Neolithic pots and potters in Europe: the end of 'demic diffusion' migratory model

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ABSTRACT – *In this paper we discuss the inventions and re-inventions of ceramic technology and pottery dispersals in foraging and farming contexts in Eurasia. We focus on narratives that operate within interpretative paradigms that suggest movements of unidirectional colonisation and 'demic' diffusion, and a correlation between pottery and human DNA haplogroup distributions in Europe in the Initial Neolithic. In addition, we present the results of ancient, Mesolithic and Neolithic mitochondrial DNA analyses, which suggest variations in population trajectories in prehistoric Europe. We comment on a hypothesis presented recently on the correlation between the distribution of the lactase (LCT) gene –13 910*T in the modern population of Europe, which has been shown to be associated with lactase persistence and dairying, and the Neolithic transition to farming in Central Europe.*

IZVLEČEK – *V članku obravnavamo večkratne izume keramične tehnologije in širitev lončarstva pri lovcih in nabiralcih ter poljedelcih v Evraziji. Osredotočamo se na različne intrepretacije v okviru interpretativne paradigme, ki temelji na predpostavki o kolonizaciji in 'demski' difuziji ter o korelaciji med distribucijami zgodnje neolitske keramike in človeških DNK haploskupin v Evropi. Predstavljamo rezultate analiz stare, mezolitike in neolitske mitohondrijske DNK, ki dokazujejo različne populacijske trajektorije v prazgodovinski Evropi. Komentiramo novo hipotezo o razširjenosti laktaznega gena –13 910*T pri modernih prebivalcih v Evropi. Povezana naj bi bila s prehodom na kmetovanje, mlekarstvom in laktazno persistenco v neolitiku v Srednji Evropi.*

KEY WORDS – *Eurasia; neolithisation; demic diffusion; pottery; human DNA and aDNA*

Introduction

The appearance and distribution of pottery have long been studied in conjunction with migrations of prehistoric populations and became highly ideologised by the Lex Kossinae that equates 'cultural province' with 'areas of particular people or tribes' (*Kossina 1911.3*). Gordon Childe agreed that Neolithic pottery was a universal indicator of both the 'cultural identities' and 'distributions of ethnic groups' (*Childe 1929.v–iv*), but he strongly disagreed that ceramic technology invention and its primary distribution can be found within Europe. He proposed that pottery arrived with Neolithic 'immigrants from South-Western Asia' who 'were not full-time specialists, but had complete mastery over their material'. The 'experienced farmers' in the Peloponnese and the Balkans thus produced 'extremely fine burnished and painted ware', whereas the 'Danubian I hoe-cultivators' in the Carpathian Basin and Central Europe produced 'unpainted and coarse and chaff-tempered vessels'. Beyond the agricultural frontier and pottery distribution on the North European plain, he recognised 'scattered bands of food-gatherers' (*Childe 1939.21, 25–26; 1958.58–60, 86–88*).

The introduction of physical anthropology and racial mapping into archaeology by Carleton Coon (*1939. 82–86, 104–107, Map 2*) related Neolithic immigrants to 'Danubian' agriculturalists', a 'new branch of Mediterranean' population in Europe that had originated in the Near East and was associated with the

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Natufian cultural context. They migrated across Anatolia and/or the Aegean into Europe, and 'up the Danube Valley into the Carpathian basin, Central Europe and farther to the west, to the Paris basin, where they met with the second group of 'Mediterranean' population, 'which entered Europe from North Africa across the Straits of Gibraltar'. It has been suggested that the first group brought 'Danubian painted pottery' that shows 'definite Asiatic similarities' into Europe. The second was associated with the dispersal of 'incised pottery with banded decoration'. These streams have been recently recognised archaeogenetically (*Sampietro* et al. *2007.2165–2166; Deguilloux* et al. *2012.29, 32*), and re-actualised archaeologically as 'Danubian' and 'Occidental' groups (*Gronenborn 2011.68, 70*).

Childe (*1951.76–77*) recognised the invention of ceramic technology and pottery making as the "*the earliest conscious utilization by man of a chemical change... in the quality of the material*" that happened in the Near East in the context of the Neolithic revolution. It later became a constituent part of the Neolithic package.

The geographical correlation of painted pottery and ceramic female figurine distribution, and the distribution of genetically identified Y-chromosome haplogroups in the modern paternal lineages of European and Near Eastern populations were hypothesised decades later to be 'the best material culture and genetic markers' of a demographic event that radically reshaped the European population structure (*King, Underhill 2002.707*). It was argued that the majority of the hunter-gatherer population in Europe was replaced in the Early Neolithic by a Near-Eastern farming population. Ceramic female figurines in this context mark the new 'expansionist' ideology that enabled the transition to the 'agricultural way of life' in the Near East first. Europe did not become neolithicised until figurines reached the Balkans (*Cauvin 2000.22–29, 204–205, 207–208*).

Childe and Coon both suggested an interpretative paradigm in which the gradual migration of farmers and the spread of agricultural frontier into Europe correlates with the boundary – that has been recognised since Herodotus – between the barbarian West and the civilized East. In this perception, the Mesolithic-Neolithic transition and/or the transition to farming in Europe correlates with the transition from barbarism to civilisation (see *Budja 1996; 1999; 2009*).

How the civilised East colonised the barbarian West

Indeed, Southeast Europe was recognised as a "*western province of Near Eastern peasant culture, created by the processes of colonisation and acculturation*" that was mirrored in the distribution of "*common traditions in pottery styles, oriental stamp-seals and female figurines, and sometimes of animals, which may relate to religious cults*" (*Piggott 1965.49–50*; see also *Roden 1965*). In John Nandris's (*1970.193, 202*) view the dispersal of the same set of artefacts marked "*cultural unity, greater than was ever subsequently achieved in this area of southeast Europe, down to the present day*".

The perception of the dichotomy of the civilised/barbarian population continued to be highly significant. The 'monochrome'[1] and painted (red, black and white) vessels achieved paradigmatic status in tracing 'waves of migrations from Asia Minor' (*Schachermeyr 1976.43–46*), and in marking the cultural and ethnic identity of the earliest Neolithic farmer diasporas in Europe (*Milojčić 1962; Theocharis 1973; Nikolov 1987; Bogucki 1996*). At the same time, coarse, 'impressed' and 'barbotine' pottery was recognised as "*so local to the Balkans that we do not believe that this primitive pottery was introduced from Asia Minor*" (*Theocharis 1967.173; cf. Thissen 2000.163*). It was, indeed, linked to 'barbarian local production' that showed 'a clear regression in pottery production' (*Milojčić 1960.32; Nandris 1970.200; Milojčić-von Zumbusch, Milojčić 1971. 34, 151*).

