

partitioned and were genetically distinct prior to the onset of the Neolithic, then different models may be taken to predict different genetic patterns.

The first model is classic "migrationism" and would involve genetic replacement, so that the sink region (Europe) should be genetically indistinguishable from the source (the Near East), except for any differentiation that had taken place within the last 8000 years. Model (7) would involve no movement of genes whatsoever – Ammerman's "indigenism" (Ammerman 1989). This would include both cultural diffusion (Dennell 1983; Barker 1985; Whittle 1996) and separate development, in which the social and ideological, rather than economic, aspects of the Neolithic take centre stage (Hodder 1990; Thomas 1996; 1998). In this case, the source and sink regions should remain genetically distinct, except for the effects of any post-Neolithic gene flow between them.

Models (2) to (6) are all "integrationist" (Zvelebil 2000) in character, involving both the arrival of new genetic lineages in an area, and the eventual acculturation of the indigenous communities. Élite dominance might show minor evidence of newcomers, although it might not be relevant to the question of the early Neolithic (Renfrew 1987). The wave of advance model predicts continent-wide genetic clines (Ammerman and Cavalli-Sforza 1984). Infiltration and leapfrog colonization would be likely to leave traces of Near Eastern lineages in the regions where they had occurred, but in patches rather than in the form of clear clines. Frontier mobility would allow for genetic exchange between colonised, newly Neolithic areas such as central Europe, and forager strongholds to the north and west. In each of these, however, any genetic discontinuities might tend to be eroded over time as the effects of subsequent gene flow acted to blur the picture.

CLASSICAL MARKERS

It has long been assumed (by population geneticists, at least), that classical markers support the Ammerman and Cavalli-Sforza (1984) model of demic diffusion by means of a wave of advance. This model depended on a view of the early Neolithic that emphasized sedentism, local population growth, and expansion into more marginal environments. Ammerman and Cavalli-Sforza (1984) modelled the expansion using Fis

The conclusions of Ammerman and Cavalli-Sforza and their colleagues were supported by Sokal and colleagues (Sokal et al. 1989; 1991), using spatial autocorrelation analysis. This approach also indicated that about a third of classical markers were arranged in a southeast-northwest cline. With this backing, the assumed model of surplus-driven population growth and expansion gained ground and began to be taken for granted amongst population geneticists. Despite the inability of these methods to quantify the demographic impact of the Neolithic newcomers, the role of the putative pioneers came to be emphasized at the expense of the indigenous Mesolithic peoples of Europe. Furthermore, the idea that the PC maps could be interpreted chronologically, like archaeological stratigraphy, also took hold (Cavalli-Sforza 1996).

However, gradually some criticisms were expressed. Why interpret the first PC solely in terms of Neolithic expansion? Europe is a small peninsula of the Eurasian landmass, and as such is likely to have been the sink for many dispersals throughout prehistory. The PC maps were much more likely to represent a palimpsest of dispersals, each one overwriting the last (Zvelebil 1989; 1998). The idea of "one PC—one migration", suggested quite specifically by Cavalli-Sforza, was highly implausible; and this disposed equally of the idea that principal components provided a genetic stratigraphy. Indeed, the problematic second PC, running southwest–northeast, was increasingly looking as if it might be explained at least in part by Lateglacial hunter-gatherer expansions, preceding the Neolithic by more than 5000 years (Torrioni et al. 1998).

