



General Palaeontology, Systematics, and Evolution

## 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.

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## R É S U M É

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.

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## 1. Abbreviations

BM	Biomass
CI	completeness index based on the proportion of range-through or Lazarus taxa (RT) with respect to the total number of taxa recorded at the time of the analysed biochronological unit
CI <sub>bda</sub>	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-FIHA	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
FIHA	First local Historical Appearance
g-TI	global Turnover index
HISO	Highest local Stratigraphical Occurrence
LFA	Local Faunal Assemblage
LIHA	Last local Historical Appearance
LISO	Lowest local Stratigraphical Occurrence
o-TI	per in-loco-origination turnover index
o-FIHA	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 Behrensmeier, 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).

The biotic response of individuals, species and communities to climatic warming and cooling events is, however, a highly complex phenomenon, making it sometimes difficult to accurately disentangle causal factors behind faunal dynamics. Some organisms, for instance, seem to have persisted over thousands to perhaps millions of years in the face of environmental perturbations and species invasions; others evolved, and others changed their range. Bioevents related to secular dispersal were particularly important during phases of marked climatic and environmental instability, e.g., during the Quaternary period, which represents a crucial transition between geological and ecological time. Any ecosystem, indeed, provides finite resources that species have to partition, optimizing the expenditure cost by reducing competition and achieving a dynamic equilibrium during periods of environmental instability. As a result, the extent of FDy mainly depends on resource shifts, in turn related to changes in physical parameters (e.g., temperature, humidity).

During the Pleistocene, particularly during the mid-Pleistocene Revolution (MPR) (Clark et al., 2006; Maslin and Brierley, 2015; Maslin and Ridgwell, 2005), climate forcing induced deep but gradual alterations and latitudinal displacements in terrestrial biomes and greatly influenced dispersal and dispersion of species. A number of species reacted to ecosystem disturbances by varying the geographic range in keeping with the displacement of biomes, acting as invasive species in the new territory they were dispersing across. Each species changed its range depending on the suitability of environmental conditions with respect to its own environmental tolerances and ecological flexibility. Such evidence is partially consistent with the Habitat Theory (Vrba, 1992), which hypothesizes that low latitude and higher latitude mammals move respectively toward higher and lower latitudes when climates become warmer and cooler, tracking the changing distributions of vegetation zones.

Whatever the extent and trajectory of dispersals should have been, discrete dispersal bioevents, merging alien species into previously existing large mammal communities, changed the faunal structure, giving rise to new internal dynamics that led to a progressive reconstruction of the mammalian fauna, although different processes predominated in different places. Dispersal hence is one among the fundamental processes in biogeography (crucial for understanding the evolutionary dynamics of organism distribution throughout time and across space) and a factor to carefully consider in analysing faunal dynamics, making correlations among distant stratigraphic sequences, and chronologically ordering faunal assemblages.

The Pleistocene fossil record of the Mediterranean region is particularly suitable for studying effects of climate change and comparing FDy at local and regional levels due to the complex physiographic and climatic heterogeneity of the region, the presence of important geographical/ecological barriers, and the long history of invasions of species of varying geographical origin and provenance.

This research aims to highlight the main aspect of FDy in selected North Mediterranean territories (Iberian Peninsula, France, Italy and Greece), each showing current

peculiar physiographic configuration and climate regime. The geological evolution of the region during the early Middle Pleistocene suggests that the main differences from one territory to another have roughly been maintained throughout the Pleistocene, differently influencing the time of dispersal and distribution patterns of taxa. The mammal FDy (shifts in biodiversity, change in taxonomic composition and ecological structure) of each territory is analyzed to verify whether or not the major modifications match climatic and environmental changes. Biogeographic insights and chronological issues are briefly discussed in the light of diachronous/asynchronous dispersal events.

### 3. Materials and methods

The database consists of taxonomically revised lists of large mammal species from selected Western (Iberian Peninsula, France and Italy) and Eastern (Greece) Mediterranean local faunal assemblages (LFAs) (a list of the species identified from the same stratigraphical horizon at a given fossiliferous site) ranging in age from about 2.6 to 0.62 Ma (from about MIS 104 to MIS 16, from the middle Villafranchian to “Epivillafranchian”/early Galerian European Land Mammal Ages, ELMAs).

Three main aspects were considered here for exploring the FDy in each studied territory: variations of diversity/richness (Estimated mean Standing Diversity, emSD, and Standing Richness, SR), changes in the taxonomic composition (Turnover index, TI; origination, OR, and extinction, ER, rates) helpful to reveal the three major components of FDy (i.e. evolution, extinction, dispersal), and modifications of the ecological structure of Faunal Complexes, FCs.

The sampling adequacy was estimated by means of two completeness indices (CI,  $CI_{bda}$ ), based on the proportion of Lazarus taxa (or range-through taxa, RT).

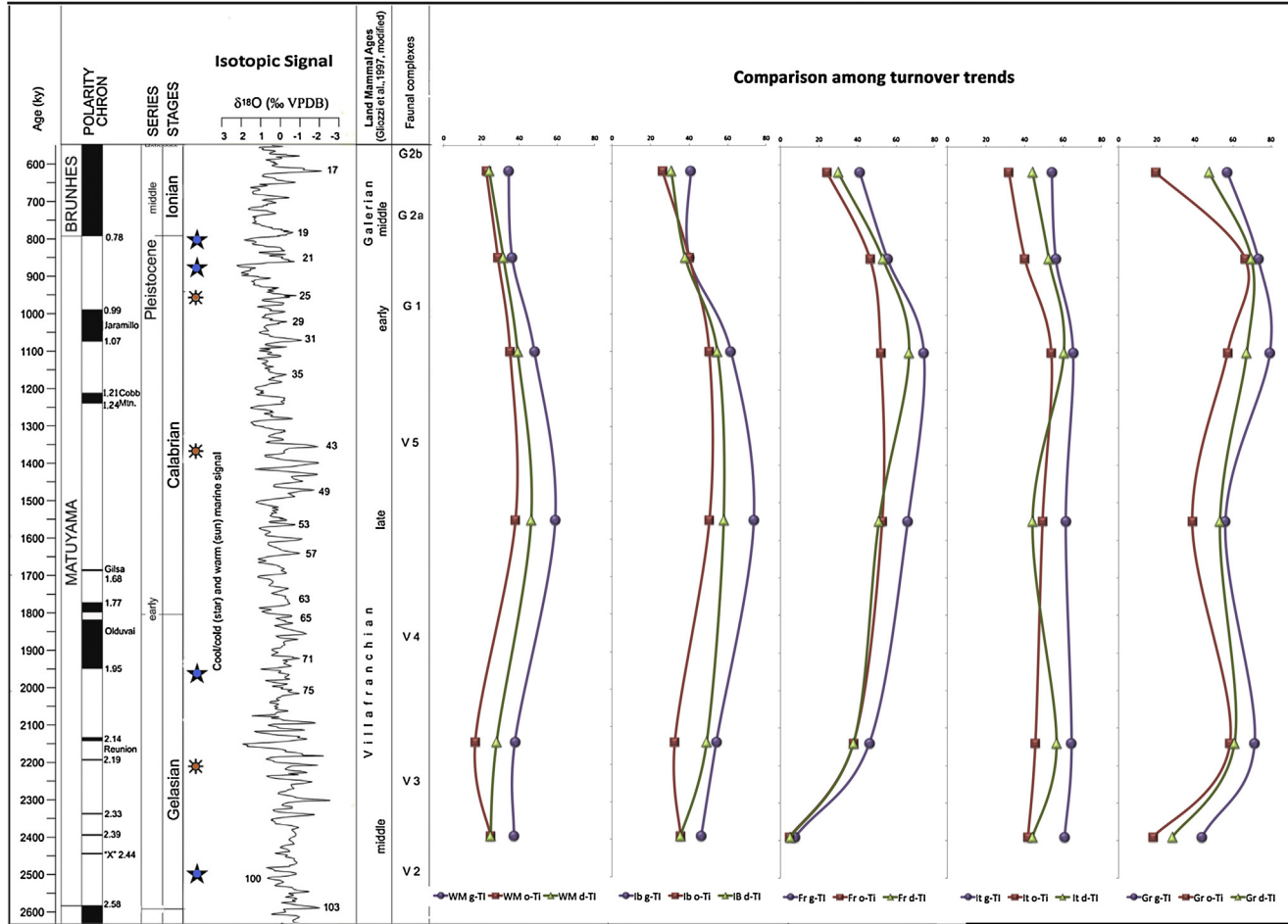
Details about material, data sources, and methods are provided in [Supplementary Information](#).

