	96.59	121.57	90.46	65.49	21.48	23.62	37.53	32.86	24.05	49.14	59.10
LUP-s	98.00	29.75	47.25	97.41	96.58	96.75	132.25	94.75	63.91	22.25	21.51	39.80	28.90	23.83	48.40	62.58
LUP-w	94.70	23.94	45.83	96.82	98.81	95.06	130.50	93.12	63.77	22.18	22.34	39.18	29.63	22.50	48.71	61.26
Meso1	102.67	27.15	52.33	98.96	100.72	97.37	132.39	95.20	65.53	22.73	20.97	40.79	31.43	23.47	50.26	62.04
Meso2	97.07	28.22	45.05	91.89	93.96	92.85	127.17	93.18	61.69	21.19	20.71	38.07	29.04	23.09	47.89	61.53
MN-Lig	96.80	25.50	42.88	96.30	96.44	96.60	123.40	91.96	60.40	20.86	23.18	39.80	30.90	24.60	46.88	58.74
MN-s	101.13	27.83	42.79	95.81	94.39	93.05	120.43	87.63	62.66	19.01	23.24	38.49	31.75	24.38	51.25	57.00
MN-s(a)	103.83	27.97	54.09	92.87	98.22	95.61	125.62	92.08	64.27	20.88	22.52	38.00	32.25	23.28	47.85	59.50
MN-w	96.63	26.85	47.10	95.09	96.46	94.97	122.67	92.87	65.55	21.85	22.66	38.72	31.33	24.00	46.73	58.69
MUP	96.93	27.88	52.30	102.75	99.56	100.02	131.88	93.65	62.96	22.63	24.46	40.17	29.00	26.44	49.45	62.06
Norse	95.33	29.84	45.16	94.02	94.60	94.85	124.44	90.15	64.25	22.29	20.64	39.20	33.22	24.18	49.16	60.11
Zalav	94.20	28.69	45.16	92.13	94.78	95.22	125.44	90.09	63.18	21.11	20.67	38.67	32.09	24.67	48.49	60.71
N total All Groups	95.51	27.98	46.25	93.95	95.99	95.34	125.63	90.90	63.50	21.53	21.65	38.98	32.03	24.29	48.47	60.38
Female S.D.																
Group	OCC	OCS	OCF	BPL	FMB	EKB	ZYB	ZMB	NPH	WMH	DKB	OBB	OBH	NLB	NLH	MAB
BA	4.28	3.44	6.55	5.66	2.65	3.89	5.91	4.47	2.81	1.75	1.94	1.24	1.70	2.35	1.38	3.59
Berg	4.95	3.55	5.86	5.15	2.83	2.66	3.97	3.85	4.05	2.01	2.16	1.20	1.86	1.72	2.97	2.98
CA	5.17	3.57	5.23	3.88	4.73	4.51	5.39	3.95	4.91	2.35	2.86	1.69	1.57	1.25	2.32	2.82
EN-e	4.98	2.40	5.81	9.28	6.28	8.02	6.24	6.80	5.17	2.40	1.41	2.92	2.17	2.30	5.15	4.03
EN-Lig	5.66	1.28	4.91	1.52	2.22	1.41	6.36	5.50	1.17	0.30	1.88	0.30	1.41	1.41	2.17	6.15
EN-s	7.27	4.30	7.48	5.88	5.79	6.78	11.20	5.61	2.14	2.36	1.13	1.50	2.13	1.64	1.02	6.63
EN-w	7.30	3.43	7.44	3.06	2.51	3.01	4.33	3.66	5.05	2.04	2.33	1.37	2.12	2.12	4.61	3.93
EUP	7.04	4.64	7.83	4.21	2.36	1.54	7.68	3.93	1.74	1.79	3.70	1.23	3.56	1.25	1.89	2.12
LN-e	6.94	3.31	6.09	7.68	2.45	3.40	4.74	6.22	5.58	2.17	1.66	1.49	2.54	2.41	3.77	2.98
LN-s	2.48	1.12	2.67	4.35	7.52	5.59	3.28	5.65	8.12	1.38	3.02	3.15	3.50	3.04	6.24	4.07
LN-w	4.12	1.69	6.30	6.27	3.17	2.07	8.22	5.53	4.76	1.88	2.33	3.42	2.78	2.16	2.56	1.48
LUP-s	6.18	5.50	3.86	4.21	1.88	0.50	2.06	2.02	3.01	2.10	2.04	0.70	1.05	0.62	1.68	1.59
LUP-w	4.10	3.40	5.77	6.39	2.31	4.88	6.10	5.45	4.83	1.59	1.18	1.66	1.83	1.80	3.21	3.16
Meso1	4.56	2.37	3.76	5.37	4.14	3.67	7.02	4.01	2.65	1.58	2.65	0.80	2.42	1.71	1.92	1.44
Meso2	4.26	3.33	5.88	8.22	2.94	2.49	7.17	7.78	4.91	1.98	2.26	1.59	1.69	1.49	4.74	2.09
MN-Lig	5.72	3.03	6.60	4.14	3.16	4.22	3.58	0.93	3.49	1.48	1.67	1.33	1.95	0.89	1.63	3.00
MN-s	8.83	2.13	3.80	1.88	4.32	1.84	4.12	3.21	5.07	1.15	4.74	1.03	1.71	2.29	2.22	2.94
MN-s(a)	10.09	3.91	12.39	5.71	4.57	3.20	5.52	4.75	2.77	1.97	1.56	1.89	3.30	2.68	3.12	3.01
MN-w	7.07	1.30	5.50	4.27	3.72	6.32	4.51	3.14	6.76	2.57	2.92	2.12	3.06	2.65	5.90	3.80
MUP	4.93	3.09	6.31	6.05	4.30	3.46	9.42	4.01	2.68	2.67	2.04	1.43	1.60	2.16	1.93	3.94
Norse	4.64	2.85	5.19	4.39	3.64	3.45	3.76	4.52	4.04	1.98	2.17	1.57	2.05	1.90	2.67	2.22
Zalav	4.16	2.73	4.27	6.31	3.26	3.31	4.10	3.45	3.59	1.99	2.39	1.72	1.76	1.65	2.54	3.30
N total All Groups	5.68	3.44	5.92	6.26	4.04	3.95	5.92	4.70	4.14	2.05	2.49	1.81	2.32	1.97	3.06	3.10

calculate a 23 × 23 D² distance matrix (see SI Table S2). This matrix underwent PCoA and NJ clustering. The plot obtained from the projection of PCo1 and PCo2 (Fig. 2a) reveals a pattern of distribution and distinction among the groups, which consistently follows chronological and cultural attributions. Notably, the Ligurian groups position themselves within the cluster formed by the early farming (EF)/Neolithic groups. All these groups are spatially distinct not only from the hunter-gatherer (HG) groups, but also from the Metal Ages (MA: Copper and Bronze Ages – CA and BA) and Recent (last millennium CE, encompassing the late Middle Ages through the modern era) groups (REC).

The R-matrix derived from 10 measurements for a total sample of 2,178 individuals across 36 groups (including the two Ligurian groups) was used to compute a 36 × 36 D² distance matrix (see SI Table S3) and this matrix underwent PCoA and NJ clustering. The plot resulting from PCoA, based on the projection of PCo1 and PCo2 (Fig. 2b), reveals a discernible pattern of distribution and differentiation among the groups, influenced partially by cultural attribution. In this pattern, the Ligurian groups position themselves within a heterogeneous cluster formed by the EF and MA groups, except for the EN-Lig group, which again shows closer proximity to the HG groups (specifically the Meso groups).

Furthermore, PCo1 and PCo2 obtained from Analyses 1 and 2 were used to produce scatterplots similar to the previous ones, but with distinctions based on a geographical-chrono-cultural criterion. The resulting pattern for Analysis 1 (reported in Fig.S1 in the SI Text & Figures) shows a clear geographical separation between the Northern, Western, and Southern EF groups, with the Ligurian groups approaching the Southern European groups.

NJ tree clustering

The relationships and distinctions observed in PCoA are further confirmed by the topology proposed by the NJ phylogram trees (Fig. 3; see SI Fig. S2 for a differently represented tree as a rectangular cladogram) obtained from the distance matrices of Analyses 1 and 2. The oldest group, EUP, was always set as an outgroup. The most basal branches consist of all HG groups, from EUP to Meso. The final branches emerging from the trees consist mostly of a few EF groups and most post-Neolithic groups, including the MA and Recent groups. Among the groups closest to the Ligurian Neolithic groups, there are: all the Southern European EF groups divided by chronology in Analysis 1; whereas, in Analysis 2, there are three Eastern European EF groups divided by chronology.

Analysis of distances

In addition to the morphological relationship patterns described through PCoA and NJ clustering, significant comparisons were made, focusing on distances of the Ligurian groups from HG groups, other EF groups, post-Neolithic groups, and within the Ligurian groups themselves (Tables 6 and 7; see also SI Tables S2 and S3).

From the statistical summary, including the median (and mean) values and interquartile ranges calculated from pairwise comparisons (Fig. 4), it is evident that the Ligurian groups show mean distances from the EF groups (specifically chrono-cultural macro-groups, such as those including all the EN, MN, and other groups) significantly lower than their distances from HG (macro-group including all Upper Paleolithic and Mesolithic groups) and REC groups. The only exception is EN-Lig in Analysis 1 (Fig. 4a), where its distances from HG groups are similar to those from other EF groups.

Focusing on the comparisons between the HG and EF macro-groups (Fig. 4c, f), EN-Lig emerges as the EF group closest to HG among all the EF chrono-cultural macro-groups, while MN-Lig does not appear to be systematically closer and is only closer than the EN macro-group for both analyses 4.

Further examination of the distance values between the Ligurian groups and the HG macro-group, as compared with other EF groups (Tables 6 and 7, see also SI Tables S2-S4), reveals that EN-Lig produces the lowest distance values first from MN-Lig (practically zero distance), followed by Southern European EF groups for both Analyses, and Eastern European EF groups for Analysis 2 only. In Analysis 2, only the distance from Meso1 places it in the 17th position in a hypothetical ranking, with 20 out of 23 comparisons showing a value < 0.1 (SI Tables S2-S4).

For MN-Lig, the lowest distance values are first from EN-Lig (obviously, by reciprocity rule), then from Southern European EF groups for both Analyses, followed by several Eastern European EF groups.

Regarding the mean distances of individual EF groups from the HG macro-group (SI Table S5), the MN groups are generally closer to HG than the EN groups based on their mean distance values. These results are consistent across both Analyses 1 and 2, and the pattern becomes even clearer when the comparison is made with a subset of the HG group consisting only of the two Mesolithic groups.

Finally, a brief mention of a non-Ligurian group, the MLN-s of Analysis 2, which includes a further Ligurian Neolithic skull: the group is associated with the Chasseén (or Chassey) culture, with specimens from southern France, except for the Ligurian individual Arma di Nasino 1 (AN1). In PCoA the MLN-s group was found to be closest to MLN-e,

Table 5 Summary descriptive statistics for Analysis 2 complete dataset. Mean, standard deviation (S.D.), and sample size of craniometric measurements are presented, stratified by sex and group. Note that the total sample size (*N* total) is slightly reduced compared to Table 2, as $n = 59$ crania lacking a reliable sex estimate were excluded from this sex-specific analysis. Abbreviations for groups follow Table 2; abbreviations for craniometric variables follow Table 3

