





Review

# Archaeogenetics and Landscape Dynamics in Sicily during the Holocene: A Review

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**Abstract:** The Mediterranean islands and their population history are of considerable importance to the interpretation of the population history of Europe as a whole. In this context, Sicily, because of its geographic position, represents a bridge between Africa, the Near East, and Europe that led to the stratification of settlements and admixture events. The genetic analysis of extant and ancient human samples has tried to reconstruct the population dynamics associated with the cultural and demographic changes that took place during the prehistory and history of Sicily. In turn, genetic, demographic and cultural changes need to be understood in the context of the environmental changes that took place over the Holocene. Based on this framework, this paper aims to discuss the cultural and demographic dimension of the island by reviewing archaeogenetic studies, and lastly, we discuss the ecological constraints related to human peopling in times of change in landscapes that occurred on the island in various periods. Finally, possible directions for future archaeogenetic studies of Sicily are discussed. Despite its long human history, Sicily is still one of the world's biodiversity hotspots. The lessons we learn from the past use of landscape provide models for sustainable future management of the Mediterranean's landscapes.

**Keywords:** ancient DNA; population genetics; anthropology; historical ecology; paleobotany; past vegetation; potential natural vegetation



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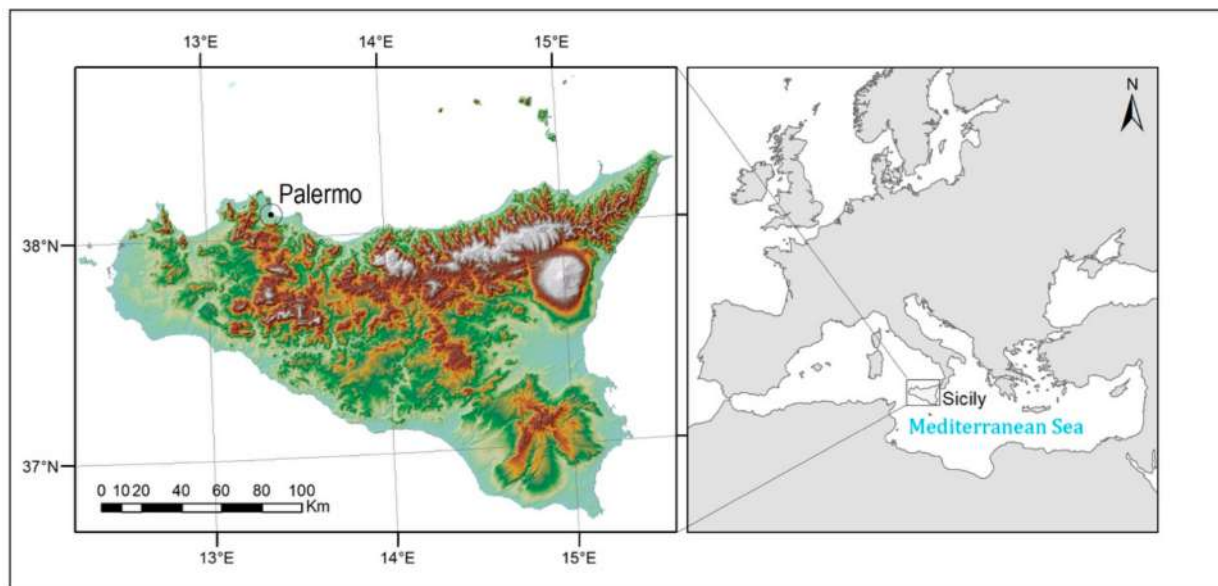
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## 1. Introduction

The emergence and spread of human populations in Italy have been reconstructed over the course of many years via archaeological and paleontological data. However, these approaches alone are insufficient to map and quantify the actual historical/evolutionary relationships between different ancient populations or groups of people. Archaeogenetic studies, together with the development of appropriate inferential and statistical methods, have provided a powerful tool to assess human demographic history and population dynamics [1].

Sicily offers the ideal context for the analysis of modern and ancient genomic data because it has always represented, since its first colonization, a crossroads of several human groups who visited and settled on the island (Figure 1). The oldest human remains in Sicily are dated to about 16,000 years ago [2]. Since then, Sicily has been settled by Neolithic peoples, Italics, Phoenicians, Greeks, Romans, Byzantines, Arabs, and Normans [3]. These complex demographic and cultural dynamics must have affected the genomic structure of the Sicilian population to different extents at different times, but the actual relative genetic impact of these migrations remains largely unknown. This is not to say that at the present time our understanding of the genetic history of Sicily is a *tabula rasa*; on the contrary, as this article documents, in the past 40 years, Sicily has been the focus of many important archaeogenetic studies. It is precisely by capitalizing on these past efforts, as well as on the

latest developments in genomic sciences, that we can reasonably hope to disentangle the as-yet-unknown layers that make up the genetic palimpsest of the Sicilian population.



**Figure 1.** Map showing Sicily, the largest island of Mediterranean Basin. Due to its position in the center of the Mediterranean, Sicily has represented a crossroads for migrations of flora, fauna, and human populations, which has made it a hotspot of biodiversity.

The international workshop, “Genetic and population history of Sicily” held at Oasi Institute in Troina (Sicily, Italy) in June of 1998 was the first and—to our knowledge—the only workshop to focus on the archaeogenetics of Sicily [4]. This was an important scientific event that offered a unique opportunity to reduce the gaps among specialists studying the history and prehistory of Sicily from different research perspectives.

Several important messages were delivered in that meeting, some of which are still relevant today and, therefore, worth recalling briefly in this paper. One message concerned open questions related to the prehistory and history of Sicily. When was the last time that Sicily was entirely de-populated? Assuming that this time was mid-Paleolithic, was there a continuity of population from the Upper Paleolithic onwards? For different historical periods, the difficulty of translating information from the large repertoire of remains (“the material culture”) made available by archaeological research, and the consultation of classical literary sources in terms of demographic dynamics, were discussed. For example, to what extent did ideology influence the accounts of the classical authors? Were the Sicels and Sicans really two distinct groups? How many Greeks stably settled in Sicily, and were they a genetically homogenous group? These questions are of remarkable relevance for population sampling and genetic analysis. The participants to that meeting have empathized that such genetic analysis should be directed towards the detection and interpretation of existing patterns of internal genetic differentiation and genetic affinity with other European and Mediterranean populations. In particular, the combined analysis of modern and ancient genomic data was considered an important step to help answer these questions. At the same time, it was stated that effort should be spent in the collection of more ancient and modern DNA samples, based on precise archaeological and historical criteria. Regarding DNA analyses, it was agreed that they should be carried out with highly polymorphic (molecular) markers, both nuclear (autosomal and Y-linked) and mitochondrial. On the other hand, the potential interest in ancient DNA from the pre-classical period was also emphasized. At the time of the meeting, ancient DNA (aDNA) analysis was still an emerging technology. As for the collection of samples, the discussion led to the decision to use a specific sampling strategy that takes into account the geographic

distribution of historical, proto-historical, and pre-historical settlements on the island, as well as the subdivision of the island into dioceses.