### 4. Results

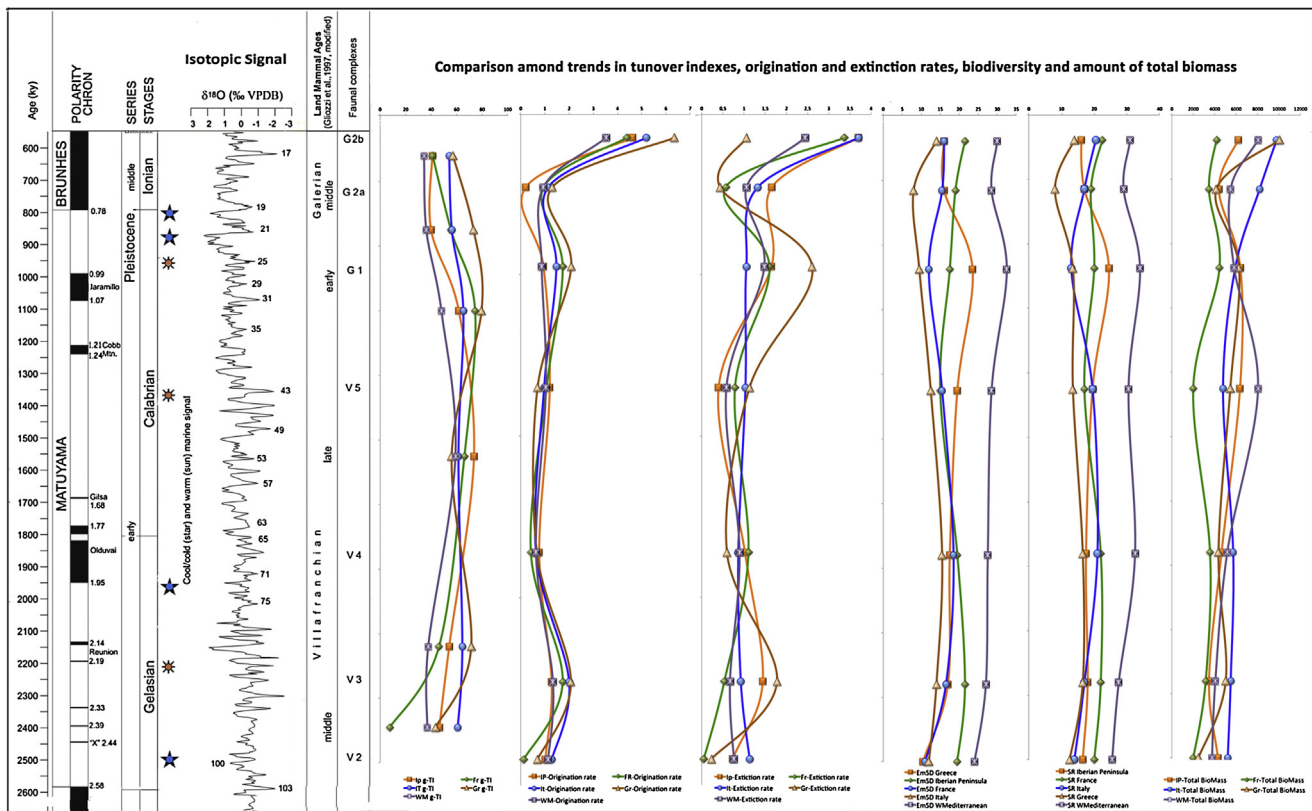
Trends in TI (Fig. 1) and in emSD and SR (Fig. 2) basically result from the same combined effect of appearances of new taxa (newcomers dispersing into the focal territory, and taxa originated by anagenetic/sympatric evolution in situ within phyletic lineages already inhabiting the area) and local disappearances/extinctions. Therefore patterns are expected to be similar throughout time, although they may vary from one territory to another, and at regional and local geographical scales.

Turnover trends in the West Mediterranean region, for instance, roughly mirror only the trend shown by the fauna from the Iberian Peninsula. Both show a high value of the three indices (global, g-TI, per in-loco-origination, o-TI, and per dispersal, d-TI, turnover indices) during nearly the entire Early Pleistocene (with a maximum during the post-Olduvai/pre-Jaramillo period), even if the value d-TI always exceeded that of o-TI. In the Iberian Peninsula, however, this aspect was more evident during the Gelasian.

The asynchrony/diachrony of local appearances due to dispersal (cf. Palombo, 2014, 2017) caused turnovers to



**Fig. 1.** Comparison among trends shown during the Early–early Middle Pleistocene by turnover indices (g-TI: global; d-TU: per-dispersal; O-TI: per-in situ origination) in Western Mediterranean (WM), Iberian Peninsula (Ip), France (Fr), Italy (It), and Greece (Gr) (methodology described in the [Supplementary Information](#))  
**Fig. 1.** Comparaison entre les tendances au cours du Pléistocène inférieur et moyen inférieur des indices de *turnover* (g-TI : globale ; d -TU : per-dispersion ; O-TI : per-origine in situ) en Méditerranée occidentale (WM), dans la péninsule Ibérique (Ip), en France (Fr), en Italie (It) et en Grèce (méthodologie décrite dans [le matériel supplémentaire](#)).



