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Population history of southern Italy during Greek colonization inferred from dental remains

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Abstract

Objectives: We are testing competing scenarios regarding the population history of the ancient Greek colonization of southern Italy using dental phenotypic evidence.

Materials and Methods: We collected dental metric and nonmetric trait data for 481 human skeletons from six archaeological sites along the Gulf of Taranto, dating to pre-colonial (900–700 BC) and post-colonial periods (700–200 BC). We are evaluating scenarios through an individual-level biodistance analysis using a three-pronged approach: (a) by analyzing levels of mobility in pre- and post-colonial periods under a model of isolation-by-distance; (b) by quantifying differences in group means and variances in pre- and post-colonial periods utilizing permutational multivariate analysis of variance and Betadisper analyses; and (c) by identifying ancestries of post-colonial individuals using naïve Bayes classification.

Results: Southern Italy during pre-colonial times was characterized by low levels of mobility and marked differences in group means and variances. During post-colonial times, mobility increased and there were no differences in group means and variances. About 18% of the people in post-colonial times were of Greek ancestry and lived equally distributed across Greek colonies and indigenous villages. Nevertheless, the overall biological composition and variability of southern Italy remained relatively unchanged across pre- and post-colonial periods.

Discussion: Our results support a scenario in which only few Greek colonists migrated to southern Italy and lived in smaller numbers alongside indigenous people in Greek colonies as well as in indigenous villages. Our results contradict a scenario in which large numbers of Greek invaders founded biologically isolated and substantially homogeneous colonial enclaves within conquered territories.

KEYWORDS
biodistance, dental metrics, dental nonmetric traits, Greek colonization, southern Italy

1 | INTRODUCTION

During the eighth century BC, people coming from ancient Greece started to settle along the coasts of the Mediterranean Basin. They founded more than 500 Greek colonies along the shores of the Black Sea, Anatolia, southern Italy, northern Africa and on the coasts of southern France and Spain (Hansen & Nielsen, 2004). The Greek colonization has been called "one of the most important cultural

encounters in world history" (de Angelis, 2016, p. 101), and its consequences in Mediterranean history were profound and long-lasting. It contributed to the creation of a Mediterranean-wide exchange network (Malkin, 2005), to the development of urbanization along its shores (Malkin, 1994), to the spread of the alphabet (Boardman, 2014), and to the diffusion of Greek artistic and architectural traditions (Greco, 1992). Among the regions settled by the Greeks, southern Italy was one of the most densely populated areas and eventually became known as *Megálē Hellás* or *Magna Graecia* (Greater Greece).

Decades of extensive research have greatly enhanced our understanding of the Greek colonization of southern Italy; however, the scale of the demographic impact and the degree of admixture between Greek colonists and indigenous groups remain unresolved. One scenario, largely drawn from ancient written sources, envisages Greek colonization as a mass migration of invaders who founded biologically isolated and substantially homogeneous enclaves within conquered territories (Yntema, 2011). In this scenario, indigenous populations were deprived of land, resources, and occasionally women to fulfill the colonies' needs, while being the object of gradual acculturation (or "Hellenization") (Boardman, 1964; Dunbabin, 1948; Greco, 2002; Pugliese Carratelli, 1996; see also Shepherd, 2005; Snodgrass, 2005). An alternative scenario, based on archaeological evidence and the adoption of post-colonial theory, envisages Greek colonization as a more gradual process, where only few Greek colonists (mostly traders, artisans, and adventurers) sailed to the shores of southern Italy and lived peacefully alongside a much larger indigenous population (Yntema, 2011). In this scenario, close collaboration resulted in intermarriage between newcomers and locals and eventually shaped new, admixed cultures (Malkin, 2002; Osborne, 1998; van Dommelen, 2012; Yntema, 2000). In recent years, demographers and geneticists have tried to tackle the question of Greek colonization and its impact on southern Italy from a different angle using census sizes documented in ancient texts and/or modern DNA data from present-day Italians. However, whereas some studies estimated a rather large number of Greek migrants (e.g., Scheidel, 2003), others have suggested a substantially smaller founding population (e.g., Tofanelli et al., 2016).

One major problem with the various arguments put forward in support of both scenarios is that they are exclusively based on indirect evidence, namely: (a) ancient texts from Greek writers; (b) archaeological objects excavated in Italy, primarily pottery; and (c) modern DNA profiles of present-day southern Italians. To rely on this evidence alone is problematic because most ancient written sources postdate Greek colonization by several centuries and portray it solely from a Greek perspective. Similarly, movements of archaeological objects do not necessarily imply migration but can also result from trade or the diffusion and adoption of stylistic fashions. Finally, present-day DNA profiles may not accurately reflect the effects of past migration events due to movements of people in more recent times.

The most promising approach for testing these two competing scenarios is to directly analyze ancient biological data from archaeological human remains. Unfortunately, endogenous DNA preservation is poor in many southern Italian skeletons, an issue that has hindered large-scale ancient DNA investigations until today. Biological distance (or "biodistance") analysis provides a powerful tool that can circumvent this problem by utilizing heritable phenotypic features for inferring genetic relationships across individuals and samples (Buikstra, Frankenberg, & Konigsberg, 1990; Konigsberg, 2006; Stojanowski & Schillaci, 2006). Surprisingly, only a handful of studies have utilized biodistance methods to address the impact of Greek colonization on southern Italy (Henneberg, 1998; Rathmann, Saltini Semerari, & Harvati, 2017; Rubini, Bonafede, & Mogliazza, 1999). These investigations found that inhabitants of Greek colonies showed marked biological differences to indigenous Italian groups, possibly due to an influx of new genes. While this is an exciting finding, these studies were limited by several factors. First, only few phenotypic variables were employed, which generally reduces the accuracy of biodistance estimates (Scott, Turner, Townsend, & Martinón-Torres, 2018, p. 242). Moreover, either metric or nonmetric data were used; however, it has been shown that combining metric with nonmetric features in a single analysis increases performance compared to using these data separately (Hefner, Spradley, & Anderson, 2014; Lease & Sciulli, 2005). In addition, all studies performed group-level biodistance analyses; however, individual-level biodistance methods are better suited for capturing the significant amount of human genetic variation within groups (Stojanowski & Schillaci, 2006). Finally, none of the previous studies used adequate comparative data from Greece, which is essential to quantifying the degree of Greek genetic contribution to southern Italy.

