Quaternary Science Reviews 164 (2017) 217–229

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

# Risky business: The impact of climate and climate variability on human population dynamics in Western Europe during the Last Glacial Maximum

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A R T I C L E I N F O

*Article history:*
Received 25 October 2016
Received in revised form
18 March 2017
Accepted 1 April 2017

*Keywords:*
Pleistocene
Paleoclimate modelling
Western Europe
Random Forest
Upper Palaeolithic
Last Glacial Maximum
Population dynamics

A B S T R A C T

The extent to which climate change has affected the course of human evolution is an enduring question. The ability to maintain spatially extensive social networks and a fluid social structure allows human foragers to "map onto" the landscape, mitigating the impact of ecological risk and conferring resilience. But what are the limits of resilience and to which environmental variables are foraging populations sensitive? We address this question by testing the impact of a suite of environmental variables, including climate variability, on the distribution of human populations in Western Europe during the Last Glacial Maximum (LGM). Climate variability affects the distribution of plant and animal resources unpredictably, creating an element of risk for foragers for whom mobility comes at a cost. We produce a model of habitat suitability that allows us to generate predictions about the probable distribution of human populations and discuss the implications of these predictions for the structure of human populations and their social and cultural evolution during the LGM.



## 1. Introduction

The Last Glacial period was marked by pronounced climate instability and decreasing global temperatures, culminating with the Last Glacial Maximum (LGM) from 19,000 to 23,000 calibrated radiocarbon years Before Present (cal. B.P.) (Mix et al., 2001). Coinciding with Greenland Stadial 2.1 (Rasmussen et al., 2014), the LGM marks the maximum global ice volume and lowest sea stand during the last Glacial period (Mix et al., 2001). Climate conditions during this interval are thought to have significantly affected human population dynamics in Europe (Banks et al., 2013; Bocquet-Appel et al., 2005; Bocquet-Appel and Demars, 2000; d'Errico and Sánchez Goñi, 2003; Gamble et al., 2004; Müller et al., 2011; Tallavaara et al., 2015; Tzedakis et al., 2007; van Andel and Davies, 2003; Verpoorte, 2009). Genetic evidence supports the existence of a Western Eurasian meta-population (including Western Europe) by 33,000 cal. B.P. (Fu et al., 2014, 2016; Posth et al.; Seguin-Orlando et al., 2014; Skorecki and Behar, 2013). Palaeogenetic data, however, indicate that large-scale population displacements occurred across Europe during the LGM (Fu et al., 2016) resulting in a loss of genetic diversity, followed by genetic turnover (Posth et al.; Soares et al., 2010). This reconstruction is consistent with paleontological evidence for the emergence of a modern European morphotype after 19,000 cal. B.P. (Churchill et al., 2000). The genetic evidence, together with the spatial distribution of archaeological sites and increasing regionalisation of Palaeolithic cultures (Gamble et al., 2004), suggest that the Western Eurasian meta-population became fragmented during the LGM. The role of climate change in shaping the social and biological history of modern human populations in Europe, therefore, is of considerable interest to scientists seeking to interpret the archaeological record.

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http://dx.doi.org/10.1016/j.quascirev.2017.04.001
0277-3791/

Archaeological evidence suggests that modern humans first entered Europe from Western Asia between 45,000 and 38,000 cal. B.P., travelling along two initial dispersal routes: west along the Danube valley to the Swabian Jura and from there south along the Rhône valley towards the Mediterranean coast; and west along the northern Mediterranean coastline (Conard et al., 2006; Conard, 2002; Conard and Bolus, 2003; Higham et al., 2012; Hublin, 2014; Mellars, 2006). This reconstruction of the timing and direction of human dispersals into Europe rests on the assumption that the early Aurignacian is the product of dispersing groups of modern humans (Davies, 2001, 2007), an assumption recently supported by physical and chronological evidence (Benazzi et al., 2015; Higham et al., 2011; Hublin, 2014). The geographical distribution of archaeological sites suggests that human populations in Europe retreated south of 49°N during the LGM (Verpoorte, 2009), contracting their range towards the southern Mediterranean peninsulas which acted as glacial refugia (Bailey et al., 2008; Gamble et al., 2004; Jennings et al., 2011; Jochim, 1987; Straus, 2015). At the same time, the archaeological record reveals the increased regionalisation of material culture (Gamble et al., 2004; Straus, 2000). Regional cultural differences existed previously, during the early Upper Palaeolithic (Vanhaeren and d'Errico, 2006), but with the onset of the LGM material culture production takes on a markedly regional expression, illustrated by the development of the Solutrean culture in Franco-Cantabria (Renard, 2011).