**Fig. 2.** Comparison among trends shown during the Early–early Middle Pleistocene by global turnover index (G-TI), the origination (OR) and extinction (ER) rates, the biodiversity (estimated as standing mean diversity, emSD, and standing richness, SR), and total the amount of biomass in Western Mediterranean (WM), Iberian Peninsula (Ip), France (Fr), Italy (It), and Greece (Gr) (methodology described in the [Supplementary Information](#)).

**Fig. 2.** Comparaison entre les tendances au Pléistocène inférieur et moyen inférieur des indices de *turnover* global (G-TI), de taux d'origine (OR), d'extinction (ER), de la biodiversité estimée en tant que diversité permanente moyenne (emSD), richesse supplémentaire (SR), et de la quantité totale de biomasse en Méditerranée occidentale (WM), dans la péninsule Ibérique (Ip), en France (Fr), en Italie (It) et en Grèce (Gr) (méthodologie décrite dans [le matériel supplémentaire](#)).

differ from one territory to another in extent and significance. By the end of the Early Pleistocene, for instance, *g*-TI and *d*-TI turnover indices reached the maximum value in Italy, while the low amount of dispersal events accounts for the low increase and the slight decrease of the *g*-TI value during the post-Olduvai/pre-Jaramillo period in France and Italy respectively. Divergences among trends also depend on disparities in the amount of dispersal events, and some asynchrony in the last local historical appearances (LIHA). The assumption is supported by some differences in ER, in particular during the Gelasian and during the post-Jaramillo Early Pleistocene. In the West Mediterranean region, Italy shows the most accentuated departures, with a nearly constant ER during the Early Pleistocene. The relatively low ER value during the post-Jaramillo Early Pleistocene is consistent with a longer duration of some Villafranchian species in Italy than in the Iberian Peninsula and France. OR, conversely, shows only minor divergences.

Dissimilarities increase comparing the trend of TI, OR and ER shown by territories of the West Mediterranean region with those of eastern Mediterranean, e.g. Greece. The Greek fauna shows pronounced fluctuations: renewal phases alternated with periods of relative stability. TI were high in the Gelasian and during the late early Pleistocene, while in the post-Olduvai/pre-Jaramillo period changes in taxonomic composition were moderate in spite of the First local Historical appearances due to dispersal (*d*-FIHA) of some species (Fig. 1). The taxonomic changes were mainly related to extinctions and, to some extent, to in situ originations as supported by the ER trend, showing peaks in ER rates during the Gelasian and in the latest Early Pleistocene (the ER value are much higher than in the western Mediterranean region). During the transition to the Middle Pleistocene, ER was definitely lower and originations prevailed (Fig. 2). As a result, the  $\alpha$ -diversity (emSD and SR) decreased on average throughout the Early Pleistocene (Fig. 2). Conversely, in the West Mediterranean diversity increased during the Gelasian and the post-Jaramillo Early Pleistocene, showing no or moderate fluctuations from about 1.6 to 1.1 Ma. The West Mediterranean trend mainly related to the emSD and SR decreases in the French and Italian FCs, while the drop in diversity in the Italian FCs in the latest Early Pleistocene was balanced by the increase in the French ones (Fig. 2).

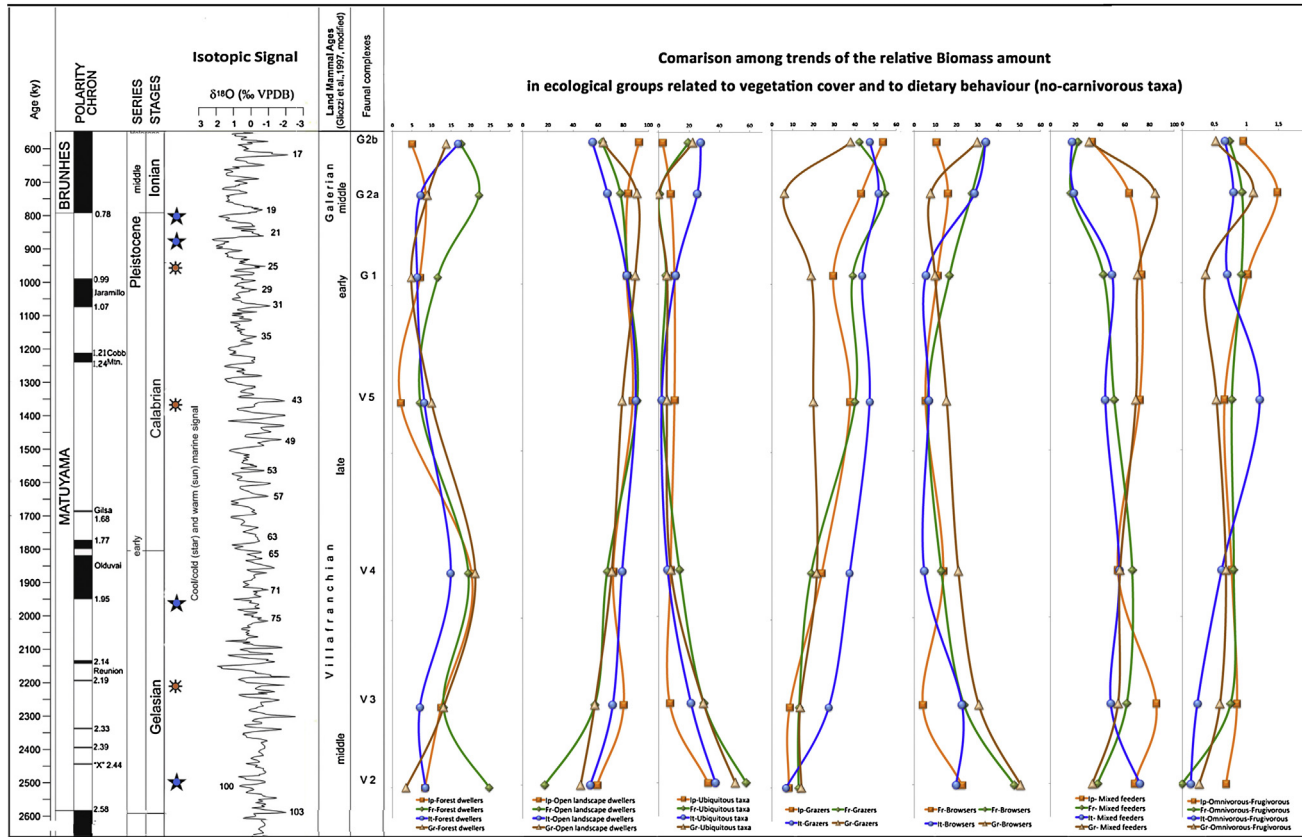
An increase/decrease in diversity does not necessarily entail an analogous increase/decrease in the biomass (BM), which is more related to the average body mass and density of the species present in a given FC rather than to their number. In the western Mediterranean region, for instance, an increase of BM occurred during most of the Early Pleistocene, peaking during the post-Olduvai/pre-Jaramillo period (as the BM of fauna from the Iberian Peninsula and Greece did), but successively dwindled, notwithstanding the opposite trend shown by the French and Italian faunas. According to the results obtained, neither trends in diversity and BM, nor trends at local and regional geographical scales are consistent with each other. Regarding the BM, for instance, a moderate decrease occurred in Italy during the Early Pleistocene followed by a noticeable increase during the early middle Pleistocene. Conversely, at the western and eastern edges of the studied area,

