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Original Article

Isolation-by-distance, homophily, and “core” vs. “package” cultural evolution models in Neolithic Europe

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ABSTRACT

Recently there has been growing interest in characterising population structure in cultural data in the context of ongoing debates about the potential of cultural group selection as an evolutionary process. Here we use archaeological data for this purpose, which brings in a temporal as well as spatial dimension. We analyse two distinct material cultures (pottery and personal ornaments) from Neolithic Europe, in order to: a) determine whether archaeologically defined “cultures” exhibit marked discontinuities in space and time, supporting the existence of a population structure, or merely isolation-by-distance; and b) investigate the extent to which cultures can be conceived as structuring “cores” or as multiple and historically independent “packages”. Our results support the existence of a robust population structure comparable to previous studies on human culture, and show how the two material cultures exhibit profound differences in their spatial and temporal structuring, signalling different evolutionary trajectories.

1. Introduction

The extent by which human culture varies over space and time is the result of a complex interplay among patterns of inheritance, interaction, and local adaptation (Beheim & Bell, 2011; Borgerhoff-Mulder, Nunn, & Towner, 2006; Crema, Kerig, & Shennan, 2014; Guglielmino, Viagnotti, Hewlett, & Cavalli-Sforza, 1995; Mace & Jordan, 2011). Distinguishing how these three types of processes generate observed patterns of cultural variation is one of the primary research questions in archaeology and anthropology.

Theoretical and empirical studies of dual-inheritance theory (Boyd & Richerson, 1985) have shown that the distribution of cultural traits over space or time are not exclusively determined by their intrinsic adaptive properties, but also by the mechanics of how the traits are transmitted from individual to individual and by the stochastic events associated with these. Despite a wide array of transmission types proposed in the literature (see Henrich & McElreath, 2003; Laland, 2004 for reviews), a general rule of thumb is to start by assuming that the frequency of cultural transmission is mostly characterised by a distance decay, where the greater the inter-distance between the donor and the recipient, the less likely is the occurrence of a transmission event. This implies that, other things being equal, the similarity of cultural traits should also decline over distance and that some degree of spatial autocorrelation is expected (Bentley, Caiado, & Ormerod, 2014; Crema et al., 2014; Premo & Scholnick, 2011). The foundation of this idea is not different from what geneticists refer to as “isolation by distance” (Wright, 1943), where limited biological dispersal determines an inverse relationship between genetic similarity and geographic proximity.

Distance friction is, however, not the only force that might generate an auto-correlation of cultural traits. Homophily, for example, can drive patterns of social and cultural interaction (Haun & Over, 2013) so that individuals sharing similar traits are more likely to engage in social learning. This can easily promote a positive feedback process that can potentially magnify initially small differences derived from stochastic noise (e.g. derived from drift-like processes) or minor differences in the likelihood of spatial interaction derived by geography (e.g., settlement pattern, topography, etc., see Manel, Schwartz, Luikart, & Taberlet, 2003). Ultimately, homophily can also determine a distance decay in cultural similarity, but this would also lead to the emergence of marked discontinuities (i.e. cultural boundaries), and the formation of distinct clusters (Axelrod, 1997; Centola, Gonzales-Avella, Eguilz, & San Miguel, 2007). Homophily is strongly linked to *population structure*, a term introduced in population genetics and referring to instances where individual subpopulations/groups exhibit low within and high between variability.

Thus, the empirical observation of clusters of cultural homogeneity raises a key question: can these groups be regarded as coherent units amenable to evolutionary analyses (e.g., implying a phylogenetic link between cultural groups), or are they, rather, an arbitrarily imposed discretisation of a continuum determined exclusively by isolation by distance? The identification of ethnolinguistic groups in the ethnographic record seems to support the former, as showcased by numerous studies on linguistic phylogenies where these have been successfully used as analytical units (Borgerhoff-Mulder, 2001; Mace & Holden,

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2005). After all, speaking the same language eases cultural interaction, and favours a homophilic positive feedback process that can eventually lead to a population structure. However, the fierce debates about the relationship between distributions of material culture attributes in prehistory and the definition of past ethnolinguistic units show how difficult it is to make inferences about such entities in the past (Shennan, 1989; Vanhaeren & d'Errico, 2006; Wotzka, 1997).

In short, identifying the existence of discrete cultural groups is not trivial. This is because, isolation by distance, homophily, and local environmental adaptation all generate confounding patterns. How can we tell whether the cultural dissimilarity measured between two locations is simply the product of a continuous gradient of change (i.e. isolation by distance), or instead the result of an underlying population structure? With very large samples, we can perhaps identify marked discontinuities that would support the latter hypothesis (e.g., Barbujani & Sokal, 1990; Safner, Miller, McRae, Fortin, & Manel, 2011), but in the majority of cases this is not possible.