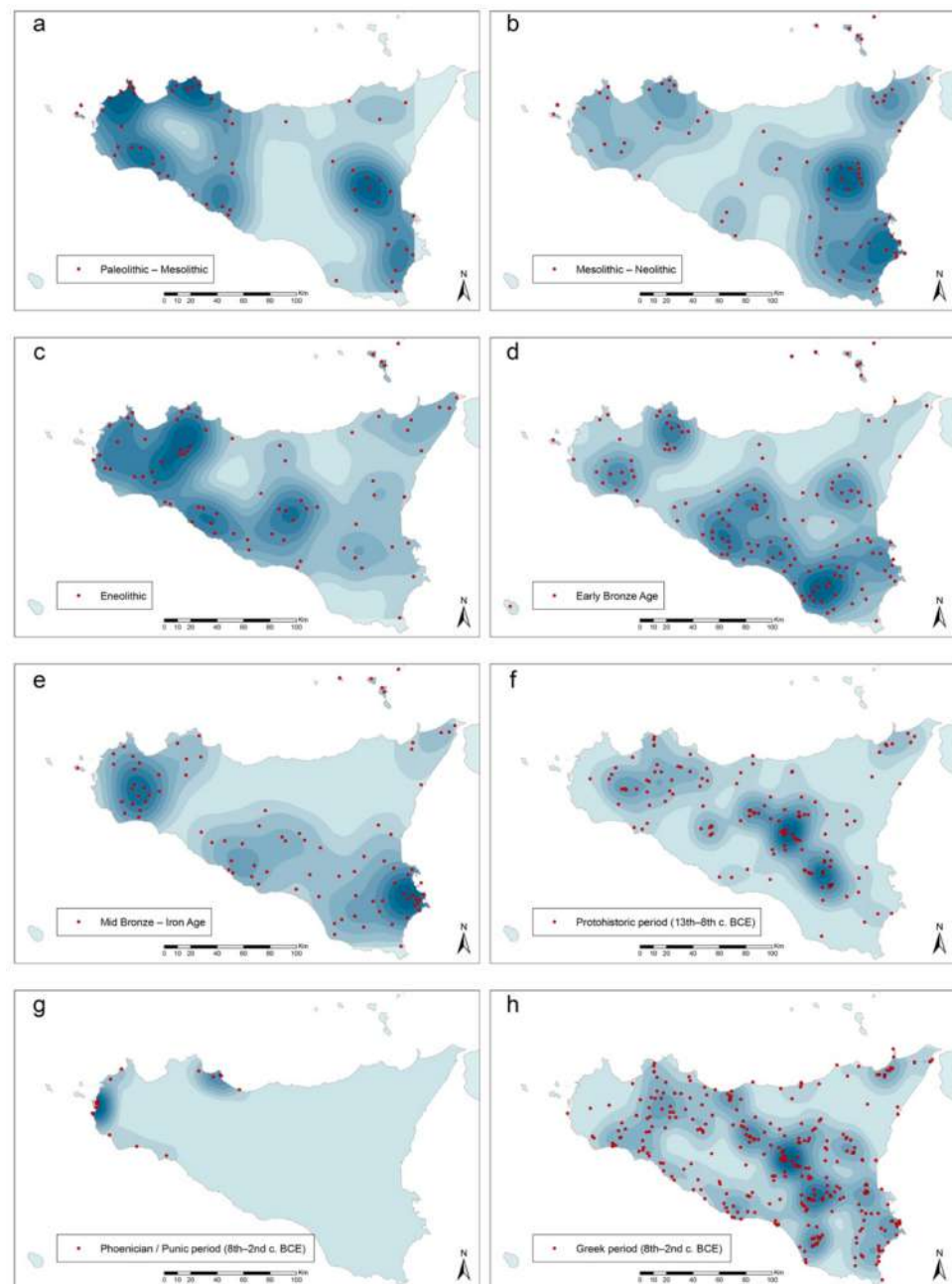
Paleobotanical (and archaeobotanical) data, through a deductive approach, may also help to understand genetic, demographic, and cultural changes that occurred in the Sicilian population over the Holocene. However, archaeogenetic and paleobotany (more generally paleoenvironment) studies have followed parallel lines of development without any contact. The cross-disciplinary approach of historical ecology that includes human populations as a component of ecosystems [5] may allow us to understand the deep relationships between biodiversities and history.

Based on this framework, this paper aims to discuss the cultural and demographic dimension of the island by reviewing past archaeogenetic studies, and we then discuss the ecological constraints imposed by the peopling of the island in relation to changes in landscape that took place in Sicily in various prehistorical and historical periods by reviewing past paleobotanical studies. Finally, possible directions for future archaeogenetic studies of Sicily are suggested.

## 2. Ethnic and Demographic Dynamics of Sicily: From Prehistory to History

In the absence of circumstantial evidence of a presumed Middle-Pleistocene human colonization of Sicily [6], the human prehistory on the island presumably begins with the arrival of the Epigravettian hunter-gatherers during the LGM (Last Glacial Maximum, from 22,000 to 17,500 years ago), who came from the Italian peninsula via a land bridge connecting, at that time, the two shores of the Messinian Strait [7–9]. These are the early people who sporadically settled the large territories of the island and with whom the Early Holocene hunter-gatherers of continental origin overlapped and mixed [10–12]. After these, came the great Neolithic movement of settlers (“Neolithic” comprises a succession of different cultural traditions). The spread of Neolithic farmers to the West from the Near East reached southern Italy ca. 6000–5800 BCE [13], and was followed by large Metal Age migratory movements [14] (Figure 2a–e).

Following the successive migratory waves of continental peoples on the island—who created the heterogeneous indigenous genetic substratum of Sicanians, Elimyans, and Sicels—and the strategic presence of Myceneans, the first great historical colonization brought about the territorial division of the Phoenicians/Punics [15] and the Greeks [16] (Figure 2f,g). This “colonization” presumably consisted of a migration of males who quickly mixed with the indigenous population. We then have to consider the phenomena of migration, deportation, and colonization operated on the island, by Republican Rome after the Punic Wars (264–146 BCE), but, above all, by Imperial (27 BCE to 284 CE) and Late Imperial Rome (284 BCE to 476 CE). In this period, we should consider the introduction of slaves for agriculture, or movements of peoples due to trade [17], with the intermittent arrival of people attracted by the economic prosperity of the country or looking for a safe place, as in the case of the diaspora of the Jewish in Late Imperial Sicily [18]. The Late Antique/Byzantine period (4th–9th c. CE) is also very significant as regards the political, cultural, and genetic relationship of the island with the Near East and Byzantine rule, and the repeatedly arising influence of barbarians such as the Vandals [19]. The long-standing (heterogeneous) and culturally intense Islamic influence, from 827 to 1061 CE, left deep cultural, and presumably genetic, footprints [20]. After 827 CE, towns and villages gradually developed in the coastal areas of Sicily, which led to a process of integration between Muslim and Jewish–Christian communities [21]. For example, Sciacca (*Al Shāqqah* in Arabic) became a flourishing center of commerce, as described by al-Idrīsī, a geographer at the court of Roger II: “Sciacca is a small town located on the shores of the western sea. There are public buildings, markets and many houses. It is currently the capital of various districts and surrounding dependencies. Its port is constantly in good repair, with ships coming in from Tripoli and (elsewhere) from Africa all the time” [22].



**Figure 2.** Distribution of archaeological sites in Sicily. Source data from Paleolithic to Iron Age (a–e) by Tusa [23]; Protohistoric period (f) and data for transition from Phoenician/Punic (g) to Greek domination (h) by Regione Siciliana [24]. The density of settlements was mapped using the Esri ArcGIS Kernel Density tool. The kernel density analysis was performed only to graphically highlight the areas of the highest concentration of sites, and it does not have any predictive meaning on the distribution of the sites.

