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Discrete dispersal bioevents of large mammals in Southern Europe in the post-Olduvai Early Pleistocene: A critical overview

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ABSTRACT

This research aims to deconstruct time and mode of dispersal of large mammals in SW Europe during the post-Olduvai Early Pleistocene, focusing on asynchronous versus diachronous appearance bioevents in the Iberian Peninsula, France and Italy. The geography of the region and its rich Quaternary fossil record is particularly suitable for studying the role (if any) of geographical/ecological barriers in either preventing some taxa to enlarge their range or causing their delayed appearances in some territories. The database consists of taxonomically revised lists of large mammalian species from selected faunal assemblages (LFAs) ranging from about 1.6 to 0.7 Ma. Results obtained show that a few diachronous appearances permit following the displacement/enlargement of species range limits across the studied region. Conversely it is a changing issue understanding which among several factors (e.g. the different impact of global climate changes in different geographic settings, differences in species resilience to habitat disturbance variability in competition and predation patterns within local faunal complexes, and heterogeneity of the fossil record) might have caused asynchronous appearances. The complex interplay of niche differentiation and biotic interactions in each region may be among the factors causing asynchronicity, though the influence of the heterogeneous consistency of the fossil record in space and time (e.g. number and richness of LFAs included in each FC), and taphonomical biases affecting the chronological reliability of local first/last appearances, cannot be discounted especially as regard to rare species.

1. Introduction

The dynamics of mammalian fauna and the evolution of terrestrial ecosystems in South Western Europe in the post-Olduvai Early Pleistocene have been receiving increasing interest during the last two decades, due to the hints these kind of studies can provide for a better understanding of factors that promoted the first appear ance of early hominids in the region at that time. This timespan includes the earliest phase of the so-called Mid -Pleistocene Revolution/Transition (in its broader meaning from about 1.2 to 0.6 Ma, Maslin and Ridgwell, 2005), which represents the final phase of the climate interval dominated by 41-ka periodicity. The new global climatic regime/system and secular trend towards more intensive global glaciation that characterizes the last few tens of millions of years (in particular from the time of Jaramillo palaeomagnetic event to the end of the Early Pleistocene) led to an increasing climatic instability that prompted important changes in the structure of terrestrial ecosystems (see e.g. among others Head and Gibbard, 2005; Trauth et al., 2009; McLaren and Wallace, 2010; Carrión et al., 2011; Joannin et al., 2011; Wu and Wu, 2011; Li, 2012; García-Medrano et al., 2014; Palombo, 2014; Bertini et al., 2015).

A number of evidence from the SW European region suggests that a remarkable change developed in both plant and large mammalian communities by the end of the Early Pleistocene, although flora and fauna answered to climate stimuli at a dissimilar pace and in different ways (see e.g. Magri and Palombo, 2013; Sadori et al., 2013; Palombo, 2014). SW European plant communities, for instance, show a certain persistence, whereas large mammals reacted to climatic stimuli more frequently by enlarging, contracting, displacing or creeping (expanding in one direction while contracting in another) their range, and from time to time by evolving in loco and producing new species (Palombo, 2014 and references therein). The climate forcing, in particular precessions that have an important control on seasonality, induced more or less gradual alterations and latitudinal displacements in terrestrial biomes and exerted great influence on dispersal and dispersion of mammalian species across and between continents.

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Dispersal (species movement away from an existing population or away from the parent organism) is one of the fundamental processes in biogeography, crucial for understanding the evolutionary dynamics of organism distribution over time and across space (Colbert et al., 2012). Simply by moving from one habitat patch to another, the dispersal of an individual has consequences not only for individual fitness, but also for population dynamics, population genetics, and species distribution in space and time. Understanding dispersal dynamics and its consequences both for evolutionary strategies at a species level and for processes at an ecosystem level, requires a detailed knowledge of the type of dispersal and mechanisms involved, and of the changes in the range of a given species during time. Studying past dispersal bioevents is of particular interest in analysing the secular active dispersal (largely depending on factors affecting habitat quality) that acts over long time intervals (thousands or millions of years) during which the range of species expands or shifts. Occasional jump-dispersal (the movement of individual organisms even over inhospitable territories by crossing barriers) and slow, progressive shifts of the species range limits, synergistically acted upon during secular-dispersal, leading to the diachronous versus asynchronous local appearances/disappearances of dispersing taxa.

