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To what extent could functional diversity be a useful tool in inferring ecosystem responses to past climate changes?

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ABSTRACT

Functional diversity (the amount of inter-specific variation in functional traits in an ecological community) has been receiving increased attention in ecological studies because it does not treat all species identically, as taxonomical diversity does, but rather according to the role they have within a community. Therefore, functional diversity (FD) can provide information capable of revealing the processes that structured past faunal complexes (FCs) (seen as "spatio-temporal" meta-communities) and promoted their dynamic changes. Each FC gathers faunal assemblages from different territories. Thus, species composition of local faunas may differ from site to site, though the ecological structure may be substantially the same. In such cases, it is appropriate to classify species into functional groups and study the changes in their relative abundance over time. This allows to quantify the functional aspect of biodiversity and to establish its relationships with ecosystem functioning and environmental constraints through changes in the amount of resource partitioning among species. The research focused on the variation of the relative abundance of mammalian ecological groups in SW European FCs, examined in the light of Early to Middle Pleistocene profound climate changes known as Mid-Pleistocene Revolution. The population density (that is marginally affected by climatic and geographical factors) is here proposed as the best proxy for the abundance of individuals of a species in a FC. This approach has the advantage of avoiding the effects of time averaging on fossil data and other sampling issues that paleontologists routinely face (e.g. taphonomic biases). Results obtained indicate that the comparison of FD variation across a region and the analysis of its changes over time can provide interesting hints for scrutinizing in detail the dynamic effect of climatic shifts in restructuring past mammalian communities.

1. Introduction

The role of climate in driving faunal dynamics along geographical gradients, through determining dispersal bioevents, sometimes removing keystone species, altering the internal equilibrium of paleocommunities, and giving rise to new inter-guild and intra-guild dynamics, is still a debated topic in paleobiology and paleoecology (e.g. inter alios Vrba, 1992, 1995, 2005; Bennett, 1997; Alroy et al., 2000; Barnosky, 2001, 2005; Gingerich, 2003, 2006; DeMenocal, 2004; Prothero, 2004; Bertaux et al., 2006; Hijmans and Graham, 2006; Millien et al., 2006; van Dam et al., 2006; Palombo, 2007; Gienapp et al., 2008; O'Regan, 2008; Figueirido et al., 2012; Schloss et al., 2012; Smith, 2012; Hua and Wiens, 2013).

The study of the Early to Middle Pleistocene the large mammal fauna of SW Europe is of particular interest due to the rich Quaternary fossil records, the long and complex history of invasion of species of varying geographical origins and provenance, competitive exclusion, origination of endemic species and the prolonged survival of some taxa in refuge areas. Moreover, although during the past climate differed from modern times, and the vegetational landscapes were generally modified following global climate pattern changes, it may reasonably be assumed that in SW Europe climatic differences from one region to another, and the presence of geographical and ecological barriers have been maintained, differently affecting both the dispersal and distribution patterns of a number of taxa. This allows us to compare faunal dynamics at local and regional scales. Therefore, analyzing the dynamics of large mammal fauna from the SW European regions (i.e. the Iberian and Italian Peninsulas and France) during the Early to Middle Pleistocene should provide important hints in inferring to what extent, if any, climate changes might have promoted ecosystem changes and

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functional diversity shifts that, in turn, may have influenced dispersals, diffusion and at least temporary settlements of archaic human populations in these regions before and during the marked global upset of Earth's climatic system known as the Mid-Pleistocene Revolution (MPR) (Maslin and Ridgwell, 2005).

Defining the ecological structure of large mammal Faunal complexes (FCs, seen as “spatio-temporal” meta-communities as in Palombo, 2007) and their changes over time and across space can be problematic because any FC gathers faunal assemblages from different territories, thus species composition of local fauna may differ from site to site, though the ecological structure may be substantially the same. In such cases, it should be appropriate to classify species into functional groups and study the changes in their relative abundance over time. This allows quantifying the functional aspect of biodiversity and establishing its relationships with ecosystem functioning and environmental constraints through changes in the amount of resource partitioning among species. This is the reason why Functional Diversity (FD, the amount of inter-specific variation in functional traits in an ecological community) has been receiving increased attention in ecological studies. FD does not treat all species identically, as taxonomical diversity does, but rather according to the role they have within a community. Therefore, FD can provide information (absent in measures of species diversity) capable of revealing the processes that structured past FCs and promoted their dynamic changes (e.g. Simberloff and Dayan, 1991; Tilman et al., 1997; Walker et al., 1999; Tilman, 2001).

This paper deals with shifts in FD of large mammal faunas in SW Europe during the Early and Middle Pleistocene, comparing trends among three focal regions (i.e. the Iberian and Italian Peninsulas and France) and scrutinizing their relationship with climate changes. In particular, the aim is to provide fresh data to the debate as to whether modifications of FD at local and regional scale may reflect changes in ecosystems that in turn may help understanding the main factors affecting dispersals and temporary or permanent settlement of human populations in SW Europe.