Soon after the Islamic period, Sicily was ruled by Normans and Swabians. These rulers promoted the occupation of internal Sicily by people from the Aleramic lands of north-western Italy, or from the Lombard territories. Later, Sicily was the final destination of people escaping from Albania, under Ottoman rule, who were present in several areas of southern Italy between the 14th and 16th centuries. As for the Modern Era, while the Angevin domination was short-lived but significant, the Iberian contribution—first made by the Aragonese and then by Imperial Spain—was long and very deep. In this context, it is worth remembering the socio-political role played by the Church of Rome in disrupting

the Spanish cultural penetration of the island, and its historical consequences. The Jews, expelled from Spain by the Inquisition, found refuge, and were forced to convert to Catholicism, in Sicily. This also had its own cultural and microdemographic consequences. Finally, in contemporary Sicily, economic immigration has created clear genetic enclaves, such as the settlements of North African fishermen in Mazara del Vallo [25]. Taken together, all the above archaeological and historical data can be summarized in a single sentence, i.e., Sicily is, in all respects, an ante litteram melting pot. In this context, aside from the Spanish domination cited above, the problem of the colonists' heterogeneity also applies to East and North African Berber and Islamic settlers. For earlier periods, we might mention the stream of very heterogeneous peoples (and genes) slowly—albeit continuously—flowing into the island from the surrounding Mediterranean regions, including the Punics of North Africa, the Iberians, and the Italics.

Archaeogenetic studies in recent years [26–50] have investigated on the actual demographic/genetic impact of this melting pot. The approaches that have been used include the following:

- (i) The application of genomic technologies to the analysis of ancient samples and extant populations;
- (ii) The selection of samples based on the careful integration of data from the material culture, literary sources, linguistics, and historical demography;
- (iii) The ascertainment of the place of birth of ancestors of blood/DNA donors from a given rural site (village, town) for at least three generations;
- (iv) The use of robust statistical techniques for data analysis.

One indirect indicator of the intensity of human occupation and landscape transformation can be found in the archaeo- and paleo-botanical records, which provide information on climate fluctuation and the exploitation of wild and cultivated plant resources.

### 3. The Archaeogenetics of Sicily: A Long Journey Lasted Forty Years

Colin Renfrew offered the first definition of archaeogenetics: “Applying molecular genetics to questions of early human population history, and hence to major issues in prehistoric archaeology, is becoming so fruitful an enterprise that a new discipline has recently come into being” [26]. Remarkably, population genetic studies in Sicily date back to at least the 1970s, and since then, they have made major methodological and conceptual developments, from classical markers to genomics, and from studies on extant populations to the more recent paleogenetic analyses. This has been an exciting undertaking involving many Italian and international researchers and scientific collaborations. In what follows, we present an extensive review of archaeogenetic studies on Sicily published over a period of nearly 40 years.

The genetic structure of Sicily was initially investigated using classical genetic markers (blood groups, proteins, and HLA) [27,28]. These studies indicated a large division between the Eastern and the Western parts of the island that, according to the authors, may reflect the demographic impacts of Greek and Phoenician colonization. A similar regional differentiation was also observed via studies on surnames [29,30]. A study on the genetic frequencies of enzyme systems and blood groups indicated a close relationship between Sicily and southern Italy. Moreover, it revealed a genetic similarity between the Sicilian and Middle Eastern populations, in accordance with the historical contribution of Islamic expansion on the island [31]. By analyzing 13 genetic markers of western Sicily, Vona et al. [32] detected a genetic variation within the island. The results also showed a Greek influence in the Sicilian and southern Italian gene pool, consistent with the Greek colonization of southern Italy and in line with a previous work by Piazza [33].

A significant development in population genetic studies came with the advent of uniparental (Y-chromosome and mtDNA) and biparental markers. Uniparental markers have been proven to be an extremely useful tool in population genetic studies. However, each of these single-locus markers offers only a partial perspective compared to genomic studies. In the last few years, advances in high-throughput SNP genotyping analysis have

allowed for a more complete description of the overall genetic variation, overcoming some of the limitations of single-locus markers.

Cali et al. [34] investigated the diffusion pattern of the IVS10nt546 mutation in the phenylalanine hydroxylase gene in several Mediterranean regions, including Sicily. This mutation is the main cause of phenylketonuria (PKU) in southern Europe. PKU is an inborn dysfunction of the metabolism causing mental retardation. These authors showed that the ancestral gene bearing this mutation probably originated in Anatolia, and then spread westward to southern Italy, Sicily, and Spain. They also interpreted the geographic pattern of diffusion as the result of the expansion of Neolithic farmers, thus suggesting the onset of this mutation to have begun at least 10,000–5000 years ago.

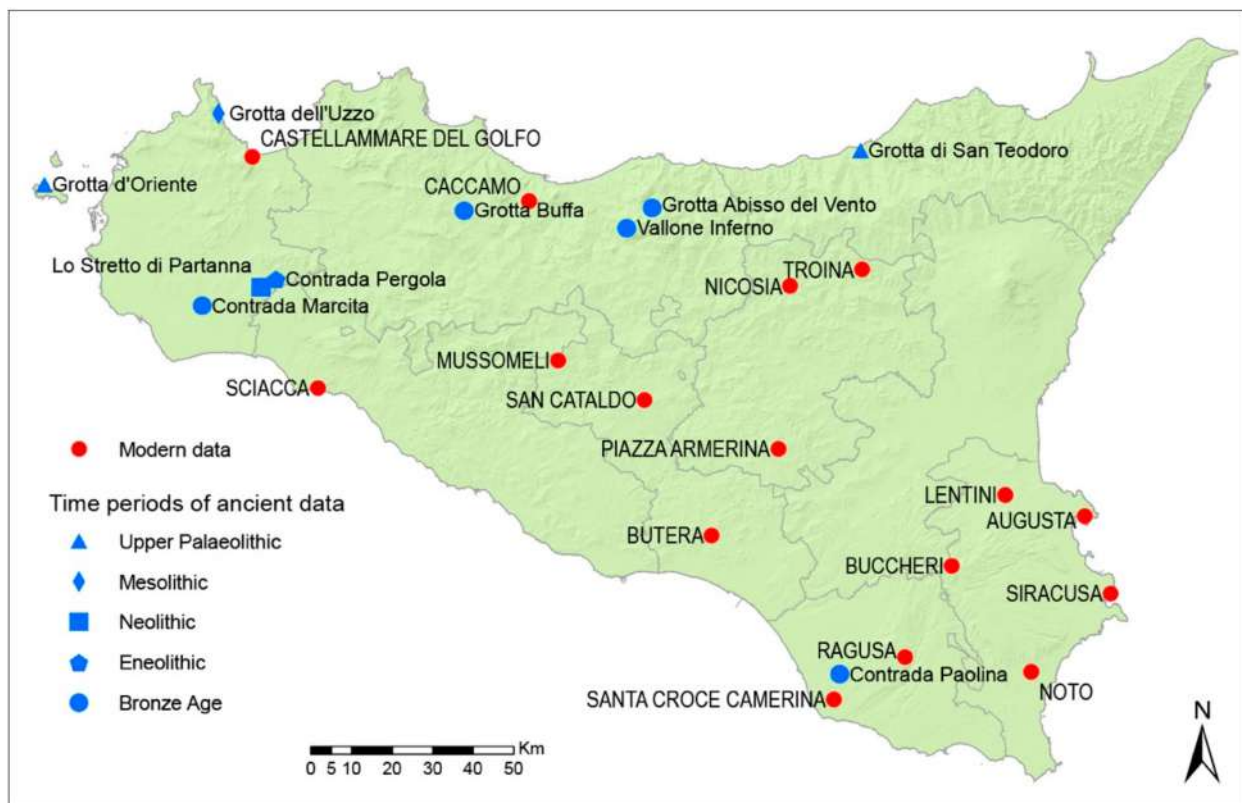
The first study reporting the analysis of mtDNA polymorphisms in Sicilians was that of Semino et al. [35], who typed six restriction enzymes in a sample of 90 individuals. A finding of particular interest in this study was that the HpaI-3/AvaII-3 complex (a polymorphism of the mtDNA), which is unique to groups of African ancestry, was found in Sicily at a frequency of 4.4%. Thus, for the first time, an estimate of the volume of gene flow from African Blacks to the Sicilian gene pool could be obtained. The existence of a genetic differentiation between the western and eastern parts of Sicily was then confirmed by two different studies conducted using mtDNA and microsatellite [36,37] markers.

