Plio-Pleistocene Mammalian Faunas from the Italian peninsula and France: species richness, turnover patterns and ecological structure

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Abstract —The large mammal fossil record of the Italian peninsula and has France been revised in order to correlate the diversity and structural dynamics of reconstructed faunal complexes with the extensive changes in environmental conditions occurring from the Middle Pliocene to the Late Pleistocene. The transition from Early to Middle Pleistocene faunas represents a major reorganisation affecting both the diversity and trophic structure of large mammal communities. Other important faunal renewals took place at the transition from the early to middle Villafranchian (from the Middle to Late Pliocene) and from the middle to late Villafranchian (from the Pliocene to Pleistocene).

Keywords — Large mammals, Palaeoecology, Turnovers, Pliocene, Pleistocene, Italy, France

1. Introduction

Changes in mammal faunal diversity over time have often been considered the result of bioevents linked to major climatic changes. On the other hand, according to the "Red Queen Hypothesis", changes in equilibrium may be due to the internal dynamics of competitive relationships, and do not necessarily indicate strict interdependence between major climatic changes and evolutionary events. The aim of this paper is: 1) to compare and provide a concise picture of evolutionary trends in French and Italian large mammal complexes from the Late Pliocene to the Pleistocene, a period of time in which the Earth made the transition from relatively warm climates to generally cooler ones; 2) to investigate whether diversity and structural changes in the course of time were more greatly influenced by biotic interactions or by disturbances to the physical environment.

2. Materials and Methods

The taxonomical composition of local faunal assemblages (LFAs, a list of the species identified from the remains retrieved at a given fossil site and recovered from the same stratigraphic horizon), ranging in age from the middle Pliocene to the Middle Pleistocene (Villafranchian to early Aurelian land mammal ages, LMAs) has been revised. Species richness, turnover and guild structure have been analysed, considering faunal complexes belonging to France and Italian biochrons (MN, and FUs; Mein, 1975; Guérin, 1990; Palombo, 2005), already erected on the basis of selected palaeobioevents, the evolutionary stage displayed by taxa belonging to a well-defined phyletic lineage or typical taxa associations.

Faunal complexes corresponding to biochrons (regarded as faunal complexes having a certain taxonomic and ecological homogeneity and living in lapses of time during which no turnover is expected) have been analysed in terms of standing richness and faunal renewal according to Foote (2000), as well as in terms of palaeoecological significance, as in Palombo (in press and references therein).

3. Results

The richness trends shown by Italian and French faunal complexes are rather different (Fig. 1). On the Italian peninsula, species richness progressively increased during the Late Pliocene and Early Pleistocene, peaking around 1.3 Ma (its highest value), after which it declined until 0.95 Ma, reaching its lowest value. Conversely, in France, richness was particularly high during the middle Villafranchian, but declined starting from the beginning of the Early Pleistocene; however, a considerable increase characterised the transition from the Early to Middle Pleistocene. Species richness shows opposite trends during the Middle Pleistocene, as, after the marked increase in taxa detectable at the beginning of the Middle Pleistocene, a progressive dwindling both in species richness and estimated mean diversity characterised Italian faunal complexes. This difference may be linked to the occurrence of some "central European" taxa in France that did not enter the Italian peninsula. Species richness in France shows roughly the same trend as on the Italian peninsula, but the appearance of new taxa seems to be "anticipated", except for the

late Middle and Late Pleistocene (peak at 0.25 Ma and the following trend). It is worth noting that the beginning of the Middle Villafranchian (about 2.6 Ma) was the starting point for a progressive increase in diversity in both Italian and French faunal complexes.