It was suggested that the second wave of migration correlated with a 'breakthrough' of white painted pottery along the Vardar, Morava and Struma rivers (*Garašanin, Radovanović 2001; Luca, Suciu 2008; Krauß 2011*), and with the "*rapid expansion of red-slipped pottery along the Black Sea coastline through the Danube River valley*" (*Özdoğan 2011. S426*). This migration resulted in the creation of a cluster of cultures in the northern and eastern Balkans and in the Carpathian Basin which shared an identical 'Neolithic package' originating in Central Anatolia and consisting of "*tubular lugs, plastic decoration in relief, anthropomorphic or zoomorphic vessels, steatopygic figurines, pintaderas, and so forth*" (*Özdoğan 2011.S425*). Differences in vessel shapes and ornamental composition, however, constituted regionally bounded Early Neolithic cultures

1 Vessels have been coated with a clay slip that gives red or brown colours after firing.

such as Starčevo, Körös, Criş and Karanovo (see *Budja 2001; Krauß 2011*).

It has been suggested recently that the new strontium isotope data from the Danube Gorges in the northern Balkans show female migration to the region in the contexts of the spread of Neolithic communities from Central Anatolia along the Black Sea coast into the Danube in the Mesolithic-Neolithic transitional phase at 6200–6000 calBC. Physical 'differences between populations' and a 'dramatic increase in the numbers of non-local, first-generation migrants' were also proposed, as five of the 45 individuals at Lepenski vir are non-local. All but one of these individuals are female; thus 'social exchange' and 'population blending' at the mobile agricultural frontier are hypothesised (*Borić, Price 2013.3301–3302, 3299*). However, such a scenario could only have happened within already established social networks (*e.g.*, kinship ties, marriage alliances, exchange partnerships and other social ties of reciprocity and obligations) between hunter-gatherers and the first farming settlements in the region (see *Zvelebil, Lillie 2000; Zvelebil 2001; 2004*). The direction and rapidity of expansion suggest the importance of existing hunter-gatherers' social contexts and routes of communication, as do the conditions of farming communities and the scale of the migration.

The third wave of migration was related to the genesis of the Linear Pottery culture (LBK) in the Carpathian Basin and its westward expansion (*Gronenborn 2007; Lünning 2007; Oross, Banffy 2009; Burger, Thomas 2011*).

The rate of spread was calculated from a series of standard ^{14}C dates available at the time. Breunig (*1987*) allocated them to temporal zones of 500-year intervals, running from the Near East to Atlantic Europe and through the 7th millennium in Southeast Europe and the 6th millennium BC in Western Europe. The southeast-northwest temporal gradient of the 'spread of the Neolithic way of life' from the Near East across Europe was thus broadly accepted (see *Biagi* et al. *2005*). A less gradual movement was hypothesised in a demographic model suggesting migrations from one suitable environment to another. Van Andel and Runnels (*1995*) suggested that Anatolian farmers first settled in small numbers on the Larissa Plain in Thessaly, as they thought this was the only region in the southern Balkans that could provide a secure and large enough harvest for significant population growth 'at the wave front' that led to the next migratory move (*i.e.*, 'leap-frog')[2] towards the Danube and Carpathian Basin. They calculated that farmers needed 1500 years to reach saturation at a 'jumping-off point' and to migrate to the northern Balkans. Paolo Biagi and Michela Spataro (*2001*), on the other hand, reviewed the radiocarbon dates from selected cave sites in the central Mediterranean and believed they had found evidence of a hiatus between the latest Mesolithic and earliest Neolithic occupations in every case. From this, it was suggested that the late Mesolithic was a period of population decline, with hunter-gatherers disappearing altogether soon after the arrival of farming (*Biagi 2003.148–150; Rowley-Conwy* et al. *2013*; for discussion see *Mlekuž* et al. *2008; Bonsall* et al. *2013; Forenbaher* et al. *2013*).

The earliest pottery productions in Southeast Europe are embedded in time spans at *c.* 6500–6200 calBC in the southern Balkans and Peloponnese, at *c.* 6440–6028 calBC in the northern and eastern Balkans (*Perlès 2001; Thissen 2005; 2009; Reingruber, Thissen 2009; Müller 1991; 1994; Budja 2009; 2010; Reingruber 2011a; b*). (Fig. 1). The southeast-northwest temporal gradient thus found no confirmation in the radiocarbon chronology of the initial Neolithic pottery distribution in Southeast Europe. The data suggest the contemporaneous appearance of pottery in regions where gradual colonisation was hypothesised.

While pottery in the southern Balkans was found in farming settlement contexts, it also appeared in the north in hunter-gatherer and farmer contexts (*Perlès 2001; Budja 2009*). At Lepenski Vir, vessels were contextualised within hunter-gatherers' burial practices and symbolic behaviour. They were embedded in trapezoidal built structures and associated with neonate burials and secondary burials (or depositions) of human and dog mandibles (*Budja 1999; 2009; Garašanin, Radovanović 2001; Stefanović, Borić 2008*)[3].

The distributions of material items such as female figurines (sometimes exaggerated in form), stamp

2 João Zilhão (*1993.37, 49*) introduced the 'leapfrog' colonization model suggesting rapid migration of east Mediterranean farmers to the West Mediterranean. The model was recently actualized in palaeogenetic studies (*Deguilloux* et al. *2011.32–34*).

3 Pottery was placed in trapezoidal built structures (Nos. 4, 24, 36 and 54). It was associated with stone sculptures, neonate burials and intentional placement of disarticulated human and dog mandibles. Neonates were buried in the rear of the structures under the red limestone floors. The burial pits were either cut into floors or dug immediately of the floor edge between the construction stones (*Stefanović, Borić 2008.139, 145–146, 149–150; Budja 2009.126–127*).