A number of recent studies have investigated the presence of population structure in cultural data, borrowing an array of statistical techniques originally designed to identify population differentiation in genetic data. Bell, Richerson, and McElreath (2009) examined human prosociality and the extent to which group selection can be supported, by evaluating evidence in support of genetic and cultural differentiation between neighbouring countries. Their results indicated significant population differentiation in both cases, but with a greater magnitude for cultural traits. More recently, evidence of population structure in cultural traits has been identified for musical variability amongst Austronesian aboriginal populations (Rzeszutek, Savage, & Brown, 2012) and folk-tale variants amongst European ethno-linguistic groups (Ross, Greenhill, & Atkinson, 2013).

Whilst these studies support the existence of a population structure, the extent to which different individual components adhere to the same overarching structure remains unquestioned. This raises the issue of whether cultural groups are coherent collections of entities that share similar evolutionary histories and spatio-temporal patterns, or in contrast are contingent assemblages of independent units that have little connection with one another. Boyd, Borgerhoff-Mulder, Durham, and Richerson (1997) suggest four hypotheses where cultural groups are defined as: 1) tightly integrated and isolated entities composed of coherent units that rarely lead to exchange between distinct groups; 2) hierarchical integrated systems with a "periphery" of units that are subject to cross-cultural borrowing and a robust "core" that remains isolated and consistent; 3) assemblages of multiple "packages" characterised by different evolutionary histories; and 4) collections of ephemeral independent entities. Whilst (1) and (4) are unlikely extremes that have little if any empirical support, the "core" (2) and the "package" (3) models are both potentially relevant here and raise the question of whether transmitted variation in the domains concerned provides support for the existence of a single shared population structure, or if they exhibit contrasting structures and independent histories.

Investigating the existence of cultural groups and, more generally, reconstructing and understanding the spatial and temporal structure of cultural variation—culture history—has been a goal of archaeology for a hundred years and continues to play a fundamental role in the field (Riede, 2011; Roberts & Vander Linden, 2011). In Europe at least it was based on the idea that correlated spatial and temporal patterns of material culture observed in the archaeological record could be taken as evidence of "peoples" and their movements, thus Childe's (1929, v-vi) famous definition, 'We find certain types of remains - pots, implements, ornaments, burial rites and house forms - constantly recurring together. Such a complex of associated traits we shall call a "cultural group" or just a "culture". We assume that such a complex is the material expression of what today we would call "a people"'. From the 1960s there was a widespread rejection of this idea, as it was argued that change in material culture could arise as a result of a variety of adaptive processes in society and economy rather than simply from the movements of peoples or contacts between them.

The introduction of the theory of cultural evolution and its associated population genetics-based quantitative methods into archaeology during the 80s has provided the basis for a new approach to inferring the processes that produced temporal and spatial variation in the past, since it offers a framework for integrating both the cultural–historical concern with cultural descent with modification and questions relating to adaptation (Lyman, O'Brien, & Dunnell, 1997). It has done this by focussing on the transmission of information in different domains and the factors acting on the variation that is transmitted (see e.g. O'Brein et al., 2008).

The objective of our paper is to contribute to this broad transdisciplinary research agenda by examining two categories of material culture, pottery and personal ornaments, from the European Neolithic period, based on information on the spatial location and date of the finds from which they come. In this prehistoric context we do not have information about linguistic affiliation, but we do have information on the cultural–historical affiliation of the finds. This refers to their categorisation by European archaeologists over the last 150 years into different named groups with a defined spatial and temporal extent, on the basis of Childe's definition of an 'archaeological culture' as given above, with particular weight generally being given to variation in pottery, as one of the most common materials and one of the most highly variable. As such, while they have rarely if ever been characterised explicitly in cultural evolutionary terms, they continue to provide the framework for the description of European prehistory because they are implicitly assumed to be units that represent areas and periods of continuity in cultural tradition. We can therefore address the question of the extent to which the cultural affiliation category of the finds structures the variation over and above that accounted for by time and space alone; in other words, whether cultural groups represent more than an illusion derived from a combination of isolation by distance and spatial–temporal biases in sampling. This corresponds to addressing whether archaeological cultures are appropriate and useful analytical units that can serve as basis for broader anthropological questions. At the same time, by analysing two categories of material culture, we can assess whether they correspond to a "cores" or "packages" model in Boyd et al.'s (1997) terms.