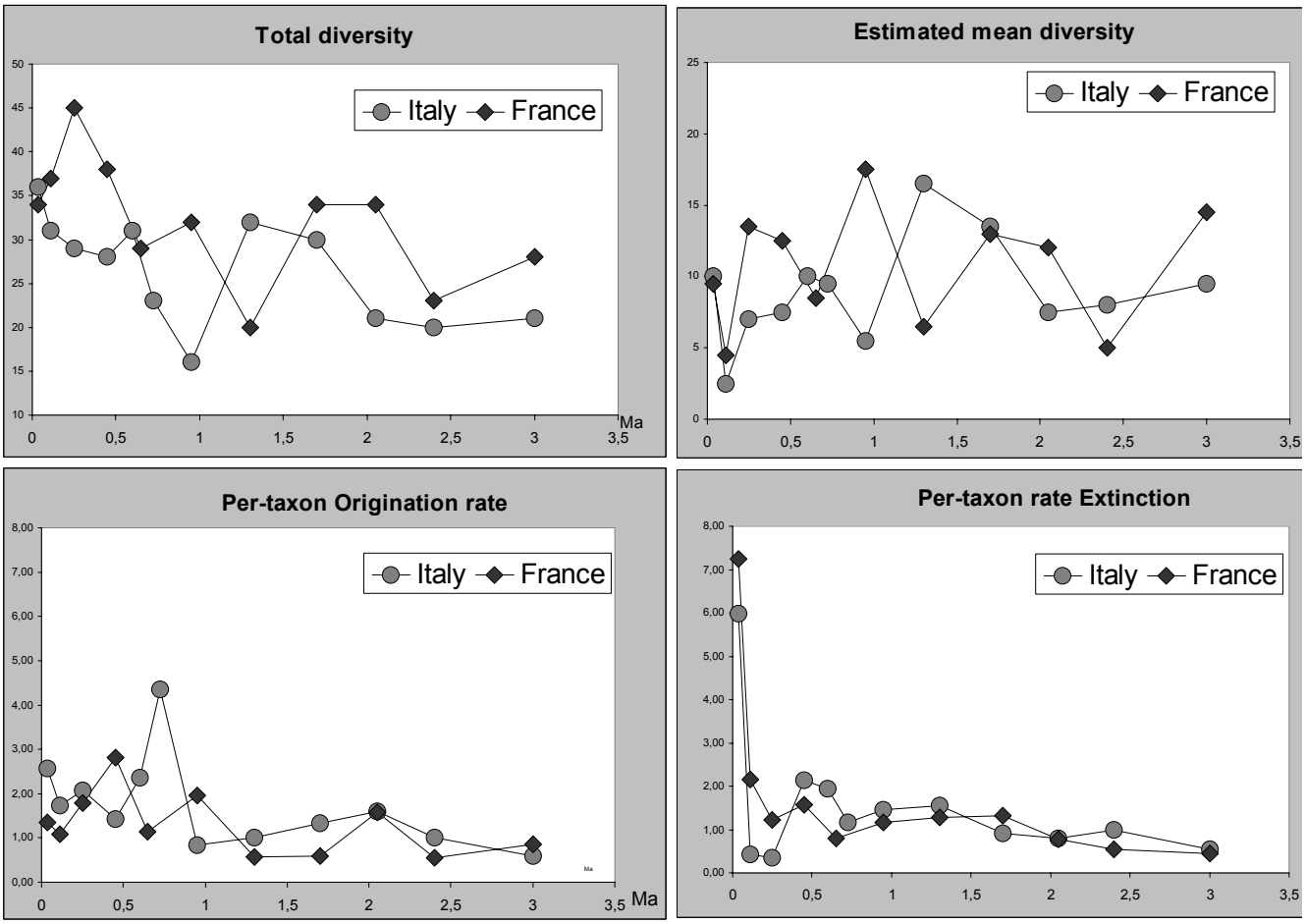

Fig. 1 — Line chart comparing richness (above), origination and extinction rates (below) in Italian and French mammalian faunal complexes from the Late Pliocene to the Late Pleistocene and faunal renewals of Italian large mammal faunal complexes from the Middle Pliocene to the Late Pleistocene. "Total Diversity" ($\mathbf{N_{tot}}$) = N_{FL} + N_{bL} + N_{Ft} + N_{bt} and "**Estimated mean standing diversity**" = $N_{tot}\,N_o/2 - N_e/2$; $\mathbf{N_o}$ (Number of originations) = N_{FL} + N_{Ft}; $\mathbf{N_e}$ Number of extinctions = N_{FL} + N_{bL}; N_{FL} = taxa that exist only in that interval; $\mathbf{N_{bL}}$ = taxa that originate before the interval but became extinct within it; $\mathbf{N_{Ft}}$ = those that originate in the interval and persist beyond it; $\mathbf{N_{bt}}$ = taxa that originate before the interval and persist beyond it (Foote, 2000). Per-taxon rates of origination and extinction are calculated as (*N*FL + *N*Ft)/*N*tot/D*t* (originations) and (*N*FL + *N*bL)/*N*tot/D*t* (extinctions), according to Foote (2000).

Origination and extinction rates calculated for Italian faunal complexes (Fig. 1) show origination peaks around 2.05, at 0.725 and 0.25 Ma (although the earlier half of this interval is biased due to poor sampling). Conversely, the extinction rate remains quite low during the first half of the interval, peaking around 0.4 Ma, is extremely low between the last Interglacial and Glacial and then increases considerably (latest Pleistocene extinctions). French faunal complexes show quite a similar trend: origination peaks can be detected at about 2.05, 0.975 and 0.45 Ma. A number of originations at 2.05 Ma leads to the high total diversity characterising middle Villafranchian faunal complexes, particularly abundant in France, where numerous fossil deposits have been found (Guérin & Faure, 2002; Palombo & Valli, 2004). Later, extinction progressively increased and richness slightly dwindled. The origination peak at 0.975 Ma and the contemporaneous extinction rate dwindling led to the "end-of-Early-Pleistocene" richness increase. During the Late Pleistocene, extinction rates in France and on the Italian peninsula were quite similar.