The archaeological aspects of Ammerman and Cavalli-Sforza's work also sustained criticism. Items in the "Neolithic package", it was pointed out, rarely moved together, except in southeast and central Europe, and they were often exchanged into Mesolithic communities (Thomas 1996; Zvelebil 1986; Price 2000). This could have led Ammerman and Cavalli-Sforza to over-estimate the impact of the Neolithic and the uniformity of its spread. More recent studies have tended to emphasize that the spread of the Neolithic was a heterogeneous

These developments have led to the development of what has been termed the "phylogeographic" approach (Richards et al. 1997; Bandelt et al. 2002). Phylogeography is a heuristic tool for interpreting complex population-genetic data that tries to make maximum use of reconstructed trees of descent, along with the geographic distribution and diversity of genealogical lineages; it is effectively the mapping of gene genealogies in time and space (Avice 2000.3). The process of testing phylogeographic hypotheses always entails making assumptions, and inevitably has to be carried out within a model or framework based on external information (such as from archaeology). Even so, the assumptions themselves can often be susceptible to empirical investigation, and may often be less unrealistic than those of more traditional population-genetics approaches (Richards et al. 2000).

MITOCHONDRIAL DNA

The first major application of phylogeographic procedures to the question of European genetic variation was an analysis of mitochondrial DNA (mtDNA) (Richards et al. 1996). This work made use of a new phylogenetic-network approach to tree reconstruction, developing new phylogeographic approaches, such as founder analysis, to the study of migration and colonization.

Founder analysis works by comparing the genetic variation in a region that has been settled by a small group of individuals (founders) to the genetic variation in a region that has been settled by a large group of individuals (colonists). The genetic variation in the founder population is expected to be lower than the genetic variation in the colonist population because the founder population is smaller and therefore has less genetic diversity. This is known as the founder effect. Founder analysis can be used to study migration and colonization events in a variety of organisms, including humans.

ment (Semino et al. 1996). However, Semino et al. (2000) teased out some of the more detailed patterns for the first time, providing some interesting parallels with the mtDNA work. They identified several potentially Neolithic markers that implied a Near Eastern Neolithic contribution to Europe as a whole of less than 25%. There have been recent criticisms of their interpretation by Chikhi et al. (2002), on the grounds that an admixture approach suggests a much higher putative Neolithic contribution than the crude estimates. However, their arguments are unconvincing, since an admixture approach seems quite inappropriate in the context of the questions under consideration, and suffers from some of the weaknesses of the classical approach (such as lack of dating).

It is noticeable, though, that the putative Neolithic lineages are markedly more common along the Mediterranean than in central Europe, which contrasts somewhat with the mtDNA picture described above. Without a founder analysis, such as has been done for mtDNA, it is certainly likely that earlier and later processes may be conflated: the palimpsest problem again. The question is to what extent. King and Underhill (2002) have argued that the high correlation between the distribution of painted pottery and anthropomorphic clay figurines and some of the putatively Neolithic Y chromosomes indicates that indeed at least some of the latter do represent early Neolithic settlement. This implies that, on the male side, intrusive lineages from the Near East only spread through the first burst of Neolithic settlement in Europe around the eastern Mediterranean basin, but were not carried to an appreciable extent into central Europe with the LBK. This in turn supports the view that high levels of acculturation took place in the Balkans prior to the LBK expansion (Gronenborn 1999; 2003). The Near Eastern lineages that spread through the eastern and central Mediterranean in the early Neolithic would have been subsequently overlaid by later Near Eastern dispersals. It

East (Gronenborn 1999). Archaeological evidence is now emerging from both ceramics and lithics for the assimilation of Mesolithic groups into LBK settlements (cf. Gronenborn 2003).

There is some evidence for further colonization from the LBK zone into the northwest, including the British Isles, whereas the pattern in Scandinavia might be explained by frontier exchange. The Atlantic west seems also to have experienced distinct, presumably maritime leapfrog colonization events from the direction of the west Mediterranean coastline. The movements into the northwest seem either not to have

involved men, or to have involved male lineages that had undergone acculturation, and were therefore indigenous to central Europe. In all or most regions of Europe, even in the LBK zone, there seems to have been substantial local adoption of agriculture.

I would like to thank Detlef Gronenborn for critical advice on an earlier version of this manuscript, and Mehmet Özdoğan and Catherine Perlès for valuable comments during the conference at which this work was presented.

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