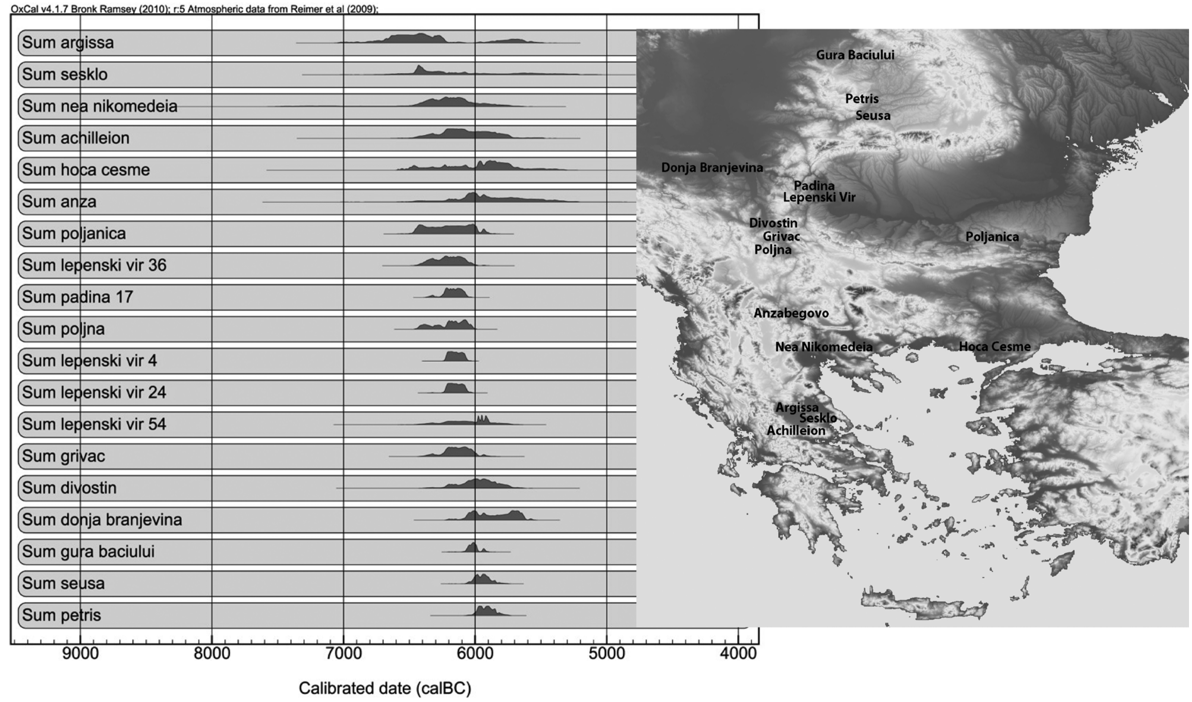

Fig. 1. Site distribution and Sum probability plot of initial Neolithic pottery distribution in Southeastern Europe (modified from* Budja 2009.Tab. 2*).

seals, anthropomorphic, zoomorphic and polypod vessels, which do indeed connect Southeast Europe and western Anatolia, support the perception of migrating farmers and the gradual distribution of the 'Near Eastern Neolithic package' (*Lichter 2005; Özdoğan 2007; 2008; 2011*). Yet it is worth remembering that the beginning of the Neolithic in Southeast Europe was marked neither by stamp seals nor ceramic female figurines. No single stamp has been found in EN I, and none of the clay figurines can be securely dated to this period. Figurines do appear in secure contexts in EN II, and stamp seals can securely be dated to EN III/MN I[4] on the southern tip of the Balkan Peninsula and in the Peloponnese (*Reingruber 2011a.301; 2011b. 135*). When figurines appeared in Southeast Europe, they remained highly schematised, sometimes to the extent that their identification as anthropomorphic is debatable (*Vajsov 1998.131; Perlès 2001.257*; for a general overview, see *Hansen 2007*).

The pottery assemblages in Southeast Europe show local and regional differences in production techniques, vessel shapes and ornaments. The combined petrographic and chemical compositional analyses of clay matrix and ceramic fabrics clearly indicate differences in pottery production. Pottery in the northern Balkans was consistently manufactured according to a single recipe, using non-calcareous micaceous clay pastes, characterised by fine well-sorted alluvial quartz sand with feldspar, and heavily tempered with organic matter (*i.e.* chaff). In the Adriatic, however, pottery was heavily tempered with crushed calcite on the east coast, and with mineral resources (*e.g.*, flint) and grog (recycled pottery) on the west coast (*Spataro 2009; 2011*). From the outset in the Aegean, pottery was made locally at a number of sites and exchanged regularly between neighbouring settlements. Some fine ware paste recipes show that pottery may have been transported over a distance of around 200km and that it may have been an item in maritime exchange networks. The unchanged ceramic matrix in some cases reflects significant continuity in pottery technology over the millennium (*Tomkins* et al. *2004; Quinn* et al. *2010*).

Two basic ornamental principles are recognised in the dispersal of pottery in Southeast Europe in the Early Neolithic. While painted motifs are limited to the Peloponnese, the Balkans and the southern Carpathian Basin, Cardium impressed ornaments mark the Adriatic coast. It is not before the Middle Neolithic that painted pottery appears on the east cost of

4 The abbreviations denote the Thessalian Early Neolithic sequence. They were introduced by Theocharis (*1967*). They were suggested to replace Milojčić's (*1959.19*) terms 'Frühkeramikum', 'Proto-Sesklo' and 'Vor-Sesklo'.

the Adriatic (*Müller 1994; Schubert 1999; Budja 2001*).

The pottery assemblages in the earliest settlement contexts on the Peloponnese and the southernmost tip of the Balkan Peninsula consist of monochrome (red-slipped) pottery, and 'a very limited use of painting' (*Perlès 2001.112*; see also *Krauß 2011.119*). Unpainted vessels were clearly the first to appear in settlements in the northern and eastern Balkans. They still prevail in the latter contexts, as painted vessels comprise from 0.2% to less than 10% of the total quantity of ceramics (*Budja 2009.126; Krauß 2009.122*). However, we cannot ignore the regionalisation evident in vessel forms (*Thissen 2009*) and ornamentation in later painted pottery (*Schubert 1999; 2005*). In southern parts of the region (Thessaly and the Peloponnese) ornaments appeared in red and black. Further to the north, in Macedonia, white was added. In northern and eastern regions of the Balkans, white ornamentation predominates in the earliest pottery assemblages. A similar pattern is seen in regional ornamental motifs distribution, as dots and grids predominate in the northern and eastern Balkans, and triangles, squares, zigzags and floral motifs in the southern Balkans and the Peloponnese.

The hypothesised southeast-northwest temporal gradient of the spread of the pottery package was broadly accepted as an indication of the spread of a Neolithic cultural identity and way of life into Europe. It was correlated with the boundaries of Early Neolithic cultures (*e.g.*, farming enclaves) and associated with the agricultural frontiers and 'demic diffusion' (see *Lünning 2007; Özdoğan 2007; Guilaine 2007; Burger, Thomas 2011*) (Fig. 2). Northeast and East Europe were marginalised, having no point of entry and remaining a blank through the period (but see *Dolukhanov* et al. *2005; 2009; Gronenborn 2007*). It is worth remembering the frontier thesis had been entertained since Herodotus recognised it as the agricultural frontier and the boundary between the civilised East and barbarian West (see *Budja 2009*).