Male means											
Group	N	M1	M8	M9	M17	M45	M48	M51	M52	M54	M55
BA-ce	163	184.91	140.18	97.53	138.53	130.85	69.46	41.43	32.27	24.88	51.29
BA-se	88	185.42	140.82	97.86	135.43	129.38	67.64	40.40	32.08	24.33	49.84
BA-sw	108	185.02	141.44	97.15	135.34	130.30	68.63	41.06	31.68	24.28	50.70
CA-e	75	185.62	140.17	96.42	136.25	129.70	69.42	40.83	31.90	24.81	50.86
CA-s	82	184.95	143.09	97.16	135.22	130.56	68.25	41.29	31.66	24.26	50.32
CA-s(a)	5	182.73	138.60	93.40	131.90	127.20	64.40	42.10	31.60	23.50	48.10
EN-e	19	185.79	140.42	97.47	138.23	131.31	67.97	40.53	32.97	26.57	49.82
EN-Lig	5	194.40	140.00	96.00	141.05	128.80	66.10	42.20	32.40	25.20	48.20
EN-s	8	189.06	138.67	96.24	138.55	129.40	68.25	40.69	32.39	24.63	51.88
EN-w	39	188.87	138.72	98.05	138.97	130.32	71.59	40.93	32.27	24.41	51.18
EUP	4	189.75	138.00	99.13	134.00	135.85	69.25	42.75	30.73	26.38	49.20
FN/CA-e	22	188.86	138.59	96.64	137.20	131.79	70.76	41.49	31.91	25.25	51.25
FN/CA-s	84	184.74	139.02	95.05	133.56	127.11	67.51	40.01	32.82	24.14	49.96
FN/CA-w	90	182.43	143.47	96.29	136.74	131.42	67.21	38.21	30.53	24.15	49.23
LN-e	37	185.20	138.30	96.49	137.98	130.04	66.11	40.30	31.88	24.61	48.58
LN-s	8	187.00	134.13	95.44	136.47	126.59	69.44	41.00	31.44	24.03	50.56
LN-w	21	187.57	138.57	96.71	136.29	129.33	67.83	40.47	31.09	24.19	49.67
LUP-s	13	193.08	141.04	96.00	139.25	141.38	67.23	43.38	30.88	24.88	49.92
LUP-w	7	194.07	140.71	98.69	135.26	144.07	71.39	41.40	29.82	24.86	51.90
Meso1	26	190.74	140.77	97.95	140.45	138.14	70.33	42.08	31.34	24.95	51.50
Meso2	41	189.06	140.15	98.47	139.38	138.83	69.76	42.23	31.02	25.19	50.47
MLN-e	6	184.42	134.00	93.17	135.32	127.33	66.90	39.83	31.00	22.92	47.67
MLN-n	22	186.45	139.41	97.96	136.71	132.11	67.55	40.23	31.50	23.91	48.75
MLN-s	6	184.00	146.50	97.17	138.16	131.50	67.37	41.33	30.83	24.67	47.50
MLN-sw	6	182.44	136.39	96.33	133.83	126.48	63.83	40.50	31.67	24.26	46.83
MLN-w	26	189.98	139.26	96.52	136.66	128.26	70.22	40.23	32.78	23.92	51.84
MN-e	25	186.28	138.72	97.48	140.31	129.89	70.16	41.41	32.94	25.71	51.36
MN-Lig	14	188.57	137.25	94.68	140.19	128.82	68.43	40.50	33.29	25.21	50.67
MN-s	6	182.83	138.75	93.75	138.25	128.88	67.82	40.25	31.58	22.78	46.83
MN-s(a)	10	187.41	139.10	96.82	139.52	129.05	67.67	40.63	31.25	22.97	49.27
MN-w	29	185.83	138.38	96.12	136.91	128.52	69.07	40.50	31.37	24.52	48.45
MUP-e	8	198.25	140.75	101.75	135.66	137.11	69.28	41.63	29.00	27.00	54.38
MUP-sw	7	196.28	141.72	102.17	136.84	140.13	64.76	45.27	29.91	26.96	50.18
Sard	21	181.76	133.02	94.26	132.98	125.24	68.88	39.95	33.12	24.43	51.60
Sicily	30	178.40	138.90	95.67	130.57	129.00	70.10	41.57	33.80	23.98	52.17
Tusc	50	181.41	141.74	98.38	135.71	131.37	70.87	42.42	33.91	24.09	52.39
N total All Groups	1211	185.58	140.25	96.96	136.59	130.69	68.71	40.86	31.97	24.54	50.47
Female means											
Group	N	M1	M8	M9	M17	M45	M48	M51	M52	M54	M55
BA-ce	146	175.27	136.60	94.40	132.40	123.64	65.30	39.61	32.49	23.79	48.27
BA-se	58	175.24	135.29	93.67	129.88	121.91	63.12	39.36	31.83	22.71	46.49
BA-sw	90	178.26	137.52	94.91	129.88	123.06	64.64	40.02	31.87	23.17	47.75
CA-e	45	176.00	136.31	93.56	130.37	122.90	63.75	38.96	31.49	23.47	47.53
CA-s	32	178.50	139.18	95.49	130.67	124.35	64.38	40.18	31.33	24.05	47.84
CA-s(a)	5	173.60	136.60	95.32	129.32	121.54	63.70	40.20	32.10	23.40	49.40
EN-e	28	178.50	136.98	93.82	132.13	123.49	66.23	39.31	32.31	24.78	48.13
EN-Lig	2	182.00	138.00	95.50	137.29	123.50	62.50	40.50	31.00	24.00	49.00
EN-s	7	183.16	136.03	95.11	136.47	123.88	67.44	40.33	32.14	23.39	49.19
EN-w	37	179.57	134.03	92.93	134.46	119.89	64.92	38.24	30.95	23.22	45.96
EUP	4	189.68	136.30	101.85	129.38	135.71	63.13	42.80	31.00	25.35	45.98

Table 5 (continued)

FN/CA-e	10	180.90	138.10	93.40	133.87	125.57	64.50	39.90	31.10	25.12	47.65
FN/CA-s	48	177.98	134.84	92.75	128.78	120.97	64.71	38.39	31.88	23.24	47.54
FN/CA-w	79	174.82	139.10	93.56	130.94	124.20	64.11	37.19	30.66	23.70	46.95
LN-e	22	179.36	133.23	92.27	133.53	121.68	64.73	38.81	31.43	24.04	46.49
LN-s	7	183.29	136.14	93.21	132.34	123.54	65.86	39.21	32.07	22.71	46.86
LN-w	16	178.63	134.50	94.00	130.24	125.31	63.97	39.50	31.63	23.20	46.97
LUP-s	6	187.67	139.58	92.00	134.83	129.83	65.13	41.67	28.92	23.75	47.00
LUP-w	7	183.00	136.86	93.29	132.14	130.50	65.54	39.01	29.63	22.43	48.47
Meso1	26	184.57	137.48	95.09	135.82	131.62	66.50	41.13	31.24	23.50	49.51
Meso2	37	179.25	136.20	94.33	131.71	129.18	65.10	39.55	29.79	23.43	48.09
MLN-e	1	167.50	148.00	101.00	131.76	130.78	68.88	39.00	32.00	21.50	51.00
MLN-n	16	179.44	134.69	94.61	134.10	119.95	63.06	39.12	32.13	22.67	45.27
MLN-s	3	172.67	139.00	89.00	125.00	120.00	64.41	37.00	31.33	23.67	45.33
MLN-sw	3	181.11	133.16	96.33	131.84	123.33	65.67	40.00	30.67	23.67	50.67
MLN-w	18	183.56	134.61	93.80	132.13	123.18	63.94	38.42	30.61	23.78	47.31
MN-e	8	179.00	134.25	92.75	135.17	121.40	63.60	37.80	30.78	24.85	47.14
MN-Lig	5	180.60	134.40	93.80	131.39	123.40	62.20	40.50	30.90	24.60	46.88
MN-s	9	179.50	135.33	93.56	132.76	123.11	66.10	40.04	32.33	23.50	49.62
MN-s(a)	7	181.52	137.05	95.56	136.70	125.40	65.13	39.93	32.57	24.16	47.53
MN-w	36	176.92	132.89	92.66	130.20	121.22	64.55	39.01	31.43	23.07	45.78
MUP-e	4	186.25	136.50	96.25	135.98	130.88	65.00	39.50	29.25	26.13	50.00
MUP-sw	6	189.17	135.83	96.83	133.82	132.34	66.58	40.50	29.00	26.00	50.70
Sard	22	176.61	128.64	90.02	124.32	117.00	64.89	38.30	33.36	23.77	48.05
Sicily	14	171.21	135.36	91.43	125.29	121.00	66.57	40.71	33.71	23.46	49.79
Tusc	50	170.96	136.48	94.36	127.52	122.42	65.55	40.63	34.00	23.36	48.74
N total All Groups	914	177.40	136.15	93.89	131.11	123.43	64.75	39.32	31.74	23.56	47.63

Male S.D.

Group	M1	M8	M9	M17	M45	M48	M51	M52	M54	M55
BA-ce	8.43	7.40	4.64	5.48	6.64	4.48	2.30	2.22	1.98	3.17
BA-se	7.76	7.05	6.31	5.10	6.59	5.01	2.37	1.91	2.06	3.65
BA-sw	7.13	5.69	4.37	5.24	5.17	4.13	1.83	2.08	1.71	3.57
CA-e	7.75	5.98	4.14	6.82	5.73	4.61	2.39	2.19	1.75	3.06
CA-s	7.35	6.69	4.38	5.72	6.77	4.77	2.52	2.04	1.79	4.24
CA-s(a)	5.79	2.88	2.51	3.23	3.70	3.44	1.43	1.34	1.94	2.84
EN-e	5.74	7.65	4.01	5.85	6.72	6.20	2.32	2.59	2.66	4.39
EN-Lig	7.37	7.58	3.67	2.58	7.40	3.40	3.70	1.95	1.64	2.28
EN-s	5.82	8.92	7.75	5.95	12.53	6.18	2.55	2.34	2.56	1.73
EN-w	6.46	4.82	4.68	6.19	5.92	4.15	1.92	2.27	1.76	3.36
EUP	8.26	7.12	4.91	5.23	4.69	7.37	2.50	2.90	0.75	5.39
FN/CA-e	7.61	6.12	3.94	5.42	7.47	5.53	2.60	2.56	1.99	4.14
FN/CA-s	6.23	5.66	4.76	6.98	6.13	4.32	2.18	2.05	1.94	3.74
FN/CA-w	6.60	7.10	4.97	6.01	6.21	3.92	2.67	2.71	1.87	3.60
LN-e	7.30	6.55	5.35	6.18	7.07	4.79	1.95	2.25	2.16	3.50
LN-s	6.59	9.88	4.07	4.55	6.57	5.67	2.14	2.01	2.28	4.98
LN-w	7.54	6.99	3.73	6.33	5.01	4.77	1.97	2.10	1.74	3.76
LUP-s	8.99	4.69	5.48	6.80	6.47	2.70	3.25	2.84	2.68	3.01
LUP-w	3.52	3.90	1.80	8.98	4.51	5.29	3.22	1.71	2.08	4.58
Meso1	4.27	4.97	4.44	4.88	6.54	5.10	2.21	2.64	2.86	2.93
Meso2	7.04	7.46	6.19	7.26	9.02	6.02	2.87	2.55	2.08	3.87
MLN-e	6.80	8.65	5.85	3.85	8.80	3.47	2.02	1.67	2.01	3.68
MLN-n	5.89	4.86	4.89	5.78	6.05	4.36	1.93	2.02	1.54	3.25
MLN-s	6.20	8.48	3.49	6.24	7.40	9.55	1.86	4.31	1.75	4.46
MLN-sw	6.49	6.87	2.94	4.15	4.51	4.54	2.26	1.37	1.17	2.71
MLN-w	6.95	4.92	4.99	5.39	8.56	4.25	2.00	1.63	2.35	3.68
MN-e	6.03	6.22	4.37	5.39	6.16	4.18	2.07	1.79	1.74	2.58

Table 5 (continued)