As noted above, pottery in particular is one of the key features used to define the affiliation of sites and assemblages to particular cultural groups. We can thus infer that if the membership of these groups still explains variation in pottery attributes even after the effects of spatial and temporal distance are taken into account, then we have identified a signal of population structure and homophily. Moreover, if ornaments and pottery are faithful proxies of the same underlying structuring in the network of cultural transmission (i.e. part of the same "core"), we should expect similar patterns in their support for the population structure defined by archaeological cultures, as well as similar correlation with geography and time (with differences confined to idiosyncrasies in the sample). Conversely, if the two show differential support for the same population structure and exhibit different degrees of correlation with space and time, we can deduce the presence of multiple and alternative networks of cultural transmission, supporting the "package" model. Existing studies on cultural cophylogenies (Jordan & Mace, 2006; Riede, 2009; Tehrani, Collard, & Shennan, 2010) suggest how both patterns can be expected, although we are unaware of any attempts to approach the problem at the level of population structure analysis.

2. Materials and methods

2.1. Data

We analysed the material culture of 361 Neolithic sites in central Europe (Fig. 1), by assessing decorative and morphological traits of pottery ($n = 195$ sites; electronic supplementary table 1) and ornaments ($n = 166$ sites; electronic supplementary table 2). Each site is described by: 1) a binary vector indicating the presence ($=1$) or absence ($=0$) of individual cultural traits (183 in the case of pottery traits and 195 in the

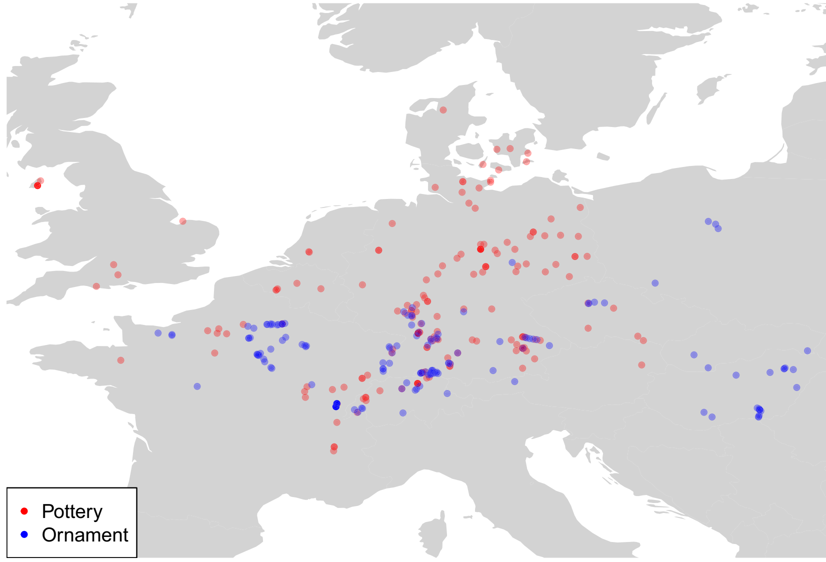

Fig. 1. Location of ornament and pottery data sites.

case of ornaments, electronic supplementary tables 4 and 5); in the case of pottery the traits are general features of shape and decoration, in the case of the ornaments they refer to different types, (e.g. copper beads or beads made of the teeth of different animals; in both cases the attributes are defined independently of the cultural affiliation (electronic supplementary material 1, and supplementary tables 6 and 7); 2) the associated Neolithic "culture"; 3) spatial coordinates (latitude and longitude); and 4) a time-span of existence based on Buchvaldek, Lippert, and Košnar (2007). Our sample covered twenty-two Neolithic cultures (electronic supplementary table 3) spanning a temporal range of ca. 4,000 years (ca 7500 ~ 3500 ya). In order to examine the consistency of our results and reduce any bias in the comparison between the ornament and the pottery data we conducted the analysis using both the complete sample (16 cultures for the pottery data and 12 cultures for the ornament data) and a subset based on six cultures common to both data sets.

2.2. Analyses[1]

2.2.1. Measuring cultural dissimilarity

We first quantified how individual sites differed in decorative and morphological traits by using Jaccard distance, equivalent to the ratio between the sum of the number of traits present in one site but not in another and the sum of the number of traits that are present in one or both the sites. The resulting numerical index is bounded between 0 (identical presences in the two sites) and 1 (complete absence of shared traits), and extremely useful for archaeological data as it ignores instances of negative matches (i.e. shared absences) that are common in sparse matrices with many absences (Shennan & Bentley, 2008). Again it is worth noting that each trait has an equal contribution to the calculation of this index, and hence the measure we deployed is independent from the cultural affiliation attributed by the archaeologist for each site.

2.2.2. Detecting isolation by distance

The correlations between geographic distance and cultural dissimilarity have been obtained using partial Mantel tests (Smouse, Long, & Sokal, 1986), as implemented in the *vegan* (Oksanen et al., 2013) and *ecodist* (Goslee & Urban, 2007) packages in R (R Core Team, 2013). Mantel tests (Mantel, 1967) are commonly used to measure the correlation between two distance matrices, where standard regression analysis cannot be used to compute the significance given that distances are not independent (i.e. removing a site would alter the entire matrix). The solution consists of comparing the observed correlation against a distribution of correlations obtained by randomly permuting the rows and the columns of one of the matrices.