Inventions and re-inventions of ceramic technologies

Hunter-gatherers used diverse ceramic technologies long before the transition to farming began. The invention of ceramic technology in Europe was associated with the making of female and animal figurines in Gravettian, Epigravettian and Pavlovian complexes in Central Europe within a period that ranges from *c.* 30 000 to 27 000 calBC[5]. It was followed in North Africa at 23 000 – 21 000 calBC and Southern

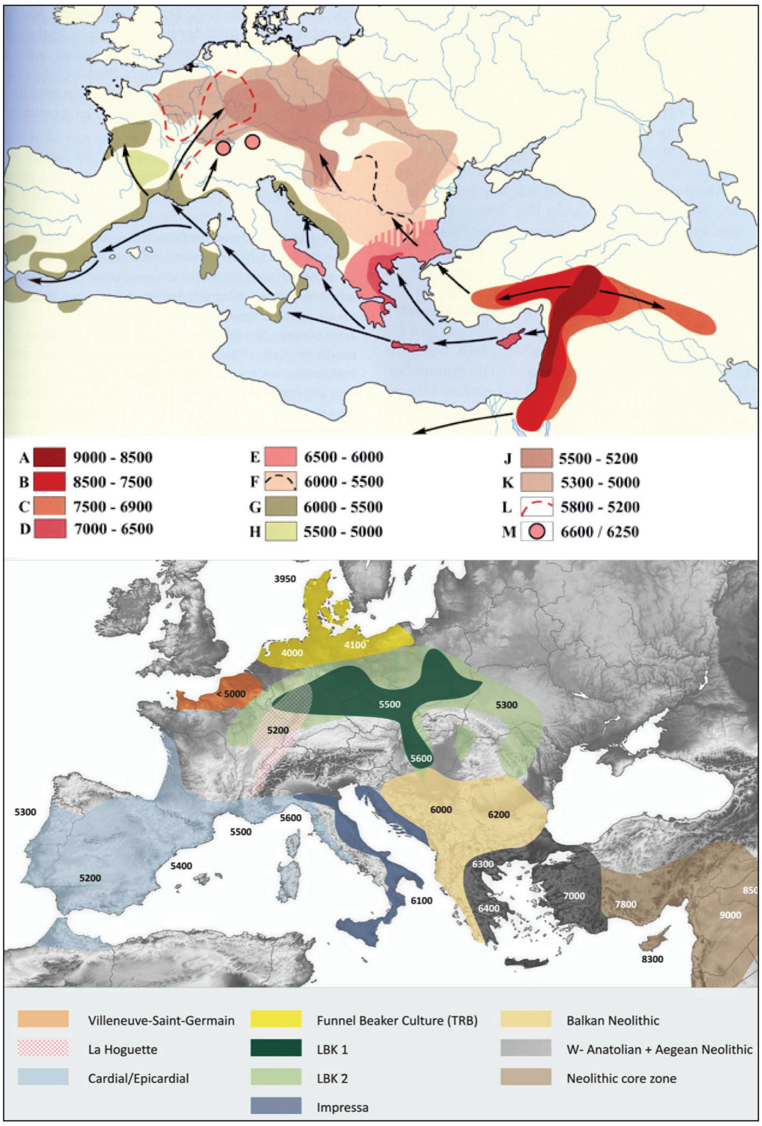

Fig. 2. The hypothesised southeast-northwest temporal gradient of the spread of the Neolithic package, cultural identities and 'demic diffusion' (from* Zimmerman 2002 *and* Burger 2010*).

5 All the ^{14}C data in the text have been calibrated at 68.2% probability (2σ), using the OxCal 4.2 programme.

Siberia at 18 000 – 17 000 calBC. In Southeast Europe, it appeared at *c.* 19 000 – 16 000 calBC in an Epigravettian context at the Vela Spila cave site on Korčula island in the Adriatic (*Verpoorte 2001.40, 59, 90; Vasil'ev 2001.10; Einwögerer, Simon 2008. 39; Farbstein* et al. *2012.4–5*) (Fig. 3).

In Central Europe, an assemblage of 16 000 ceramic objects – more than 850 figural ceramics – have been found in Gravettian and Pavlovian hunter-gatherer camps at Dolní Věstonice, Předmostí, Pavlov I and Krems-Wachtberg (*Verpoorte 2001.95–100, Tab. 5.1*). At Dolní Věstonice and Pavlov, the ceramic distributions seem to be associated with the central position of oven-like hearths. The available statistics indicate that almost all the figurines and statuettes were deliberately fragmented, although many of the pellets and balls which comprise a large quantity of the ceramic inventory were found intact (*Verpoorte 2001.56, 69, 95–100, Tab. 5.1*). Recently, 36 ceramic artefacts (fragments of horse or deer figurines) from the cave site at Vela Spila on Korčula Island offer the first evidence of ceramic technology in the Epigravettian in the Adriatic (*Farbstein 2012*). However, more than 10 000 years separate the Palaeolithic ceramics and the earliest Neolithic pottery in the region.

The anthropomorphic ceramic figurine at the Palaeolithic site Maininskaia (Maina) in Southern Siberia predates the introduction of the first fired-clay vessels in East Eurasian hunter-gatherer contexts by less than a millennium. The introduction of ceramic vessels first occurred among small-scale sedentary or semi-sedentary hunter-gatherer communities in Southern China (Yuchanyan Cave) at *c.* 16 500 – 15 500 calBC (*Boaretto* et al. *2009; Lu 2010*). On the Japanese archipelago, it appeared at *c.* 14 000–13 100 calBC (*Taniguchi 2009.38*). In the Russian Far East, the time span is much broader, from 15 990 to 7710 calBC (*Keally* et al. *2003; Kuzmin 2006; Kuzmin* et al. *2007*).