In spite of the above-mentioned differences, the most evident important peaks in origination rates, in France as well as on the Italian peninsula, matching or immediately preceding richness peaks, took place at the transition between the Early and Middle

Pleistocene, when a major turnover in both faunas has been highlighted (Palombo & Valli, 2005). This faunal renewal coincides with a period of climatic worsening revealed by the spread of grassland supporting more abundant 'cold' taxa, such as *Rangifer* (Caune de l'Arago, France; de Lumley et al., 1998).

Even if faunal renewals are related to extinctions, origination/immigration and local evolution affecting faunal richness, a turnover does not always imply structural reconstruction of mammal communities. However, changes in community structure can be detected throughout the whole time span examined here. Forest-dwelling taxa progressively decreased during the Late Pliocene and early Pleistocene, even if some oscillations can be detected in both the Italian and French faunal complexes. Conversely, the most ecologically-flexible taxa or taxa inhabiting grass- and/or bush lands increased in various degrees. As far as herbivores are concerned, the percentage of grazers increased, both on the Italian peninsula and in French faunal complexes (Fig. 2). At the beginning of the middle Villafranchian (at 2.6 Ma, Palombo, 2005 and references therein), grazers became more frequent in both countries, this trend being consistent with the marked cooling event taking place during the same period (Azanza et al., 2000; Palombo et al., 2003, Palombo in press and references therein). Furthermore, during the last 0.45 Ma, grazers dominated French faunas, whereas browsers markedly decreased. On the other hand, the faunal complexes' structure shows a more complex trend in Italian faunas, due to a more marked fluctuation in the percentage of mixed feeders. The geographical position of the Italian peninsula (further south than France), its physiography and the great influence exerted by the seas surrounding the peninsula, possibly favoured more microclimatic differences and environmental fragmentation. In any case, the percentage of grazers globally improved on the Italian peninsula as well, starting at the beginning of the middle Villafranchian and reaching its acme in the last Interglacial.

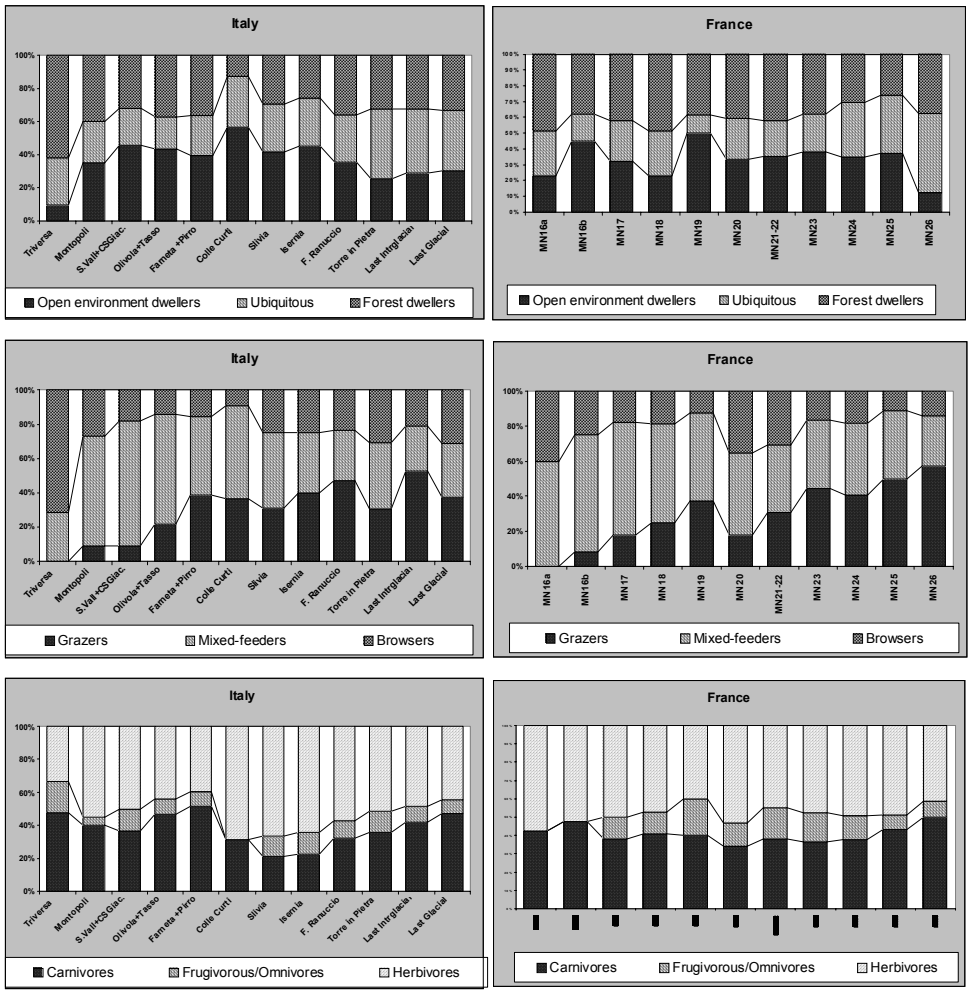

Fig. 2 — Bar charts comparing the frequency of ecological categories in Italian and French mammalian faunal complexes from the Late Pliocene to the Late Pleistocene.