The correlation between geographic distance and cultural dissimilarity can however be confounded by temporal distances. Two sites located at close distance in space might be separated by a large temporal distance, which in turn, depending on the rate of cultural evolution, might determine a large Jaccard index. In order compute the correlation between Jaccard and geographic (or temporal) distances, we need to de-trend the effect of temporal (or geographic) distance. We thus computed a partial Mantel test, which enables the computation of the partial correlation between two matrices, holding the effects of one or more additional matrices (Smouse et al., 1986).

We obtained significance levels comparing the observed partial correlations against 1,000 random permutations of the data. Great-circle (spatial) distance has been retrieved from the latitude and longitude data, while we used the Euclidean distance between median culture dates as a proxy for the temporal distance between pairs of sites.

2.2.3. Detecting population structure

We examined the degree to which cultural affiliation is comparable to an actual population structure by using the analysis of molecular variance (AMOVA; Excoffier, Smouse, & Quattro, 1992). This provides a quantitative measure of whether and to what degree the observed population (our ornament and pottery data) is characterised by more or less distinct groups (archaeological cultures). We followed Ross et al. (2013) and used the Φ_{ST} statistic given its flexibility to rely on distance matrices rather than variant frequencies (Excoffier et al., 1992). This provides a scaled measure of the amount of variance explained by the population structure. The test statistic Φ_{ST} is in fact obtained by dividing the variance among populations by the sum of the variance among populations and the variance within populations. The result will be equal to 0 when there is no variation in the material culture among sites attributed to different cultures. In other words, the observed diversity between sites would not be explained by cultural affiliation. At the other extreme, a Φ_{ST} approaching 1 will indicate that most of the diversity in the data set is explained by a population structure. All sites attributed to the same culture will be identical (thus with a Jaccard distance of 0) and differences between any pair of sites will be observed only if they are affiliated to different cultures. We calculated significance levels of our

[1] R source codes of all analyses can be found on the online electronic supplementary codes S1 and S2.

Table 1
Partial Mantel tests using Jaccard distance between individuals sites as predicted variable (n pottery sites = 195; n ornament sites = 166).

Variables	Pottery r^2	Pottery p	Ornament r^2	Ornament p
Jaccard distance ~ geography (holding time)	0.005	0.041	0.023	0.001
Jaccard distance ~ time (holding geography)	0.005	0.993	0.093	0.001
Jaccard distance ~ cultural affiliation (holding geography + time)	0.073	0.001	0.008	0.001
Jaccard distance ~ geography, (holding cultural affiliation + time)	0	0.849	0.014	0.001
Jaccard distance ~ time (holding cultural affiliation + geography)	0.025	1	0.057	0.001

statistics with a permutation test (1,000 iterations) using the *pegas* package in R (Paradis, 2010).

We further examined, again using partial Mantel tests, how much variation in our data is explained by cultural affiliation when distances in space and time are simultaneously controlled. While a slight confounding effect of isolation by distance is still expected (see Meirmans, 2013 for a detailed analysis on this problem), this approach enables us to de-trend its effect and identify the underlying population structure by different means (cf. Drummond & Hamilton, 2007).

2.2.4. Detecting correlation between population structure, space, and time

We further hypothesised that Φ_{ST} statistics are most likely affected by the way the cultures we examined are distributed in space and time. If these are located at greater spatial and temporal distance we should expect higher Φ_{ST} values. In order to examine this hypothesis we first computed Φ_{ST} statistics between all possible pairs of cultures. This was obtained by using the standard procedure described above, but taking into consideration only two cultures at the time. The resulting statistic thus gives a measure of population differentiation for each possible pair of archaeological cultures that can then be used to generate a matrix of pairwise Φ_{ST}. This can then be examined using partial Mantel tests, defining the temporal and spatial coordinates of each culture as the average median date and the average latitude and longitude of the sampled sites.

In order to visualise the relationship between the degree of population structure defined by each material culture type, geography, and temporal distance, we employed DISTATIS analysis (Abdi, Valentin, O'Toole, & Edelman, 2005), using the *DistatisR* package (Beaton, Fatt, & Abdi, 2013) in R. This is a variant of multidimensional scaling that allows the simultaneous assessment of multiple distance matrices through the creation of a compromise matrix that represent the best aggregate between the original matrices. The observations are projected on a compromise space, together with vectors representing each source distance matrix. DISTATIS thus enables visual depiction of the differences and similarities between the different distance matrices for each culture, providing information additional to the partial mantel tests.