In western Siberia, the initial distribution of pottery was hypothesised as lying within the time span *c.* 8300–6400 calBC (*Zakh 2006.77*). Further to the west, in the Western Urals and Middle Volga River, the oldest pottery was contextualised in small seasonal Elshanka (Yelshanian) sites scattered over a vast forest-steppe area. Vessels with conic and flat bases were made from salty clay tempered with organic matter, fish scales and crushed animal bones. They are decorated with imprints of pits, notches and incised lines. The earliest dates, based on freshwater mollusc shells, range between *c.* 8300 and 7300 calBC. However, they should be considered too old, as the reservoir age value for the East European Plain is not known. However, the dates on bone samples and carbonised food residuals range between 7070–6509 calBC (*Viskalin 2006; Zaitseva* et al. *2009.799–800, Tab. 1; Vybornov* et al. *2013. 15–18*).

In the northern East European Plain, on the Upper Volga and Oka rivers, the earliest pottery sites are embedded in a time span of 6218–5811 calBC (*Tsetlin 2008.234, Tab. 66; Zaretskaya, Kostyliova 2008. Tab 1*). Further north, in Karelia, the early pottery was contextualised at hunter-gatherer sites on the southern shores of Lake Onega. The earliest context (Tudozero V) is dated to *c.* 6209 – 6049 calBC, and the later (Sperrings) to *c.* 5512 – 4947 calBC. The

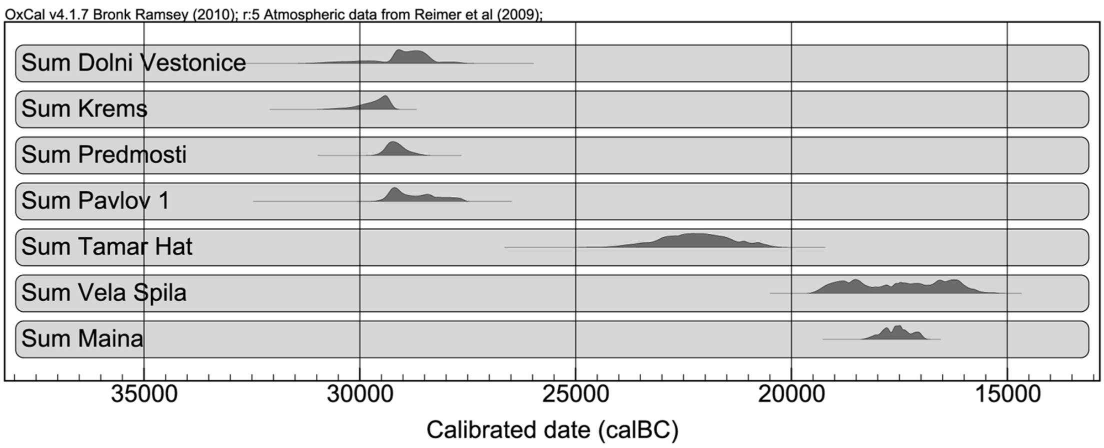

Fig. 3. The ^{14}C distribution of ceramic figurines in pre-Neolithic contexts in Eurasia. The sequence is based on ^{14}C data sets from Dolní Věstonice, Pavlov I, Předmostí and Krems-Wachtberg in central Europe (**Verpoorte 2001.40, 59, 90; Einwögerer, Simon 2008.39*****), from Vela Spila on the Korčula Island in Adriatic (*****Farbstein 2012.4–5*****), from Tamar Hat in northern Africa and Maina in Siberia (*****Farbstein 2012.11*****).***

point-based vessels were decorated with impressions of fish vertebrae, later replaced by comb and punctuated lines (*German 2009*). In the southern Baltic, early pottery dispersals are embedded in a time span of c. 5462 – 5303 on the east coast (Narva), *c.* 5611 – 5471 on the central coast (Neman), and *c.* 5466 – 5316 calBC on the west coast (Ertebølle) (*Hallgren 2009*) (Fig. 4). The pottery assemblages in all cultural contexts show similarities in having common features such as sparse and simple decoration, coiling techniques and pointed vessel bases (*Piezonka 2012*).

The earliest pottery production in the Near East was embedded in farming social contexts. The pottery was painted and dated at 7066 – 6840 calBC (*Özdoğan 2009; Nieuwenhuyse* et al. *2010*).

All these data indicate that ceramic technology was invented and reinvented more than once in different Palaeolithic and Neolithic contexts, and that hunter-gatherer communities made ceramic vessels elsewhere in Eurasia. The various pottery-making techniques, vessel shaping and ornamentation reflect different, but parallel production methods and distributions before and after the transition to farming. Thus, in Western Eurasia, initial pottery distributions occurred in two almost contemporaneous, but geographically and culturally distinct areas. The northern distribution was embedded in mobile and semi-mobile hunter-gatherer contexts on the East European Plain; the southern is associated with subsistence farming in the Near East. It is worth remembering that, while the first was ignored for much of the time (but see *Davison* et al. *2007; 2009; Gronenborn 2011*), the latter is constantly discussed in archaeogenetic studies (*King* et al. *2008; Battaglia* et al. *2009; Burger 2010; Thomas* et al. *2013*). As mentioned above, the first was associated with the distribution of the genetically determined Y-chromosome haplogroup (hg) J in modern European populations. The second then correlates, paraphrasing King and Underhill, with the 'best genetic predictors': the Y-chromosome hg N in modern populations (*McDonald 2005; Rootsi* et al. *2007; Derenko* et al. *2007*) and the ancient mitochondrial hg U4, U5 and H (*Der Sarkissian* et al. *2013*) (Figs. 5 and 6).

The southeast-northwest temporal gradient of the spread of the pottery package has been correlated with frequency gradients of genetic marker distributions in modern populations in Western Eurasia since Luigi Cavalli-Sforza and Albert Ammerman introduced demographic and genetic studies into archaeology. They postulated a continuous southeast-northwest oriented movement of Early Neolithic Levantine farmers across Europe, a 'demic diffusion' at an average of 1km per year (*Ammerman, Cavalli-Sforza 1971; 1984*; but see *Currat 2012*).