Here, we expand on previous biodistance studies on the Greek colonization of southern Italy by: (a) analyzing a new dataset from several important archaeological sites along the coastal area of the Gulf of Taranto, dating from pre- to post-colonial periods (900–200 BC); (b) employing a large battery of phenotypic variables; (c) combining metric with nonmetric traits; (d) performing individual-level biodistance analyses; and (e) integrating comparative data from Greece. Our analysis is based on dental phenotypic data for several practical reasons. First and foremost, teeth are generally well-preserved in many southern Italian samples, even when associated skeletal preservation is poor. Their better state of preservation results in teeth being recovered in higher quantities than other skeletal elements and, therefore, allowed us to employ larger samples and more robust statistical analyses. Moreover, tooth crowns develop relatively early in the life of an individual and their form remains unchanged once fully developed, except by wear or pathology. More importantly, tooth form has been proposed to be highly heritable and selectively neutral, thus providing an excellent proxy for neutral genetic data (Hillson, 1996; Scott & Turner, 1997). In fact, several recent studies have demonstrated the utility of dental phenotypic data in reconstructing genetic relatedness across human populations on different geographic scales (Hubbard, Guatelli-Steinberg, & Irish, 2015; Rathmann et al., 2017) and even between individuals within a population (Paul & Stojanowski, 2015, 2017; Ricaut et al., 2010; Stojanowski & Hubbard, 2017). Finally, dental phenotypic data can be sampled in a nondestructive, cost-efficient, and straightforward manner using crown width and length measurements (dental metrics) and visual scoring of crown and root shape variants (dental nonmetric traits). Analytically,

we aim to address the two competing colonial scenarios through a three-pronged approach:

1. By analyzing levels of mobility in pre- and post-colonial time periods;
2. By quantifying differences in group means and variances through space (between archaeological sites within a period) and time (between pre- and post-colonial periods);
3. By identifying ancestries of individuals living in Greek colonies and indigenous villages in post-colonial southern Italy.

If the colonization process was driven by large groups of Greeks founding biologically isolated and substantially homogeneous enclaves within southern Italy (Scenario 1), then we would expect to see evidence of a substantial increase in mobility from the pre-colonial period to the post-colonial period (due to migration influx of new people). In addition, we would expect to see that inhabitants of Greek colonies are biologically different from indigenous populations, with the former exhibiting lower levels of variability than the latter (due to isolation and genetic drift). Moreover, we would expect that Greek colonies are predominantly inhabited by individuals of Greek ancestry whereas indigenous villages are predominantly inhabited by individuals of Italian ancestry. Lastly, we would expect to see a general increase in biological variability and a change in the overall biological composition of southern Italy from the pre-colonial period to the post-colonial period (due to the transfer of new genes into the southern Italian gene pool).

Alternatively, if only few Greek colonists migrated to southern Italy and lived in small numbers alongside indigenous people in Greek colonies as well as in indigenous villages (Scenario 2), then we would expect to see evidence of a moderate increase in mobility from the pre-colonial period to the post-colonial period. In addition, we would expect to see that inhabitants of Greek colonies are biologically similar to indigenous populations with both exhibiting similar levels of variability (due to the homogenizing effect of gene flow). Moreover, we would expect that individuals of Greek and Italian ancestry are equally distributed across Greek colonies and indigenous villages. Lastly, we would expect to see similar levels of biological variability and a largely unchanged overall biological composition of southern Italy from the pre-colonial to the post-colonial period (because numerically negligible gene flow will not significantly alter the southern Italian gene pool).

2 | MATERIALS AND METHODS

2.1 | Skeletal samples

We collected osteological data from 481 human skeletons with well-preserved dentitions from six archaeological sites from the coastal area of the Gulf of Taranto, southern Italy, dating to pre-colonial (900–700 BC) and post-colonial periods (700–200 BC) (Figure 1). The dataset was collected by a team from the University of Tübingen between the years 2014 and 2018 at the storage rooms of the National Archaeological Museums of Policoro, Metaponto, and Taranto. Several of the skeletal remains were hitherto inaccessible and the majority had not been published before.

The study region is of special importance to scholars concerned with the Greek colonization of *Magna Graecia*, because it is home to several major Greek colonies and features a wealth of well-studied indigenous sites (Bianco, 2012; Carter, 2006; De Siena & Tagliente, 1986; Greco, 1999; Yntema, 2000). Our dataset comprises skeletons from three indigenous Italic settlements: Incoronata, Santa Maria d'Anglona, and Passo di Giacobbe. These sites share a distinct indigenous cultural package, defined by specific grave good assemblages,
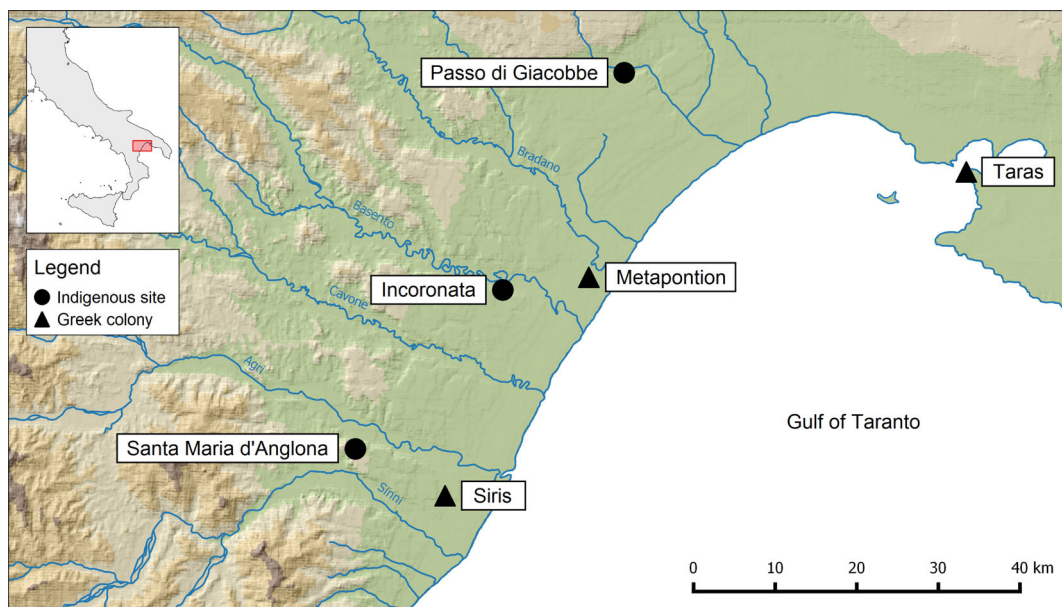

FIGURE 1 Map of the Gulf of Taranto region showing the geographic locations of the archaeological sites analyzed in this study

flexed burial positions, and gender-specific burial orientations. Moreover, our dataset includes skeletons from three Greek colonies: Metapontion, Siris, and Taras. According to ancient written sources, the colonies were founded in the course of the late eighth to sixth centuries BC by Greek settlers from Achaia, Ionia, and Laconia (Strabo, n.d., p. 6.1.14, 6.1.15, 6.3.2). The early colonies gradually grew into full-fledged urban centers, amassed a great amount of wealth owing to the region's fertile farmland, and erected temples and monumental public buildings.

Table 1 gives summary information about the skeletal samples under study, including cultural affiliation, dating, total number of examined skeletons, as well as subsamples used for different statistical analyses (see Methods section below). More detailed sample descriptions and references for the individual archaeological sites are provided in Appendix S1. All skeletons were dated based on grave good assemblages, including pottery and metal artifacts.

2.2 | Data recording

Sex and age-at-death estimates are fundamental to any osteological analysis. Sex estimation was based on pelvic and cranial morphology using standard osteological techniques (Buikstra & Ubelaker, 1994). Age-at-death estimates were based on dental development, fusion of epi- and apophyses, cranial and palatal suture closure, and morphological changes of the pubic symphyseal and auricular surfaces (Buikstra & Ubelaker, 1994).

