Quaternary Science Reviews 96 (2014) 50–71

Contents lists available at ScienceDirect

Quaternary Science Reviews

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

Deconstructing mammal dispersals and faunal dynamics in SW Europe during the Quaternary

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ARTICLE INFO

Article history:
Received 15 July 2013
Received in revised form
27 April 2014
Accepted 1 May 2014
Available online 17 June 2014

Keywords:
Biochronology
Biodiversity
Dispersal
Turnover
Large mammals
SW Europe
Pleistocene

ABSTRACT

This research aims to investigate the relationships between climate change and faunal dynamics in south-west Europe, disentangling the asynchronous and diachronous dispersal bioevents of large mammals across geographical and ecological boundaries, analysing biodiversity and its changes through time. The analysis of local versus regional biological dynamics may shed new light on whether turnovers and ecological and evolutionary changes developed because of global climate changes and related phenomena, or because of intrinsic biological factors. The SW European Quaternary fossil record is particularly suitable for studying the role of climate change at local and regional levels because of the complex physiographic and climatic heterogeneity of the study area, the presence of important geographical/ecological barriers and the complex history of invasions of species of varying geographical origin and provenance. The data base consists of taxonomically revised lists of large mammal species from selected SW European local faunal assemblages ranging in age from the Early to the late Middle Pleistocene (middle Villafranchian to early Aurelian European Land Mammal Ages). The new biochronological scheme proposed here allows for the comparison of local turnovers and biodiversity trends, yielding a better understanding of the action of geographical/ecological barriers that either prevented the range of some taxa from reaching some regions or caused delays in the dispersal of a taxon in some territories. The results obtained provide evidence that major environmental perturbations, triggering dispersal events and removing keystone species, modified the structure of the pre-existing mammalian faunas, merging previously independently-evolved taxa into new palaeo-communities. The coupled action of climatic changes and internal biotic dynamics thus caused the Quaternary SW European faunal complexes to significantly restructure. Diachroneity in local turnover across the study area probably relates to differences in local dynamic patterns of competition/coevolution, although different manifestations of global climate changes in different geographic settings would have contributed to the scale of local bioevents.

1. Introduction

This paper deals with dispersal events, shifts in biodiversity and taxonomical turnovers of large mammals in SW Europe. It compares trends among three focal territories, i.e. the Iberian Peninsula, France and Italy, with the aim of providing a fresh perspective on the debate as to whether climate and ecosystem changes may have affected dispersals of hominin populations towards SW Europe in the late Early Pleistocene.

The multifaceted and intriguing evolutionary history of mammals, which culminated in the biodiversity and biogeographical patterns seen today, has been deeply influenced by the palaeogeographic, climatic and environmental changes experienced by our planet, especially during the Cenozoic. Nonetheless, the actual role of climate in driving both faunal dynamics along geographical gradients and human evolution, through determining dispersal routes and settlement in new territories (i.e. in southern Europe and subsequent expansion northward) is still a hotly debated topic in palaeobiology, palaeoanthropology and palaeoecology.

Despite the growing amount of data and the increasing interest in establishing the baseline factors that may have promoted the earliest dispersals of hominins towards Western Europe, we are still far from deciphering the complex relationships between climate changes and vegetation, fauna, and human evolutionary dynamics. A number of questions as to the causal mechanisms promoting human diffusion and permanent settlement in focal areas still

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http://dx.doi.org/10.1016/j.quascirev.2014.05.013
0277-3791/

remain open to discussion. When did hominins first disperse towards southern Europe and from which "core" population? Did such dispersals coincide with those of other mammalian taxa? To what extent (if any) did changes in the environment and particularly in mammalian palaeo-communities have a role in shaping the timing and mode of human population dynamics? (for contrasting views, in addition to the papers quoted in Palombo, 2013a, see *inter alios* Eriksson et al., 2006; Fís, 2010; Westaway, 2010; deMenocal, 2011; Dennell et al., 2011; Joordens et al., 2011; Messager et al., 2011; Anton and Snodgrass, 2012; Dennell and Petraglia, 2012; Issar et al., 2012; Louys and Turner, 2012; MacDonald and Roebroeks, 2012; MacDonald et al., 2012; Potts, 2012, 2013; Preece and Parfitt, 2012; Rodríguez et al., 2012, 2013; Stewart and Stringer, 2012; Tourloukis and Karkanas, 2012; Bar-Yosef and Belfer-Cohen, 2013; Bermúdez de Castro et al., 2013; D'Errico et al., 2013; Finlayson, 2013; Garcia et al., 2013; Groves, 2013; Hertler et al., 2013; Huguet et al., 2013; van der Made, 2013; Magill et al., 2013; Mosquera et al., 2013; Parés et al., 2013; Rodríguez-Gómez et al., 2013; Tipple, 2013; Toro-Moyano et al., 2013).