MN-Lig	6.51	3.68	3.97	4.80	4.40	4.26	2.02	2.81	1.52	2.65
MN-s	6.88	7.63	3.95	4.96	6.53	3.99	2.36	1.37	1.79	4.12
MN-s(a)	6.11	4.12	4.18	4.44	7.61	6.61	1.88	2.70	1.42	3.68
MN-w	6.77	4.95	5.71	5.75	4.89	3.91	1.90	2.04	2.10	3.37
MUP-e	7.03	4.77	2.96	4.29	6.86	5.40	1.92	2.14	2.96	4.87
MUP-sw	5.77	6.74	4.89	8.30	8.11	5.08	2.83	4.47	1.71	4.69
Sard	7.95	6.22	4.91	4.59	3.67	4.36	1.82	1.57	1.74	2.85
Sicily	5.39	4.34	5.03	6.27	5.30	5.05	2.22	1.54	1.66	2.86
Tusc	6.76	5.92	4.87	6.02	5.87	4.53	2.01	2.28	1.88	3.12
N total All Groups	7.63	6.60	4.92	6.15	7.00	4.79	2.49	2.36	2.01	3.65
Female S.D.										
Group	M1	M8	M9	M17	M45	M48	M51	M52	M54	M55
BA-ce	7.79	6.00	3.44	5.18	5.38	4.14	2.12	2.13	1.78	3.46
BA-se	7.48	6.12	4.85	4.44	4.87	3.66	2.29	2.73	2.63	4.09
BA-sw	6.71	4.96	3.61	5.22	5.38	3.87	1.89	2.00	1.99	3.16
CA-e	5.98	6.26	4.90	6.21	5.60	5.05	1.92	2.04	1.77	3.70
CA-s	5.55	5.55	4.62	5.47	6.38	5.28	2.65	1.64	1.83	3.44
CA-s(a)	4.72	8.96	5.97	3.94	1.80	2.22	1.60	1.52	3.21	3.13
EN-e	6.83	3.96	4.24	4.01	5.75	3.73	2.87	1.98	1.82	3.15
EN-Lig	1.41	1.41	3.54	0.41	6.36	2.12	0.71	1.41	1.41	2.83
EN-s	6.74	5.85	3.08	6.79	9.81	2.06	2.58	2.29	2.24	2.04
EN-w	6.07	5.69	4.80	4.28	5.96	4.01	2.15	1.87	1.96	3.30
EUP	7.83	3.79	3.57	6.87	8.29	1.35	2.07	1.15	0.45	2.50
FN/CA-e	5.76	7.78	4.27	6.50	6.59	4.79	2.38	1.97	1.95	2.55
FN/CA-s	5.93	4.00	4.60	5.76	5.62	3.49	2.33	2.18	1.80	3.20
FN/CA-w	6.25	5.06	3.59	5.74	4.98	3.84	2.18	2.64	2.02	3.89
LN-e	7.20	6.70	3.28	5.47	4.84	4.53	1.88	2.58	2.20	3.14
LN-s	4.82	3.53	2.64	4.77	3.82	4.88	2.48	2.62	3.73	4.18
LN-w	6.28	6.41	3.78	6.42	5.66	2.72	2.11	2.47	2.05	3.60
LUP-s	9.23	5.35	4.60	6.47	4.12	3.02	1.75	1.36	0.61	2.61
LUP-w	4.40	4.85	2.87	4.91	6.10	5.16	2.29	1.83	1.81	3.99
Meso1	5.53	7.20	5.17	6.52	6.55	4.52	1.99	2.78	1.66	4.28
Meso2	6.18	5.81	4.40	5.85	7.48	5.30	2.08	2.21	1.53	4.08
MLN-e	\	\	\	\	\	\	\	\	\	\
MLN-n	7.34	6.35	5.93	4.27	5.42	3.59	2.33	1.63	1.20	2.96
MLN-s	6.66	5.00	2.00	7.55	4.58	1.97	1.00	0.58	4.51	2.31
MLN-sw	7.00	6.52	3.21	1.32	4.93	7.09	1.00	0.58	1.53	2.89
MLN-w	6.04	3.52	3.51	6.57	6.73	6.11	3.04	2.76	2.80	3.07
MN-e	7.03	4.06	3.28	4.36	2.38	4.20	2.37	1.42	1.68	2.69
MN-Lig	4.93	2.30	4.87	4.32	3.58	3.77	1.12	1.95	0.89	1.63
MN-s	5.97	4.00	2.32	4.53	6.58	3.50	1.60	1.41	2.50	3.51
MN-s(a)	7.90	4.37	3.78	8.30	6.07	5.06	2.05	2.44	2.36	3.29
MN-w	7.07	4.86	3.19	5.44	4.11	4.61	1.66	1.91	1.99	2.97
MUP-e	4.19	8.70	5.32	5.35	9.22	2.16	1.29	2.87	1.93	1.83
MUP-sw	7.81	3.37	3.92	2.77	4.19	2.87	2.26	1.67	1.26	1.62
Sard	6.05	4.73	4.28	5.18	5.42	3.27	0.96	1.84	1.90	2.70
Sicily	6.05	5.24	4.20	5.51	3.44	4.73	2.20	2.95	1.80	3.19
Tusc	7.40	6.97	4.12	5.82	5.15	3.71	1.58	1.87	1.74	3.12
N total All Groups	7.43	5.87	4.20	5.85	6.16	4.19	2.31	2.38	2.01	3.53

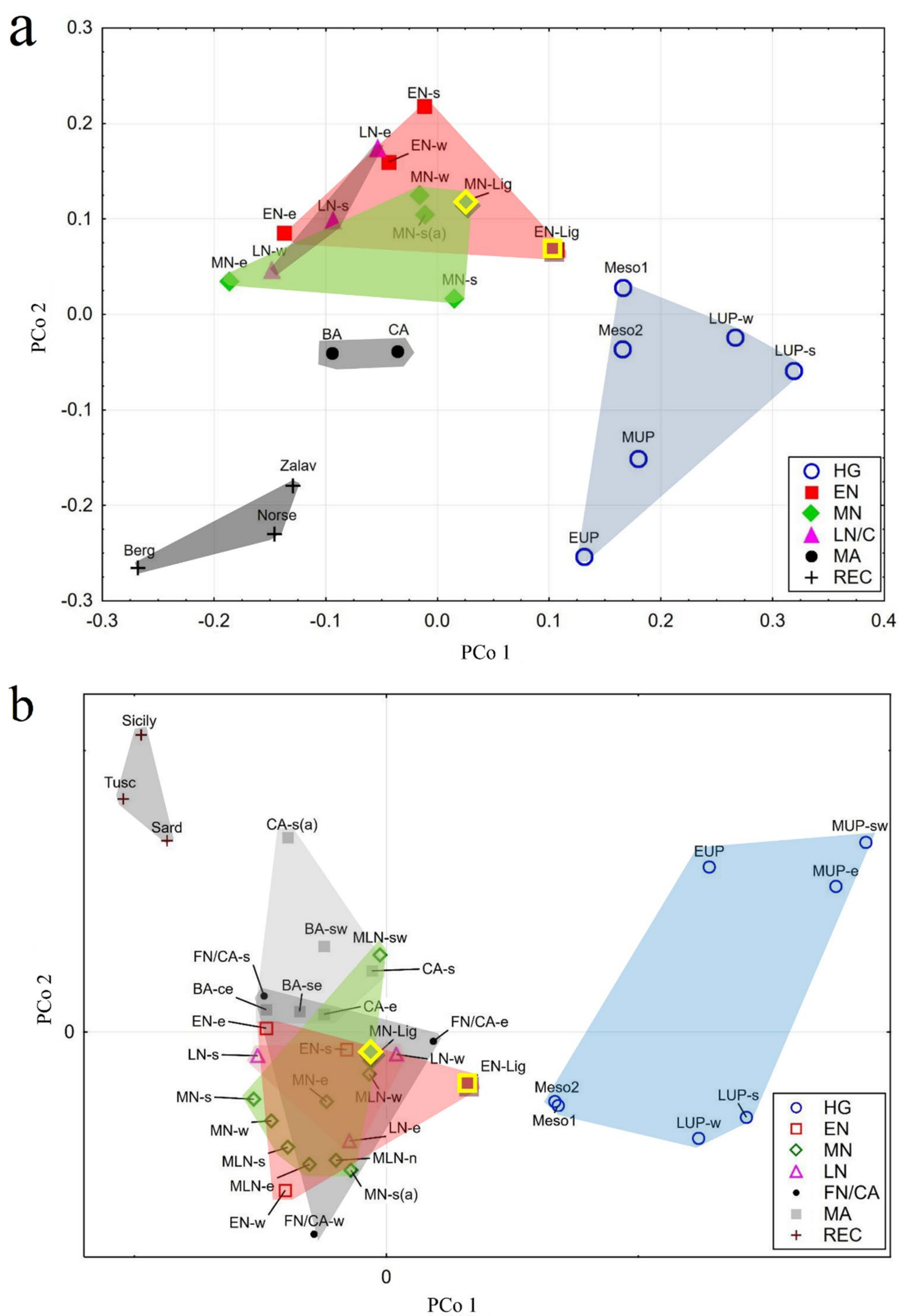

Fig. 2 Plot of principal coordinates 1 and 2 from R-matrix analysis for Analysis 1 (**a**) and Analysis 2 (**b**). Ligurian Neolithic groups' symbols are enlarged and highlighted. Convex hulls delimit the groups according to their inclusion in six and seven chrono-cultural macro-groups, respectively

MN-w and MN-s; in the NJ analysis tree it was found to be linked to FN/CA-w, CA-s and CA-e (in this order).

DFA

DFA was used for the classification of the 27 Ligurian Neolithic crania (Table 8). This analysis was performed on both the Analyses 1 and 2 datasets, starting with four and five "a priori" groups, respectively. These groups are nearly identical in their composition to the macro-groups used in the distance matrix analysis, with the Ligurian crania considered as "ungrouped cases".

Focusing on the "ungrouped" Ligurian Neolithic crania, an examination of their most probable posterior classifications for Analysis 1 (Table 8a) reveals that two EN-Lig crania (AC2T and AM252) were better classified as HG. Additionally, three

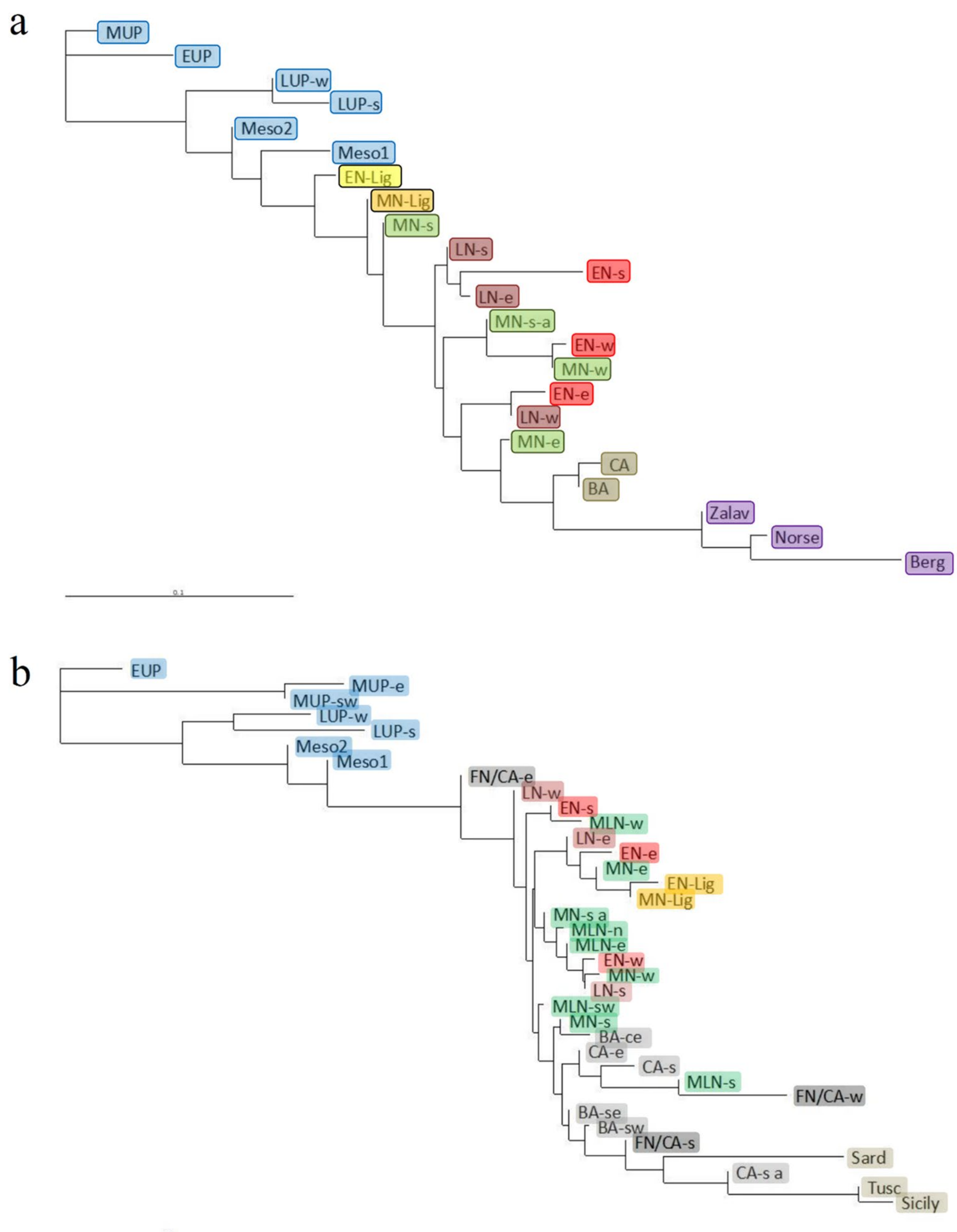

Fig. 3 Phylogenetic trees obtained by clustering the distance matrices for Analysis 1 (**a**) and Analysis 2 (**b**) by the neighbor-joining method. Trees are represented as phylograms, with EUP used as the outgroup. Different colors used for the hulls identify different macro-groups, as follows: light blue: HG, yellow: Ligurian groups, red: EN, green: MN, pink: LN/C, grey: MA, FN/C, light purple: REC

MN-Lig crania (ACIII, ACVI, and PO13) were better classified as HG, and the only LN cranium (AN1 Chasseén) was also better classified as HG. Specifically, this means 2 out of 7 EN-Lig crania (28.6%), 3 out of 19 MN-Lig crania (15.8%), and 1 out of 1 LN cranium (100%) were classified as HG.

Regarding Analysis 2 (Table 8b), the most probable posterior classifications again revealed two EN crania (AC2T and AA2R) classified as HG, two MN crania (ACVI and ACVII) classified as HG, and the only LN cranium (AN1) classified as HG. This corresponds to 2 out of 7 EN-Lig crania (28.6%), 2 out of 19 MN-Lig crania (10.5%), and 1 out of 1 LN cranium (100%) being classified as HG.