For our biological distance analysis we collected dental metric and dental nonmetric trait data. The dental metric dataset consists of 32 mesiodistal (MD) and buccolingual (BL) crown and cervical diameters of the permanent teeth recorded for each individual. Only polar teeth were recorded (UI1, UC, UP3, UM1, LI2, LC, LP3, LM1) in order to reduce genetic covariation between traits, and to minimize potential effects of fluctuating asymmetry and ontogenetic plasticity on

adult tooth size (Butler, 1939; Dahlberg, 1945; Sciulli & Cook, 2016; see also Stojanowski, 2003, 2004; Thompson, Hedman, & Slater, 2015). Only left teeth were measured, but when a left tooth was missing, damaged, or affected by wear or pathology, the corresponding right antimere was measured. Maximum MD and BL crown diameters were recorded according to the procedures detailed in Mayhall (1992) and Buikstra and Ubelaker (1994). MD and BL dimensions of the cervix at the cement-enamel junction were recorded according to the procedures detailed in Hillson, Fitzgerald, and Flinn (2005). All measurements were taken using a Mitutoyo pointed blade digital sliding caliper accurate to 0.01 mm. A table listing the summary statistics of the dental metric dataset is provided in Appendix S1, Table S1.

The dental nonmetric trait dataset consists of observations for 34 morphological variables in the permanent dentition of each individual. All traits were recorded according to the reference standards of the Arizona State University Dental Anthropology System (ASUDAS) described in Turner, Nichol, and Scott (1991). This system comprises a set of dental casts illustrating expression levels for various traits and specific instructions to ensure a standardized scoring procedure that minimizes observer error. Only traits on key teeth were recorded (Scott, Maier, & Heim, 2016). Scoring followed the individual count method, where a trait was counted only once per dentition, regardless of whether or not the trait appeared bilaterally. In cases where a trait was expressed asymmetrically, the side with the highest expression level was scored (Delgado et al., 2019; Edgar, 2007; Irish & Konigsberg, 2007; Scott, 1980; Sutter & Verano, 2007; Turner, 1985; Turner & Scott, 1977). To ensure accuracy, any observation that was potentially affected by dental wear, caries, or calculus was treated as missing data. We followed the standard procedure and dichotomized the ordinal-scaled dental trait scores into binary categories of absence (0) or presence (1) in order to reduce observer error and simplify data analysis. The applied dichotomization thresholds follow established breakpoints (Irish, 2016; Turner, 1987) that have proven useful for

TABLE 1 Archaeological sites and sample sizes used in this study

Archaeological site	Cultural affiliation	Time period	Necropoleis	Sample date	Number of skeletons[a]	Analytic subset 1[b]	Analytic subset 2[c]
Incoronata	Indigenous settlement	Pre-colonial	Incoronata Indigena	900–750 BC	99	14	—
			San Teodoro	900–750 BC	40	6	—
Santa Maria d'Anglona	Indigenous settlement	Pre-colonial	Conca D'oro	850–700 BC	85	18	—
			Sorigliano	800–700 BC	17	3	—
Passo di Giacobbe	Indigenous settlement	Post-colonial	Passo di Giacobbe	625–300 BC	105	21	15
Metapontion	Greek colony	Post-colonial	Crucinia	600–200 BC	94	15	12
			Pantanello	650–200 BC	12	3	5
			Torre di Mare	600–200 BC	3	2	3
Siris	Greek colony	Post-colonial	Madonelle	700–500 BC	18	7	8
			Zona C	700–500 BC	1	1	1
Taras	Greek colony	Post-colonial	City center	700–500 BC	7	1	1

[a]Total number of skeletons for which at least one dental metric or nonmetric trait was recorded.
[b]Subset of skeletons submitted to isolation-by-distance, permutational multivariate analysis of variance and Betadisper analyses.
[c]Subset of skeletons used as test individuals for the naïve Bayes ancestry classification.

effectively capturing variation across human populations in the Mediterranean Basin (Coppa, Cucina, Lucci, Mancinelli, & Vargiu, 2007; Irish, Lillios, Waterman, & Silva, 2017; McIlvaine, Schepartz, Larsen, & Sciulli, 2014; Parras, 2004; Rathmann, Saltini Semerari, & Harvati, 2017; Ullinger, Sheridan, Hawkey, Turner, & Cooley, 2005). A table listing the summary statistics of the dental nonmetric dataset is provided in Appendix S1, Table S2.

All osteological data were collected by the lead author (H.R.). The dataset is publicly available via an online data repository (https://github.com/HannesRathmann/GCSI). The data sheet provides individual-level information about sex, age-at-death, dental metrics, dental nonmetric traits scores, and dichotomized dental nonmetric traits.

2.3 | Data preprocessing

A number of data preprocessing steps were used to ensure that patterns of dental phenotypic variation most closely approximate underlying genotypic variation. First, H.R. quantified his level of intra-observer error by re-measuring a subsample of individuals from Santa Maria D'Anglona (n = 30) in two sessions separated by an interval of 1 week. Dental measurements from the two sessions were compared using Student's t tests performed with the t.test function in R (R Core Team, 2016). None of the comparisons exhibited a significant difference with $p < 0.05$ (Appendix S1, Table S3). Dichotomized dental nonmetric traits from the two sessions were compared using Cohen's Kappa tests using the cohen.kappa function from the psych package in R (Revelle, 2017). The resulting coefficients ranged from 0.621 to 1.000 with a significance of $p < 0.05$ for all comparisons (Appendix S1, Table S4). All comparisons indicated that intra-observer error was negligible.

Second, sexual dimorphism on dental characters was analyzed using Student's t tests for metric variables and Fisher's exact tests for dichotomized nonmetric variables using the t-test and fisher.test functions in R. For comparison, we only included individuals with secure sex determinations (n = 61). We found that 53% of the metric variables (15 of 28) showed significant differences between sexes with $p < 0.05$ (Appendix S1, Table S5). For the dichotomized nonmetric variables we found that 4% (1 of 25) exhibited a significant difference between the sexes with $p < 0.05$ (Appendix S1, Table S6). Hence, all further analyses have to correct for sexual dimorphism on metric features (see Methods section below), while levels of sexual dimorphism in nonmetric features are within an acceptable range as detailed by previous ASUDAS studies (Irish, 2016; Matsumura & Oxenham, 2014; Reyes-Centeno, Rathmann, Hanihara, & Harvati, 2017; Scott & Turner, 1997).