A world-wide mitochondrial DNA database and a geographical information system (mtRadius) were used to identify the regions of the world with the highest frequencies of matching HVR1 mtDNA types [38]. The analysis identified western Sicilians as “Europeans”, while a few types were found to be typical African (2%) or Asian (5%) sequences. In this study, the ancestry of typed individuals was traced maternally to the province of Agrigento for two or three generations. In a subsequent analysis performed on the mtDNA sequences of 1082 Sicilians, 17 (1.6%) were found to have Sub-Saharan African mtDNA types, belonging to various African L lineages. These lineages stand out clearly among the mainly European mtDNA lineages of Sicily. Strikingly, the African lineages were observed predominantly along the Sicilian coast, on average, only 3.3 miles (5.4 km) inland, i.e., generally within one hour’s walk from the gently sloping seashore (Forster and Romano, unpublished).

Romano et al. [39] analyzed the mtDNA haplogroups and autosomal microsatellite frequencies of 465 Sicilians (Figure 3). Their results were consistent with those for settlements of people that occurred at different times. In particular, the divergence times inferred from the microsatellite data seem to suggest that the genetic composition of the town of Sciacca is mainly derived from settlements after the Roman conquest of Sicily (First Punic war, 246 BCE), while all the other divergence times occurred between the second and first millennia BC, and, therefore, seem to backdate to the pre-Hellenistic period.

In order to investigate the population structure across the Mediterranean, Capelli et al. [40] investigated Y-chromosome variation in a large dataset of Mediterranean populations. Their analyses identified four main clusters, labeled North Africa, Arab, Central-East, and West Mediterranean. In particular, the relatively high frequencies of Y-chromosome haplogroup E-M81, as well as a subset of J1-M267-derived lineages, found in Sicily are consistent with the long-term Muslim expansion across the Mediterranean.

The study of Di Gaetano et al. [41], performed using the combination of Y-chromosome haplogroups and short tandem repeats from several areas of Sicily, has shown that traces of genetic flow in the island, still visible on the basis of the distribution of some lineages, are likely due to ancient Greek colonization and a northern African contribution. The genetic contribution of Greek chromosomes to the Sicilian gene pool has been estimated to be about 37%, whereas the contribution of North African populations is estimated to be around 6%.



**Figure 3.** Geographic distribution of sites sampled for ancient genome analysis (blue symbols) and DNA analysis of extant Sicilians (red symbols).

The genetic history of Sicily was also investigated by Sarno et al. [42] through the analysis of Y-chromosome and mtDNA genetic markers. Their results showed a significant genetic homogeneity within the island, as well as between Sicily and southern Italy, thus suggesting different demographic patterns for the maternal and paternal lineages. In particular, while mtDNA genetic variability seems to be linked to pre-Neolithic and post-glacial migration events, the Y-chromosome results reveal a tight connection with the Balkan Peninsula dating back to Neolithic and post-Neolithic times.

A study investigating the proportions of admixture among present-day Europeans has shown that the Sicilian population, as well as Maltese and Ashkenazi Jews, have a strong affinity with the populations of the Near East [43]. These data are consistent with the abundant archaeological evidence of long and intense relations between the island and the Near East in the prehistoric and protohistoric periods.

In a recent paper, Busby et al. [44] estimated the different ancestral contributions of source groups to western Eurasian populations. Their results showed that southern European groups, including Sicilians, derive their ancestry from African and Near Eastern regions. Interestingly, they showed evidence of a specific West African genetic contribution to southern Italians and Sicilians dating back to 882–1250 CE, which is consistent with the Arabic conquest of the Mediterranean.

Tofanelli et al. [45], by analyzing both the Y-chromosome and mtDNA haplotypes, detected the contribution of Greek colonizers to present-day southern Italian and Sicilian communities. They observed a clear signature of Greek ancestry in East Sicily, consistent with the settlement from Euboea during the Archaic Period (1000–400 BCE). They also suggested that the colonization process was driven by a few thousand breeding men, with a minor contribution of Greek breeding women.

More recently, a genome-wide study based on the comparison between modern and ancient populations provided evidence of a “Mediterranean genetic continuum”, extending from Sicily to Cyprus [46]. Furthermore, admixture analyses showed that modern Sicilians

harbor a predominant genetic Neolithic-like ancestry, as well as significant contributions from post-Neolithic Caucasian and Levantine-like ancestries, with lower frequencies of the European hunter-gatherer component arising. These findings corroborate the idea that Sicily and southern Italy have long represented one of the most important Mediterranean crossroads in the peopling history of Europe.

Starting with the pioneering studies performed in the 1980s [47,48], the field of ancient DNA (aDNA) is now able to explore many aspects of human genetic history better than ever. The development of next generation sequencing (NGS) technologies, along with the application of sophisticated bioinformatics pipelines, has enabled the generation of an unprecedented quantity of genomic data from past populations [14,49,50].

A paleogenetic study by Mannino et al. [51] on the Mesolithic Oriente B individual, restricted to the mitochondrial DNA (mtDNA) HVR1 region, assigned the specimen to the HV1 haplogroup, and suggested that early Holocene Sicilians might have descended from the Late Epigravettians who migrated from the Italian Peninsula around the LGM. Recently, two genome-wide analyses reported a U2'3'4'7'8'9 mtDNA haplogroup for the Upper Paleolithic Oriente C individual, suggesting that the “Western Hunter Gatherers” were a genetically homogeneous population widely distributed between the Atlantic seaboard of Europe in the west and Sicily in the south, and the Balkan Peninsula in the southeast [10,11]. More recently, Modi et al. [12] also categorized the Mesolithic Oriente B individual into the U2'3'4'7'8'9 mtDNA haplogroup, estimating the emergence date of a “Sicilian clade” to 23,248 years BP. Interestingly, new ancient sequences from a Paleolithic individual in Grotta di San Teodoro and from two Early Mesolithic individuals in Grotta dell'Uzzo seem to corroborate the idea that U2'3'4'7'8'9 was the only mitochondrial lineage in Sicily during the Late Pleistocene and Early Holocene [49,50]. Taken together, all these findings are consistent with the hypothesis of a genetic continuity between Paleo-Mesolithic hunter-gatherers in Sicily.