The geneticists shifted the focus from phenotypes to genotypes, from cranial characteristics to classic genetic markers, from races to populations. They linked the first principal component (PC) of 38 gene frequencies of 'classic' marker distributions in modern European populations with the Early Neolithic

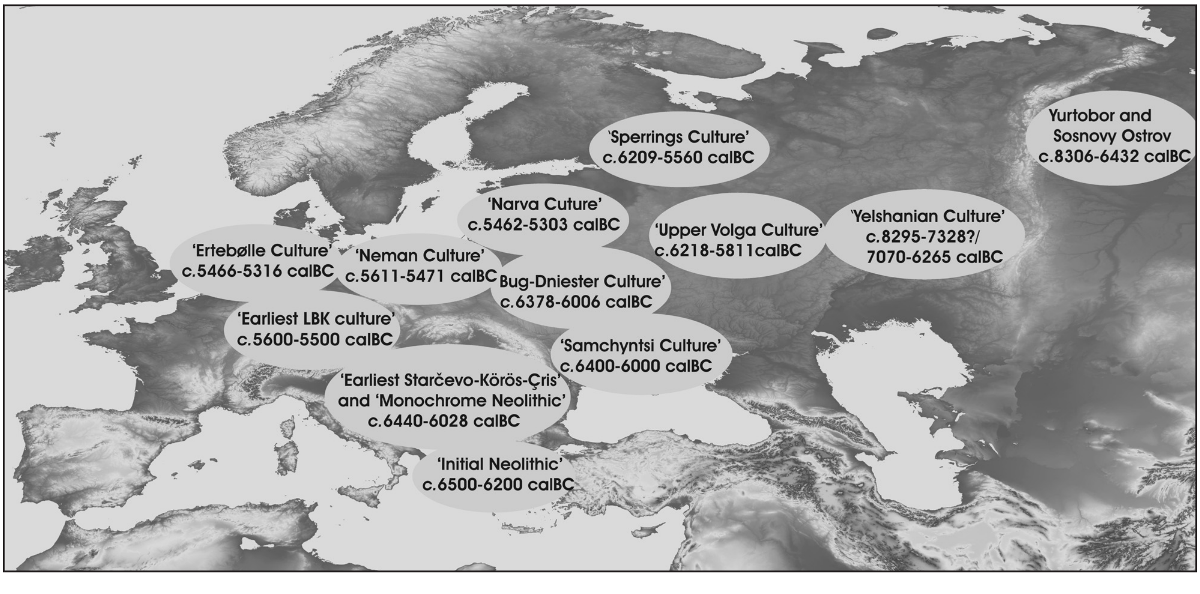

Fig. 4. The ^{14}C time spans of initial pottery distributions in hunter- gatherer groups in northeastern and eastern Europe, and in farming groups in southeastern, central and western Europe. For cultural contexts and ^{14}C dates see text with references.

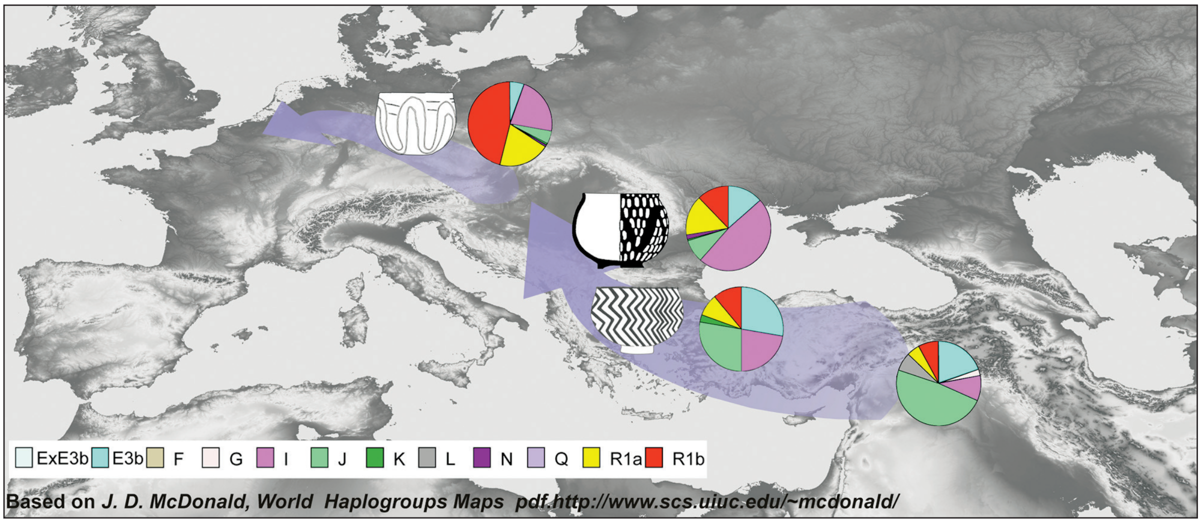

Fig. 5. The southeast-northwest cline of frequencies for Y-chromosome haplogroups J and E within modern European populations were hypothesised to be associated with Levantine male contribution to the European Neolithic. It was suggested they geographically overlap with the distribution of Early Neolithic painted pottery and settlements distributions in Southestern Europe. Northeast and East Europe were marginalised, having no point of entry and remaining a blank through the period. The haplogroups distribution is based on McDonald's World Haplogroups Maps (**McDonald 2005*****).***

'wave of advance' or 'demic diffusion' of farmers from the Near East into Europe. The gradual changes in allele frequencies summarised on spatially interpolated 'synthetic maps' of allele-frequency distributions are due to the absorption of local hunter-gatherer populations into farming communities. During the 'demic diffusion' process, the local admixture of indigenous hunter-gatherers in the advancing wave of farmers was hypothesised as minimal. The 'first demic event' was believed to have significantly reshaped European population structure, and the current European gene pool was interpreted as consisting mainly of genetic variations originating in Near Eastern Neolithic populations, with only a small contribution from Mesolithic Europeans. It was suggested that 'demic diffusion' generated a genetic continuity between the Neolithic and modern populations of Europe (*Menozzi* et al. *1978; Cavalli-Sforza* et al. *1994*). However, the 'demic diffusion' model was criticised because the local features of the PC 'synthetic maps' are mathematical artefacts that "*do not necessarily indicate specific localized historical migration events*" (*Novembre, Stephens 2008.646*). The PC gradients can occur even in the context of cultural diffusion, when there is no population expansion, and paradoxically, a 'very large level of Paleolithic ancestry' is necessary to produce the southeast-northwest gradient axis (*Arenas* et al. *2013.60*). The highest haplotype diversity in European population is found not in Southeast Europe, but on the Iberian Peninsula, thus suggesting a south-north gradient and trans-Mediterranean gene flow with northern Africa (*Novembre, Ramachandran 2011.259–260*).