Third, inter-trait correlations between dental metric and nonmetric traits were analyzed using the mixed.cor function from the psych package in R. The mixed.cor function computes a heterogeneous correlation matrix consisting of Pearson correlations for metric variables, tetrachoric correlations for dichotomized variables, and biserial correlations for mixed variables. Correlations were generated using all observations with valid data for a pair of variables. The resulting inter-trait correlation matrix is provided in Appendix S2, Sheet 1. The

correlation matrix was further visualized using the corrplot function from the corrplot package in R (Wei & Simko, 2017) (Appendix S1, Figure S1). In summary, we found a high amount of integration among dental metric variables (with 71% of all 496 pairwise comparisons exceeding $r > 0.5$), but general independence among dichotomized traits (with only 7% of all 465 pairwise comparisons exhibiting correlations of $r > 0.5$ or $r < -0.5$) as well as general independence among dichotomized and metric features (with only 5% of all 942 pairwise comparisons exhibiting correlations of $r > 0.5$ or $r < -0.5$). All subsequent biodistance analyses require independence among dental features. The high amount of integration among dental metric variables was removed using data reduction techniques (see Methods section below). The few instances of inter-correlation between dichotomized descriptors and between dichotomized and metric features were removed by dropping variables from analysis that had the fewest observations overall or that were correlated with multiple variables. Consequently, 18 variables were removed prior to biodistance analysis: Tuberculum Dentale UI1, Tuberculum Dentale UC, Distal Accessory Ridge UC, Distal Accessory Ridge LC, Odontome P1-P2, Mesial and Distal Accessory Cusps UP1, Peg-shaped UI2, Cusp 6 LM1, Cusp 7 LM1, Enamel Extension LM1, Root Number LM2, UP1-MD-CROWN, LP1-MD-CROWN, LM1-MD-CROWN, LI2-BL-CROWN, LI2-MD-CROWN, LI2-BL-CERVIX, and LI2-MD-CERVIX. This reduction procedure resulted in a dataset of 475 individuals and 48 variables (25 metric and 23 nonmetric traits).

2.4 | Analyzing levels of mobility in pre- and post-colonial southern Italy

We analyzed mobility under a model of isolation-by-distance (IBD). The IBD model states that individuals that are geographically close to each other tend to be genetically more similar than individuals that are farther apart because of spatially limited gene flow (Wright, 1943). Therefore, a positive correlation is expected between genetic distance and geographic distance. However, the strength of this correlation depends on the level of mobility. If mobility was low, then we would expect genetic distances to be strongly correlated with geographic distances, whereas if mobility was high, we would expect genetic distances to be weakly correlated with geographic distances (Loog et al., 2017). In physical anthropology, IBD models are traditionally used to explain genetic variation using populations as the unit of analysis (e.g., Konigsberg, 1990; Ragsdale & Edgar, 2015; Relethford, 2004). Here, we take a different approach and apply the model to single individuals, a procedure that is well-established and commonly performed in genetics. To analyze mobility through time, we compared the IBD pattern of individuals living in pre-colonial southern Italy (900–700 BC) to the IBD pattern of individuals living in post-colonial southern Italy (700–200 BC). Sample sizes for these tests are detailed in Table 1.

IBD patterns were quantified by estimating the association between inter-individual biological distances (B) and geographic distances (G) using Mantel tests. Mantel tests measure the correlation between two distance matrices against a null model and assess statistical significance via a permutation procedure (Mantel, 1967). We also

performed partial Mantel tests to control for the effects of a third distance matrix during our comparisons (Smouse, Long, & Sokal, 1986). This test was used to account for the fact that not all individuals in our analysis are contemporaneous (Konigsberg, 1990; Pinhasi & Cramon-Taubadel, 2009; Reyes-Centeno et al., 2017; Schillaci, Irish, & Wood, 2009). Partial Mantel tests assessed the correlation between biological distances (B) and geographic distances (G), while holding temporal distances (T) constant. Computationally, the partial Mantel test design calculates the correlation of the residuals from the independent regressions B ~ T and G ~ T. Mantel computations were performed using the *mantel* and *mantel.partial* functions from the vegan package in R (Oksanen et al., 2016). For all Mantel tests, correlation significance was determined after 1,000 permutations.

Biological distances among individuals were estimated on the basis of dental metric and nonmetric data using the Gower similarity coefficient (Gower, 1971), following the protocol set forth by Paul, Stojanowski, and Butler (2013). Gower coefficients have been extensively used in inter-individual biological distance analyses (e.g., Howell & Kintigh, 1996; Ricaut et al., 2010; Stojanowski & Hubbard, 2017; Stojanowski & Schillaci, 2006) because they can incorporate multiple variable scales (metric and nonmetric traits) and allow for missing data. Nevertheless, the amount of missing data should be reduced as much as possible in order to prevent the comparison of two individuals who share no traits in common. Because not every tooth could be observed in each individual due to poor preservation, wear, or pathology, our dataset comprises large amounts of missing values. We therefore removed the most incomplete variables and individuals from analysis in a systematic stepwise manner to ensure that no more than one-third of the variables were missing for any individual included in the analysis. We removed all MD crown diameters from the analysis because of excessive levels of missing data for these measurements (UI1-MD-CROWN, UC-MD-CROWN, UP1-MD-CROWN, UM1-MD-CROWN, LC-MD-CROWN, LP1-MD-CROWN, and LM1-MD-CROWN). Furthermore, we removed dental nonmetric variables that were monomorphic (Double Shoveling UI1, Mesial Ridge UC, and Root Number LM1) or too data sparse (Anterior Fovea LM1, Deflecting Wrinkle LM1). These reduction procedures left us with a dataset of 91 individuals and 39 variables (21 metric and 18 nonmetric traits), with less than 13% of values missing.

Gower coefficients allow for missing values, thus, in principle, no data imputation is required. Nonetheless, we imputed missing dental measurements because complete metric data rows per individual are necessary for subsequent data processing steps (see below). Missing metric data were imputed following Kenyhercz and Passalacqua (2016) using the *k*-nearest neighbor (kNN) algorithm using the *knn* function from the VIM package in R (Kowarik & Templ, 2016). The kNN algorithm searches the entire dataset for cases most similar to the one with missing data and generates a mean to replace the missing value(s). Missing nonmetric trait data were not imputed because they are generally independent (see Data Preprocessing section), making the estimation of missing values difficult or impossible (Stojanowski & Hubbard, 2017).

Dental measurements were then converted into shape variables by dividing each measurement by the geometric mean for all the measurements in each individual (Jungers, Falsetti, & Wall, 1995). This standardization procedure removes gross size from the data in order to assess differences in the proportionate contribution of individual variables to overall tooth size (Harris & Lease, 2005; Hemphill, 2013, 2016; Irish, Hemphill, de Ruiter, & Berger, 2016; Irish & Kenyhercz, 2013; Paul et al., 2013; Romero, Ramirez-Rozzi, & Pérez-Pérez, 2018; Scherer, 2007). Furthermore, this procedure adjusts for size differences between individuals that may result from sexual dimorphism.

Because the Gower coefficient requires trait independence, we transformed the highly correlated 21 dental metric variables into a smaller subset of uncorrelated factor scores by performing principal component analysis (Pilloud & Kenyhercz, 2016) using the *principal* function from the psych package in R. Seven unrotated principal components with eigenvalues ≥1 were retained (Kaiser, 1960). Together these components account for 77% of the total variance in the dental measurements. Each component's loadings, eigenvalues, and variance explained are listed in Appendix S1, Table S7. Individual factor scores are provided in Appendix S2, Sheet 2, as well.

Finally, the seven factor scores for individuals were combined with the 18 dental nonmetric trait variables, and we generated a matrix of pairwise Gower distance values among individuals using the *daisy* function from the cluster package in R (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2017). The *daisy* function estimates Gower distances by converting the Gower similarity coefficient (S_{ij}) into a distance measure by subtracting its value from one ($1 - S_{ij}$). The Gower distance matrix is presented in Appendix S2, Sheet 3.