In a study focusing on the spread of the Bell Beaker cultural complex across western Europe, Olalde et al. [52] also obtained genome-wide data from Early Bronze Age individuals associated to the Bell Beaker culture. They found that Sicilian individuals showed low proportions of ancestry derived from populations related to Early Bronze Age Yamnaya pastoralists from the Eurasian steppe. More recently, Fernandes et al. [14], in analyzing genome-wide data from ancient Sicilians from the Middle-Neolithic to Late Bronze Age, detected evidence of early European farmers' ancestry in Middle-Neolithic individuals. They also identified signs of steppe pastoralist ancestry in Early Bronze Age individuals who arrived in Sicily around 2200 BCE, mainly from Iberia. Furthermore, they found an Iranian-related ancestry associated with the Minoan and Mycenaean cultures in Middle Bronze Age (1800–1500 BCE) Sicily, which could have reached Sicily before the Greek period. Their results also showed, in extant Sicilians, a significant presence of North African-related ancestry, which probably spread onto the island in the Iron Age and afterwards.

The genetic reconstruction we have discussed does not currently allow us to define exhaustive scenarios. However, the prospects are very promising and are still based on the definition of targeted sampling, especially in the case of the analysis of aDNA. The demographic dimension of human events can potentially be reconstructed, but the big interpretative problem remains. A paleoenvironmental analysis that aims at the discovery of anthropization markers could provide further important insights in this sense.

#### 4. Past Vegetation, Climate and Landscape Dynamics during the Holocene

The Holocene landscape of Sicily is the result of a long history of paleogeographic and paleoecological events that, together with human actions, have shaped the distribution of flora and phytocoenoses. The geographical position and bioclimatic conditions of this part of the Mediterranean allowed the survival of many species during the LGM, including many remnants of the “palaeotropical geoflora” [53,54], and the permanence of some species known as “glacial relicts” [55]. During the Late Pleistocene, the Italian Peninsula



and Sicily were a refuge area for many plant species (e.g., *Fagus sylvatica*) and allowed post-glacial recolonization [56]. The first hunter-gatherers that arrived on the island with the LGM had a very limited impact on natural ecosystems. The causal relationship between humans and their environment is the consequence of the ecological transition that starts with the end of the Würm.

The evolution of vegetation throughout the Holocene in Sicily since 11,750 cal yr BP (9700 BCE) has been reconstructed using different paleoenvironmental records, such as pollens, charcoals, and isotope analysis of lacustrine deposits. Lacustrine deposits are crucial in both the understanding of paleobiogeography and the identification of human ecological prints, and intensity. In Sicily, lacustrine sediments have been investigated at different sites, such as Lago di Pergusa [57–63], Gorgo Basso, Lago Preola, and Biviere di Gela on the southern coast [64–66], and Gorgo Tondo, Gorgo Lungo, Urgo Pietra Giordano, Gorgo Pollicino, Marcato Cixè, and Urio Quattrocchi in the northern mountains of the island [67–69] (red dots in Figure 4).

The Early Holocene (11,750–8200 cal yr BP; 9700–6250 BCE) was characterized by a climatic trend toward warmer and wetter conditions than the Younger Dryas. This climate change favored the transition from steppe-like or grasslands to Mediterranean broadleaf forests, which reached their maximum expansion between 9000 and 7000 cal yr BP (7050–5050 BCE) [70,71]. The most profound changes in vegetation occurred in the Early Holocene as a result of insolation, temperature, and rainfall increases [56]. Sadori and Narcisi [57] reconstructed the paleoenvironmental evolution that took place between the Last Glacial period and the Holocene at Lago di Pergusa (670 m a.s.l.). The pollen data records from 10,000 cal yr BP (8050 BCE) indicate the presence of xeric steppes in the glacial period, dominated by *Artemisia* sp., Chenopodiaceae, and Poaceae. In the Sicilian inland region, wetter conditions arose after 9000 cal yr BP (7050 BCE), which allowed the beginning of the afforestation process. The transition from herbaceous plants to the woody vegetation of the Early Holocene was synchronous throughout Sicily. However, while the hilly interior and the mountains were colonized by mixed broadleaved forests, the southern coast was covered with maquis formations [64].

In coastal areas, postglacial afforestation started later than in other areas of the Mediterranean Basin [71]. At Gorgo Basso (6 m a.s.l.), the pollen record shows the predominance of grasslands populated by *Urtica dioica*, Poaceae, Brassicaceae, *Peucedanum*, Cichorioideae, and *Artemisia* up until 9750 cal yr BP (7800 BCE) (Figure 5) [63]. After this period, herbaceous communities were replaced by Mediterranean shrublands dominated by *Pistacia* sp. and *Phyllirea* sp., as well as *Tamarix* sp., *Chamaerops*, *Juniperus* sp., *Erica* sp., *Ephedra* sp., and *Cistus* sp. Since 9500 cal yr BP (7550 BCE), *Pistacia* shrublands have colonized the coastland as a consequence of increases in environmental moisture and related reductions in the occurrence of natural fires. The palynological record from Gorgo Basso also reveals an expansion of *Olea* woods between 8400 and 8200 cal yr BP (6450–6250 BCE), followed by a reduction [65] that is probably related to the 8200 cal yr BP (6250 BCE) dry/cold event [72]. About a thousand years would pass before the evergreen forests returned to the area.

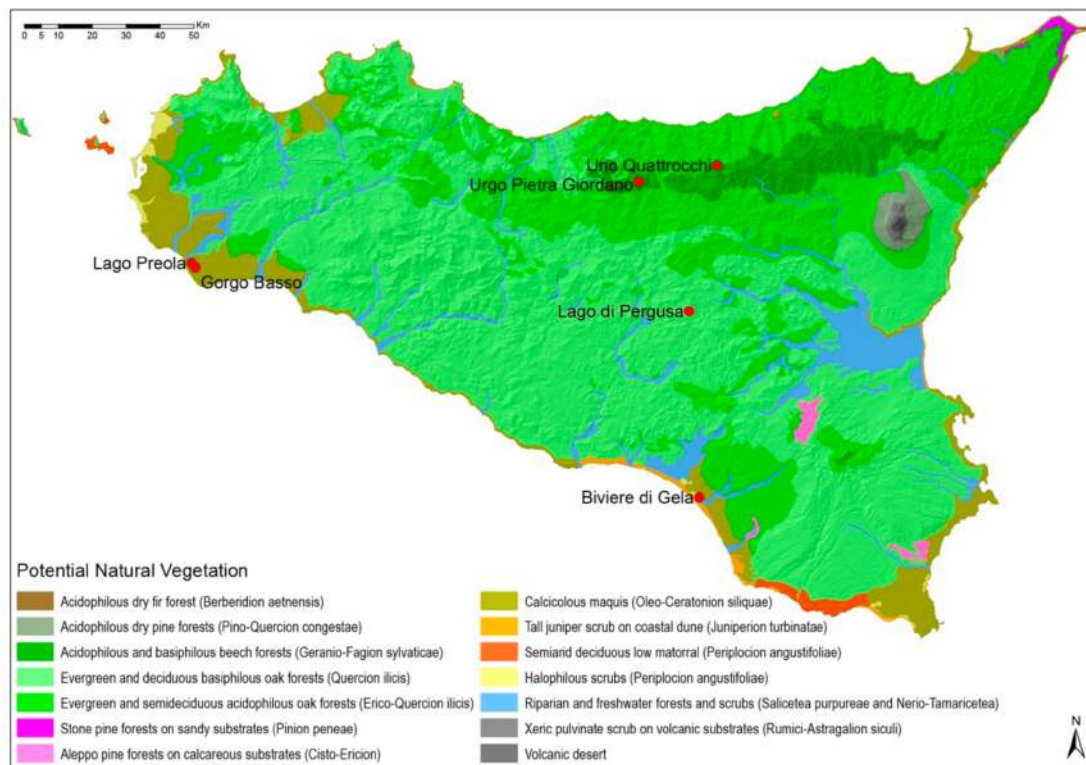
At higher altitudes, in the Urio Quattrocchi area (1044 m a.s.l.), open forest ecosystems dominated by deciduous and evergreen oaks (today growing at lower altitudes) appeared at ca. 10,250 cal yr BP (8300 BCE). Since 10,000 cal yr BP (8050 BCE), the forests have begun to close and became more mesic, reaching maximum coverage at 9700 cal yr BP (Figure 5). The general increase in environmental moisture in this phase of the Holocene allowed the spread of broadleaved forests of *Quercus cerris*, *Fagus sylvatica*, *Quercus ilex*, and *Fraxinus* spp. [68]. The same transition from open communities to *Fagus* and *Abies* forests was observed at Urgo di Pietra Giordano (1323 m a.s.l.) in ca. 10,000 cal yr BP (8050 BCE) by Bertolani Marchetti et al. [67]. ca. 10,000 cal yr BP (8050 BCE).