To assess the discriminatory effectiveness of these analyses, we referred to the absolute and relative frequencies of correctly classified cases (SI Table S7). The results for Analysis 1 demonstrate strong discriminatory power, with percentages of correct classifications ranging from ~98% to ~78% across the four a priori groups, yielding an overall average of 87.06%. In contrast, Analysis 2 revealed lower discriminatory efficacy, with percentages of correct classifications ranging from ~69% to ~24% across the five a priori groups, yielding an overall average of 39.41%. However, both the HG and Recent groups achieved a good percentage of correct classification (~69%).

Table 6 Analysis 1: distance matrix for 23 groups calculated from a R-matrix with 30 variables, displayed as a heatmap. Ligurian Neolithic group values are enlarged and highlighted

	HG						LIG		EN			MN				LN/C			MA		REC		
Group	EUP	MUP	LUP-w	LUP-s	Meso1	Meso2	EN-Lig	MN-Lig	EN-e	EN-s	EN-w	MN-e	MN-s	MN-s-a	MN-w	LN-e	LN-s	LN-w	CA	BA	Norse	Zalav	Berg
EUP		0.063	0.134	0.147	0.254	0.155	0.223	0.224	0.220	0.346	0.238	0.239	0.119	0.200	0.212	0.304	0.221	0.205	0.205	0.212	0.180	0.174	0.257
MUP	0.063		0.081	0.130	0.179	0.123	0.128	0.163	0.230	0.222	0.227	0.207	0.149	0.150	0.195	0.216	0.196	0.211	0.176	0.185	0.200	0.194	0.287
LUP-w	0.134	0.081		0.005	0.017	0.036	0.086	0.146	0.225	0.147	0.167	0.196	0.077	0.075	0.124	0.198	0.152	0.179	0.118	0.156	0.247	0.211	0.346
LUP-s	0.147	0.130	0.005		0.071	0.010	0.093	0.141	0.300	0.247	0.215	0.260	0.113	0.163	0.168	0.211	0.197	0.249	0.220	0.210	0.281	0.207	0.395
Meso1	0.254	0.179	0.017	0.071		0.030	0.051	0.097	0.171	0.141	0.161	0.176	0.054	0.060	0.134	0.173	0.126	0.136	0.081	0.108	0.213	0.160	0.304
Meso2	0.155	0.123	0.036	0.010	0.030		0.049	0.075	0.140	0.173	0.156	0.156	0.020	0.070	0.109	0.124	0.100	0.124	0.107	0.099	0.175	0.109	0.258
EN-Lig	0.223	0.128	0.086	0.093	0.051	0.049		0.000	0.133	0.055	0.155	0.116	0.041	0.100	0.118	0.103	0.061	0.093	0.064	0.083	0.173	0.156	0.301
MN-Lig	0.224	0.163	0.146	0.141	0.097	0.075	0.000		0.082	0.041	0.098	0.089	0.002	0.056	0.071	0.039	0.030	0.074	0.089	0.072	0.166	0.141	0.279
EN-e	0.220	0.230	0.225	0.300	0.171	0.140	0.133	0.082		0.140	0.109	0.064	0.034	0.054	0.090	0.044	0.042	0.000	0.139	0.123	0.180	0.142	0.202
EN-s	0.346	0.222	0.147	0.247	0.141	0.173	0.055	0.041	0.140		0.093	0.076	0.084	0.044	0.121	0.071	0.040	0.099	0.118	0.133	0.247	0.225	0.340
EN-w	0.238	0.227	0.167	0.215	0.161	0.156	0.155	0.098	0.109	0.093		0.043	0.075	0.016	0.000	0.090	0.058	0.068	0.147	0.098	0.256	0.163	0.298
MN-e	0.239	0.207	0.196	0.260	0.176	0.156	0.116	0.089	0.064	0.076	0.043		0.070	0.041	0.055	0.073	0.012	0.000	0.087	0.040	0.108	0.056	0.093
MN-s	0.119	0.149	0.077	0.113	0.054	0.020	0.041	0.002	0.034	0.084	0.075	0.070		0.007	0.079	0.076	0.019	0.008	0.074	0.043	0.108	0.068	0.194
MN-s-a	0.200	0.150	0.075	0.163	0.060	0.070	0.100	0.056	0.054	0.044	0.016	0.041	0.007		0.018	0.072	0.010	0.024	0.044	0.033	0.193	0.117	0.217
MN-w	0.212	0.195	0.124	0.168	0.134	0.109	0.118	0.071	0.090	0.121	0.000	0.055	0.079	0.018		0.070	0.043	0.034	0.126	0.097	0.215	0.155	0.264
LN-e	0.304	0.216	0.198	0.211	0.173	0.124	0.103	0.039	0.044	0.071	0.090	0.073	0.076	0.072	0.070		0.028	0.102	0.170	0.125	0.228	0.181	0.270
LN-s	0.221	0.196	0.152	0.197	0.126	0.100	0.061	0.030	0.042	0.040	0.058	0.012	0.019	0.010	0.043	0.028		0.013	0.084	0.057	0.120	0.094	0.184
LN-w	0.205	0.211	0.179	0.249	0.136	0.124	0.093	0.074	0.000	0.099	0.068	0.000	0.008	0.024	0.034	0.102	0.013		0.088	0.068	0.112	0.077	0.140
CA	0.205	0.176	0.118	0.220	0.081	0.107	0.064	0.089	0.139	0.118	0.147	0.087	0.074	0.044	0.126	0.170	0.084	0.088		0.000	0.125	0.098	0.160
BA	0.212	0.185	0.156	0.210	0.108	0.099	0.083	0.072	0.123	0.133	0.098	0.040	0.043	0.033	0.097	0.125	0.057	0.068	0.000		0.096	0.046	0.113
Norse	0.180	0.200	0.247	0.281	0.213	0.175	0.173	0.166	0.180	0.247	0.256	0.108	0.108	0.193	0.215	0.228	0.120	0.112	0.125	0.096		0.032	0.070
Zalav	0.174	0.194	0.211	0.207	0.160	0.109	0.156	0.141	0.142	0.225	0.163	0.056	0.068	0.117	0.155	0.181	0.094	0.077	0.098	0.046	0.032		0.052
Berg	0.257	0.287	0.346	0.395	0.304	0.258	0.301	0.279	0.202	0.340	0.298	0.093	0.194	0.217	0.264	0.270	0.184	0.140	0.160	0.113	0.070	0.052	

To visualize the Ligurian individuals within a discriminatory morphospace, we generated scatterplots by projecting the first two canonical variates (CV1 and CV2) obtained via DFA for both datasets in Analyses 1 and 2 (Fig. 5).

In Analysis 1, where the sample was divided into four "a priori" groups (with the exception of the 27 Ligurian Neolithic crania as "ungrouped cases"), the scatterplot reveals a noticeable differentiation among HG, EF, and the other groups, although some overlap exists (Fig. 5a). When summarizing each macro-group by their 90% normal distribution ellipses, a separation among the HG, EF, and REC groups is evident, with the MA group overlapping largely with the previous three (Fig. 5b).

For Analysis 2, where the sample was divided into five "a priori" groups, the scatterplot reveals some differentiation among HG, EF, and the other groups, although substantial mixing occurs (Fig. 5c). When summarizing the extent of the macro-groups by their 75% normal distribution ellipses (Fig. 5d), both HG and EF show some separation from each other and from the REC group, although the EF ellipse overlaps extensively with the FN/CA and MA groups. The HG and REC groups extend largely without overlap. The Ligurian Neolithic individuals predominantly cluster in the area occupied by EF individuals, with significant overlap.

Other Ligurian crania cluster with HG; for example, the EN individual AC2T was consistently classified as more similar to HG, as was AA2R in three out of four instances. Similarly, the MN individual ACVI was consistently classified as more similar to HG, and the LN individual AN1 was always found to be more similar to HG.

Table 7 Analysis 2: distance matrix for 36 groups calculated from a R-matrix with 10 variables, displayed as a heatmap. Ligurian Neolithic group values are enlarged and highlighted