Geographic distances among individuals were measured as straight-line distances in meters between the global positioning system (GPS) coordinates for the location of each individual burial. For simplicity, burials from the same necropolis were assigned the same GPS coordinate, taken at the center of the necropolis. Further information about the number of necropoleis belonging to the archaeological sites under investigation are provided in Table 1 and Appendix S1. Geographic distances were generated with the *distm* function from the geosphere package in R (Hijmans, 2017) and can be found in Appendix S2, Sheet 4.

Temporal distances among individuals were measured as Euclidean distances between the mean age estimates of the date ranges of each individual burial. Many of the burials in our dataset are well-dated with date ranges within a 10–60 year span. In these instances, the mean age estimate may be an adequate approximation of the actual burial's age. However, we note that an equivalent number of burials in our dataset are poorly dated with date ranges within a 200–300 year span. For these burials the mean age estimate may be only a rough approximation of the burial's actual age. The temporal distance matrix is provided in Appendix S2, Sheet 5.

2.5 | Analyzing differences in group means and variances within and between pre- and post-colonial southern Italy

We analyzed differences in group means and variances using a permutational multivariate analysis of variance (PERMANOVA). PERMANOVA

compares groups of individuals to test the null hypothesis that the centroids (means) and dispersions (variances) of the groups are equivalent across groups (Anderson, 2001). PERMANOVA shares some resemblance to univariate analysis of variance (ANOVA) in that both partition the sum-of-squares between and within groups and make use of F tests to compare between-group to within-group variance. However, while ANOVA tests the significance of the generated result based on the assumption of normality, PERMANOVA tests the significance directly from the data via a permutation procedure. Moreover, while ANOVA is restricted to univariate datasets with variables measured on a continuous scale, PERMANOVA is based on any inter-individual distance matrix calculated prior to analysis. This allows researchers to choose among a wide range of useful distance measures, including those that have been designed for complex datasets that violate the assumption of normality, that consist of mixed data types, or that contain more variables than individuals. Because of its flexibility, PERMANOVA is widely used in ecology and genetics, but, surprisingly, it is rarely applied in biological anthropology, with a few recent exceptions, for example, Allen and Cramon-Taubadel (2017). For each time period, we explored diversity through space by comparing group centroids and group dispersions across archaeological sites. Furthermore, we analyzed diversity through time by comparing the group centroid and group dispersion of individuals living in pre-colonial southern Italy (900–700 BC) to the group centroid and group dispersion of individuals living in post-colonial southern Italy (700–200 BC). Sample sizes for these tests are detailed in Table 1.

The PERMANOVA analysis was performed using the *adonis* function implemented in the *vegan* package in R, based on inter-individual Gower distances of dental metric and nonmetric data (see Method section above). To confirm that significant results in our PERMANOVA analysis reflect differences in group centroids rather than group dispersions, we checked for homogeneity of group dispersions using a multivariate analogue of Levene's test (Anderson, 2006) implemented in the *betadisper* function from the *vegan* package in R. For all tests, statistical significance was determined after 1,000 permutations. To further ease the interpretation of inter-individual relationships, we visualized the Gower distance matrix using principal coordinates analysis (PCoA). Group dispersions were visualized using boxplots. All graphics were created in R using functions described above and the ggplot2 package (Wickham, 2009).

2.6 | Identifying individual ancestries in post-colonial southern Italy

We identified individual ancestry using naïve Bayes classification based on dental nonmetric traits. Naïve Bayes is a simple yet powerful classification technique based on Bayes' theorem (Cichosz, 2015). Conceptually, this technique classifies an individual of unknown ancestry (i.e., the test individual) based on a single trait into pre-defined ancestry groups (in our case, Italians and Greeks) by calculating its posterior probability of belonging to Italians, $P(I)$, or to Greeks, $P(G)$, and assigning it to the group with the higher posterior probability. The approach can be extended to multiple traits by sequentially applying Bayes' theorem. The method is flexible as it allows for

missing variables. If a trait is missing in a test individual, the calculation of the posterior probability for this particular trait is skipped in the chain of sequentially applied Bayes' theorems. Naïve Bayes classification makes two assumptions. First, it assumes that a test individual certainly derives from one of the reference groups ($P[I] + P[G] = 1$). This assumption seems reasonable in our case, however, we will consider this issue further in the discussion below. Second, when applied to multiple traits, it assumes that the traits are independent. This assumption generally holds true when using dental nonmetric trait data as discussed in the previous section (see Appendix S1, Figure S1 and Appendix S2, Sheet 1). Because naïve Bayes classification is conceptually simple, allows for missing variables, and has few assumptions, it is widely used in classification studies based on dental nonmetric trait data (Bailey, Weaver, & Hublin, 2009; Edgar, 2005; Herrmann, Plemons, & Harris, 2016; Scott et al., 2018).

We trained our naïve Bayes model with two ancestry reference groups, Italians and Greeks. The Italian reference sample ($n = 241$) consists of pooled data from two sites in southern Italy (Incoronata and Santa Maria d'Anglona) dating to the pre-colonial period (900–700 BC). The Greek reference sample ($n = 116$) consists of pooled data from three sites in central and southern Greece (Corinth in Corinthia, Akraiphia in Boeotia, and Karystos in Euboea) dating from the prehistoric to the Classical period (1100–350 BC). The dental nonmetric trait data from Greece were previously gathered by two of us (B.K. and E.N.) (McIlvaine et al., 2014; Nikita, Schrock, Sabetai, & Vlachogianni, 2019). All dental data from Greece were collected from the same key teeth as those utilized in this study (Scott et al., 2016) and were dichotomized using the same criteria detailed above. Prior to analysis we removed traits that showed strong inter-correlations in our southern Italian sample (see Data Preprocessing section above) and we dropped traits that were monomorphic across ancestry reference groups (Double Shoveling UI1). Ultimately, this reduction procedure left us with a training dataset comprising 237 Italians and 100 Greeks, characterized by a battery of 21 dental nonmetric trait variables.

None of the three observers whose data contributed to the naive Bayes classification observed the same dentitions; thus, an inter-observer error test could not be performed. However, each observer followed the same ASUDAS definitions to score dental nonmetric traits, which ensures a standardized scoring procedure with minimal observer error. Moreover, all three observers are experienced in collecting data of this kind. In a previous study on inter- and intra-observer reliability, Nichol and Turner (1986) reported that most dental traits can be observed with adequate levels of replicability. In their study, misclassification of ranked traits by more than one grade was low (6–10%) for between-observer comparisons. Our trait dichotomization approach reduces inter-observer error even further by collapsing ranked trait scores into simplified categories of "present" or "absent" in such a way that slight scoring discrepancies are eliminated. Thus, we consider inter-observer error, although potentially present, to be negligible.

Classification algorithms are sensitive to unbalanced sample sizes, biasing the prediction model towards the more common reference

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group. Therefore, prior to analysis we created equal sample sizes for our two reference groups by randomly removing individuals from the Italian sample until both Greek and Italian reference groups had identical sample sizes of 100 individuals.

We constructed our naïve Bayes classification model using the *naiveBayes* function from the e1071 package in R (Meyer, Dimitriadou, Hornik, Weingessel, & Leisch, 2017). The estimated conditional probabilities for the 21 dental nonmetric traits are presented in Appendix S1, Table S8. We then applied the classification model to our test data consisting of 45 individuals from post-colonial southern Italy (Table 1) with no more than one-third of variables missing (i.e., at least 14 of 21 dental nonmetric traits preserved).