3. Results

3.1. Correlation in space and time of individual sites

Correlations between the Jaccard and spatial and temporal distances show consistently different outcomes for the ornament and pottery data (Table 1). Variation in the former exhibits weak, but statistically significant correlation with the two matrices ($p < 0.002$), with approximately 2% of the variance explained by geography, and 9% of the variance explained by temporal distance between individual sites. On the other hand, pottery data show significant correlation only for distance in space, but with less than 1% of the variance explained. Log-transformed distances showed similar results for both datasets (electronic supplementary table S8). Analyses on the subset of individual sites from the 6 cultures common to both datasets (see electronic supplementary table S9) confirm the stronger spatio-temporal correlation in the ornament data (6 ~ 9% of variance explained by geography and time). The pottery data show some degree of correlation with time (ca. 4% of variance explained) but not with space.

Table 2
Partial Mantel tests using pairwise Φ_{ST} between cultures as predicted variable: subset including only cultures with statistically significant Φ_{ST} (n pottery cultures = 13; n ornament cultures = 10).

Variables	Pottery r^2	Pottery p	Ornament r^2	Ornament p
Pairwise Φ_{ST} ~ geography (holding time)	0.074	0.078	0.335	0.002
Pairwise Φ_{ST} ~ time (holding geography)	0.27	0.001	0.003	0.486

3.2. Population structure

The global Φ_{ST} statistic indicates that both ornament and pottery show a statistically significant population structure, although the latter exhibits a slightly higher magnitude in both the complete dataset ($\Phi_{ST} = 0.134$ for pottery and $\Phi_{ST} = 0.109$ for the ornament data, both with $p < 0.001$) and the subset comprising the six common cultures ($\Phi_{ST} = 0.126$ for pottery and $\Phi_{ST} = 0.087$ for the ornament data, both with $p < 0.001$). Both figures show values consistent with previous studies where the population structure was inferred from language or political boundaries, including Ross et al.'s (2013) analysis of European Folktales ($\Phi_{ST} = 0.091$), Rzeszutek et al.'s (2012) study on musical variability amongst Austronesian aboriginal populations ($\Phi_{ST} = 0.021$), and Bell et al.'s (2009) work on human prosociality ($F_{ST} = 0.08$).

We conducted further partial Mantel tests on the individual site data (Table 1) including this time a binary distance matrix representing cultural affiliation (0 = same culture, 1 = different culture). For the pottery data, approximately 7.3% (3.7% for the six cultures dataset) of the cultural dissimilarity between individual sites is explained by cultural affiliation even when holding geography and time, whereas no significant correlation with these is observed (except for about 0.5% of variance explained by time in the six culture dataset). On the other hand, cultural affiliation explains only 0.8% (1% in the six culture subset) of the inter-site cultural dissimilarity in the ornament data, with time (5.7%, 3.3% in the six culture subset) and geography (1.4%, 8% in the six culture subset) providing more explanatory power. Despite the fairly low R^2 resulting from the partial Mantel tests, cultural affiliation in the pottery data explains a higher amount of variation than ethnolinguistic identities in Ross et al.'s (2013) analysis of the folktale data, which explains 3.7% of the variation when geography is taken into consideration. The continuing strength of cultural affiliation even when the effects of spatial and temporal variation on pottery variation are controlled is striking.

3.3. Population structure, geography, and time

The analysis of the pairwise culture Φ_{ST} (electronic online supplementary tables S10-S11) provides a more detailed view of the range

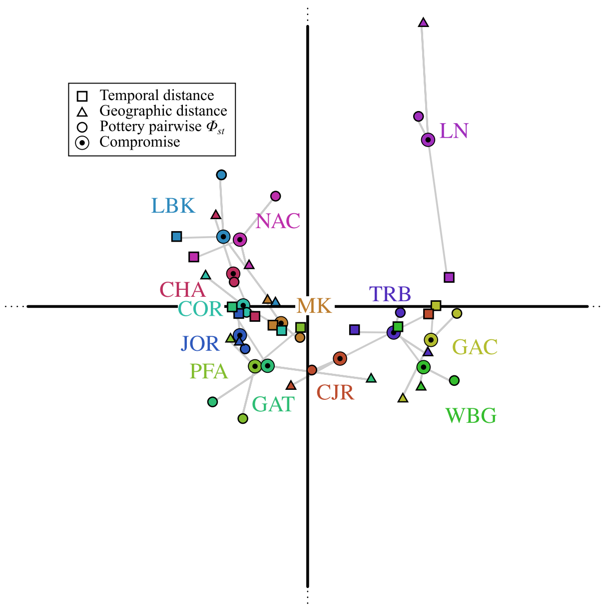

Fig. 2. DISTATIS analysis of the pottery data, based on the subset of the 13 cultures with statistically significant Φ_{ST} (CHA = Chasseen/Middle Neolithic of Burgundy; CJR = Cham/Jevisovice B/Rivnac; COR = Cortaillod; GAC = Globular Amphora Culture; GAT = Gatersleben; JOR = Jordanow/Schulterband/Schussenried; LBK = Linearbandkeramik; LN = British Late Neolithic; MK = Michelsberg; NAC = Nachfolgekulturen; PFA = Pfyn/Altheim; TRB = Funnel Beaker (Trichterbecher); WBG = Walternienburg/Bernburg).