faunas from the Iberian Peninsula and Greece show some increase in the large mammal BM since Olduvai time, a quasi-stationary phase in the latest Early Pleistocene followed by a marked decrease after the transition to the middle Pleistocene. Despite such disparities, the differences in the total amount of BM were not so important during the late Gelasian and the successive Early Pleistocene, except for the French fauna, which shows a low value throughout the studied period, with a minimum during the post-Olduvai/pre-Jaramillo time and a moderate increase in the following Early Pleistocene (Fig. 2).

The differences in the BM trends would suggest some differences in the ecological structure of FCs, and in turn in the habitats, at a local geographical scale across the studied region. The hypothesis, however, is hardly supported by the somehow similar BM trends of the ecological groups related to the vegetational cover (Fig. 3). The BM of forest dwellers, for instance, decreased during most of the Early Pleistocene in all the studied territories, although at different degrees and paces, reaching the minimum value during the post-Olduvai/pre-Jaramillo period, as it occurred to the BM of more ecologically flexible large mammals, and on average of browsers. During this time span, the BM of taxa inhabiting open environments increased, as that of grazers did in the West Mediterranean area, except in Greece. The fluctuation of mixed-feeder BM differs at local geographical scale, although since Olduvai time analogous trends characterised France and Italy. These trends are opposed to that shown by both the Iberian Peninsula and Greece, suggesting one again some environmental similarities between these two distant territories.

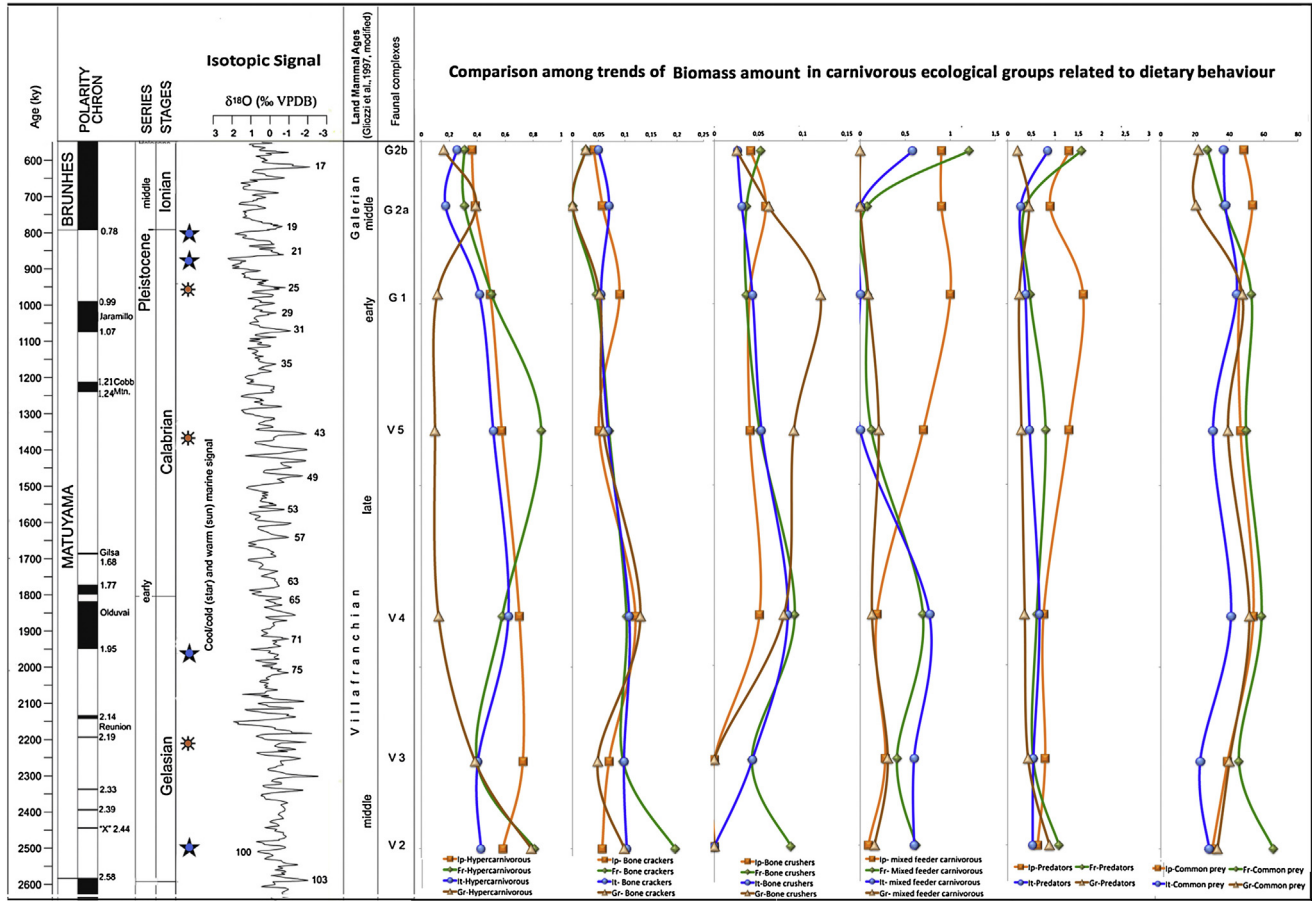
All in all, the increased difference in the trends of BM shown by ecological groups related to vegetational cover and to the dietary behaviour of primary and non-carnivorous secondary consumers in the latest early and the beginning of the Middle Pleistocene (Fig. 3) suggests an increasing environmental heterogeneity across the North Mediterranean region in a period of climate instability, roughly coinciding with the most pronounced phases of the MPR. In that time, temperature and humidity on average decreased and grassland and savannah-like environments spread especially in Spain, Greece and southern Italy (Magri and Palombo, 2013 and references therein).