Validation of the classification model was performed using the leave-one-out cross-validation method (LOOCV), where a single individual in the training data is removed and used to validate the model constructed on all other individuals in the training data. This procedure is repeated such that each individual in the training data is used once for validation. The LOOCV procedure was performed for all individuals that had at least 14 of 21 dental nonmetric traits preserved.

3 | RESULTS

3.1 | Levels of mobility in pre- and post-colonial southern Italy

Table 2 displays the Mantel test results of IBD for pre- and post-colonial southern Italy. A positive and statistically significant Mantel correlation indicates a presence of IBD caused by limited regional mobility, whereas a negligible or negative and statistically insignificant Mantel correlation signals an absence of IBD caused by higher levels of regional mobility. For the pre-colonial period, the Mantel test revealed presence of IBD as indicated by a positive and statistically significant correlation between inter-individual biological distances and geographic distances. A similar result was obtained when we performed a partial Mantel test to control for temporal variation due to differential burial dates. In contrast, for the post-colonial period, the Mantel test revealed absence of IBD as indicated by a negligible and negative and statistically insignificant correlation between inter-individual biological distances and geographic distances. Results were

TABLE 2 Mantel tests of isolation-by-distance (IBD) for pre- and post-colonial time periods[a]

Time period	IBD	*r*	*p*
Pre-colonial	B ~ G	0.126	0.001[b]
	B ~ G, T	0.127	0.001[b]
Post-colonial	B ~ G	−0.020	0.615
	B ~ G, T	−0.008	0.569

[a]Simple Mantel tests correlating inter-individual biological distances (B) against geographical distances (G). Partial Mantel tests correlating B and G, while controlling for the effect of temporal distances (T). Shown are Pearson correlation coefficients (*r*) and probability values (*p*).
[b]Statistically significant difference at the 0.05 level.

similar when we performed a partial Mantel test to control for temporal variation in burial dates.

3.2 | Differences in group means and variances within and between pre- and post-colonial southern Italy

Table 3 displays the PERMANOVA and Betadisper results of differences in group means and group variances through space (between archaeological sites within a period) and time (between pre- and post-colonial periods). Figure 2 illustrates the PERMANOVA and Betadisper results in PCoA plots and boxplots, respectively. We performed three comparisons. First, we compared individuals in different archaeological sites during the pre-colonial period (i.e., Incoronata and Santa Maria d'Anglona). PERMANOVA analysis revealed a statistically significant difference in group centroids and/or group dispersions. Betadisper analysis indicated that the significant PERMANOVA result was due to nonhomogeneous group dispersion and estimated the average dispersion for Santa Maria d'Anglona as 0.205, whereas the average dispersion for Incoronata was estimated as 0.168. Thus, inhabitants of Santa Maria d'Anglona were about one and a half times more variable as those living in Incoronata. Nevertheless, the PCoA plot also indicates some degree of biological separation between the centroids of the two sites. Second, we compared individuals in different archaeological sites during the post-colonial period (i.e., Passo di Giacobbe, Metaponto, and Siris). PERMANOVA found no significant difference in group centroids and group dispersions. Note that for this analysis we removed the single individual from Taras because PERMANOVA and Betadisper analyses require that groups consist of at least two entities. Third and last, we compared individuals in pre-colonial southern Italy to individuals in post-colonial southern Italy. PERMANOVA analysis estimated that there was no significant difference in group centroids and group dispersions.

3.3 | Individual ancestries in post-colonial southern Italy

Validation of the naïve Bayes ancestry classification model revealed that Italians and Greeks of known ancestry in the training data were correctly classified in 80% of cases, which corresponds to a misclassification rate of 20% (Appendix S1, Table S9). Thus, our classification model produced relatively accurate results. The model misclassified Greeks more often (23%) than Italians (17%). Misclassified individuals had lower posterior probabilities for group membership (on average: 0.67) than correctly classified individuals (on average: 0.73). The classification results for test individuals in post-colonial southern Italy are provided in Appendix S1, Table S10. Overall, classification identified the majority of the test individuals as Italian (82%) and only a few as Greek (18%). Classified individuals had relatively high posterior probabilities for group membership (on average: 0.83). Table 4 displays the classification results for test individuals in post-colonial southern Italy from different archaeological sites (indigenous villages and Greek colonies). Individuals classified

TABLE 3 Analysis of variance tables for permutational multivariate analysis of variance (PERMANOVA) and Betadiper models testing differences in centroid (mean) and dispersion (variance) of inter-individual Gower distances across sites and time periods[a]

Test	PERMANOVA						Betadisper			
	df	SS	MSS	F	R²	p	SS	MSS	F	p
Differences across sites in pre-colonial period	1	0.152	0.152	3.868	0.090	0.001[b]	0.014	0.014	6.097	0.018[b]
Residual	39	1.531	0.039		0.910		0.088	0.002		
Differences across sites in post-colonial period[c]	2	0.046	0.023	0.541	0.023	0.882	0.002	0.001	0.338	0.715
Residual	46	1.975	0.043		0.977		0.131	0.003		
Differences across pre- and post-colonial periods	1	0.072	0.072	1.704	0.019	0.129	0.001	0.001	0.001	0.985
Residual	89	3.747	0.042		0.981		0.220	0.002		