The Mid-Holocene (ca. 8200–4300 cal yr BP; 6250–2350 BCE) was a period of climatic instability and intense cultural change in the Mediterranean region [71]. A warming period, which characterized the Holocene's optimum climate, occurred from approximately 7500 to 5500 cal yr BP (5550–3550 BCE), which was immediately followed by a dry/cold event,

peaking at 4200 cal yr BP (2250 BCE) [73]. These climate oscillations had an impact on the plant landscape of Sicily and presumably reduced the efficacy and demographic expansion of pre-Neolithic peoples.

Paleobotanical records from Lago di Pergusa by Sadori and Narcisi [57] have revealed changes in floristic composition taking place after 8000 cal yr BP (5950 BCE). The pollen of *Olea* and Mediterranean trees increased after 7200 cal yr BP (5250 BCE), reaching their maximum expansion at around 3200 cal yr BP (1250 BCE). The Mediterranean plants' pollens (*Olea* sp., *Phillyrea* sp., *Quercus ilex*-type, *Rhamnus* sp., *Cistus* sp., *Pistacia* sp., etc.) increased in accordance with the attainment of an optimum climate.

The end of the Mid-Holocene was characterized by increases in *Olea* vegetation cover (4300 cal yr BP; 2350 BCE), despite the lower temperature (Figure 5). Wild olive is one of the dominant elements of the xerophilous forests in Sicily [74,75], and is a component of thermophilous oak forests, both semideciduous and evergreen [76]. The increase in *Olea* incidence is an indicator of the anthropogenic perturbation of forest cover, which then led to vegetation rich in sclerophyllous. *Olea* growth may also have been facilitated by humans, because archaeobotanical data confirm the use of olive tree wood [77], and probably its fruits, during the Bronze Age (ca. 4300–2900 cal yr BP; 2350–950 BCE) [78] (Figure 2d,e).



**Figure 4.** Potential Natural Vegetation of Sicily and locations of paleobotanical sites that have been surveyed in the literature. Vegetation types are indicated at the level of phytosociological alliances (see Bazan et al. [76]).

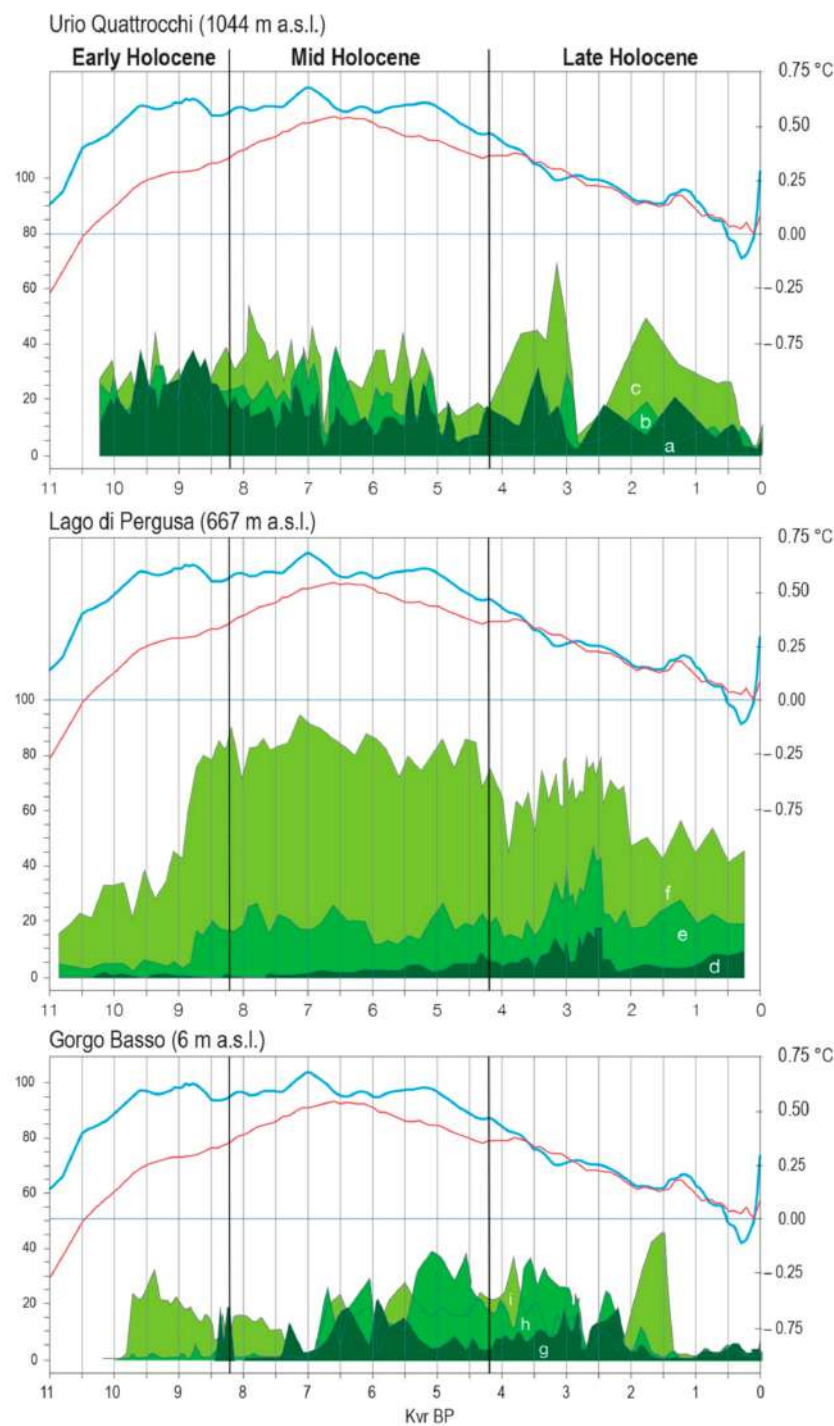
On the southern coast (Gorgo basso), there was also an expansion of *Quercus ilex* and *Olea* forests in ca. 7000 cal yr BP (5050 BCE) that replaced the open environments (grasslands, shrublands), probably resulting from the warmer/wetter conditions and related reductions in natural fire events [65]. After the afforestation of this period, the woods maintained their structure more or less consistently throughout the whole Mid-Holocene. Tinner et al. [65] argued that the climatic conditions of the Sicilian coast between 7000 and 2000 cal yr BP (5050–50 BCE) were similar to those found today. Consequently, the natural vegetation that could have grown is also similar to that seen in the present day (Figure 4). The landscape of the coastal belt was dominated by evergreen oak forests, primarily of *Olea* sp., *Pistacia* sp., *Phillyrea* sp., *Chamaerops* sp., *Juniperus* sp., *Tamarix* sp.,

*Erica* sp., *Ephedra* sp., and *Cistus* sp. [64]. Paleobotanical indicators (*Ficus carica* and Cerealia-type pollens) and archaeobotanical remains (wheat, lentil, and fig) at Lago Preola and Gorgo Basso suggest timid farming activities in the Neolithic period (prior to 7300 cal yr BP; 5350 BCE) (Figure 2b), which had a smaller impact on coastal forests than it had inland [65].