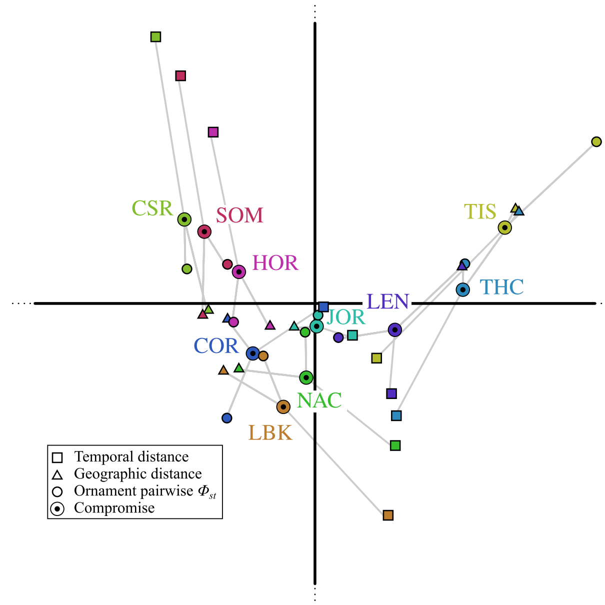

Fig. 3. DISTATIS multidimensional analysis of the ornament data, based on the subset of the 10 cultures with statistically significant Φ_{ST} (COR = Cortaillod; CSR = Civilisation Saone-Rhone; HOR = Horgen; JOR = Jordanow/Schulterband/Schussenried; LBK = Linearbandkeramik; LEN = Lengyel; NAC = Nachfolgekulturen; SOM = Seine-Oise-Marne/Clairvaux/Ferrieres; THC = Tisza-Herpaly-Csoszhalom Gruppe; TIS = Tiszapolgar).

of observed Φ_{ST} values, the degree to which each culture exhibits a population structure, and possible correlation with space and time. Most pairwise Φ_{ST} values showed statistically significant evidence of population structure, although ca. 6% of the pairs from the ornament data and 11% of the pairs from the pottery data showed a p-value above 0.05. We thus reduced our sample, excluding cultures that contributed to the generation of these non-significant p-values. The distribution of the Φ_{ST} obtained from these subsets (10 cultures for the ornament data, 13 cultures for the pottery data) showed a range between 0.018 and 0.395 with a mean of 0.132 for the ornament data, and a range (13 cultures) between 0.037 and 0.272, with a mean of 0.15 for the pottery data. Again these ranges are comparable to those observed by previous studies (Bell et al., 2009; Ross et al., 2013; Rzeszutek et al., 2012) although our dataset includes cultures that are not contemporary.

In order to investigate how much of the variation in inter-culture Φ_{ST} is explained by spatial isolation and how much by temporal distance we conducted partial mantel tests following the same procedure we used for the analysis of variability between individual sites. The results (Table 2) show, once again, a profound divergence between the two datasets. The pairwise Φ_{ST} in ornament data is correlated with space but not with time, whilst the pottery data exhibit the opposite relationship, with time being a stronger explanatory variable than geography. Similar results have been obtained with the subset of six cultures (see electronic online supplementary table S12).

The difference between the two datasets can be visualised with DISTATIS analysis (Figs. 2 and 3, see electronic supplementary table S3 for the full list of cultures). Pottery data show a fairly good compromise between the three matrices, with the location of each culture defined by a fairly equal pull of the three distance matrices into opposite directions. British Late Neolithic (LN) is the only significant outlier and an exception to the overall stronger correlation of Φ_{ST} with time. Geography and population structure are in fact both determining its isolation in the multidimensional compromise space, despite a closer proximity in time to other cultures such as *Globular Amphora Culture* (GAC) and *Cham/Jevisovice B/Rivnac* (CJR). The ornament data exhibit a clear disagreement on the temporal dimension, in line with the results of the partial Mantel tests. *Civilisation Saone-Rhone* (CSR), *Seine-Oise-Marne/Clairvaux/Ferrieres* (SOM) and *Horgen* (HOR) are chronologically closer and isolated, but their spatial distance and Φ_{ST} values place them in proximity to *Cortaillod* (COR), *Linearbandkeramik* (LBK) and *Jordanow/Schulterband/Schussenried* (JSS). This distinct patterning of space and time in relation to the two material cultures is also visible with the DISTATIS analysis of the subset of six cultures (Fig. 4). Here the distinct pattern of between-culture space, time, and the pairwise Φ_{ST} of the pottery and ornament data can be directly visualised. Both *Cortaillod* (COR), and *Michelsberg* (MK) are spatially isolated from other temporally closer cultures, i.e. *Pfyn/Altheim* (PFA) and *Jordanow/Schulterband/Schussenried* (JSS). The Φ_{ST} of the ornament data follows this pattern, but the pottery data show the opposite trend and exhibit a closer affinity to PFA and JSS.