[a]Shown are factor and residual degrees of freedom (*Df*), sum of squares (*SS*), mean sum of squares (*MSS*), *F*-statistic values (*F*), proportion of explained variance (R^2) and probability values (*p*).
[b]Statistically significant difference at the 0.05 level.
[c]To assess differences across sites during the post-colonial time period, we removed the single individual from Taras because PERMANOVA and Betadisper analyses require that groups consist of at least two entities.
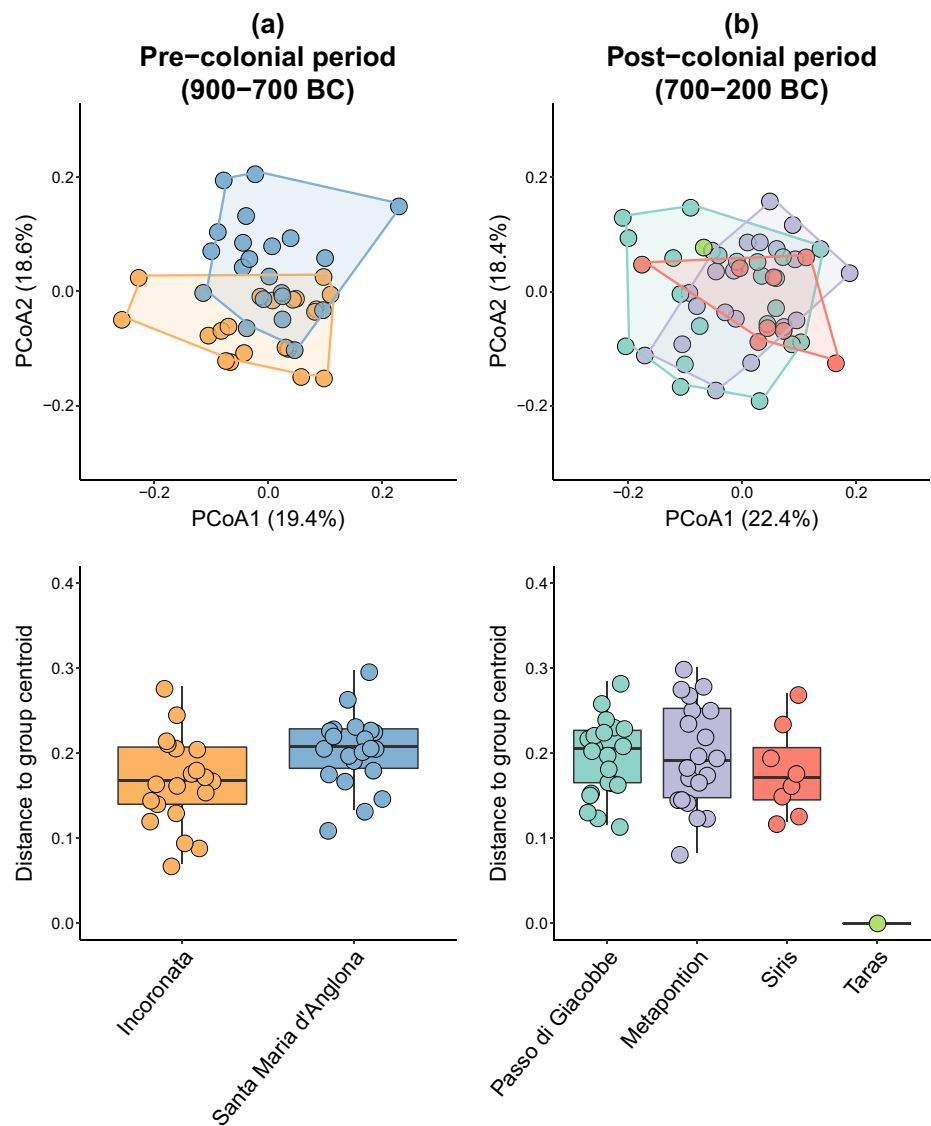

FIGURE 2 Population structure of southern Italy during (a) pre-colonial and (b) post-colonial times. Figures show principal coordinates analysis plots of inter-individual Gower distances (top) and boxplots represent distances to group centroids (bottom). Color-coding indicates archaeological sites

TABLE 4 Naïve Bayes ancestry classification results for test individuals in post-colonial southern Italy

Archaeological site	Italians	Greeks
Passo di Giacobbe	80.0% (n = 12)	20.0% (n = 3)
Metapontion	80.0% (n = 16)	20.0% (n = 4)
Siris	88.9% (n = 8)	11.1% (n = 1)
Taras	100.0% (n = 1)	0.0% (n = 0)
Total study region	82.2% (n = 37)	17.8% (n = 8)

as Greek were scattered across the study region without any significant differences across sites (Fisher's exact test, p = 1.000).

4 | DISCUSSION

In this study, we aimed at evaluating competing scenarios regarding the ancient Greek colonization of southern Italy. For this purpose we applied a set of individual-level biodistance analyses to a comprehensive dataset of archaeological human dental remains from several Greek colonies and indigenous settlements along the Gulf of Taranto. We found that the mobility of indigenous Italic people in pre-colonial times was limited (evidenced by a presence of IBD) and that inhabitants of different settlements differed in terms of group means and group variances (measured by PERMANOVA and Betadisper analyses). During the Greek colonization, mobility in southern Italy increased (evidenced by an absence of IBD) and there were no differences in group means and variances across inhabitants of different settlements, regardless of whether the settlement was a Greek colony or an indigenous village (as measured by PERMANOVA and Betadisper analyses). About 18% of the people in post-colonial southern Italy were of Greek ancestry (revealed by naïve Bayes classification). These people lived equally distributed across Greek colonies and indigenous settlements. Nevertheless, we found that the overall biological composition and variability of southern Italy remained relatively unchanged across pre- and post-colonial periods (as measured by PERMANOVA and Betadisper analyses).

Taken together, our results support a colonization scenario in which few Greek colonists settled in southern Italy and lived in small numbers alongside indigenous people in Greek colonies as well as in indigenous settlements. This scenario is favored by scholars inspired by post-colonial theory who have challenged the traditional colonial narratives surviving in ancient Greek texts and consider the colonization process as an interplay of actions of both colonizers and colonized (Malkin, 2002; van Dommelen, 2012; Yntema, 2000). It is also supported by several archaeological discoveries associated with the early phases of Greek colonization, indicating close interaction between the first generations of Greek newcomers and local Italic populations (Carter, 2006; Crielaard & Burgers, 2012; Denti, 2018). For example, settlement and burial data from Siris suggest that the early colony was an open, dispersed village with burial plots including a mix of Greek- and indigenous-style funerary practices (Berlingò, 1993). A similar conclusion was drawn from the archaeological

evidence from the early colony of Taras (Yntema, 2000). At early Metapontion, the ceramic assemblage from an indigenous-style included mostly Greek-style pottery and a smaller proportion of indigenous wares (De Siena, 1986). Archaeological signs of Greek-indigenous coexistence have also been found in many indigenous sites in the hinterland of the coast. At the indigenous site of Passo di Giacobbe, for example, several burials contained Greek-style pottery (Schojer, 2010).

Our results contradict a colonization scenario in which large numbers of Greek invaders founded biologically isolated and substantially homogeneous colonial settlements in hostile native lands. This more traditional interpretation of Greek colonization is largely based on ancient written sources from Greek writers (Boardman, 1964; Dunbabin, 1948; Greco, 2002; Pugliese Carratelli, 1996). Drawing from these historical sources, it is thought that the colonies (or *apoikiai*) were centrally organized expeditions sent out by a "mother city" under the auspices of the Delphian oracle. They were led by an official founder (the *oikistes*), who chose the location and proceeded to divide the land in regular allotments distributed to the colonists. The *oikistes* was also responsible for establishing local cults (largely derived from the mother cities) and public spaces. In this framework, the role of local populations, if at all considered, is essentially passive (Burgers, 2004; Shepherd, 2005).

We estimated an overall Greek contribution of 18% to the population of southern Italy along the Gulf of Taranto during the post-colonial period (700–200 BC). Our estimated Greek contribution is close to the size spectrum proposed by historical demographers, who suggested 10% Greeks in pre-Roman southern Italy (Beloch, 1886). Our finding is also in line with preliminary strontium isotopic evidence, indicating that 10% (n = 20) of the post-colonial individuals in the study region are of nonlocal origin (Vos, 2018). Interestingly, our results also broadly agree with biodistance and isotopic studies conducted at other Greek colonies across the Mediterranean Basin (Keenleyside, Schwarcz, & Panayotova, 2011; McIlvaine et al., 2014; Stallo, Schepartz, Grimes, & Richards, 2010), which suggest that colonized territories were generally characterized by few Greek newcomers living alongside a much larger indigenous population. Our estimated Greek contribution of 18% differs from genomic estimates of the ancient Greek contribution to southern Italy derived from present-day DNA profiles. Di Gaetano et al. (2009) used the haplogroup lineage E-V13 to estimate a Greek contribution of 37% to the population of Sicily and attributed the migration influx to the Classical period (2,380 years before present, with a 95% confidence interval ranging between 6,940 and 675 years ago). A potential explanation for the discrepancy between our estimate and their genomic reconstruction could be that proportions of specific genetic lineages surviving in present-days populations may not be good proxies for assessing the effects of past migration events (Tofanelli et al., 2016). Moreover, their genomic estimate of the timing of the migration influx has a wide confidence interval spanning several millennia. The estimate provided in this study is directly derived from archaeological human remains and may therefore be a more accurate reconstruction of the initial Greek genetic contribution to southern Italy (but see further discussion below).