As far as carnivores are concerned, in French faunas their percentage ranges between 30% and 50% during the whole interval considered, being slightly lower (or at least equal to, as during the last Glacial) than the percentage of herbivores. In any case, carnivores are particularly abundant in French faunas at the beginning of the middle Villafranchian and at the end of the Pleistocene (Fig. 2). Conversely, the percentage of Italian carnivores fluctuated more, being between 20% and 60%. Carnivores were more abundant than herbivores in the time span from 1.9 to 1.2 Ma, peaking at the Pirro FU. The increase in the percentage of carnivores at the beginning of the Early Pleistocene was mainly related to the spread of hunting-pack dogs and scavenging hyenas, inhabiting open environments (the so-called "wolf-event"; Azzaroli, 1983; Azzaroli et al., 1988; Palombo & Sardella, in press). At the end of the Early Pleistocene, starting with the Colle Curti FU (but see Palombo, 2005), the percentage of carnivores fell dramatically, increasing again at the end of the Middle Galerian (*sensu* Gliozzi et al., 1997).

4. Discussion and Conclusions

Since the Late Pliocene, a series of climatic cycles have caused latitudinal displacements of vegetational cover and biomes in Europe. Actually, it seems that, with the passing of time, climatic events exerted great influence on mammalian species diffusion and dispersion, thus influencing the composition of regional faunas (see e.g. Jansson & Demetrius, 2002). Moreover, climatic changes facilitated immigration of new taxa, and during the Plio-Pleistocene, mammals more frequently reacted to climate changes not by evolving and producing new species, but by expanding their diffusion area or migrating as the climate changed (see for example: Koenigswald, 2002, and references therein as far as the alternation of "temperate faunas" in the interglacials and "cold faunas" typical of glacial periods in Central Europe is concerned; Spassov, 2003 for Eastern European faunal turnovers). In other respects, most Pleistocene mammals persisted through many climatic cycles, and relatively few evolutionary changes can be directly attributed to climatic change. On the other hand, very poor correlation between turnover pulses and climatic variation has been inferred, e.g., for African Plio-Pleistocene (Hill, 1995; Behrensmeyer et al., 1997) and North American Cenozoic mammals (Alroy, 1995, 1997, 1998).

However, with reference to Italian and French large mammals, analysis results confirm that during the late Pliocene and Pleistocene, the most important faunal renewals (due both to originations/ immigrations and extinctions) were linked to major global climatic changes. Nonetheless, there is little evidence of cyclical, climatically-driven turnovers corresponding to "glacial/interglacial" alternations. The Late Villafranchian and Middle-Late Galerian present only minor phyletic adjustments and support a model of protracted minor faunal changes that seem to result more from complex forcing factors rather than merely from climatic changes.

All in all, patterns of Italian and French faunal complexes suggest that climatic control clearly acts as an important factor in driving faunal structural changes, but in a rather complex way, and intrinsic biotic controls may also be essential in determining faunal complex evolution (see e.g. Prothero, 1999).

Temporarily alternating, more or less frequent climatic stimuli seem to produce very few responses on the part of all mammal fauna: a few species produced specialist adaptations, others developed flexible adaptations and still other generalist species having broad niches survived major environmental changes. On the other hand, peaks in mammalian fauna renewals can be directly linked to climatic changes producing migratory waves in multiple taxa. In addition, climatic changes should remove keystone species; this, along with migratory responses to climate change, may also lead to evolutionary change, causing new internal dynamics in competitive relationships within reconstructed faunal complexes. We can eventually hypothesize cause-and-effect relationships between climatic oscillations and faunal changes that may be present at the level of individual species; moreover, evolutionary divergences (more frequently sub-speciation) developed during multiple climatic cycles.

The results obtained support the argument that climatic changes (especially decreasing in temperature and increasing in aridity) should be a forcing factor, especially in large mammal first appearances, whereas global reconstruction of the structure of faunal complexes may also be affected by the internal dynamics of competitive relationships and does not necessarily indicate strict dependence on major climatic changes. Moreover, progressive shifts in faunal composition suggest that migratory and evolutionary responses to climate change, physical-environmental disturbances and biotic interactions globally contribute to faunal evolution.

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