At the beginning of the Mid-Holocene, on the northern mountains of Sicily, according to paleobotanical records, dense forests were widespread, indicating a period with less human disturbance [69]. In the Madonie mountains, around Marcatò Cixè (1200 m a.s.l.) and Urgo Pietra Giordano (1323 m a.s.l.), forests of *Fagus sylvatica* (dominant), *Quercus pubescens*, *Q. petraea*, *Ilex aquifolium*, and *Abies nebrodensis* were present [65,67]. At Gorgo Tondo (783 m a.s.l.) and Gorgo Lungo (877 m a.s.l.), the forests were dominated by mesophilous species, such as *Quercus cerris* and *Q. pubescens* [68], which were in catenal contact with the thermophilous wood of the deciduous and evergreen broadleaf trees of the hilly belt [61,69]. From 7000–6500 cal yr BP (5050–4550 BCE) (data from at Urgo di Pietra Giordano), forest coverage began to thin out, and grassland (Poaceae, Cichorioideae, *Achillea*, *Aster*) took its place [69]. According to archaeological evidence, the transformation of the landscape took place at the same time as the first Neolithic crops were established in coastal northern Sicily (Grotta dell'Uzzo), dated to 5711–5558 BCE [78] (Figure 3). Animal husbandry (bovids, sheep, and goat) was introduced in the area of Grotta dell'Uzzo around 6000 cal yr BP (4050 BCE) [79]. According to Bisculm et al. [68], in the Nebrodi mountains (Urio Quattrocchi), due to anthropogenic fires, the forests also began to decrease after 7000 cal yr BP (5050 BCE) (Figure 5).

The Late Holocene (after 4200 cal yr BP; 2350 BCE) was an epoch characterized by significant human-induced landscape transformations related to the cultural transitions of human societies. The Middle–Late Holocene boundary has been placed at 4200 cal yr BP (2350 BCE), corresponding to an aridification event (the so-called “4.2 ka event”) that may have played an important role in the decline of major ancient civilizations in the Mediterranean area [73]. According to recent temperature reconstructions spanning the past 10 millennia, the Mid-Holocene was followed by a progressive cooling period, culminating in the Little Ice Age, around 1550–1800 CE [80,81]. However, the influence of the climate trend on landscape transformation in this last period has been masked by anthropic processes. Human-induced landscape transformation is not necessarily the symptom of an increased demography but is rather an indication that humans began the process of sub-intensively cropping and burning.

In central Sicily, landscape changes began in 3200 cal yr BP (1250 BCE) with the increase in olive formations and continued in the following millennia. The increase in sclerophyllous Mediterranean taxa (*Olea* sp., *Pistacia* sp., *Phyllirea* sp., *Quercus ilex*) compared to the drop in mesophilous species indicates that opening up and structural degradation occurred in forest formations, and these were related to human disturbance. Even today, the main potential natural vegetation (Figure 4) that can grow in the central clayey soils of the Sicilian countryside is mixed wood (*Oleo-Quercetum virgiliana*), mainly thermophilous oaks and a variety of Mediterranean species (*Olea europaea* var. *sylvestris*, *Pistacia lentiscus*, *Phillyrea angustifolia*, etc.), which indicate a degree of environmental xericity [76] as a consequence of forest canopy openness. Another interesting aspect of the palynological data offered by Sadori et al. [61] is the development in 2600 cal yr BP (650 BCE) of certain anthropogenic taxa (Caryophyllaceae, Urticaceae, Asteroideae, Cichorioideae, Pooideae, *Papaver* sp., *Plantago*, *Polygonum*, *Rumex*, *Vitis* sp., etc.). The paleobotanical data are in accordance with the archaeological evidence. During the Iron Age, between 3200 and 2700 cal yr BP (1250–750 BCE), the area around the Lago di Pergusa was strongly exploited and disputed by Sicels and Sicanians [82] (Figure 2f).



**Figure 5.** Schematic trends of pollen percentage: Urio Quattrocchi (a—*Quercus pubescens*; b—*Q. ilex-t*; c—*Q. cerris*) within the Evergreen and semideciduous acidophilous oak forests (*Erico-Quercion ilicis*) PNV (see Figure 4); Lago di Pergusa (d—*Olea* sp.; e—Mediterranean vegetation; f—Arboreal pollen) within the Evergreen and deciduous basiphilous oak forests (*Quercion ilicis*) PNV; Gorgo Basso (g—*Olea* sp.; h—*Quercus ilex-t*; i—*Pistacia* sp.) [59,65,68] within the Calcicolous maquis (*Oleo-Ceratonion siliquae*). Trends of average temperature variations by Marcott et al. [80] (red line) and Kaufman et al. [81] (blue line) during the Holocene.

During the last 2000 years, according to Sadori et al. [83], farming has been practiced continuously, as recorded in lacustrine sediments. Fluctuations in the concentration of pollen from species related to cultivation indicate changes in the productivity of agricultural system. For example, cereal pollens peaked during the Byzantine period (fifth and seventh

centuries CE) [83] as an effect of temperature and humidity increases, which favored the late Roman economy of intensive grain production. This period was followed by a cooling that may have been important in determining the collapse of Byzantine society in Sicily and favoring the success of the Arab conquest, which spread new agricultural techniques on the island. During the Islamic domination, irrigated agriculture was widespread all over the island, and was integrated with non-irrigated agriculture and husbandry as part of a complex productive system. The great novelty of the medieval “Arabic agricultural revolution” concerned the new techniques, new species, and new social and economic conditions that all came together. In fact, the “green revolution” may have had such a huge impact on the agricultural landscape thanks not only to new agricultural and technical innovations, but also to the fact that these developments were rooted in innovations and improvements of agronomic techniques inherited from the Greeks, Phoenicians, and Romans [84]. Archaeobotanical and archaeozoological evidence from the medieval site of Contrada Castro in Monti Sicani (late 8th to 11th CE) showed that the transition between the Byzantine and Arab periods manifested no radical change in agricultural strategy, wood exploitation, or the management of animal resources [85]. Recent papers by Bazan et al. [86,87] highlight the *Long-Durée* of the landscapes of the Sicilian rural countryside, which have displayed strong continuity throughout the last millennium.

The drastic reduction in evergreen forests (Figure 5) on the coastland between Gorgo Basso and Lago Preola have been dated back to ca. 2700 cal yr BP (750 BCE) by Tinner et al. [65] and Calò et al. [66], corresponding to the period of Greek colonization, which started in 734 BCE (2684 cal yr BP) [78] and which had a demographic impact on Sicily [27,28] (Figure 2h). This is evident in the first increase in *Pistacia* shrublands that was followed in subsequent centuries (after 1500 cal yr BP; 450 CE) by a drastic reduction in natural vegetation due to human-caused disturbances in the period of great prosperity in nearby Selinunte [88]. Since the Mid- and Late Holocene (6000–2600 cal yr BP), the climate conditions and potential natural vegetation present on the coastlands of Sicily have steadily evolved into those seen today (Figure 4) [64,65].