Group	HG							LIG		EN			MN										LN			FC/CA			MA						REC		
	EUP	MUP-e	MUP-sw	LUP-w	LUP-s	Meso1	Meso2	EN-Lig	MN-Lig	EN-e	EN-s	EN-w	MN-e	MN-s	MN-s(a)	MN-w	MLN-e	MLN-n	MLN-s	MLN-sw	MLN-w	LN-e	LN-s	LN-w	FN/CA-e	FN/CA-s	FN/CA-w	CA-e	CA-s	CA-s(a)	BA-ce	BA-se	BA-sw	Tusc	Sicily	Sard
EUP		0.225	0.047	0.190	0.187	0.176	0.139	0.220	0.271	0.283	0.278	0.308	0.289	0.310	0.261	0.243	0.258	0.212	0.329	0.131	0.270	0.236	0.258	0.166	0.174	0.302	0.461	0.259	0.247	0.280	0.310	0.238	0.231	0.425	0.439	0.401
MUP-e	0.225		0.012	0.194	0.287	0.234	0.239	0.279	0.311	0.401	0.280	0.423	0.344	0.451	0.361	0.477	0.419	0.401	0.459	0.266	0.258	0.357	0.423	0.279	0.229	0.377	0.417	0.305	0.294	0.393	0.400	0.359	0.317	0.647	0.614	0.535
MUP-sw	0.047	0.012		0.192	0.125	0.166	0.172	0.179	0.274	0.377	0.274	0.420	0.329	0.392	0.310	0.414	0.389	0.343	0.422	0.201	0.301	0.310	0.398	0.240	0.200	0.383	0.483	0.296	0.257	0.300	0.364	0.323	0.290	0.565	0.562	0.546
LUP-w	0.190	0.194	0.192		0.095	0.062	0.042	0.324	0.282	0.338	0.230	0.262	0.309	0.227	0.208	0.257	0.119	0.213	0.238	0.220	0.190	0.229	0.273	0.133	0.164	0.256	0.230	0.210	0.225	0.312	0.297	0.238	0.227	0.488	0.447	0.431
LUP-s	0.187	0.287	0.125	0.095		0.054	0.093	0.130	0.209	0.341	0.225	0.325	0.288	0.233	0.196	0.305	0.246	0.257	0.253	0.244	0.272	0.229	0.342	0.192	0.151	0.324	0.379	0.250	0.223	0.278	0.309	0.288	0.278	0.509	0.504	0.544
Meso1	0.176	0.234	0.166	0.062	0.054		0.007	0.085	0.076	0.153	0.053	0.125	0.100	0.067	0.040	0.140	0.060	0.088	0.140	0.087	0.106	0.076	0.136	0.053	0.037	0.146	0.184	0.083	0.097	0.142	0.103	0.108	0.114	0.260	0.277	0.306
Meso2	0.139	0.239	0.172	0.042	0.093	0.007		0.157	0.125	0.150	0.099	0.128	0.119	0.080	0.067	0.116	0.043	0.087	0.118	0.075	0.133	0.080	0.132	0.049	0.051	0.157	0.146	0.083	0.103	0.148	0.109	0.104	0.113	0.263	0.276	0.304
EN-Lig	0.220	0.279	0.179	0.324	0.130	0.085	0.157		0.000	0.083	0.000	0.084	0.028	0.056	0.000	0.117	0.141	0.058	0.116	0.040	0.054	0.032	0.101	0.065	0.023	0.102	0.250	0.075	0.070	0.096	0.093	0.081	0.091	0.279	0.337	0.276
MN-Lig	0.271	0.311	0.274	0.282	0.209	0.076	0.125	0.000		0.019	0.000	0.059	0.000	0.023	0.011	0.084	0.092	0.056	0.116	0.039	0.033	0.001	0.055	0.047	0.004	0.049	0.180	0.038	0.092	0.096	0.043	0.063	0.083	0.194	0.215	0.128
EN-e	0.283	0.401	0.377	0.338	0.341	0.153	0.150	0.083	0.019		0.043	0.062	0.007	0.037	0.055	0.057	0.086	0.063	0.040	0.050	0.073	0.021	0.055	0.063	0.027	0.040	0.114	0.025	0.075	0.098	0.027	0.043	0.067	0.126	0.149	0.116
EN-s	0.278	0.280	0.274	0.230	0.225	0.053	0.099	0.000	0.000	0.043		0.015	0.000	0.000	0.000	0.056	0.022	0.020	0.087	0.003	0.000	0.011	0.008	0.007	0.000	0.020	0.144	0.002	0.033	0.039	0.012	0.015	0.018	0.134	0.160	0.126
EN-w	0.308	0.423	0.420	0.262	0.325	0.125	0.128	0.084	0.059	0.062	0.015		0.024	0.004	0.000	0.013	0.004	0.014	0.066	0.049	0.035	0.025	0.000	0.035	0.042	0.061	0.131	0.044	0.100	0.147	0.060	0.050	0.069	0.207	0.241	0.164
MN-e	0.289	0.344	0.329	0.309	0.288	0.100	0.119	0.028	0.000	0.007	0.000	0.024		0.023	0.011	0.055	0.077	0.049	0.100	0.042	0.056	0.001	0.029	0.056	0.005	0.073	0.150	0.034	0.099	0.133	0.026	0.064	0.088	0.184	0.220	0.149
MN-s	0.310	0.451	0.392	0.227	0.233	0.067	0.080	0.056	0.023	0.037	0.000	0.004	0.023		0.000	0.000	0.000	0.000	0.016	0.006	0.034	0.002	0.000	0.000	0.020	0.013	0.100	0.000	0.033	0.007	0.000	0.000	0.012	0.082	0.105	0.110
MN-s(a)	0.261	0.361	0.310	0.208	0.196	0.040	0.067	0.000	0.011	0.055	0.000	0.000	0.011	0.000		0.028	0.000	0.000	0.049	0.006	0.025	0.000	0.016	0.001	0.020	0.051	0.104	0.017	0.043	0.067	0.017	0.011	0.036	0.164	0.224	0.205
MN-w	0.243	0.477	0.414	0.257	0.305	0.140	0.116	0.117	0.084	0.057	0.056	0.013	0.055	0.000	0.028		0.000	0.018	0.040	0.029	0.069	0.029	0.000	0.026	0.051	0.054	0.143	0.044	0.096	0.098	0.064	0.040	0.057	0.169	0.187	0.128
MLN-e	0.258	0.419	0.389	0.119	0.246	0.060	0.043	0.141	0.092	0.086	0.022	0.004	0.077	0.000	0.000	0.000		0.000	0.031	0.012	0.032	0.016	0.000	0.000	0.058	0.032	0.056	0.019	0.061	0.065	0.038	0.000	0.024	0.144	0.172	0.153
MLN-n	0.212	0.401	0.343	0.213	0.257	0.088	0.087	0.058	0.056	0.063	0.020	0.014	0.049	0.000	0.000	0.018	0.000		0.058	0.007	0.040	0.005	0.019	0.005	0.055	0.053	0.109	0.040	0.075	0.095	0.050	0.015	0.048	0.180	0.238	0.186
MLN-s	0.329	0.459	0.422	0.238	0.253	0.140	0.118	0.116	0.116	0.040	0.087	0.066	0.100	0.016	0.049	0.040	0.031	0.058		0.095	0.088	0.061	0.090	0.055	0.046	0.047	0.029	0.020	0.014	0.085	0.062	0.034	0.043	0.160	0.176	0.243
MLN-sw	0.131	0.266	0.201	0.220	0.244	0.087	0.075	0.040	0.039	0.050	0.003	0.049	0.042	0.006	0.006	0.029	0.012	0.007	0.095		0.039	0.013	0.008	0.000	0.032	0.035	0.150	0.013	0.038	0.000	0.026	0.000	0.004	0.123	0.152	0.110
MLN-w	0.270	0.258	0.301	0.190	0.272	0.106	0.133	0.054	0.033	0.073	0.000	0.035	0.056	0.034	0.025	0.069	0.032	0.040	0.088	0.039		0.045	0.030	0.019	0.032	0.015	0.134	0.032	0.071	0.104	0.080	0.039	0.040	0.219	0.216	0.118
LN-e	0.236	0.357	0.310	0.229	0.229	0.076	0.080	0.032	0.001	0.021	0.011	0.025	0.001	0.002	0.000	0.029	0.016	0.005	0.061	0.013	0.045		0.030	0.017	0.021	0.051	0.103	0.028	0.082	0.096	0.034	0.032	0.065	0.188	0.227	0.153
LN-s	0.258	0.423	0.398	0.273	0.342	0.136	0.132	0.101	0.055	0.055	0.008	0.000	0.029	0.000	0.016	0.000	0.000	0.019	0.090	0.008	0.030	0.030		0.016	0.038	0.032	0.175	0.030	0.092	0.078	0.045	0.030	0.037	0.139	0.149	0.070
LN-w	0.166	0.279	0.240	0.133	0.192	0.053	0.049	0.065	0.047	0.063	0.007	0.035	0.056	0.000	0.001	0.026	0.000	0.005	0.055	0.000	0.019	0.017	0.016		0.021	0.028	0.110	0.013	0.041	0.042	0.045	0.008	0.016	0.160	0.172	0.134
FN/CA-e	0.174	0.229	0.200	0.164	0.151	0.037	0.051	0.023	0.004	0.027	0.000	0.042	0.005	0.020	0.020	0.051	0.058	0.055	0.046	0.032	0.032	0.021	0.038	0.021		0.049	0.138	0.010	0.039	0.088	0.039	0.047	0.044	0.177	0.177	0.157
FN/CA-s	0.302	0.377	0.383	0.256	0.324	0.146	0.157	0.102	0.049	0.040	0.020	0.061	0.073	0.013	0.051	0.054	0.032	0.053	0.047	0.035	0.015	0.051	0.032	0.028	0.049		0.121	0.018	0.055	0.041	0.054	0.020	0.022	0.122	0.111	0.066
FN/CA-w	0.461	0.417	0.483	0.230	0.379	0.184	0.146	0.250	0.180	0.114	0.144	0.131	0.150	0.100	0.104	0.143	0.056	0.109	0.029	0.150	0.134	0.103	0.175	0.110	0.138	0.121		0.084	0.117	0.192	0.116	0.097	0.130	0.275	0.303	0.310
CA-e	0.259	0.305	0.296	0.210	0.250	0.083	0.083	0.075	0.038	0.025	0.002	0.044	0.034	0.000	0.017	0.044	0.019	0.040	0.020	0.013	0.032	0.028	0.030	0.013	0.010	0.018	0.084		0.015	0.024	0.012	0.007	0.009	0.104	0.112	0.124
CA-s	0.247	0.294	0.257	0.225	0.223	0.097	0.103	0.070	0.092	0.075	0.033	0.100	0.099	0.033	0.043	0.096	0.061	0.075	0.014	0.038	0.071	0.082	0.092	0.041	0.039	0.055	0.117	0.015		0.012	0.043	0.023	0.012	0.114	0.133	0.221
CA-s(a)	0.280	0.393	0.300	0.312	0.278	0.142	0.148	0.096	0.096	0.098	0.039	0.147	0.133	0.007	0.067	0.098	0.065	0.095	0.085	0.000	0.104	0.096	0.078	0.042	0.088	0.041	0.192	0.024	0.012		0.034	0.013	0.000	0.032	0.037	0.121
BA-ce	0.310	0.400	0.364	0.297	0.309	0.103	0.109	0.093	0.043	0.027	0.012	0.060	0.026	0.000	0.017	0.064	0.038	0.050	0.062	0.026	0.080	0.034	0.045	0.045	0.039	0.054	0.116	0.012	0.043	0.034		0.022	0.037	0.068	0.106	0.149
BA-se	0.238	0.359	0.323	0.238	0.288	0.108	0.104	0.081	0.063	0.043	0.015	0.050	0.064	0.000	0.011	0.040	0.000	0.015	0.034	0.000	0.039	0.032	0.030	0.008	0.047	0.020	0.097	0.007	0.023	0.013	0.022		0.005	0.094	0.124	0.134
BA-sw	0.231	0.317	0.290	0.227	0.278	0.114	0.113	0.091	0.083	0.067	0.018	0.069	0.088	0.012	0.036	0.057	0.024	0.048	0.043	0.004	0.040	0.065	0.037	0.016	0.044	0.022	0.130	0.009	0.012	0.000	0.037	0.005		0.094	0.102	0.131
Tusc	0.425	0.647	0.565	0.488	0.509	0.260	0.263	0.279	0.194	0.126	0.134	0.207	0.184	0.082	0.164	0.169	0.144	0.180	0.160	0.123	0.219	0.188	0.139	0.160	0.177	0.122	0.275	0.104	0.114	0.032	0.068	0.094	0.094		0.012	0.163
Sicily	0.439	0.614	0.562	0.447	0.504	0.277	0.276	0.337	0.215	0.149	0.160	0.241	0.220	0.105	0.224	0.187	0.172	0.238	0.176	0.152	0.216	0.227	0.149	0.172	0.177	0.111	0.303	0.112	0.133	0.037	0.106	0.124	0.102	0.012		0.107
Sard	0.401	0.535	0.546	0.431	0.544	0.306	0.304	0.276	0.128	0.116	0.126	0.164	0.149	0.110	0.205	0.128	0.153	0.186	0.243	0.110	0.118	0.153	0.070	0.134	0.157	0.066	0.310	0.124	0.221	0.121	0.149	0.134	0.131	0.163	0.107	

PCA

To further investigate the morphometric variation among the Ligurian Neolithic crania and the comparative sample, a PCA was performed on both the dataset of Analyses 1 and 2, including the 27 Ligurian specimens. The PCA was conducted using correlations among the variables, and the results were visualized in a two-dimensional plot, which captures the largest sources of variation in the dataset (Figs. 6 and 7). The first PCA (Analysis 1) yielded seven PCs with eigenvalues > 1, collectively explaining 58.22% of the total variance in the craniometric data (SI Table S8). The second PCA (Analysis 2), which utilized a partially different subset of variables and samples, yielded three PCs with eigenvalues > 1, explaining 62.53% of the total variance (SI Table S8). The difference in the number of PCs extracted to retain a similar proportion of variance between the two analyses is attributed to the difference in the input variable and sample subsets used for each respective analysis.

Among the six plots obtained from the seven PCs for Analysis 1 (Fig. 6) and in the two plots obtained from the three PCs for Analysis 2 (Fig. 7), plots formed by PC1 vs. PC2 and PC2 vs. PC3 show a certain distinction between the HG, EF and REC crania, although the overlap between

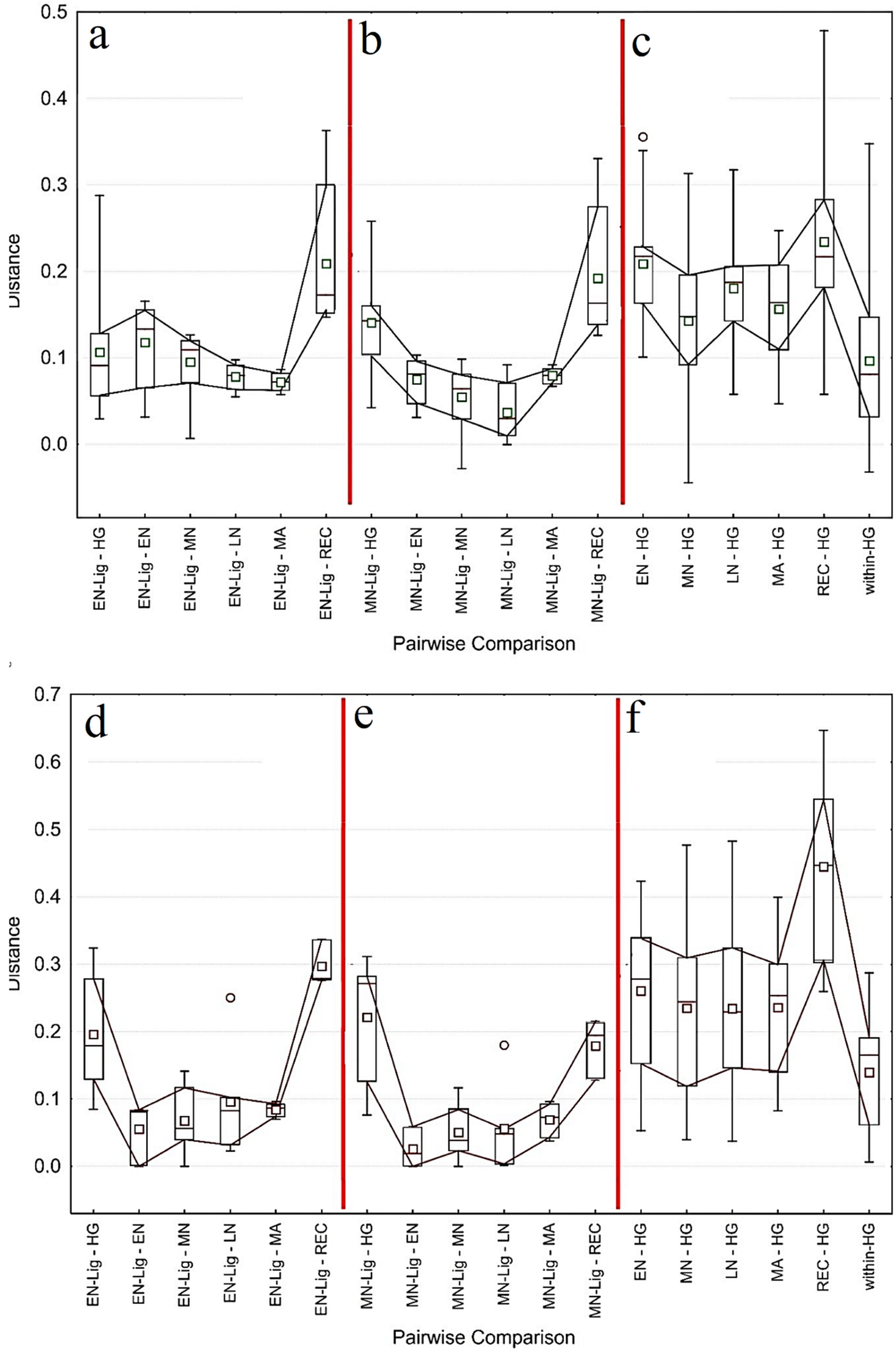

Fig. 4 Summary of the distribution of cumulative pairwise distances for between-group/macrogroup comparisons for Analysis 1 (**a-c**) and Analysis 2 (**d-f**). From left to right, comparisons between EN-Lig and others (**a, d**), between MN-Lig and others (**b, e**), between HG and others (and within HG) (**c, f**). Boxes represent the interquartile range (25% to 75% of quartiles), with a horizontal line inside indicating the median and a small square inside indicating the mean. Whiskers represent 1.5 times the interquartile range, with small circles indicating outliers

groups is extensive (Figs. 6a-b and 7). The majority of the Ligurian specimens cluster within the region occupied by the EF crania, but a few crania show some proximity to HG groups in the morphospace. In the other four plots of Analysis 1 (Fig. 6c-f), the overlap between the different macrogroups generally appears even more accentuated, although in two of them, those formed by PC5 vs. PC6 and PC6 vs. PC7, a partial distinction between HG and EF is again observable, with some Ligurian specimens again falling within the overlapping area between EF and HG groups, or even in the exclusively HG zone of the morphospace (Fig. 6e-f).