The end of 'demic diffusion' migratory model

Since the revolution in the study of the human genome, studies have focussed on nuclear genetic DNA markers, *i.e.* mitochondrial (mt) and Y-chromosomal (*Renfrew 2000; Renfrew* et al. *2000; Thomas* et al. *2013*). The first is present in both sexes, but inherited only through the maternal line, while the latter is present only in males, and inherited exclusively through the male line (see *Jobling* et al. *2004*). Because they are non-recombinant and highly polymorphic, they are seen as ideal for reconstructing human population history and migration patterns. Thus different human nuclear DNA polymorphic markers (polymorphisms) of modern populations have been used to study genomic diversity, to define maternal and paternal lineage clusters (haplogroups), and to trace their (pre)historic genealogical trees, and chronological and spatial trajectories (*Goldstein, Chikhi 2002; O'Rourke 2003; Richards 2003; Torroni* et al. *2006; Olivieri* et al. *2013*). Particular attention has been drawn to the power of Y-chromosome biallelic markers, as they allow the construction of intact haplotypes and thus male-mediated migration can be readily recognised. We already mentioned above, it was hypothesised that the southeast-northwest cline of frequencies for selected Y-chromosome markers and related haplogroups indicates the movement of men with Levantine genetic ancestry, and

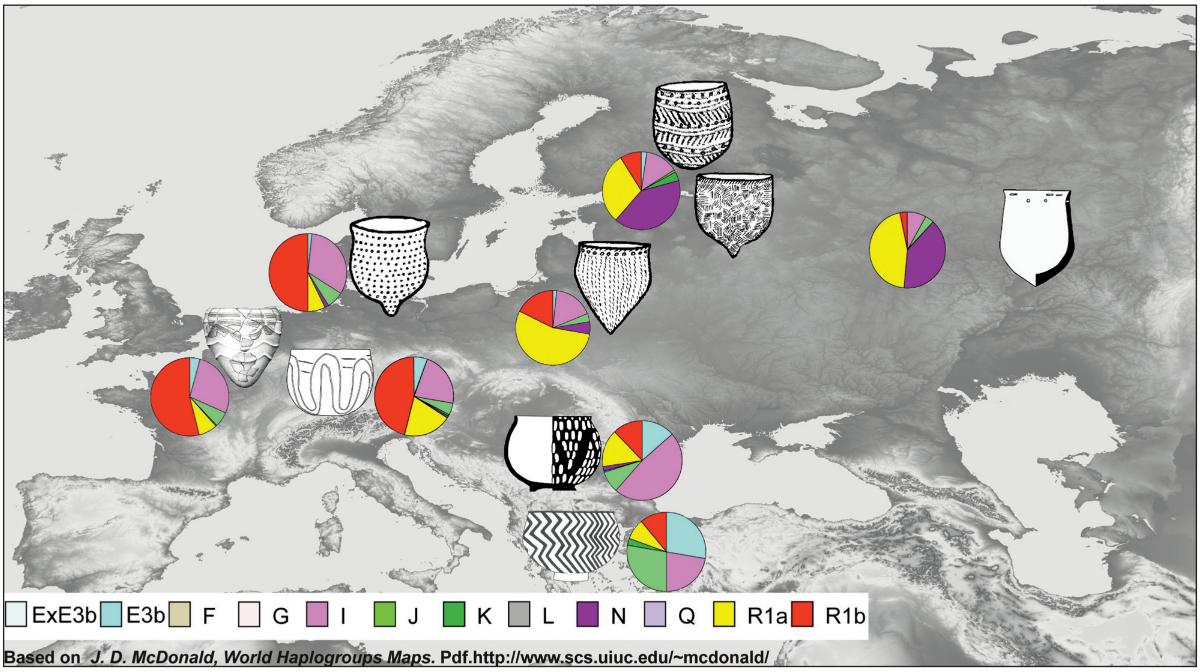

Fig. 6. The parallel clines of frequencies of Y-chromosome haplogroups J, E and N in modern populations in Europe and initial pottery distributions in Neolithic Europe. The haplogroup distribution is based on McDonald's World Haplogroups Maps (*McDonald 2005*).

that this coincides with the distribution of Early Neolithic painted pottery and ceramic female figurine distributions in Europe (*King, Underhill 2002*).

Indeed, recent genetic studies suggest that the modern peopling of Europe was a complex process, and that the view of a single demic event in the Early Neolithic is too simplistic (*Pinhasi 2012*). The paternal heritage of the modern population of Southeast Europe reveals that the region was both an important source and recipient of continuous gene flows. The studies of the Y-chromosomal hg J1 (M267), J2 (M172), E (M78) and I (M423) strongly suggest continuous Mesolithic, Neolithic and post-Neolithic gene flows within Southeast Europe and between Europe and the Near East in both directions. In addition, the low frequency and variance associated with I and E clades in Anatolia and the Middle East support the European Mesolithic origin of these two haplogroups. The Neolithic and post-Neolithic components in the gene pool are most clearly marked by the presence of J lineages. Its frequency in Southeast European populations ranges from 2% to 20%, although some lineages may have arrived earlier than the Neolithic, which has led to the level of Neolithic immigration being overestimated (*King* et al. *2008; Battaglia* et al. *2009*). However, the mitochondrial genome dataset and timescale for lineages show that possible candidates for Neolithic immigration from the Near East would include hg J2a1a and K2a. It seems, however, that the immigration was minor (*Soares* et al. *2010*).

The lactase persistence paradox

Dairying and lactose tolerance in European populations, marked by the –13 910*T allele, are thought to have evolved in a relatively short period in the northern Balkans and were introduced to Central Europe by lactase-persistent farmers within the 'first demic event' at 'around 6256–8683 years BP' (*Itan* et al. *2009.7;* see also *Itan* et al. *2010; Burger, Thomas 2011; Gerbault* et al. *2011. Leonardi* et al. *2012;* for discussion see *Budja* et al. *2013*). A simulation model of the evolution of lactase persistence suggests that natural selection began to act on a few lactase persistent individuals of the Starčevo and Körös cultures in the northern Balkans. Lactase persistence frequencies rose rapidly in the 'gene-culture co-evolutionary process on the wave front of a demographic expansion into central Europe' and overlap well with the region where Linear Pottery culture (LBK) developed (*Itan* et al. *2009. 8; Leonardi* et al. *2012.95*). The raw milk fats and dairy fat residues (*i.e.*, lipids) preserved in ceramic vessels indeed show that milk was exploited in the Carpathian Basin between 6000–5500 calBC (*Evershed* et al. *2008*). However, the scenario of lactase-persistent farmers in Central Europe seems to be unrealistic. The palaeogenetic analysis of Neolithic skeletons suggests "*that lactase persistence frequency* *was significantly lower in early Neolithic Europeans than it is today, and may have been zero*" (*Leonardi* et al. *2012. 93*). Indeed, the analysis revealed an absence of the –13 910*T allele in Central Europe, in western Mediterranean and the Baltic (*Burger* et al. *2007; Burger, Thomas 2011; Lacan 2011; Linderholm 2011; Nagy* et al. *2011*).