The presence of carnivores in a given territory, and consequently the diversity of the carnivore guild, has generally been regarded as affected, on average, more by the resources (prey) availability/abundance and food-web functioning rather than by abiotic (e.g. climate) factors, although some complex, rarely direct relationships exist between environmental changes and shifts in the diversity of Carnivora (i.e. forest dweller species and the most specialized ones) (see among several others Carbone and Gittleman, 2002; Carbone et al., 2007, 2011; Chesson, 2000; Palombo et al., 2009; Pettorelli et al., 2011). The trends shown by the BM of carnivores in ecological groups related to their feeding behaviour (Fig. 4) suggest that the major local changes, as well as the dissimilarities from a region to another, mainly relate to the appearance/disappearance (sometimes diachronous, sometimes asynchronous) of selected species (cf. Palombo, 2017 and references therein). The pick in BM of French



**Fig. 3.** Comparison among trends shown during the Early–early Middle Pleistocene by the biomass amount in habitat-related ecological groups and in groups related to the feeding behaviour of non-carnivorous species in the Western Mediterranean (WM), the Iberian Peninsula (Ip), France (Fr), Italy (It), and Greece (Gr) (methodology described in the [Supplementary Information](#)).

**Fig. 3.** Comparaison entre les tendances au Pléistocène inférieur et moyen inférieur de la quantité de biomasse des groupes écologiques définies par rapport à l'habitat préférentiel des toutes les espèces et au régime alimentaire d'espèces non carnivores en Méditerranée occidentale (WM), dans la péninsule Ibérique (Ip), en France (Fr), en Italie (It) et en Grèce (Gr) (méthodologie décrite dans le [Matériel supplémentaire](#)).



**Fig. 4.** Comparison among trends during the early–early middle Pleistocene of the biomass amount in carnivorous ecological groups related to their dietary behaviour.  
**Fig. 4.** Comparaison entre les tendances durant le Pléistocène inférieur et le Pléistocène moyen inférieur de la quantité de biomasse des carnivores, regroupés selon leur comportement alimentaire.



hypercarnivorous species in the post-Olduvai/Pre-Jaramillo Early Pleistocene depends, for instance, on the late appearance in this area of large felids (e.g. *Panthera gombaszoegensis*). During the same period, a nearly contemporaneous decrease of bone-cracker BM occurred in the Mediterranean region, which was likely due to the disappearance of *Pliocrocota perrieri*. In the following Early Pleistocene, the contemporaneous presence of *Crocota* in the North of the Iberian Peninsula and *P. brevirostris* in the South, accounts for the increase of the bone-cracker BM.

The predator-prey interaction is an important component of FDy and evolution of large mammal community structure. The diversity of predators and prey within the system, the relative proportion of body size groups of both prey and the predators, the availability of the most suitable prey for which predators are competing, and the presence of alternative prey are among the factors that mostly influence the predator-prey interaction (e.g. Cohen, 1977; Croft, 2006; Sinclair et al., 2003; Van Valkenburgh and Janis, 1993).

The BM trends of predators and common prey (i.e. carnivores and primary and secondary consumers whose interaction is within the common rule), suggest the tendency of a progressive reduction of the predation pressure during the whole Early Pleistocene in the North Mediterranean region, except for the Iberian Peninsula where the BM of predators increased in the latest Early Pleistocene more than that of prey. As underlined above, at this time, the spotted hyaena is recorded for the first time in northern Spain (TD4W level, Atapuerca) (Garcia and Arsuaga, 2001), while *P. brevirostris* was still present in Southern Spain (Vallparadís EVT7, Catalonia) (Madurell-Malapeira et al., 2010). The ecological traits of the Pleistocene European *Crocota* suggest that the species cannot have been successful in competing with the short-faced hyaena. Therefore, the BM of Spanish predators in this period may be regarded as overestimated if *Pachycrocota* had already disappeared from the Cantabrian territory by the latest Early Pleistocene, and the two species never coexisted in any Spanish palaeocommunity.

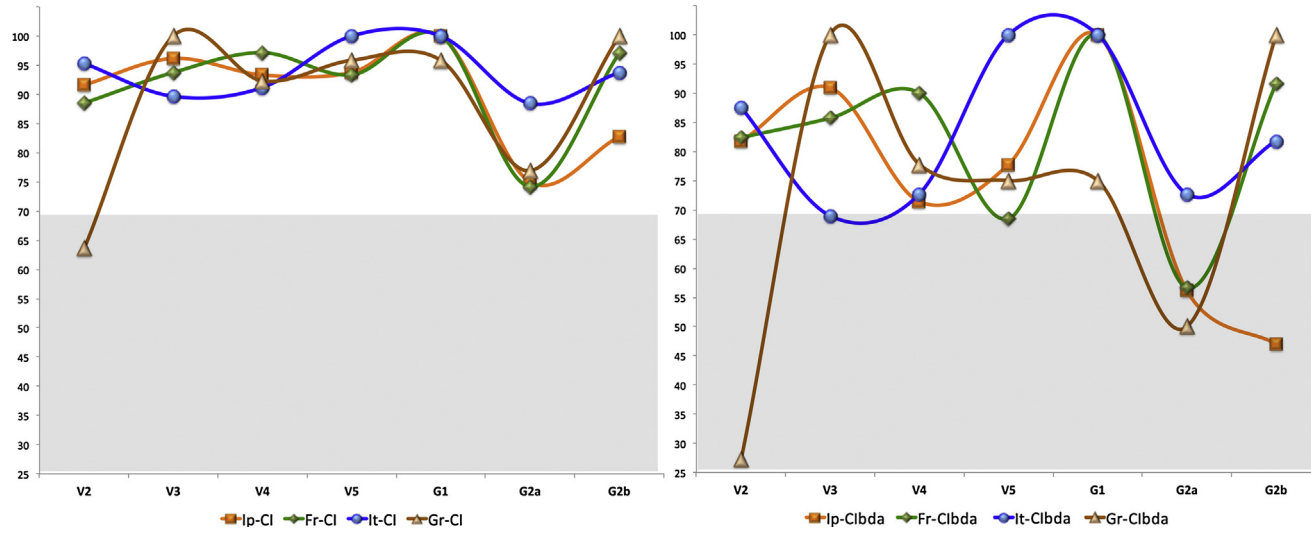
All things considered, the analysis of the FDy in the North Mediterranean mammalian FCs and the comparison among trends in taxonomical turnovers, biodiversity and changes in ecological structure indicate significant modifications at regional geographical scale of the mammalian fauna during the Early Pleistocene, particularly during the MPR. The faunal change, however, developed at different pace and with different timings and modes at local geographical scale, underlining the important role played by the dynamics of single dispersal events in changing the fauna composition and structure in each studied territory. The peculiarity of FDy at local geographical scale mainly depends on palaeogeographical factors that may have prevented or slowed the appearances of some taxa in some territories, the different biological response of species to the local manifestation of the effect of global climate changes, and the resilience of local mammalian palaeocommunities in face of the arrival of invasive species and environmental perturbations. In addition, the nature of the data may have contributed to differentiate the FDy trends during time and across space. Large mammal LFAs,