Table 8 DFA classification results for 27 Ligurian Neolithic crania included as non-grouped cases for Analyses 1 (a) and 2 (b). The best classifications for Ligurian crania within the macro-groups are determined by the highest posterior probability (the darkest color) and the lowest D^2 distance. The darker the color for the D^2 distance, the higher the value within the overall results for all crania

Specimen	Cult. group	a) Analysis 1									b) Analysis 2										
		Best macro-group post. class.	Posterior probability of membership				D^2 distance from macro-groups				Best macro-group post. class.	Posterior probability of membership					D^2 distance from macro-groups				
			HG	EF	MA	REC	HG	EF	MA	REC		HG	EF	FN/CA	MA	REC	HG	EF	FN/CA	MA	REC
Arene Candide 2 Tinè	EN-Lig	*HG*	0.99	0.01	0.00	0.01	26.47	36.34	40.69	38.97	*HG*	0.37	0.29	0.20	0.13	0.01	7.17	7.61	8.41	9.18	15.58
Arma del Morto 252	EN-Lig	*HG*	0.49	0.21	0.18	0.11	28.07	30.03	28.83	33.18	*MA*	0.12	0.19	0.17	0.39	0.12	5.81	4.85	5.12	3.42	5.73
Arma dell'Aquila R1	EN-Lig	*EF*	0.41	0.57	0.01	0.01	29.92	29.47	35.80	39.76	*EF*	0.05	0.44	0.09	0.33	0.10	11.81	7.36	10.62	7.93	10.36
Arma dell'Aquila R2	EN-Lig	*MA*	0.40	0.01	0.59	0.00	87.60	96.51	85.56	98.74	*HG*	0.80	0.10	0.01	0.08	0.01	32.72	36.84	40.78	37.44	41.85
Arma dell'Aquila R5	EN-Lig	*MA*	0.11	0.08	0.79	0.03	25.76	26.49	20.52	30.81	*MA*	0.04	0.31	0.21	0.37	0.06	9.31	5.37	6.15	5.03	8.79
Matta-Sanguineto 01083	EN-Lig	*REC*	0.01	0.11	0.25	0.63	37.58	33.83	30.61	32.19	*FN/CA*	0.03	0.28	0.47	0.20	0.02	12.74	8.04	7.01	8.70	13.47
Matta-Sanguineto 01085	EN-Lig	*MA*	0.00	0.47	0.52	0.00	49.40	40.39	38.74	51.97	*EF*	0.07	0.55	0.06	0.26	0.06	11.07	6.91	11.19	8.43	11.20
Arene Candide 1 Tinè	MN-Lig	*MA*	0.01	0.00	0.91	0.07	30.77	33.06	20.66	29.06	*MA*	0.13	0.21	0.27	0.30	0.09	8.72	7.69	7.20	7.03	9.41
Arene Candide 7PE	MN-Lig	*EF*	0.07	0.92	0.00	0.00	41.81	36.98	47.19	50.28	*FN/CA*	0.07	0.25	0.47	0.18	0.04	9.43	6.80	5.52	7.43	10.69
Arene Candide 8PE	MN-Lig	*EF*	0.04	0.55	0.10	0.31	21.80	16.63	18.51	19.70	*REC*	0.06	0.19	0.16	0.19	0.41	6.92	4.74	5.09	4.75	3.17
Arene Candide I Issel (3407-3408 Ge)	MN-Lig	*MA*	0.00	0.20	0.75	0.05	55.00	37.36	33.30	42.12	*REC*	0.00	0.09	0.01	0.07	0.82	25.20	16.88	20.46	17.14	12.34
Arene Candide III	MN-Lig	*HG*	0.56	0.32	0.10	0.01	26.43	27.78	28.56	36.15	*EF*	0.15	0.37	0.18	0.26	0.04	6.82	5.09	6.49	5.79	9.39
Arene Candide III Issel (5700 Pig)	MN-Lig	*EF*	0.01	0.98	0.01	0.00	56.96	48.22	55.87	66.96	*EF*	0.24	0.31	0.24	0.17	0.04	11.67	11.15	11.64	12.34	15.39
Arene Candide IV	MN-Lig	*MA*	0.21	0.02	0.67	0.10	35.13	40.27	31.58	38.83	*MA*	0.07	0.24	0.22	0.37	0.11	9.12	6.55	6.70	5.66	8.11
Arene Candide IV Issel (5690 Pig)	MN-Lig	*EF*	0.00	0.94	0.01	0.04	32.28	21.99	29.04	30.03	*EF*	0.32	0.36	0.08	0.11	0.13	10.02	9.76	12.73	12.11	11.78
Arene Candide IX	MN-Lig	*EF*	0.03	0.97	0.00	0.00	138.37	131.38	154.21	146.87	*EF*	0.03	0.35	0.09	0.25	0.28	13.22	8.44	11.27	9.10	8.94
Arene Candide V Issel (5733 Pig)	MN-Lig	*EF*	0.02	0.50	0.06	0.42	26.84	20.29	22.94	22.59	*EF*	0.02	0.58	0.22	0.16	0.02	23.06	16.40	18.35	18.97	23.51
Arene Candide VI	MN-Lig	*HG*	0.84	0.15	0.01	0.00	29.12	32.83	36.28	45.76	*HG*	0.92	0.04	0.01	0.03	0.00	4.41	10.79	13.07	11.53	18.66
Arene Candide VII	MN-Lig	*EF*	0.22	0.48	0.00	0.30	23.65	22.29	33.45	25.18	*HG*	0.34	0.18	0.20	0.23	0.05	9.32	10.61	10.39	10.06	13.16
Bergeggi 2	MN-Lig	*EF*	0.00	0.97	0.01	0.02	43.77	30.36	37.83	39.93	*EF*	0.00	0.38	0.14	0.29	0.18	22.82	13.81	15.84	14.35	15.29
Pollera 1 Tiné	MN-Lig	*EF*	0.01	0.98	0.01	0.00	27.08	18.51	26.22	33.12	*MA*	0.14	0.28	0.17	0.30	0.11	5.02	3.68	4.62	3.49	5.52
Pollera 12	MN-Lig	*EF*	0.09	0.63	0.23	0.05	20.18	16.61	17.21	23.73	*MA*	0.13	0.26	0.18	0.33	0.10	6.15	4.79	5.51	4.34	6.76
Pollera 13	MN-Lig	*HG*	0.80	0.17	0.00	0.03	65.37	68.70	78.80	74.02	*EF*	0.20	0.26	0.16	0.19	0.18	6.82	6.22	7.17	6.85	7.00
Pollera 30	MN-Lig	*EF*	0.03	0.73	0.23	0.00	24.01	18.05	18.91	30.18	*EF*	0.10	0.51	0.11	0.25	0.04	9.17	5.86	8.92	7.33	11.16
Pollera 33	MN-Lig	*EF*	0.02	0.58	0.38	0.02	31.42	25.26	24.63	34.42	*EF*	0.07	0.39	0.21	0.28	0.06	4.98	1.46	2.72	2.14	5.10
Pollera 6246	MN-Lig	*EF*	0.03	0.75	0.05	0.17	32.01	25.84	29.88	30.69	*EF*	0.03	0.27	0.57	0.12	0.01	13.14	8.56	7.12	10.24	14.96
Arma di Nasino 1	LN-s	*HG*	1.00	0.00	0.00	0.00	26.16	39.11	42.53	46.06	*HG*	0.91	0.02	0.04	0.03	0.00	13.63	21.45	19.85	20.59	30.10

To interpret the morphological variation underlying the principal components, the factor loadings for the first three principal components (PC1, PC2, and PC3) and for the other two PCs found to be partially effective in distinguishing HG and EF (PC5 and PC6), were examined (SI Fig. S3 and Table S8). The factor loadings indicate the relative contribution of each craniofacial measurement to the overall variation captured by each principal component. For PC1 in Analysis 1, the factor loadings reveal that this component is primarily influenced by craniofacial breadth dimensions (SI Fig. S3 a and Table S8a). Specifically, variables related to cranial breadth and facial width

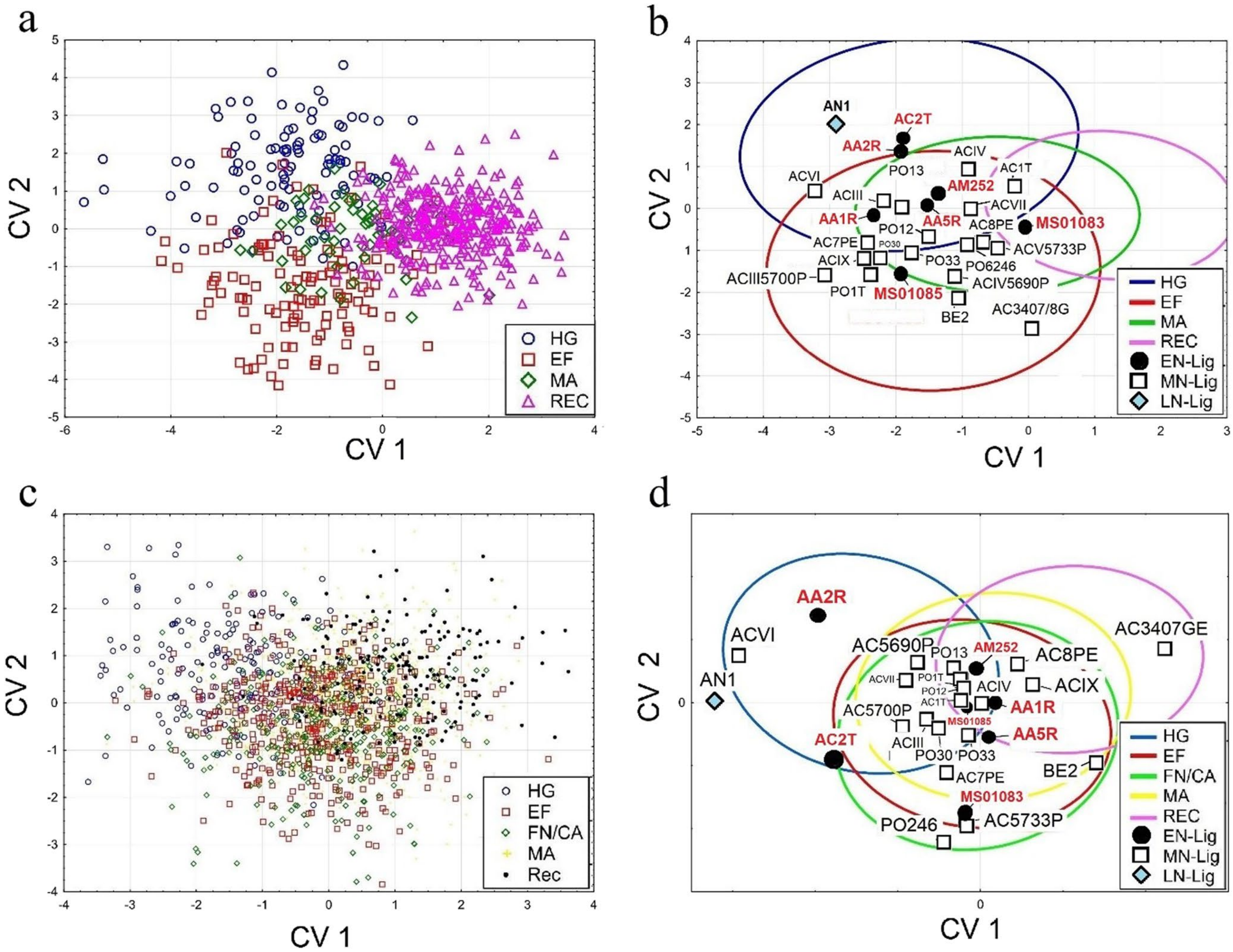

Fig. 5 Scatterplot of canonical variates (CV) 1 and 2 resulting from the DFA on four "a priori" macro-groups for Analysis 1 (**a-b**) and on five "a priori" macro-groups for Analysis 2 (**c-d**). The total sample sizes are 602 for Analysis 1 and 2152 for Analysis 2. All the scored "a priori" cases (**a, c**) and the 27 Ligurian Neolithic crania (**b, d**) projected onto the discriminant plane are represented. The macro-groups are summarized by their 90% and 75% normal distribution ellipses, respectively (b, d). The names of EN-Lig crania are in red