Mesolithic and Neolithic human DNA

Recent phylogenetic analyses of ancient mitochondrial and Y-chromosomal DNA (aDNA), extracted from Mesolithic and Neolithic human remains have revealed a genetic structure that cannot be explained by a southeast-northwest oriented 'wave of advance' or 'demic diffusion' of Near Eastern farmers and hunter-gatherer population replacements. Advances in aDNA methods and next-generation sequencing allow new approaches which can directly assess the genetic structure of past populations and related migration patterns. Mitochondrial aDNA analyses thus suggest variations in population trajectories in Europe. In central Europe, Neolithic farmers differed in various genetic markers from both Mesolithic hunter-gatherers and from modern European populations (*Haak* et al. *2005; 2010; Bramanti* et al. *2009; Burger, Thomas 2011*). The characteristic mtDNA type N1a, with a frequency distribution of 25% among Neolithic LBK farmers in Central Europe, is in contrast with the low frequency of 0.2% in modern mtDNA samples in the same area (*Haak* et al. *2005*). It was not observed in hunter-gatherer samples from Western and Northern Europe. On the contrary, hg H dominates (40%) present-day Central and Western European mitochondrial DNA variability. It was less common among Early Neolithic farmers and virtually absent in Mesolithic hunter-gatherers. Phylogeographic studies suggest that it arrived in Europe from the Near East before the Last Glacial Maximum, and survived in glacial refuges in Southwest Europe before undergoing a post-glacial re-expansion. Recently published analyses of the maternal population history of modern Europeans and hg H mitochondrial genomes from ancient human remains show that Early Neolithic lineages "*do not appear to have contributed significantly*" to present-day Central Europe's hg H diversity and distribution (*Brotherton* et al. *2013.7*). The hg H was associated with LBK culture, but lineages were lost during a short phase of population decline after 5000 calBC. The current diversity and distribution were largely established by the strong post-LBK population growth and by "*substantial genetic contributions from subsequent pan-European cultures such as the Bell Beakers expanding out of Iberia in the Late Neolithic, ... after which there appears to have been substantial genetic continuity to the present-day in Central Europe*" (*ibid. 7*; see also *Lee* et al. *2012.577*).

A rather different picture emerges from the Iberian Peninsula, where the Neolithic composition of the haplogroup population (*e.g.*, hg H, T2, J1c, I1, U4, W1) "*is not significantly different from that found in the current population from the Iberian Peninsula*", but differs from the Near Eastern groups (*Sampietro* et al. *2007.2165*). Interestingly, there is no evidence of the mt aDNA hg N1a in either Spain or France (*Lacan* et al. *2011*). Two Mesolithic individuals, on the contrary, carried a mitochondrial U5b haplotype which does not cluster with modern populations from Southern Europe (including Basques), as suggested recently (*Sánchez-Quinto* et al. *2012; Behar* et al. *2012*).

The mt aDNA sequences from contemporary hunter-gatherer and farmer populations in Scandinavia and the Baltic differ significantly. These populations are unlikely to be the main ancestors of either modern Scandinavians or Saami, but indicate greater similarity between hunter-gatherers and modern eastern Baltic populations (*Linderholm 2011*). It has also been suggested that Scandinavian Neolithic hunter-gatherers shared most alleles with modern Finnish and northern Europeans, and the lowest allele sharing was with populations from Southeast Europe. In contrast, Neolithic farmers shared the greatest fraction of alleles with modern Southeast European populations, but were differentiated from Levantine populations and showed a pattern of decreasing genetic similarity to 'populations from the northwest and northeast extremes of Europe' (*Skoglund* et al. *2012. 469*). The most recent arhaeogenetic study reveals an extensive 'heterogeneity in the geographical, temporal and cultural distribution of the mtDNA diversity' in Northeast Europe. While some mt aDNA sequences from hunter-gatherer sites show a genetic continuity in some maternal lineages (*e.g.*, hg U4, U5 and H) in Northeast Europe since the Mesolithic, and also genetic affinities with extant populations in Western Siberia, the precise genetic origins of the others is more difficult to identify. They all display clear haplotypic differences with contemporary Saami populations. The major prehistoric migration in the area was thought to have been associated with 'the spread of early pottery from the East' (*Der Sarkissian* et al. *2013.10–12*).

Unfortunately, we still do not know what happened to the Mesolithic hunter-gatherer and Neolithic populations in Southeast Europe, as no aDNA studies have yet been carried out in the region.

Instead of concluding remarks

Initial pottery distribution in Europe shows two almost contemporary, but geographically distinct, trajectories. While the northern is embedded in hunter-gatherer contexts, it has been suggested that the southern was associated with the expansion of farming into the region. The pottery assemblages in both contexts differ in terms of vessel shapes, production techniques and decoration. While vessels with conic bases were not modelled in Southeast Europe, coloured ornaments were never attached to vessels in the north-east or north-west. Unpainted vessels were clearly the first to appear in Europe in the 7th millennium calBC. Since coloured ornaments were attached to pots in Southeast Europe, a dichotomy of colour and motif applications in the European Early Neolithic becomes evident. Red and brown geometric and floral motifs were limited to the Peloponnese and the southern Balkans; white painted dots and spiral motifs were distributed across the northern and eastern Balkans and southern Carpathians.

Geneticists suggest that the processes of peopling Europe in prehistory were far more complex and variable than was first thought. The palimpsest of Y-chromosomal paternal and mitochondrial maternal lineages in modern populations reveals the signatures of several demographic expansions within Europe over millennia, and gene flows between Europe and western Asia in both directions. These processes have been suggested for the Mesolithic, Neolithic and Chalcolithic periods and seem to be more visible in the frequency of Y-chromosome markers in modern populations in the Balkans and Mediterranean than in other regions. Recent analyses of ancient DNA and palaeodemographic reconstructions show a complex picture of varied population trajectories elsewhere in Europe, and while such studies have yet to be conducted for Southeast Europe, a similar picture may be expected.

We suggest that the Mesolithic-Neolithic transformation, too, was also a far more complex and variable process than previously hypothesised. The introduction of ceramic technology and initial pottery distributions in Eurasia show a wide-spread appearance of different pottery-making techniques and ornamental principles in different cultural and chronological contexts. The pattern cannot be explained by way of a narrow and gradual southeast/northwest oriented spread of both people and vessels across Europe in a 'wave of advance' and within a 'first demic event'. We suggest that both were embedded in continuous social networks established long before the advent of the Neolithic in the Levant.

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