Hominin presence in Southern Europe in the earliest Pleistocene (middle Villafranchian European Land Mammal Age, ELMA) has been claimed at a number of controversial sites, including supposed artifacts at Dealul Mijlociu Hill (Romania), found in sandy gravels overlying a faunal assemblage referred to the MN 17 "biozone" (Radulescu et al., 2003), alleged pebble tools reported from Chillac III, (Haute Loire, France) (Guth, 1974; Texier, 1985) [(inferred age bracketed by the underlying Varennes lava flow (2.47 Ma) and the overlying Les Sognes lava flow (2.0–1.6 Ma) (Boivin et al., 2010)], lithic implements (likely geo/tephrofacts, Raynal and Magoga, 2000) from the French Central Massif deposits of Saint-Eble (2.1–2.5 Ma, Bonifay, 1989) and les Etouaires (about 2.5 Ma, G.U.E.R.P.A. et al., 1984). Archaeological evidence indicates the existence of hominin groups in the early post-Olduvai Pleistocene, around 1.5 Ma, both in southern France (Lézignan Le-Cèbe, Hérault, Crochet et al., 2009) and southern Italy (Pirro Nord, Apulia, Arzarello et al., 2012), whereas some uncertainties exist concerning the actual age of lithic implements found in Eastern European sites (Moncel, 2010), such as Kozarnika (Bulgaria, estimated age from 1.6 to 1.4 Ma, Guadelli et al., 2005; Sirakov et al., 2010) and Sandalja 1 (Croatia, possibly pre-Jaramillo age, Spassov, 2003). The claimed presence of hominin groups in the Lower Don valley in Russia, based on scratches identified as cut-marks on a metatarsal of the middle Villafranchian species *Paracamelus alutensis* found in the Liventsovka local faunal assemblage (LFA) (Khaprovian faunal complex, 2.1–1.97 Ma) (Sablin and Girya, 2010), requires further support.

Geological and anatomical evidence indicate that a hominin population showing a high morphological variation was settled at the gates of Europe, in the southern Caucasus region, from about 1.85 to 1.77 Ma years ago (Lordkipanidze et al., 2007, 2013; Garcia et al., 2009; Agustí and Lordkipanidze, 2011; Ferring et al., 2011; Margvelashvili et al., 2013; Bermúdez de Castro et al., 2014). The Caucasus has been therefore regarded as a potential core area for the dispersal of hominin groups towards both Asia and Europe, although available data do not conclusively confirm the hypothesis that first European homin settlers dispersed from Caucaso. In SW Europe, *Homo* remains are first recorded in Spain in deposits whose ages range from about 1.4 (Barranco Léon, Orce Basin, Toro-Moyano et al., 2013) to 1.3–1.2 Ma (Atapuerca, Sima del Elefante T9, Carbonell et al., 2008). The arrival of hominin groups in SW Europe possibly resulted from a second "Out of Africa" dispersal event, across the Levantine corridor and maybe the Balkan region, but the hypothesis can at present be neither confirmed nor refuted.

Whatever the source area and the number and routes of dispersals, a body of evidence confirms that between about 1.5 and 1.1 Ma, the presence of archaic human groups was restricted to Southern Europe (see e.g. Dennell and Roebroeks, 2005; Hughes et al., 2007; Dennell, 2010, 2011; MacDonald and Roebroeks, 2012; MacDonald et al., 2012; Bermúdez de Castro et al., 2013; Palombo, 2013a, with bibliography), with a subsequent diffusion into Central Europe at the time of the Jaramillo event (Untermassfeld, Germany; Landeck, 2010; Garcia et al., 2013) or even later (Happisburgh III in Norfolk and Pakefield in Suffolk, UK, Parfitt et al., 2005, 2010).

Analysing the dynamics of the large mammal fauna from the SW European regions (i.e. the Iberian Peninsula, France and Italy) during the Early Pleistocene is, therefore, of crucial importance to infer to what extent, if any, climate changes might have promoted dispersals, diffusion and at least temporary settlements of archaic human populations in these regions before and during the marked global transition in Earth's climatic system known as the Mid-Pleistocene Revolution (MPR) (Maslin and Ridgwell, 2005). Focal territories allow us to compare faunal dynamics at local and regional scales because of their rich Quaternary fossil records, the long and complex history of invasion species of varying geographical origin and provenance, competitive exclusion, origination of endemic species and the prolonged survival of some taxa in refuge areas. Although the specifics of past Quaternary climates differed from those at the present day and vegetation generally responded to these global climate changes, it may be reasonably assumed that climatic differences from one region to another, and the presence of geographical and ecological barriers have been maintained, differently influencing the dispersal and distribution patterns of a number of taxa.

With the challenging goal of investigating the relationships between climate change, faunal dynamics and human dispersals and for a more comprehensive understanding of the complex interplay of the underlying causal forces, it is crucial to provide a firm chronological framework in order to distinguish between asynchronous and diachronous dispersal bioevents and to define local versus regional diversity of large Pleistocene mammals and its changes over time. It is hoped that the resulting reconstruction of faunal dynamics and evolution may improve our understanding of the scenario leading to temporary or permanent hominin settlement in the focal area.

2. Material and Methods

A detailed explanation of the criteria for selecting the sources of data, ordering the SW European Local Faunal Assemblages (LFAs) within a common chronological framework and validating it at a regional scale, and for estimating the entity of dispersals and faunal changes at regional (SW Europe) and sub-regional (Iberian Peninsula, France and Italy) scales is given in Supplementary Information.

3. Results

3.1. Chronological ordering of SW European local faunal assemblages (LFAs)

The succession of SW European Faunal Complexes (FCs) is shown in Fig. 1. The resulting biochronological setting for large mammals in the study area (Supplementary Information, Tables 1 and 2) can be regarded as the "best-fit" currently allowed by the available data.

3.2. Dispersal bioevents and first appearances across the focal region

Data on first/last appearances and the chronological ranges of large mammals in SW Europe (Supplementary Information Tables 1