4. Discussion

The aim of this paper was to assess the evidence for population structuring in prehistory as represented by the cultural affiliations that archaeologists assign to their finds, in opposition to the idea that these designated affiliations arise from the irregular sampling of continuous variation in space and time. We found good support for population structure in the pottery data, as suggested by both AMOVA and partial Mantel tests. The latter showed how the affiliation to archaeological cultures is a stronger predictor of inter-site variation in pottery style than geography and time, indicating how a pure isolation by distance model is not sufficient to characterise the structured pattern in our data.

The R^2 values showed high values compared to other studies (e.g. Ross et al., 2013), but in absolute terms less than 10% of the variance has been explained by isolation by distance and population structure. There are a number of possible reasons that we can speculate about for these results. Apart from the high degree of noise dictated by

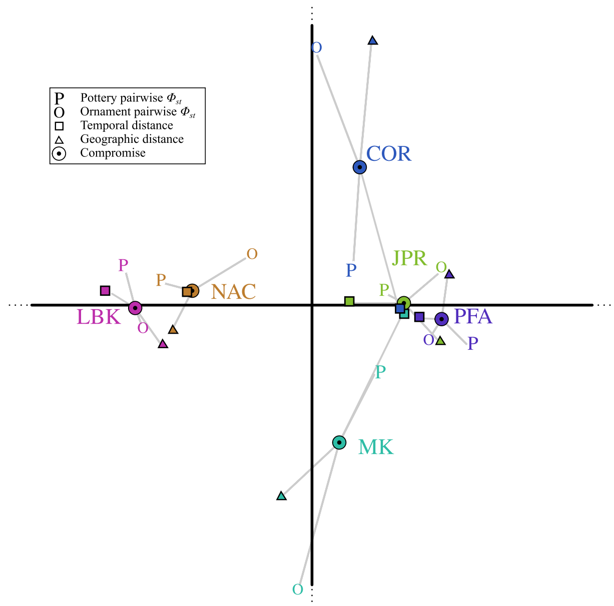

Fig. 4. DISTATIS multidimensional analysis of the pottery (P) and the ornament (O) data, based on the subset of the 6 common cultures (COR = Cortaillod; JOR = Jordanow/ Schulterband/Schussenried; LBK = Linearbandkeramik; MK = Michelsberg; NAC = Nachfolgekulturen; PFA = Pfyn/Altheim).

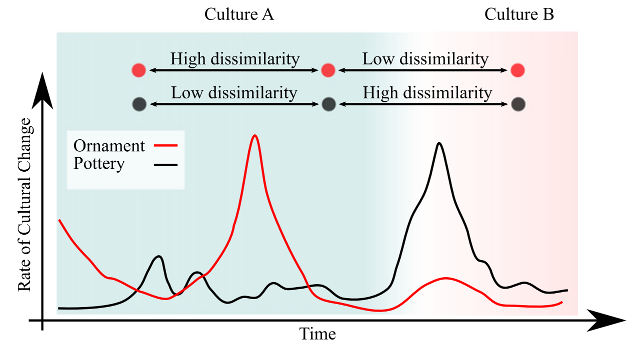

Fig. 5. Inferred relationship between the population structure as defined by pottery style and the inter-site dissimilarity in pottery and personal ornament.

sampling biases in archaeological data, isolation by distance assumes isotropy in the pattern of cultural interaction. This can be a useful approximation in many studies, but the presence of preferred routes of interactions, constrained for instance by topography, will undoubtedly determine a decrease in R^2 values. Some of the traits examined could also be adaptive to specific environmental conditions. However, in many cases environmental gradients are correlated with geographic distance (i.e. sites that are closer in space are more likely to share similar environment and vice-versa), so our partial Mantel tests should have, at least in part, isolated their effect in detecting population structure. Nonetheless, discrepancies and non-linearity between geographic and environmental distance are likely to lower observed R^2. It is however reassuring that a recent study on the faunal assemblages from 13 Neolithic cultures in Europe, has shown that between 10 and 13% of the variation in the frequencies of cattle, pig, roe and red deer is explained by cultural affiliation even when the effect of ecological and environmental variables are accounted for (Manning et al., 2013). It is also worth mentioning that even if we assume that traits being examined are selectively neutral, the underlying environment can still constrain or promote cultural interaction. Instances of cultural hitchhiking (Ackland, Signitzer, Stratford, & Cohen, 2007), might in fact promote situations where neutral traits are carried together with selective ones, leading to significant patterns of correlation that are in fact indirect.