2. Material and methods

2.1. Source of data

The database consists of taxonomically revised lists of mammal species from selected Pleistocene Iberian, French, and Italian Local Faunal Assemblages (LFA = a list of the species identified from the remains retrieved from the same stratigraphic horizon at a given fossiliferous site) (see Palombo, 2014). Small mammals (Rodentia, Soricomorpha and Chiroptera) are not included in the analysis because their highly limited ecological interaction with hominins, as well as Lagomorphs and Lutrini because of their non-uniform documentation in time and space across the studied region.

The lists were compiled by revising and updating those resulting from previous studies of the Pleistocene mammals from SW Europe (see Palombo, 214 and references therein), and adding data from recently published papers (e.g. Demuro et al., 2013, 2014a,b; Arnold et al., 2014; Bourguignon et al., 2014; Breda, 2014; Duval et al., 2014; Ghezzo et al., 2014; Gómez-Olivencia et al., 2014; Nomade et al., 2014; Palmqvist et al., 2014; Prado et al., 2014; Santos et al., 2014; Siori et al., 2014; Stiller et al., 2014; Vallverdú et al., 2014; Lozano-Fernández et al., 2014a,b; 2015; Breda et al., 2015; Falguères et al., 2015; Gibert and Ferrandez-Canadell, 2015; López-García et al., 2015; Persico et al., 2015). For providing a uniform baseline for the study material, a taxonomical uniform view was applied even for taxa/specimens whose taxonomy, systematics, and identification are controversial. The faunal list of selected LFAs ranging in age from the late Early to the early Middle Pleistocene (latest Villafranchian to Galerian European Land Mammal Ages, ELMAs) is reported in Supplementary information 1, Table SI 1.

2.2. Chronological ordering of SW European local faunal assemblages

Ordering LFAs within a chronological framework and validating them at a regional scale is crucial to making correlations between distant sequences, which in turn may allow us to disentangle asynchronous and diachronous dispersal bioevents across geographical and ecological boundaries and to define local versus regional FD changes over time. Nonetheless, numbers and characteristics of SW European LFAs (e.g. depositional context and taphonomic signatures in turn affecting richness, evenness, and number of ecological groups) greatly differ from one geographic area to another, making any comparison between single LFAs difficult and not very informative. Therefore, chronologically ordered LFAs were assembled into FCs. A FC is here regarded here as a proxy of a “biochronological unit”, representing a complex of faunas assumed to be characterized by a virtual taxonomical homogeneity that lived in a time span (Biochron) during which significant taxonomical and functional turnovers are not expected (coordinated stasis, Brett et al., 1996). Although FCs are thus unlikely to capture attributes arising from processes operating at small spatial and temporal scales, they should do well at summarizing the average structure and characteristics of the meta-communities living during the biochron's time and thus are a valuable basis for analyzing the large-scale processes that determined long term faunal evolution.

Biochronological principles are applied here for gathering LFAs into FCs and then ordering them in a chronological sequence based on selected LFAs for which chronological constraints (stratigraphy, radiometric dating, paleomagnetism etc.) are available. New discoveries and absolute chronological assessments of LFAs may substantially change the chronological extent of any already defined biochron, making any previously established biochronological scheme predisposed to change. Hence, the successions of SW European FCs here proposed (Fig. 1) and the resulting chronological assessment of SW European LFAs can be regarded as the “best-fit” allowed by available data.

2.3. Data consistency

Any estimate of diversity dynamics during a time interval within a given geographic area could be misrepresented because the distribution of sites is generally heterogeneous in time and space, rare species are often sparsely represented and ghost lineages are not uncommon. This joined with either taphonomic or ecological factors and sampling biases, should make our knowledge of the actual composition of regional and local faunas at the best imperfect. The number of LFAs gathered within each FC and species richness could markedly fluctuate between successive biochrons. Studying a rich fossil record within a quite restricted geographic area (i.e. the Pleistocene record of large mammals from SW Europe) may contribute to reduce these drawbacks. Sample size and species richness could sometimes correlate throughout the analyzed record, negatively affecting the reliability of the results (e.g. Badgley and Gingerich, 1988; Badgley, and Fox, 2000). Therefore, an evaluation of the effects of “sampling” is a basic prerequisite for investigating the significance of faunal dynamics. The Spearman non-parametric rank-order test (Fieller et al., 1957) was here used for testing whether the richness of species in a FC depends on the number of LFAs the FC includes. Results obtained show that the species richness and the number of Spanish, French and Italian LFAs do not significantly correlate (SW Europe: $\rho = 0.168$ $P = 0.487$;

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