indeed, mostly come from deposits sparse in space and time. Therefore, a low number of LFAs included in some FCs and chronological insufficient controls may result in large uncertainties in the age of the appearance and disappearance of taxa and detection of geographical patterns and diachrony/asynchrony of biological events. The hypothesis that the differences at local geographical scale may depend on the disproportion among fossil records finds, however, only a little support in the quality of fossil record as estimated by means of the completeness indices (Fig. 5). The quality of the fossil data is crucial for validating results and conclusions, because the fluctuating frequencies of coexisting species may depend simply on sampling bias. In the analysed sample, the value of the completeness index CI is consistently high through the Early Pleistocene, except the Greek earliest Pleistocene fauna, as expected due to the dramatic paucity of LFAs known at that time. The value of the more conservative  $CI_{bda}$  index is generally higher than the minimum value ( $>70$ ) regarded as suitable for accepting estimates of originations, extinctions, turnover, and diversity/richness (Maas et al., 1995). In two cases (Italy and France in the late Gelasian and the post-Olduvai/pre-Jaramillo time respectively) the value is slightly lower, but close to the minimum. The low values of the  $CI_{bda}$  index shown at the beginning of the Middle Pleistocene would be expected due to the relatively large ratio of LIHA/FIHA with respect to the number of Early Pleistocene taxa that were present even in the following early Middle Pleistocene.

## 5. Discussion

### 5.1. Dispersal

Considerable evidence underlines the key role that climate driven dispersal bioevents had in shaping FDy and evolution, and in conditioning the biodiversity and biogeography of land mammalian fauna at any point in time in any region. In the course of the secular long distance dispersal, the progressive extension/deformation or fragmentation of the range of a land mammal taxon is constrained to a large extent not only by the existence of physical connections and ecological and physical barriers, but also by the availability of environments suitable to sustain viable populations and demographic increase. FDy and evolution actually result from a complex network of interactions (and relate feedback processes) among differently acting factors (climate forcing, environment characteristic, resource amount and distribution, patterns of mammal dispersal, biotic competition and resilience of resident species in face of perturbation of the community equilibrium by the arrival of dispersing species) that affect the time of species appearances and disappearances (i.e. FIHA/LIHA, and hence chronology and correlation among LFAs) and their distribution across space (i.e. the biogeographical context). However, the low spatial and temporal resolution of the fossil record in the terrestrial domain, taphonomic biases, and the lack of firm chronological constraints make it sometimes difficult to interpret causal factors behind the delayed or asynchronous appearance of a taxon in some territories, or the absence of a species in an area that would have been part of its range because



**Fig. 5.** Comparison among the early–early Middle Pleistocene Completeness indices in the Western Mediterranean (WM), the Iberian Peninsula (Ip), France (Fr), Italy (It), and Greece (Gr) (methodology described in [Supplementary Information](#)).

**Fig. 5.** Comparaison durant le Pléistocène inférieur et le Pléistocène moyen inférieur des indices d'exhaustivité en Méditerranée occidentale (WM), dans la péninsule Ibérique (Ip), en France (Fr), en Italie (It) et en Grèce (méthodologie décrite dans le [Matériel supplémentaire](#)).

it was located along the alleged trajectory connecting the source area with those inhabited by the focal taxon during the dispersal. As regard to the North Mediterranean region, it is challenging to individuate the causal factors behind the asynchronous appearances of some species. This happens especially if the chronological order of FIHAs across the region does not mirror the hypothetical trajectory drawn by the progressive displacement of the focal species range (see Palombo, 2017). Such a pattern should be expected assuming that species responded to Pleistocene climatic and environmental fluctuations following a Gleasonian model (Gleason, 1926). According to the model, indeed, species respond to environmental changes modifying the geographical range at different time, extent and direction in accordance with their individual tolerance limits. As a result, different species shift their range with varying rates, at different times, and in divergent directions, although under the pressure of the same climatic changes. The model markedly differs from the Clementsian model (Clements, 1926), sometimes implicitly followed by some researchers to explain the “mixed” (warm/cold) character of some fauna, such as those recorded during the Pleistocene in central Europe. The model hypothesizes the persistence through time of cold and warm adapted long-lasting groups of species in equilibrium. The groups would have moved successively to the north or the south during warm (interglacial) and cold (glacial) periods.

Evidence resulting from the analysis of FDy and turnover during the Pleistocene strongly supports the hypothesis of a climatic driven displacement of a number of taxa. Mammals, however, did not generally move in multi-species dispersal waves, but each species enlarged, displaced or contracted its geographic range as the environmental conditions were suitable or not for it. Although changes in the climatic system and vegetational background triggered, for instance, the dispersal of some large mammals from Africa and Asia toward and across southern Europe, other biotic and abiotic factors contribute to differentiate time and mode of dispersion from species to species. As a result, discrete dispersal bioevents succeeded each other, shaping the progressive change of the North Mediterranean Pleistocene fauna, but at a different pace and rate in different territories, making it sometimes problematic to depict a compelling biogeographic scenario.

In the following paragraphs the most intriguing and debated potential dispersal bioevents from Africa are briefly discussed.

Various Plio-Pleistocene dispersal events from Africa towards SW Asia and Europe have been proposed by a number of authors (e.g. among others, out of Africa by bovids about ~2.7–2.5 Ma, Vrba, 1995b; Elephantini about 2.5–1.5 Ma, Tchernov and Shoshani, 1996; *Megantereon whitei* about 2.0–1.9 Ma, Arribas and Palmqvist, 1999; *Bos primigenius* about 0.7–0.6, Martínez-Navarro et al., 2007), and widely reported and reviewed in the palaeontological literature.

The ancestors of some Eurasian Pleistocene species stemmed from African lineages that had already moved towards Eurasia during the Late Pliocene, before the cooling phases culminated with the growth of the Arctic ice-sheet at about 2.520 Ma (MIS 100) (Zachos et al.,