Estimates of Φ_{ST} between pairs of archaeological cultures showed a wide range of values, meeting our expectations that these were caused by differences in the temporal extent (i.e. cultures with longer duration in time are expected to exhibit higher inter-site variability), but more importantly by the temporal and spatial distances between cultures. However, partial Mantel tests showed significant correlation only with time. This implies that the geography of Neolithic cultures does not exhibit a neat decay in similarity over space. When we ignore cultural affiliation, and consider only the effect of time, the dissimilarity between sites shows in fact almost no correlation with geography, possibly as a consequence of shared ancestry (branching) intertwined with horizontal cultural transmission (blending).

The positive correlation between pairwise cultural Φ_{ST} and temporal distance contrasts with the substantial lack of correlation between inter-site Jaccard distance and time. This pattern could possibly imply that the temporal variation in the pottery attributes was punctuated by sudden changes, corresponding to archaeologically defined cultural transitions, rather than a stationary continuum arbitrarily sliced by archaeologists. This supports a "temporal" population structure and once again highlights the presence of a process beyond simple isolation by distance.

The ornament data show a different picture. We still observe good support for population structure from both AMOVA and the site-level partial mantel tests, but the signal is weaker, with geography and time providing much greater information compared to the pottery data.

The structure of the within vs. between population dissimilarity in personal ornaments also shows a contrasting pattern to the pottery data. Time, in fact, does not explain the variation in the pairwise Φ_{ST}. This might be a consequence of how archaeological cultures are defined primarily from pottery rather than ornaments. Marked temporal discontinuities in pottery design are interpreted as temporal "boundaries" of archaeological cultures (Fig. 5), hence the within cultural similarity of pottery design will be higher than the between culture similarity, in turn leading to higher Φ_{ST} values, and a correlation with time. We expect to see the same pattern from the ornament data only if peaks in the cultural rate of change match those observed in the pottery design. If major temporal discontinues are recorded within the chronological boundary of a culture we would observe higher dissimilarity between pairs of sites within the same culture, and conversely if we do not see peaks in cultural discontinuities at the chronological boundaries we might observe lower dissimilarity between sites of different cultures (Fig. 5). The consequence of this can be observed in a generally lower Φ_{ST}, a lack of correlation of between pairwise Φ_{ST} and time contrasted by a positive correlation between time and the dissimilarity of individual sites. Pairwise Φ_{ST} and geography, on the other hand, exhibit fairly high levels of correlation, suggesting how, with increasing distance, the proportion of variation among individual sites is increasingly occurring between, rather than within, cultures.

Our results suggest distinct evolutionary histories in the spatial and temporal variation of personal ornament and pottery, with different rates of innovation, patterns of descent, and dynamics of diffusion. Ornament data do show statistically significant values of Φ_{ST} using pottery-defined population structures, but the magnitude is extremely small, and partial Mantel tests suggest that much of this pattern is explained by isolation by distance. These results are in line with a model of culture represented by independent "packages" of multiple coherent units rather than one characterised by a distinct and fairly isolated "core" surrounded by a "periphery" of elements prone to cross-cultural transmission. The alternative hypothesis is that one element was part of the "core" tradition, whilst the other was peripheral. This scenario is however less likely given that both elements are generally regarded as expression of local lines of transmission and/or signalling. The robust support for a population structure in the pottery data shows that some degree of homophily must have biased the transmission process, but this bias was confined within the single "package", rather than affecting other aspects of the material culture. In other words similarity (or dissimilarity) of pottery style was not influencing the transmission process of personal ornaments and vice-versa. If this was the case, we should have observed a stronger agreement between in the spatio-temporal distribution of the two datasets, a pattern we failed to observe. Personal ornaments are often seen as group-identity markers, but the fact that our study appears to indicate a stronger role for isolation by distance in accounting for variation in ornaments suggests that this assumption may not be valid, or alternatively that these groups cross-cut the archaeological cultures traditionally recognised. Thus, while our study has provided strong evidence of population structure affecting patterns of cultural interaction, in this case at least the distinct patterns observed point to a modular, 'package' model. It has also shown that we can identify population structuring from the evidence of the archaeological record without continuing to attempt the fruitless task of correlating its patterns with past ethnolinguistic units.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2014.09.006.

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