Beech and mesophilous forests have maintained their potential range since the Late Holocene in the mountains of northern Sicily [69]. The mountain forest ecosystem of Sicily has shown remarkable resilience against past climate change and increasing human pressure (burning, cutting, or overgrazing).

Paleoecological studies have shown that different climatic fluctuations caused no significant changes in the ecological setting of Sicily, demonstrating the high adaptability of natural ecosystems and human societies. On the other hand, the long-term agrosilvo-pastoral exploitation of land since the Neolithic period has transformed the natural ecosystems into agroecosystems that have played an important role in maintaining biodiversity and endemic, rare plant species [89–91]. In general, the Neolithization of Sicily led to the development of the first agroecosystems, which evolved in tandem with the introduction of new species that accompanied human migrations. New populations brought with them new domesticated species (even in areas where wild varieties were present) and new cultivation practices. An important role in the domestication of landscape was played by the spread of the three “key stone species” of the Mediterranean agroecosystems: wheat, olive, and grapevine.

The archaeobotanical remains of the first Neolithic phase from Grotta dell’Uzzo (5711–5558 BP; 3751–3608 BCE) (Figure 3) have documented the exploitation of wheat (*Triticum aestivum* and *T. compactum*), fava bean (*Vicia fava*), bitter vetch (*Vicia ervilia*), pea (*Pisum* sp.), fig (*Ficus carica*), wild olive (*Olea europaea* var. *sylvestris*), etc. [78]. The oldest olive oil production, however, has been dated by Tanasi et al. [92] to the end of the third and beginning of the second millennium BCE, in the Early Bronze Age settlement of Castelluccio (Noto), while the earliest attested presence of winemaking was identified at the Copper Age site of Monte Kronio (Sciacca). The presence of wine was indicated by the presence of tartaric acid and its sodium salt in storage jars, which dated to the third millennium

BCE [93]. Therefore, archaeobotanical findings have confirmed that, in the Early Bronze Age, the cultivation of wheat, olive, and grapevine were already well-established practices.

These agroecosystems and associated agrobiodiversity have changed over time, starting with plant selection processes (agrarian archaeophytes) and changing in relation to migrations, commerce, and the introduction of new species (agrarian neophytes). Co-evolution processes between human culture and cultivated plants have favored symbiotic growth and mutual expansion [94]. These changes are evident in the first agricultural revolutions, which occurred during the Neolithic period, during the medieval “Arabic agricultural revolution”, and at the end of 15th century AD. The “discovery of America” and its extraordinary richness of species introduced new species (at that time Sicily was under the Spanish Imperial Rule) that changed the agrobiodiversity of the Old World. In many cases, plant crops coming from other continents became very important beyond their places of origin, and even shaped the landscape in areas where farming has been affirmed to have taken place (e.g., the prickly pear in Sicily). Therefore, the landscape of Sicily has been profoundly shaped by the cultural transformations and stratifications that occurred during different historical periods with similar climate settings, which have in turn defined its identity.

## 5. Discussion

The extensive survey of the archaeogenetic studies of Sicily since the Troina meeting presented in this paper verifies that many of the predictions and plans made at that meeting have been realized. Nevertheless, it is worth remembering that the reconstruction of the genetic history of the island is a growing field of investigation, and this survey of the published efforts clearly indicates that there are many difficulties that remain. This is somewhat inevitable, given that the analyses conducted thus far have only involved a small part, perhaps not even representative, of the extensive archaeological and historical evidence pertaining to the island, containing (by a previous outdated prediction) over 3000 registered sites. This contrast is better illustrated by comparing the map of archaeological sites surveyed to date (Figure 2) and the map of sites sampled for DNA analyses (Figure 3).

The new NGS technologies will undoubtedly have important effects. As a first step, it is necessary to increase the coverage of ancient genomes by focusing on the cultural and bio-demographic processes that have shaped the current genetic landscape. In our opinion, the extent of the genetic contribution made by Iron Age indigenous peoples is a highly debated issue that needs to be addressed (Figure 2e), as this contribution may have been masked by subsequent migration events.

Another fundamental area of focus will be forming a better understanding of the impact on the present-day Sicilian gene pool of Greek and Punic colonizations, beginning with the founding events of the eighth and the sixth centuries BCE (Figure 2g). The evaluation of the demographic dimension of colonization may be indirectly inferred through changes in vegetation cover recorded by paleoecological analyses. The movement of people and the effective genetic impact of their settlements is tied to ecological and environmental factors. The evaluation of the ecological and paleo-botanical characteristics of the territory is thus important, as this helps in reconstructing the diffusion and demographic repercussions of the different Holocene human flows.

In our opinion, it is necessary to proceed, with reinvigorated effort, with the integrated study of modern and ancient genomes, in order to achieve a complete and more accurate picture of the population history of Sicily. We would like to mention here the research project AGED “1000 Ancient Italian Genomes: Evidence from ancient biomolecules for unravelling past human population Dynamics”, begun in 2020, which aims to study the dynamics of population that have characterized the Italian peninsula via a multidisciplinary approach based on the paleogenomic, isotopic, and radiometric analysis of ancient biological samples from the Paleolithic to Middle Age. As far Sicily is concerned, the AGED project aims to provide an interpretation of genetic data for Sicily via a detailed

examination of the population dynamics associated with the cultural, demographic, and environmental changes that took place during the prehistory and history of the island. In turn, the genetic, demographic, and cultural changes need to be understood in the context of the environmental changes that took place over the Holocene.

## 6. Concluding Remarks

While, on one hand, the literature surveys on the three themes (ethnic/archeological, archeogenetics, past vegetation/landscape) discussed in this review were intended to offer the reader a systematic knowledge about the state of art of studies performed on various aspects of the prehistory, protohistory, and history of Sicily, on the other hand, we wish to suggest here a few ideas for future studies on Sicily, hoping they will serve as a useful general theoretical framework. First of all, we underscore the importance of pursuing an interdisciplinary approach to gain a deeper understanding of the complex dynamics that have characterized the past timeline of Sicily. More specifically, we think that the most effective and appropriate way to implement such an interdisciplinary approach is to undertake a systems level analysis of Sicily by which to investigate the many crosstalk events that have occurred between the cultural and biological evolutions during the Holocene. Indeed, as it was extensively discussed in the landscape section of this review, the two types of evolution have interacted and influenced each other at different periods and places within the island. Moreover, we propose that such evolutionary changes would be better understood if they are considered in terms of the changes in biodiversity and sustainability of the Sicilian ecosystem. Here, the term biodiversity is used to include the genotypic as well as phenotypic changes of the humans, animals, and plants that have lived in the island throughout this time frame. From this perspective, changes of sustainability can be causally linked to changes in biodiversity of the Sicilian ecosystem. In turn, such changes need to be studied as a response to natural (e.g., climatic, geological) and cultural (e.g., transition from a hunter-gatherer to agricultural economy) influences. Within this framework, the contribution of archaeogenetic studies will help to reconstruct the dynamics of human populations. Throughout the Holocene, these dynamics have constituted the main driver of the prehistoric and historical changes of Mediterranean landscapes. Despite its long human history, the Mediterranean is still one of the world's biodiversity hotspots and Sicily is one of its important areas [95]. The lessons we learn from the past use of landscape provide models for the sustainable future management of the Mediterranean's landscapes.

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