2001). Some lineages spread across the entire Eurasia, some extended the geographic range only to restricted region of Asia (e.g. *Damalops*, *Oryx*, *Hippotragus*, *Sivacobus* whose descendants are recorded in the Indian subcontinent), or did not reach Europe (e.g. among others *Elephas*), some others are only recorded in the Levant (e.g. *Kolpochoerus*, *Pelorovis*, ?*Oryx gazella*, ?*Equus tabeti*). *Mammuthus* and *Palaeoloxodon* are among the best-known and best-represented species in the Pleistocene fossil record of Eurasia. Few remains of *Mammuthus* showing archaic morphology (mostly referred to *M. rumanus*) are first recorded in Eurasia since about 3.5–3.2/3.0 Ma in Romania (Radulesco and Samson, 1995); ?Bulgaria (Markov and Spassov, 2003), Greece (Kostopoulos and Koulidou, 2015), and North China (Wei et al., 2006). The wide but punctuated geographic distribution (from the Balkan area eastward to China) of primitive mammoth populations during the Late Pliocene suggests a rapid dispersal. The scarce fossil record, however, challenges an understanding of potential taxonomic implications (if any) of the contradicting morphological variation among specimens (Kostopoulos and Koulidou, 2015). Moreover, the poorly constrained chronology of the Eurasian sites and the possibility that two elephantid taxa (*Elephas* and a primitive mammoth intermediate between African *M. subplanifrons* and European *M. rumanus*) are present in the late Pliocene/early Pleistocene in SW Asia (Bethlehem, Israel) (Rabinovich and Lister, 2016) hampers our ability to specify time and patterns of dispersal. Considering the chronological range of the potential African population source of Eurasian mammoths [*Mammuthus* sp., Hadar morphotype, is recorded from about 3.8 to 3.2 Ma in eastern Africa, at Woranso-Mille, dated to about 3.8–3.6 (Sanders and Haile-Selassie, 2012), and in the Sidi Hakoma and Denen Dora members of Hadar Formation, dated from about 3.4 to 3.2 Ma (Brown et al., 2013)], the hypothesis that mammoth populations dispersed via the Levantine Corridor during the late Piacentian cool phase recorded at about 3.3–3.2 Ma, and concomitantly with the emergence of a thermic seasonality in the Mediterranean terrestrial domain (Bertini et al., 2010), cannot be discounted.

The dispersal of *Palaeoloxodon* took place much later, likely by the end of the Early Pleistocene as supported by the roughly contemporaneous presence of straight-tusked elephants in Israel (Gesher Benot Ya'akov, ~0.8 Ma = *P. antiquus* in Goren-Inbar et al., 1994; *P. cf. recki atavus* in Saegusa and Gilbert, 2008), Croatia (<0.9 Ma) and Italy (Slivia, ~0.8 Ma), suggesting dispersal phases triggered by the latest Early Pleistocene cooler and dryer climatic oscillations (MIS 24–22) (cf. Palombo, 2014, 2017 for a discussion).

The climate instability in the post-Olduvai Early Pleistocene, which preludes the MPR, promoted the dispersal toward Europe of some species inhabiting open environments, mostly of Asian provenance (see below). Among the African species believed to have reached SW Europe during that time, the unique presence of a few baboon remains at Cueva Victoria (Spain) and the alleged occurrence of a caprine close to the extant *Ammotragus levia* in Spain and France pose intriguing questions.

*Theropithecus* is recorded in Eurasia by very few, scattered remains in the Levantine Corridor (Ubeidiya, 1.5 Ma), India (Mirzapur,  $\approx 0.6$  Ma) and in SW Spain (Cueva Victoria,  $\sim 0.9$ – $0.85$  Ma). The presence of the baboon in Spain in deposits older than the Indian ones prompted Gibert et al. (2016) to conjecture a dispersal of *T. oswaldi* from Africa to Eurasia across the Strait of Gibraltar, which would have acted as a filter bridge for both baboons and humans during the MIS 22 sea level lowering. This hypothesis has to be considered with great caution, because dispersal across the Gibraltar Strait during the Early Pleistocene for terrestrial mammals would have been hardly probable if not impossible (Turner and O'Regan, 2015). It seems rational to suppose that small *Theropithecus* populations reached SW Asia about 1.5 Ma, and then moved toward the Eurasian continent across a patchy mosaic of desert and grassland. The disjointed geographic range of *Theropithecus* was possibly related to sub-optimal climatic and environmental conditions of some areas that caused low population densities and consequently a sparse fossil record. A similar context may be advocated to explain the sparse distribution in space and time of the Early Pleistocene European giraffids recently ascribed to the genus *Palaeotragus* (Athanasios, 2014), known in Spain (Fonelas 1,  $\approx 2.0$  Ma) and from the Balkan area, Greece, throughout the Caucasus to the Kazakhstan in LFAs ranging in age from the Late Pliocene to the late early Pleistocene.

The renewal of the European Early Pleistocene ungulates due to dispersal bioevents was mainly related to the arrival of species from Eurasia (e.g. scrofic suids, large deer, bovine and caprine). The number and dispersal dynamics of species believed to be of African origin are debated. The arrival via the Levant of *Hippopotamus* is indeed the only unquestioned the early Pleistocene dispersal event from Africa to the western Mediterranean, but the time of dispersal is uncertain. Hippopotamuses are first recorded in Greece and may be in Italy in the middle Villafranchian, while a hippo closely related to the European *H. antiquus* is recorded in the southern Levant not earlier than 1.5 Ma (Ubeidiya LFA). Assuming that the absence of hippos in SW Asia would be related to taphonomic biases, it should be hypothesised that *H. gorgops* dispersed from the North of Africa during the short mid-Gelasian warm event, recorded in both the oceans and the Mediterranean Sea, around 2.2 Ma, when the steppe-like vegetation averagely decreased (Bertini et al., 2010). Whether the successive absence of a hippo fossil record till about 1.5–1.4 Ma (Venta Micena LFA, Spain) was related to a scanty presence in a restricted area, or to a disappearance of *Hippopotamus* from most of the area, followed by a new dispersal from either the Levant or some “refugium” territories, remains an unsolved issue.

The biogeographic origin of the slender equid *E. altidens* and the caprine *Ammotragus mediterraneus* has been questioned. *E. altidens* was regarded either as an indigenous European species originated from *E. stenonis*, or a new Early Pleistocene immigrant that originated from the Chinese lineage of *E. qinyangensis*, or from the African species *Equus tabeti*, recorded, for instance, in the Magreb at Ain Hanech ( $\approx 1.8$  Ma) (Sahnouni et al., 2013), and in the Levant at Ubeidiya ( $\approx 1.5$  Ma) (Belmaker and O'Brien, 2017). The middle-sized horse from Selvella (Italy,  $\approx 1.5$  Ma) is the

key sample providing morphological and dimensional evidence to support the hypothesis of an origination of *E. altidens* from a stenonoid European lineage (cf. Alberdi and Palombo, 2013; Palombo and Alberdi, 2017).

The name *A. mediterraneus* was proposed for some caprine remains found in the LFAs of Fuente Nueva (Spain,  $\approx 1.3$  Ma) and Le Vallonnet (France,  $\approx 1.1$  Ma), and believed to be closely related to the extant Barbary sheep (Moullé et al., 2004). Whatever the accuracy of the taxonomic identification of remains from the French site of Le Vallonnet would be (cf. Crégut-Bonnouire and Dimitrijevic, 2006 for a discussion), the alleged presence of *Ammotragus* in Europe poses a question about the trajectory and the time of dispersal of the ancestor of the extant Barbary sheep lineage. As Geraads (2010) pointed out, the genus *Ammotragus* could be the end product of a North African lineage, or alternatively could be of European origin, if actually present in SW Europe during the Early Pleistocene.