As is often observed in secular dispersal models, Pleistocene mammals did not generally move in multi-species waves of dispersal. Rather, each species changed its range depending on the suitability of environmental conditions in respect to its own environmental tolerances and ecological flexibility. In particular, in SW Europe the presence of important physical/ecological barriers may have prevented some taxa from reaching some territories or caused long delays in their dispersal, leading to diachronicity/asynchronicity in local first appearances. Moreover, resilience of already established species to alien species invasion and habitat disturbance could have slowed the spread of new taxa into some areas. Therefore, factors driving the remodelling of the range of a species, and time and mode of its dispersal and diffusion into a given region may have differed from species to species as well from one territory to another. As a result, correlations and biochronological assessments of local faunal assemblages may be difficult especially when firm chronostratigraphical constraints are unavailable.

This work critically synopsizes the main dispersal events of large mammals toward and across SW Europe in the post-Olduvai Early Pleistocene with the aim of evaluating whether asynchronous appearances mainly depended on the action of geographical/ecological barriers or they are, at least partially, a by-product of our incomplete knowledge of the fossil record and of taphonomical biases.

2. Material and methods

The database consists of taxonomically revised lists of large mammal species (with a body mass of at least 10 kg) from selected Iberian, French and Italian local faunal assemblages (LFAs, i.e., a list of the species identified from the remains retrieved from the same stratigraphical horizon at a given fossiliferous site), ranging in age from the post-Olduvai Early Pleistocene to the beginning of the early Middle Pleistocene (from about 1.7 to 0.7 Ma). Besides LFAs with a sound stratigraphic control, isolated finds having particular taxonomical or chronological relevance were added to the analysis. The lists were compiled by revising and updating those resulting from previous studies on the Pleistocene mammals from SW Europe (see e.g. Palombo, 2014, in press and references therein). Lutrini were not included in the study because of the scantiness and disproportion in time and space of their remains across the studied region. To provide a uniform baseline for the study material, the identifications of species was based by using a taxonomical uniform view, even for species/specimens whose taxonomy, systematics, and identification are controversial.

In order to disentangling asynchronous and diachronous dispersal bioevents across geographical and ecological boundaries, a tentative correlations among distant sequences was made by ordering LFAs within the chronological framework proposed by Palombo (2014) (Fig. 1). The chronologically ordered LFAs are assembled into Faunal Complexes (FCs), regarded as a proxy of a "biochronological unit" (= non-overlapping and "ecologically adjusted groups of animals within specific geographic limits and a chronologic range", Tedford, 1970) (see Palombo and Sardella, 2007; Palombo, 2009 for a discussion). Given that any established biochronological scheme is predisposed to change because new discoveries may substantially change the chronological extent of any already defined biochron, for the purpose of this study and if numerical chronological data were available, the first local appearance of focal taxa in each territory was treated in the analysis as contemporaneous with their lower stratigraphical occurrence. Time and patterns of dispersals were inferred by considering the centre of dispersion (if known) and the first local appearance of each focal taxon in the territories where they spread, moving towards SW Europe.

3. Lights and shadows in dispersal events of large mammals during the post-Olduvai Early Pleistocene

Based on the most compelling stratigraphical and chronological data, during the Early Pleistocene local appearances of taxa that dispersed into SW Europe from both Asia and Africa and, rarely, from Central Europe, were sometimes diachronous but rather frequently asynchronous (Palombo, 2014) (Fig. 2). During the Middle Villafranchian LMA (Gelasian Epoch partim), most of the newcomers spread across all of the SW European studied area, while successively nearly synchronous per-dispersal appearances within the different territories (Iberian Peninsula, France, Italy) were rare. Since the Olduvai palaeomagnetic event, inter-regional dispersals of multiple, potentially interacting species affected each territory in different ways (Fig. 2). Therefore the entity of the dispersal phenomenon greatly varied across the studied region an over time (Fig. 3). Time and mode of the range displacement of each mammalian taxon vary according to its own environmental tolerance, ecological flexibility, trophic requirement and its chance to be successful in competition with species inhabiting the territory across it dispersed. Dispersal patterns differed among species and ecological groups, as it results from comparing the time and mode of dispersal of primary and secondary consumers in SW Europe during the post-Olduvai Early Pleistocene.

3.1. Main dispersal bioevents in carnivore lineages

Dispersal events of larger carnivores (canids, hyaenids and felids) during the Early Pleistocene, merging new taxa into previous communities and changing the structure of carnivore guild, may yield significant information about factors affecting dispersal patterns throughout Europe of hominins, who likely had to compete for meat and other resources with other secondary consumers.

The structure of the carnivore guild documented in SW Europe by the end of Olduvai palaeomagnetic event, results from discrete dispersal events that started during the Gelasian (middle Villafranchian ELMA) (if not earlier for *Canis*, see e.g. Lacombat et al., 2008; Sotnikova and Rook, 2010) with the progressive (though asynchronous and geographically discontinuous) appearance of large canids, hyaenids and felids. Dispersal bioevents involved

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