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Faunal dynamics in SW Europe during the late Early Pleistocene: Palaeobiogeographical insights and biochronological issues

Dynamique faunistique en l'Europe méridionale à la fin du Pléistocène inférieur : évidences paléobiogéographiques et problèmes biochronologiques

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ABSTRACT

The Pleistocene fossil record of the Mediterranean region is particularly suitable for studying the role of climate change on faunal evolution, and comparing faunal dynamics (FDy) at local and regional levels because of the complex physiographic and climatic heterogeneity of the region, and the complex history of invasions of species of varying geographical origin. This research aims to analyze and compare FDy trends in selected North Mediterranean territories (Iberian Peninsula, France, Italy, Greece), showing current differences in physiographical configuration and climate regime that may be supposed to have roughly been maintained throughout the Pleistocene, differently influencing time of dispersal and distribution patterns of mammalian species. The mammal FDy (changes in biodiversity, taxonomic composition and ecological structure) of each territory is analyzed to verify to what extent the major modifications match climatic and environmental changes. Biogeographic insights and chronological issues are discussed in the light of diachronous/asynchronous dispersal events.

RÉSUMÉ

Le record fossile du Pléistocène de la région méditerranéenne (caractérisée par une importante hétérogénéité physiographique et climatique et une histoire complexe d'invasions d'espèces d'origines géographiques différentes) est particulièrement approprié pour étudier le rôle des changements climatiques sur l'évolution des faunes au niveau local. La dynamique faunique du Nord de la Méditerranée est analysée, en comparant des territoires caractérisés aujourd'hui par une géographie physique et un climat différents. La géographie de la région méditerranéenne a peu changé pendant le Pléistocène et les principales différences d'une région à l'autre, les barrières géographiques/écologiques qui ont affecté

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le temps de dispersion et la distribution des espèces ont été à peu près les mêmes pendant tout le Pléistocène. La dynamique faunique des mammifères (biodiversité, composition taxonomique, structure écologique) de chaque territoire est analysée pour vérifier dans quelle mesure les changements climatiques et environnementaux entraîneront ses modifications. Les problèmes biogéographiques et chronologiques sont brièvement discutés.

1. Abbreviations

BM	Biomass
CI	completeness index based on the proportion of range-through or Lazaus taxa (RT) with respect to the total number of taxa recorded at the time of the analysed biochronological unit
CI_{bda}	completeness index based on the proportion of RT with respect to the number of taxa recorded before, during and after the time of the analysed biochronological unit
d-TI	per dispersal turnover index
d-FlHA	per dispersal First local Historical Appearance
ELMA	European Land Mammal Age
emSD	estimated mean Standing Diversity
ER	Extinction rate
FC	Faunal Complex
FDy	Functional Diversity
FlHA	First local Historical Appearance
g-TI	global Turnover index
HlSO	Highest local Stratigraphical Occurrence
LFA	Local Faunal Assemblage
LlHA	Last local Historical Appearance
LlSO	Lowest local Stratigraphical Occurrence
o-TI	per in-loco-origination turnover index
o-FlHA	per in-loco-origination First local Historical Appearance
OR	Origination rate
RT	range-through or Lazarus taxa
SR	Standing Richness
TI	Turnover Index

2. Introduction

> "...if true that the juxtapositions of ideas and data from largely independent studies can inspire new hypotheses, then mammalogy is surely a marvelous substrate for discoveries within the evolutionary paradigm. In total range and strength, mammalian research is unrivalled in biology." (Vrba, 1992, p. 2)

The multifaceted and intriguing evolutionary history of mammals, which led to their current biodiversity and biogeographical setting, is tightly linked with palaeogeographic, climatic and environmental changes. The complex synergistic action of physical and biological factors shaped faunal evolution, species originations and extinctions, and the timing and mode of species dispersal through time and across continents.

The ecological and evolutionary responses of mammalian faunas to stimuli perturbing the internal dynamic equilibrium of palaeocommunities varies with the temporal and spatial scales at which such factors acted. Climate changes have been considered by some scholars as the most influencing causal factor in triggering species evolution and faunal diversity (FDy) at ecological and geological temporal scale, hypothesising that evolutionary change (e.g. speciation events) may be less frequent in times of ecosystem stability rather than during phases of variability triggered by physical environmental events (e.g. Alroy et al., 2000; Barnosky, 2001, 2005; Bennett, 1997; Berteaux et al., 2006; Eldredge, 1999; Gienapp et al., 2008; Hua and Wiens, 2013; Jansson and Dynesius, 2002; Smith, 2012; Vrba, 1992; Vrba, 1995a, 2005; Webb, 1995; Webb and Barnosky, 1989).

Some scholars believed extrinsic factors to have a minimal effect on species evolution, and that intrinsic biological factors must be the most important. Accordingly, changes in ecosystem equilibria and faunal turnovers may be due to the internal dynamics of competitive relationships, without necessarily indicating a strict interdependence between major climatic changes and evolutionary events (e.g. Jaeger and Hartenberger, 1989; Prothero, 1999, 2004; Tsubamoto et al., 2004). The statement may be actually true especially as regards to macroevolutionary events at a high taxonomic level in deep time, but some evidence has demonstrated that climatic changes related to geological/Quaternary time may have profound effects on patterns of mammalian FDy even at a continental scale (e.g. Blois and Hadly, 2009; Figueirido et al., 2012; Gingerich, 2003, 2006; Saarinen et al., 2014; Webb et al., 1995 Woodburne et al., 2009). During times of environmental normality, indeed, interactions among ecosystem species evolve in a regime of dynamic equilibrium. Perturbations of physical parameters produce disequilibrium by causing the extinction of the most specialized species. The resulting unbalanced structure of the community stimulates new individual responses of other species, de facto causing ecosystems to significantly restructure (Graham and Lundelius, 1984).

Climate and biotic interactions, however, likely contribute to faunal evolution in successive phases: climate changes and physical-environmental disturbances, altering the ecosystem structure and functioning, acted as a trigger factor in promoting functional and taxonomic turnovers, while internal dynamics of competitive relationships constrained the faunal reorganization leading to a new equilibrium (e.g. Faith and Behrensmeyer, 2013; Palombo, 2007, 2014). Some researchers, conversely, assumed that although global climate changes may have influenced longer-term evolutionary trends, species interactions and local environmental changes were the most influential factors at shorter time scales (Bibi and Kiessling, 2015).