Very little is known about the population structure of indigenous Italic communities prior to Greek colonization (Rathmann, Saltini Semerari, & Harvati, 2017). Our study provides additional insights into this hitherto underexplored topic by finding that the inhabitants of the two pre-colonial indigenous sites under investigation, Santa Maria d'Anglona and Incoronata, shared a similar yet not identical biological makeup. Moreover, Santa Maria d'Anglona showed significantly higher internal variability, which may be explained by a more diverse or less isolated gene pool. This interpretation would support previous theories, based on the relative wealth of its necropoleis, that the settlement of Santa Maria d'Anglona held greater regional importance compared to Incoronata, and was thus able to attract a greater number of inhabitants from abroad. The role of Santa Maria d'Anglona as a central place of regional importance may also support its identification as *Pandosia*, the seat of a king (or *basileus*) (Greco, 1992, p. 34–40). On the other hand, the lower internal variability found in Incoronata may be explained by the site's genetic isolation. This interpretation would support previous theories of a relatively homogeneous population inhabiting the site, as inferred from the higher degree of uniformity in grave goods found in the necropoleis (De Siena, 1990).

Lastly, it has to be noted that our results deviate from the findings of our previous dental biodistance study in the Gulf of Taranto region (Rathmann, Saltini Semerari, & Harvati, 2017), where we found a significant separation between the inhabitants of indigenous Italic sites and the Greek colony of Metapontion, which evidenced a higher amount of variability. The study presented in this manuscript expands and improves upon our previous investigation. First, we expanded sample sizes by including additional individuals from the Greek colonies of Taras and Siris. Second, we employed a larger battery of dental phenotypic variables, which generally improves the accuracy of biological distance estimates (Scott, Turner, et al., 2018, p. 242). Third, we analyzed metric and nonmetric trait data because combining both data types in a single analysis increases performance compared to using these features separately (Hefner et al., 2014; Lease & Sciulli, 2005). Fourth, we performed individual-level biodistance analyses because they are better suited to capturing the significant amount of human variation within groups than group-level analyses based on simplified centroid estimates (Stojanowski & Schillaci, 2006). Fifth, we integrated comparative data from Greece in order to identify individual ancestries and to quantify the Greek contribution to southern Italy.

4.1 | Limitations to the study and areas for future research

Although our study constitutes the largest biodistance investigation of the Greek colonization of southern Italy to date, it is nevertheless limited to a few dozens of individuals coming from only a handful of archaeological sites along the Gulf of Taranto. Future research should therefore increase sample sizes and expand the study area to Calabria and Sicily in order to generate a more comprehensive picture of the colonial history of the entire *Magna Graecia*. We also note that our diachronic analysis is based on two simplified time slices, pre-colonial

(900–700 BC) and post-colonial (700–200 BC). Finer temporal resolution was not possible, as there are only rough relative dates available for the study samples. Future research should therefore attempt to generate absolute dates for the individuals used in our analysis, allowing for a more refined assessment of changes of population structure through time. This study provides a conceptual template for coming research in this area, and the provided raw data allow for repeatability.

We also believe that there is a need to improve the reference samples used for the naïve Bayes ancestry classification. In our study, we used two reference samples as potential ancestry sources: Italians and Greeks. However, the high degree of mobility across the Mediterranean Basin involving a multiplicity of actors in addition to Greek seafarers (e.g., Phoenicians and Etruscans) leaves open the possibility that multiple agents might have been involved in the colonial process, not all of them necessarily coming from ancient Greece. Given our simplified two-sample study design, such individuals would be forced to be classified as either Italian or Greek, regardless of their "true" ancestry. Moreover, our Greek sample was rather small (*n* = 100) which forced us to down-sample our Italian sample to ensure a balanced reference data design. This is problematic because Italians and Greeks share a very similar "Mediterranean" genetic makeup (Sarno et al., 2017) and, for biologically similar populations, large samples are needed to effectively identify differences between populations. Perhaps these two issues were the reason why cross-validation of the naïve Bayes model revealed a misclassification of Italians and Greeks 20% of the time. Because the misclassification rate is higher than our estimated Greek contribution of 18%, our results should be treated with caution. Using a large number of robust reference samples from Italy, Greece, and different regions across the Mediterranean would address this issue and, furthermore, open the possibility to explicitly test for the bio-geographical origin of the colonists.

We note that classifying individuals into binary ancestry categories of "Italian" or "Greek" does not recognize admixed individuals. Several test individuals in our naïve Bayes ancestry classification have posterior probabilities for group membership close to 0.5 and, thus, are quasi intermediate. Such intermediate ancestry assessments may indicate individuals with mixed Italian-Greek ancestry (Konigsberg, Algee-Hewitt, & Steadman, 2009). However, interpreting classification probabilities as ancestry proportions is difficult because the reference groups may already contain considerable degrees of admixed individuals. Moreover, intermediate ancestry assessments may also be the result of missing diagnostic dental morphological traits in these individuals, or relate to small and insufficient reference samples (see above). Further analyses of the individuals with intermediate ancestry assessments are underway, including isotopic analyses and comparisons of grave goods, to see if a multidisciplinary investigation can provide additional evidence to clarify our classifications.

Finally, it could be that dental phenotypic data may not adequately capture neutral genetic variation for geographically fine-scaled analyses. In fact, dental phenotypic data are considered to be most effective at higher geographic scales of study, particularly continental or global (Scott & Turner, 1997). Recent research has confirmed this and identified congruence in dental phenotypic and neutral genetic datasets from

globally distributed populations, with correlations as high as $r = 0.635$ (Rathmann, Reyes-Centeno, et al., 2017). Slightly lower correlations have been found for populations at a regional level, with an agreement of $r = 0.500$ (Hubbard et al., 2015). At the within-population level, mixed results have been found, ranging from moderate to strong concordance (Paul & Stojanowski, 2015, 2017; Stojanowski & Hubbard, 2017). However, it has to be noted that all previous studies used either metric or nonmetric data, although it has been shown that combining metric with nonmetric markers in a single analysis increases performance compared to using the features separately (Hefner et al., 2014; Lease & Sciulli, 2005). In our study, we used a comprehensive set of mixed metric and nonmetric data with a trait battery outnumbering the variables employed in the previous studies mentioned above. We therefore think our approach is adequate for detecting subtle genetic structures on a local scale. Nevertheless, future work should systematically test the association of large mixed metric and nonmetric dental datasets and neutral genomic variation on a local scale to identify dental data combinations that are most useful for reconstructing local population structure and history.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in GitHub at https://github.com/HannesRathmann/GCSI

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