Conversely to ungulates, the renewal of the South European Early Pleistocene large predator/scavenger guild has been regarded as mainly related to species coming from Africa, while *Canis* species and *Xenocyon* dispersed from Asia (see Palombo, 2014 for a discussion). Some issues, however, concern the biogeography of hyaenas and pantherines.

The African origin of *Pachycrocuta brevirostris* may be reconsidered. The short-faced hyaena is first recorded in the North Mediterranean at about 2 Ma and its dispersal, though diachronous, has been regarded as the key signal of the beginning of the late Villafranchian (“*Pachycrocuta* event” sensu Martínez-Navarro, 2010). Scant remains are recorded in Kenya about 3.6–3.2 Ma, but the species had already disappeared from East Africa at the time of its FHA in SW Europe (Lewis and Werdelin, 2007). In Asia, however, the FHA of *P. brevirostris* (= *P. licenti*) in the Nihewan Basin (North China) postdates that in Europe (Ao et al., 2013). Therefore, an Asian origin of the short-faced hyaena seems unlikely.

The dynamics of spotted hyaena dispersal is rather complex and as challenging to evaluate as the African history of the genus *Crocuta* is (Lewis and Werdelin, 2007). In Eurasia *C. crocuta* is first recorded in India between about 2.5 and 1.8 Ma (Nagrota formation), in the Levant at about 1.5 Ma (Ubeidiya, Israel), and in Europe about 0.9 Ma (Atapuerca, Spain). Whether *Crocuta* moved from Africa once or twice, the Levant was reasonably the source area for its dispersal toward SW Europe.

As for felids, the European jaguar-like cat *Panthera* ex gr. *P. gombaszoegensis* (= *Panthera onca*) is first reported in the late middle Villafranchian in the Netherlands; subsequently, shortly before and during the Olduvai subchron, its geographic range extended from Italy to the Balkan area (Bulgaria, Greece) to the Caucasus region, and later, about 1.5 Ma, in the Levant. The biogeographic scenario is complex because on the one hand the diachronous appearances might support a European origin for the jaguar-like cat, and on the other the presence of a pantherine in the Tibetan Himalaya in the late Miocene–early Pliocene, along with evidence from new molecular phylogenies, may suggest an Asian origin. The mixed characteristics of

lion, leopard, and tiger genera shown by the 3.5 Ma old *Panthera* remains found at Laetoli (Tanzania) would support, however, an African origin of *Panthera* (see references in Palombo, 2017).

Some doubts concern the African origin of *Megantereon whitei*, a sabre-toothed cat that most researchers hypothesized to have dispersed from Africa to Eurasia at roughly the same time as the earliest hominins, while others considered it the most advanced representative of a European lineage (see, e.g., Lewis and Werdelin, 2010; Palmqvist et al., 2007). The scenario is further complicated by the discovery in Early Pleistocene deposits (about 2.0 Ma) of South China of a small *Megantereon* with dental features similar to those of *M. whitei* and more advanced than those of Chinese sabre-toothed cats having roughly the same chronology (Palombo, 2017 and references therein). All things considered, however, a dispersal from Africa seems to be the most conceivable.

## 5.2. Biochronological notes

Factors driving the remodelling of the range of a taxon, and time and mode of its dispersal and diffusion into SW Europe differed from one territory to another. This led on the one hand to some diachrony/asynchrony in the local first appearances of North Mediterranean species (especially in the post-Olduvai Early Pleistocene), on the other to dissimilarities in the resilience of resident species to the perturbation of community' equilibria, and in the disappearances of the most specialized taxa. In addition, the geographic ranges of some species apparently restricted to a single territory (e.g. but not only, Greece) may be suggesting some kind of endemism. As a result, correlations and biochronological assessments of LFAs may be difficult especially when firm chronological constraints are unavailable, challenging any attempt to properly define biochronology units having short temporal extents. This is the case, for instance, of the so-called "Epivillafranchian" LFAs fauna, which undoubtedly shows a peculiar composition due to the discrete appearances of new taxa since about 1.5 Ma and the persistence of some Villafranchian species, some of which survived to the Middle Pleistocene. Evidence from SW Europe suggests that the chronological range of the "Epivillafranchian" (whatever its biochronological rank could be) might span from about 1.5 to 0.85 Ma (i.e. Lowest local Stratigraphical Occurrence, LISO datum, of, among others, *Homo*, *Xenocyon lycaonoides*, *Canis ex gr. C. mosbachensis*, *Megantereon whitei*, advanced stenoroid horses, *Praemegaceros*, *Bison*, and Highest local Stratigraphical Occurrence, HISO datum, of *X. lycaonoides*, *M. whitei*, *Puma pardoides*) (Palombo, 2016 and references therein). Nonetheless, taking into account the negative influence of factors such as controversial identifications of some specimens/taxa, and uncertainties in LFAs chronology, several lines of reasoning suggest an informal use of the term Epivillafranchian, pending a complete revision of the Villafranchian ELMA, in particular the number of its subdivisions and their rank.

## 6. Conclusion

During the late Early Pleistocene, the climate forcing known as mid-Pleistocene Revolution (MPR) induced deep, more or less gradual alterations and latitudinal displacements in European terrestrial biomes and exerted great influence on dispersal and dispersion of mammalian species. The discrete dispersal bioevents that progressively contributed to the changes in taxonomic composition and ecological structure of the large mammal fauna of North Mediterranean mainly concern species of Palearctic origin, especially bovids and cervids, and some Nearctic groups, such as equids of the genus *Equus*. The arrival of a few species of African origin (baboon, elephants, hippos, and large carnivores) is comparatively rare and sometimes contentious. The Levantine Corridor has generally been accepted as the preferential route of dispersals from Africa. The region possibly acted as a sort of a "filter" corridor because a few African large mammals recorded in the Levant never dispersed further into the Eurasian continent.

Mammals did not generally move in multi-species waves of dispersal; rather each species changed its range depending on the suitability of environmental conditions with respect to its own environmental tolerances and ecological flexibility. As a result, the remodelling of the geographic range of a taxon, and the time and mode of its dispersal and diffusion into SW Europe, differed from species to species as well as from one territory to another, leading to diachronicity/asynchronicity in FIHA/LIHA. This and other factors (e.g. heterogeneous consistency of the fossil record in space and time, weak or unavailable chronological constraints of LFAs, exclusive presence of some species in confined areas, confusing taxonomic treatment of some taxa, and effects of depositional context, preservation and taphonomical biases in determining the chronological reliability of FIHA/LIHA and patterns of presence/absence especially of rare species) make it difficult to order LFAs in correct chronological sequences and gathered them in short-time chronological units.

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## Appendix A. Supplementary information

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