(AUB, XCB, ZYB, XFB, ASB, EKB) exhibit high positive loadings, whereas cranial length and height dimensions (PAC, BBH, PAF, GOL, BNL) have negative loadings. For PC2, the factor loadings indicate a shift in the relative importance of cranial breadth versus height (SI Fig. S3 a-b and Table S8a). Cranial and facial height measurements (OCS, FRC, NLH, OBH) exhibit high positive loadings, whereas facial breadth measurements (FMB, EKB, ZMB, PAS) are associated with negative loadings. For PC3, the factor loadings show a pattern in which neurocranial breadth dimensions and frontal/parietal measurements (XCB, XFB, FRS, ASB, PAC) are positively correlated, whereas facial height and length measurements (NPH, WMH, NLH) exhibit negative loadings (SI Fig. S3b and Table S8a). Finally, PC5 arises from a contrast between DKB (interorbital distance), NLB (nasal width), FRS (frontal profile height), OCF (occipital squama height), and WMH (zygomatic height) with positive factor loadings, and GOL (maximum cranial length), OBB (orbital width), ASB (biasteric occipital width), BNL (cranial base length), and PAC (parietal length) with negative factor loadings (Table S8a). HG specimens show a greater tendency toward negative PC scores, while EF specimens show more positive scores (Fig. 6e). PC6, conversely, arises from a contrast between OBH (orbital height), BNL (cranial base length), NLH (nasal height), XFB (maximum frontal width), and FRC (frontal length) with positive factor loadings, and OCS, OCF, OCC (three dimensions of the occipital), WMH (zygomatic height), and ZYB (maximum facial width) with negative factor loadings (Table S8a). HG sample exhibits more negative PC scores, while EF exhibits more positive scores (Fig. 6f).

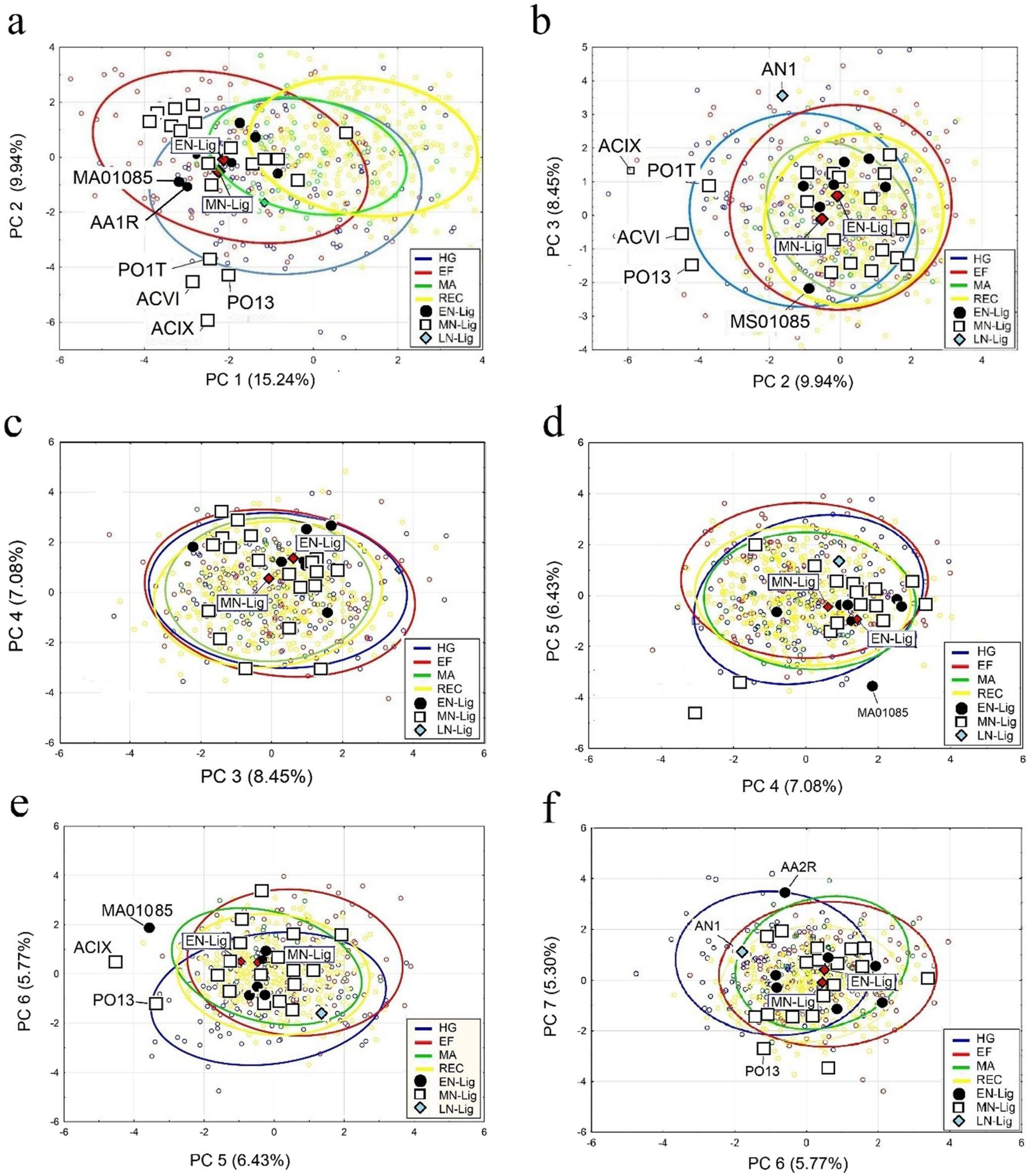

Fig. 6 PCA scatterplots showing the distribution of the 27 Ligurian Neolithic crania along the first seven principal components, together with the other crania from the Analysis 1 dataset. The total sample size is $n = 602$. Each point represents an individual cranium, with color coding corresponding to the identification of groupings explained in the legend. Red diamond symbols indicate the position of centroids of the EN-Lig and MN-Lig groups. The ellipses represent the 90% confidence intervals for each macro-group, and the axes represent the main sources of variation in cranial morphology

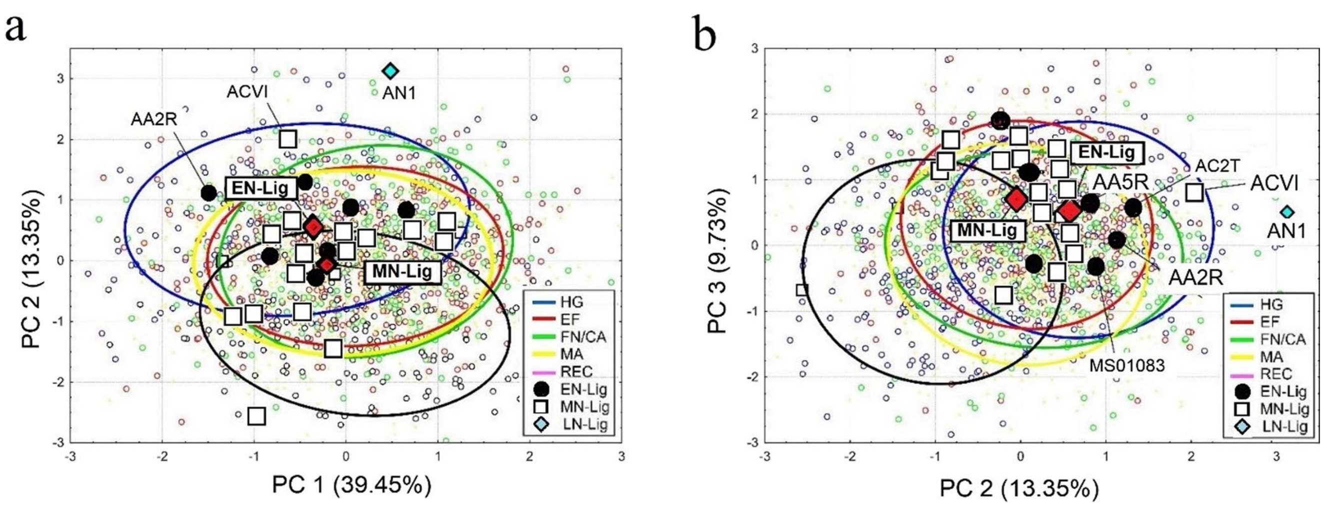

Fig. 7 PCA scatterplots showing the distribution of the 27 Ligurian Neolithic crania along the first three principal components, together with the other crania from the Analysis 2. The total sample size is $n = 2152$. Each point represents an individual cranium, with color coding corresponding to the identification of groupings explained in the legend. Red diamond symbols indicate the position of centroids of the EN-Lig and MN-Lig groups. The ellipses represent the 90% confidence intervals for each macro-group, and the axes represent the main sources of variation in cranial morphology

Similarly, an examination of the factor loadings for Analysis 2 indicates that PC1 is primarily driven by overall size variation, as all variables have the same algebraic sign (negative), with facial dimensions M45, M48, and M55 showing the highest absolute values (SI Fig. S3c and Table S8b). PC2 reflects an opposing developmental trend between cranial breadth and height, with minimum frontal and maximum facial breadth dimensions (M17, M8, M45, M9) contributing positively, whereas orbital, nasal, and upper facial height dimensions (M52, M55, M48) contribute negatively (SI Fig. S3 c-d and Table S8b). PC3 represents an inverse relationship between cranial length and height, as well as nasal breadth dimensions (M1, M54, M17) on the positive side, and cranial maximum breadth dimensions (M8) on the negative side (SI Fig. S3 d and Table S8b).

Discussion

Liguria – a narrow strip of land between mountains (western Alps and the Apennines) and the Mediterranean Sea – constitutes a crossroad and chokepoint for movements between southern France and the Italian peninsula. As such, it has always been a fundamental area for our understanding of the movement of people and artifacts in the prehistory of the northwestern Mediterranean (Maggi et al. 2023; Negrino et al. 2023). In this study, we employed a cranial morphometric approach to investigate the biological makeup and evolutionary trajectories of the Neolithic groups from Liguria, which began spreading into the Liguro-Provençal Arc around 5800 cal BCE (Biagi and Starnini 2016; Binder et al. 2017; Bruschini et al. 2023). Specifically, we examine the relationship between these early farmers – culturally belonging to the ICC – and indigenous foragers, a topic that remains subject to debate (Binder 2013; Binder and Maggi 2001). This debate stems from uncertainties surrounding the precise geographic and temporal overlap of Neolithic farmers and the last Mesolithic foragers (Biagi et al. 1988; Perrin and Manen 2021; Negrino et al. 2023; Perrin 2025). Similarly, the population dynamics of subsequent farming groups in the Middle and especially the Late Neolithic remain to be clarified.

The results of this study, based on cranial morphology and employing various multivariate methods – particularly principal coordinate analysis (PCoA), neighbor-joining (NJ) cluster analysis, and distance analysis – collectively indicate that the Early and Middle Neolithic groups from Liguria are morphologically closely associated with other Neolithic populations and thus integrated into the broader biological and cultural network of European Neolithic groups. However, they also reveal that the EN-Lig group is notably closer to hunter-gatherers, particularly those from the Mesolithic period, than most other early farming groups, including both contemporary EN groups and those from later periods. Indeed, several Ligurian Neolithic crania are better classified as HG in the DFA. The close proximity between the two Ligurian groups is further underscored in the NJ cluster analysis, where they appear closely connected within the same branch. Collectively, these findings suggest that, while the Ligurian Neolithic groups are part of broader European Neolithic variability, they exhibit marked morphological heterogeneity that sets them apart. The morphological affinities between early Ligurian Neolithic individuals and HG groups suggest a significant degree of genetic interaction between these incoming farmers and the foragers they encountered. For further insights, see SI Text.

It should be noted, however, that our EN-Lig sample does not include the earliest Neolithic settlers with their Impressed Ware culture, but the later bearers of Cardial Ware. Thus, the genetic contribution from HG that we detected may not have involved the first pioneering wave bearing the Impressed Ware, while it is likely to have left a legacy in the Cardial people.