A full and convincing explanation for the successful initial expansion of modern human populations and the apparently rapid re-colonisation of northern Europe following the LGM remains elusive. It has been suggested that modern humans were dispersible and quick to take advantage of climatic upturns (Conard, 2011; Grove, 2015; Müller et al., 2011; Pinhasi et al., 2011; Tzedakis et al., 2007). This would have conferred an advantage during periods of climate instability, such as the period preceding the LGM and the period immediately following it, as the climate began to warm again. A reorganisation of human society with the “release from proximity” (Gamble, 1998), i.e., the ability to maintain relationships beyond the constraints of physical proximity, enabled the creation of spatially extensive social networks and may well have equipped modern human populations with a heightened ability to deal with environmental instability, or ecological risk, by facilitating information and resource sharing (Burke, 2012; Whallon et al., 2011). These hypotheses cannot be assessed, however, until we have identified a means of quantifying ecological risk under past climate regimes and fully tested the sensitivity of human systems to it, alone and in combination with topography and climate.

### *1.1. Hunter-gatherers and risk*

Upper Palaeolithic populations pursued a mobile, hunting and gathering way of life. As (Kaplan, 2000) states on p.311: “One of the perennial problems confronted by virtually all hunter-gatherers is not only the seasonal variation in resources, but more significantly the periodic failure of all major resources”. The ethnographic, ethnohistorical and archaeological records suggest that hunter-gatherers are capable of adapting to a wide range of conditions. Seasonal variability may be a recurrent problem, but to the extent that it is predictable it doesn't constitute risk. Seasonal fluctuations in productivity can be anticipated and counter-measures applied, generating recurring patterns in the archaeological record (e.g., patterns of seasonal mobility and site occupation). Unpredictable variation in the distribution of resources, on the other hand, constitutes ecological risk since it means the outcome of foraging behaviour is uncertain (Winterhalder et al., 1999). Ecological risk, therefore, is not the same thing as resource scarcity. Unpredictable shifts in productivity are more difficult to manage and their impact is scale dependant. For example, whereas the failure of a single resource may be countered by substituting other resources, the failure of a key resource (or multiple resource failure) may force a spatial reorganisation of the hunter-gatherer system.

The ability to deploy a variety of strategies to mitigate ecological risk is deeply embedded in the social, technological and economic structure of human hunting and gathering groups. Rather than simply engaging the world around them on a day-to-day basis, hunter-gatherers anticipate and actively evaluate strategies that minimize risk over the long term (Kelly, 2013) p.164. These strategies include technological innovation, such as the introduction of storage mechanisms to even out energy imbalances (Rowley-Conwy and Zvelebil, 1989), changes in diet (Stiner, 2001; Stutz et al., 2009; Winterhalder, 1981), the use of social mechanisms such as food-sharing and reciprocity (Bird-David, 1992; Cashdan, 1985; Smith, 1988; Weissner, 1982; Winterhalder, 1986; Winterhalder, 2001) and of course, mobility (Binford, 1981; Grove, 2009, 2010; Morgan, 2009; Yellen, 1986). These risk-reducing strategies allow human systems to manage resource fluctuations while minimising disruption - in other words, they confer resilience. Risk management strategies have social and emotional costs, however, and may affect the size and cohesiveness of hunter-gatherer social groups (Kelly, 2013) as well as other aspects of human culture (Collard et al., 2011). One expects, therefore, that trade-offs between different strategies will be carefully weighed (Winterhalder et al., 1999).

Repositioning people on the landscape is a common strategy for countering ecological risk (Morgan, 2009) and the nature of the response is linked to the scale of the risk (Collard et al., 2011). Hunter-gatherers may counter short-term variability in the distribution of resources by shifting from logistical to residential mobility strategies, for example (Morgan, 2009). In a residential strategy, base camps are abandoned when the resources within their local catchment are exhausted (*sensu* (Vita-Finzi and Higgs, 1970)), whereas a logistical strategy extends the effective catchment of base camps through the use of special purpose camps, located some distance away and exploited by small work parties (Binford, 1982). At a larger scale, however, ecological variability may induce more disruptive changes which come at a greater cost, both socially (as local groups disband) and physiologically, because mobility has energetic costs commensurate with the distances involved (Kelly, 1992) and the structure of the environment. In addition, mobility carries an element of risk, due to incomplete knowledge of conditions at distal locations (Winterhalder et al., 1999), that is scaled to distance: the further away the move, the greater the risk. Information sharing removes some, but not all of the uncertainty associated with residential mobility (Kelly, 1992; Whallon, 2006; Whallon et al., 2011). Ultimately, accurately predicting resource availability at distal locations is only possible if climate conditions generate consistent and predictable patterns.

The distribution of archaeological sites in Europe indicates human range contractions during the LGM, suggesting that environmental conditions exceeded the ability of hunter-gatherer systems to adapt and disrupted their spatial organisation. In this research, we aim to develop a robust and parsimonious predictive statistical model of habitat suitability which will allow us to identify the key environmental stressors that affected human population dynamics during the LGM and investigate the role of ecological risk in shaping their spatial distribution.

### *1.2. Climate change, climate variability and risk*

Climate affects human systems at different spatial and temporal scales. Climate change, which refers to changes in climate conditions occurring on a decadal scale or greater, is thought to have