It is essential to acknowledge that while craniometric affinities offer a robust reflection of overall biological relatedness, they cannot, in isolation, definitively disentangle the underlying processes of admixture, shared ancient ancestry, or developmental plasticity (phenotypic response to environmental/dietary change). Our finding that Early Neolithic Ligurian crania cluster closer to Mesolithic individuals is interpreted here as a proxy for the rapid assimilation of WHG ancestry, aligning with the strong evidence for high WHG introgression observed in adjacent genomic studies (Arzelier et al. 2022). This interpretation is strengthened by the fact that the observed pattern (convergence toward HG) directly contradicts the anticipated initial 'pristine' EEF signal.

While direct paleogenetic results for Ligurian Neolithic remains are currently unavailable, similar studies from southern France offer insights into the biological relationships of geographically and culturally close Neolithic farmers. Rivollat et al. (2020) present evidence of genetic admixture between early farmers and western hunter-gatherers, with varying patterns of ancestry reflecting regional differences in Neolithic expansion. They show that Neolithic groups in southern France, part of the Mediterranean expansion route of ICC, exhibit a higher HG component compared to groups from the continental route. The analyzed sites, Pendimoun and Les Breguieres (two successfully genotyped individuals for each site), dated to 5400–4700 BCE, that is 400 or more years after the first coastal settlements in Liguria, Provence, and Mediterranean Languedoc, suggest a recent local admixture event. These results are in agreement with archaeological research hypothesizing greater interaction between incoming farmers and indigenous HGs in the western Mediterranean, particularly in areas where chronological and geographic overlapping is better demonstrated, such as in southern France (Gomart et al. 2017). In Italy, such an area could be the Tuscan-Emilian Apennines, which is not far east from Liguria (Binder 2000). However, admixture may have occurred in Liguria itself, as the apparent lack of overlap – or even signs of avoidance – between Early Neolithic and Late Mesolithic groups may be influenced by preservation bias (see Introduction). On the contrary, ICC individuals from the eastern Adriatic coast show little HG ancestry and greater affinity with Central European groups (Rivollat et al. 2020), and this finding could be in line with the differentiation of technical traditions within the material cultures observed on both sides of the Apennines in Italy: an Adriatic tradition linked to the Balkans and a Tyrrhenian tradition of unknown origin (Gomart et al. 2017). It is tempting to associate a high HG component on the Tyrrhenian side of ICC with the characteristic ceramic traditions observed in this region and consider these traditions the result of HG reinterpretation (Gomart et al. 2017); however, the scarcity of genomic data available for central and southern Italy currently prevents direct testing of this hypothesis (but see below regarding the results obtained by Antonio et al. 2019; Raveane et al. 2022; and Yu et al. 2022).

A hypothetical genetic profile of the Ligurian EN population must be understood against the backdrop of three major human ancestral components that, on the basis of paleogenomic studies (Lazaridis et al. 2014), shaped modern European diversity: Early European Farmers (EEF), Western Hunter-Gatherers (WHG), and Ancient North Eurasians (ANE). The Ligurian coast, specifically, sits at the critical juncture of the Western Mediterranean Neolithic expansion and the established hunter-gatherer presence on the Italian peninsula, making it an ideal region to investigate the nature of initial farmer-forager interactions. The EEF component, originating in the Near East (Anatolia), was the primary vector for the dispersal of agriculture across Europe. Initial farmer groups entering Europe via the Balkans were characterized by near-pure Anatolian Neolithic ancestry (98%) (Mathieson et al. 2018). This "pristine" farmer ancestry rapidly spread along both the Danubian and Mediterranean routes, forming the core of all EN populations (Lazaridis et al. 2016). The HG component – the local European substrate – was composed of WHG ancestry descended from groups belonging to the Villabruna/Oberkassel cluster (Posth et al. 2023). This ancestry was established across the Italian peninsula as early as 17,000 cal BP, having likely dispersed from the Balkans into Northern Italy (Posth et al. 2023; Raveane et al. 2022). These foragers, adapted to the post-LGM environment, were the human groups that the incoming EEF populations first encountered.

Migrations and admixture always played a fundamental role in shaping the genetic make-up of European populations in post-Glacial times (Allentoft et al. 2024). The process of admixture between EEF and WHG was not uniform across the continent or even within Italy (Raveane et al. 2022). The timing and intensity of this interaction frame the significance of any high HG affinity in Liguria: limited initial admixture was frequent in Europe, where first wave of farmers into both the Balkans and Central Europe produced demic replacement (Lazaridis et al. 2014; Mathieson et al. 2018). Early, high regional admixture is rarely found, e.g. Iron Gates (Serbia) and Malak Preslavets (Bulgaria), showing admixture with local HG reaching 15% (Mathieson et al. 2018). A finding of a high HG affinity in EN Liguria would contradict the low initial admixture model seen in the Balkan entry point (98% EEF) (Mathieson et al. 2018) and the early Central Italian models (5% WHG) (Antonio et al. 2019). Instead, it would align with the high, early admixture (e.g., 14–28% WHG) documented in geographically adjacent Southern France (Arzelier et al. 2022). Antonio et al. (2019) found that Neolithic individuals from central Italy (6th millennium BCE; $n = 10$) share 95% ancestry from central Anatolia or northern Greece (i.e., from the direct sources of origin of Neolithization across Europe; see e.g. Hofmanová et al. 2016), but also have about 5% local HG ancestry, indicating different source populations for the Neolithic transition in Italy compared to central and western Europe. According to Yu et al. (2022), Early Neolithic farmers in Sicily were genetically most similar to farmers in the Balkans and Greece, with only 7% ancestry from local Mesolithic HGs.

With regard to population dynamics following the initial spread of the Neolithic, a notable contrast to the Ligurian EN and MN samples emerges from our comparisons with other EF groups: while many EF groups display a general trend of increasing morphological proximity to HG over time, this pattern is absent in the Ligurian dataset. An interesting trend can be seen in the comparison of the mean distances of individual EF groups from the HG macro-group (SI Table S5). The MN groups are generally closer to HG than the EN groups based on their mean distance values. The only exceptions are the two groups, EN-Lig and EN-s, which may be closely connected due to sharing the same cultural matrix (ICC). These results are consistent across both Analyses 1 and 2, and the pattern becomes even clearer when the comparison is made with a subset of the HG group consisting only of the two Mesolithic groups. Specifically, mean distance values show that Middle Neolithic groups in several regions are closer to HG populations than their Early Neolithic counterparts, a trend interpreted as evidence of a genetic "HG resurgence" likely driven by admixture (HG "resurgence" refers to the distinct, widespread increase in Western Hunter-Gatherer ancestry observed in European farming populations beginning primarily in the Middle/Late Neolithic and Copper Age, signifying a later, substantial re-introduction of forager genes into the farmer gene pool).

This interpretation aligns with paleogenetic findings indicating a recurring pattern of increased HG gene flow into farming populations long after initial contact. Such phenomena have been evidenced through genetic analysis across the Iberian Peninsula, northern and central Europe, the Carpathian Basin, and the Balkans (Haak et al. 2015; Lipson et al. 2017). More updated genome-wide data from 28 individuals from Southern France dated to ca. 5500–2500 BCE (Arzelier et al. 2022) highlight the role of HG resurgence also in the Neolithic populations of southern France, showing the persistence of HG ancestry and multiple events of HG introgression in farming communities throughout the Neolithic.

Our results suggest that this process did not occur in the nearby Ligurian Neolithic. When considered alongside paleogenetic evidence from southern France, the present study indicates that the Early Neolithic ICC specimens from the Finalese area may have originated from EF groups that migrated into the region and subsequently admixed with local HG populations, either locally, in the Italian peninsula, or in nearby southern France (scenario 3 in the Introduction). In contrast, the results for the Middle Neolithic SMP specimens appear more consistent with scenario 1, in which this group derived exclusively from the preceding Early Neolithic population with no significant genetic input from HG groups, although some influence from neighboring Neolithic cultures cannot be ruled out.

The absence of the HG resurgence – a continental trend found across Central Europe and Iberia during the MN-LN and Copper Age (Mathieson et al. 2018) – is directly explained by the high HG affinity already present in the Ligurian EN and MN samples. The high morphological affinity of EN Ligurians to HG groups, which aligns with the high, early WHG admixture (14–28% WHG) documented in adjacent Southern France (Arzelier et al. 2022; Rivollat et al. 2020), suggests the Ligurian EN population represents a localized, immediate, and intense interaction zone. If HG mixing happens immediately in the EN, as suggested by our morphological data, the resulting population already harbors a high WHG component. Therefore, there is no longer a need for a large subsequent genetic resurgence (HG resurgence) in the MN or later periods, which explains the anomaly observed in the Ligurian dataset compared to the European trends. Naturally, given the small sample size, these conclusions should be interpreted with appropriate caution.

Regarding the Late Neolithic of Liguria, the available sample consists of a single individual from Arma di Nasino (directly dated to 4200−4000 cal BCE; Sparacello et al. 2020; SI Fig. S4), who was classified as HG in the DFA. Beyond this result, the study offers limited insight into population dynamics during the later Neolithic in the region. Nevertheless, it is noteworthy that the group including Chasséen individuals (MLN-s) was never found to cluster closely with the Ligurian Early and Middle Neolithic groups in any of our analyses. On the contrary, in some cases, the MLN-s group displayed affinities with populations from the Metal Ages, particularly with Copper Age groups, including CA-s, which encompasses Italian sites.

The Chassey culture expansion towards Liguria originated in Southern France (Crepaldi 2001), a region known for high Neolithic/HG admixture. Paleogenomic data from this core area confirm high HG ancestry in both Early and Late Neolithic groups, supporting multiple pulses of gene flow persisting throughout the period (Arzelier et al. 2022). Given this context, the LN specimen's HG-like morphology may signal a population discontinuity related to Chassey influence; the individual may represent a new group arriving from Southern France, bringing a population component already morphologically and genetically closer to HG lineages than the preceding, homogenous SMP population. This distinctiveness breaks the morphological pattern of the local MN group, anticipating the broader demographic shifts that characterize the subsequent Metal Ages (Palmisano et al. 2021).

This scenario is supported by archaeological evidence from Arene Candide Cave in Liguria and other cave sites of this region. Here, an abrupt interruption of the SMP sequence around 4300 BCE (Maggi, 1997; see also Sparacello et al. 2020), is followed by assemblages including Chassey pottery, knapped flint tools made of southern France raw materials, and a different variety of sheep (Bruschini et al. 2023; Crepaldi 2001; Maggi and Starnini 1997; Maggi and Tinè 2023; Rowley-Conwy 1997). By the end of the fifth millennium BCE, the Chassey culture had spread in northern Italy (Ferrari et al. 2002; Maffi 2014), while the Square Mouthed Pottery persisted only in the northeastern portion of the peninsula (Mottes 2021). The degree and nature of interaction between these groups is unclear, but our result may reflect a disruption in genetic continuity and a substantial population turnover, traces of which may persist into the Metal Ages. However, this hypothesis will require validation through future genomic research.

Conclusions

This study contributes to the understanding of Neolithic population dynamics in Liguria by applying cranial morphometric analysis to Early and Middle Neolithic human remains. The results indicate that Ligurian Neolithic groups are integrated into the broader biological variability of European Neolithic populations, yet they display distinctive morphological heterogeneity. In particular, Early Neolithic individuals from the Finalese area show closer affinities to Mesolithic hunter-gatherers than other early farmer groups, suggesting a significant degree of admixture.

In contrast, the Middle Neolithic group from the Square Mouthed Pottery context appears more homogeneous and distinct from hunter-gatherer groups, supporting a model of population continuity with limited external input. This diverges from broader European trends where increasing hunter-gatherer genetic influence is often observed in Neolithic populations over time.

The Late Neolithic phase remains poorly understood, represented here by a single individual with HG-like morphology. Preliminary evidence suggests a possible discontinuity between the Middle and Late Neolithic, potentially corresponding to the arrival of the Chassey culture and broader demographic shifts visible in later periods. However, these hypotheses await confirmation through future genomic research.

The results of this study underscore the importance of considering both genetic and cultural factors in understanding the population dynamics of prehistoric Liguria. Obviously, we are aware that the results of the analysis of craniometric data must be taken with due caution, given the possible influences of non-genetic factors.

Future research should expand the geographic and temporal scope of analysis to include Late Mesolithic cranial samples from northwestern and central-western Italy, which are currently unavailable. Additionally, the integration of paleogenetic data, specifically high-coverage nuclear genome sequences, would be particularly valuable in elucidating the genetic underpinnings of the observed biological and cultural patterns.

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Author contributions GD'A, VS, and ES conceptualized the manuscript. GD'A and SDM performed the statistical analyses. GD'A, MS, ID, AV, LS and VS performed data collection. ES curated the archaeological contextualization. All authors revised the drafts of the manuscript and the final submission.

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Declarations

Competing interests The authors declare no competing interests.

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