Pliocene to Pleistocene large mammal diversity and turnover in North Mediterranean region: the Greek Peninsula with respect to the Iberian and Italian ones

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ABSTRACT

During the Plio-Pleistocene several important climatic events constrained faunal renewal phases, affecting the structure of mammal communities, their richness and diversity. In order to complete the analysis of the Pliocene to Pleistocene large mammal faunal renewal in North Mediterranean region, the Greek turnover and diversity patterns from Ruscinian (about 5 Ma BP) to the end of middle Pleistocene (about 175-127 ka BP) are compared with those of Italy and Spain. The analysis takes into account the changes in the taxonomical composition and ecological structure of the Greek, Italian and Spanish succession of regional faunal complexes, which correspond to high rank biochrons (Mammal Ages or Mammal Subages) or they are provided from a cluster analysis.

KEY WORDS
Large mammals,
Plio-Pleistocene,
diversity,
turnover,
Southern Europe.

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The results indicate a Villafranchian longitudinal diversification from Greece to Spain and a significant early Pleistocene (Galerian) faunal renewal that affected more or less simultaneously the entire North Mediterranean region as a response to the establishment of cooler-dryer climatic conditions around the Jaramillo magnetochron.

RÉSUMÉ

Diversité et changement des faunes de grands mammifères plio-pléistocènes sur le pourtour nord de la Méditerranée : comparaison des faunes de la péninsule grecque avec celles d'Italie et d'Ibérie.

Pendant le Plio-Pléistocène plusieurs événements climatiques importants ont provoqué des phases de renouvellement faunique, affectant la structure des communautés à mammifères, et également leur richesse et leur diversité. Dans l'objectif de compléter l'analyse des changements des faunes à grands mammifères dans la région nord-méditerranéenne du Pliocène au Pléistocène, le renouvellement et la diversité faunique de la Grèce ont été comparés à ceux de l'Italie et de l'Espagne, du Ruscinien (environ 5 Ma BP) à la fin du Pléistocène moyen (175-127 ka BP). L'analyse prend en compte les changements de composition taxonomique et de structure écologique des successions des complexes fauniques régionaux de Grèce, d'Italie et d'Espagne. Ils correspondent aux complexes biochronologiques majeurs (« Mammal Ages » ou « Mammal Subages ») ou dérivent de l'analyse de regroupement par comparaison (« cluster analysis »). Les résultats montrent qu'il se vérifie, pendant le Villafranchien, une diversification longitudinale de l'est vers l'ouest (de la Grèce jusqu'à l'Espagne), et qu'il se produit un renouvellement significatif concernant, plus au moins à la même époque (Pléistocène inférieur, Galérien), toute la région nord-méditerranéenne. Ce renouvellement est la réponse à l'établissement des conditions climatiques froides et sèches correspondant au magnétochron de Jaramillo.

MOTS CLÉS
Grands mammifères,
Plio-Pléistocène,
diversité,
turnover,
Europe du Sud.

INTRODUCTION

The crucial role of both the physical and the biotic factors in configuring mammal communities has been extensively discussed by several authors, who propose different models to explain the regulation of faunal diversity with respect to time (e.g., Van Valen 1973; Turner 1995; Vrba 1995; Brett *et al.* 1996; Behrensmeyer *et al.* 1997; Alberdi *et al.* 1997; Azanza *et al.* 1999, 2003, 2004; Palombo *et al.* 2003; Fortelius *et al.* 2006 and literature therein). Physical and biotic environmental conditions exert great influence on the biogeographic distribution of mammalian species, affecting the taxonomical composition and the structure of mammal communities through time. Environmental changes were assumed to be a driving force in changing diversity: taxonomic groups undergo long periods of quasi-static dynamic that are interrupted by intervals of especially high rates of extinction/emigration and origination/immigration (Vrba 1985, 1995; Azanza *et al.* 2004; Palombo & Valli 2004). With respect to the role played by biotic factors in mammal radiation and extinction the "Turnover pulse hypothesis" (Vrba 1993, 1995) suggests that most of lineage turnovers occurred when groups of organism spread in pulses correlated with changes in the physical environment. Furthermore, renewal patterns might be constrained by climatic-driven effect at intermediate to large temporal scales. Hence, changes in mammal faunal diversity have often been considered as the result of bioevents, correlated with major climatic changes, which, in their turn, can determine concurrent bioevents in multiple lineages.

Apparently, the composition of regional faunal complexes is the result of both ecological and historical factors that control the structure of communities even inside a particular biogeographic area. Indeed, the possibility of dispersion, diffusion and survival of taxa – especially when forced by climatic events – were greatly affected by the physiography, the microclimate conditions, and the availability of ecological niches. As far as the North Mediterranean is concerned, past and present large mammal distribution is not homogeneous. Although the South European realm is supposed to outline a uniform zoogeographic province, its environment and topography are highly heterogeneous. Despite general similarities, the three well separated peninsulas maintained different configuration through time and had different biogeographic significance because of geographical and ecological barriers, represented by local mountain chains, relations between their latitudinal and longitudinal extension (e.g., Spain versus Italy), and influence of the Mediterranean Sea on their climatic conditions. From the end of Miocene, the "Greek arm" of the Balkan Peninsula constituted a reception and diffusion area of several migration waves directed mainly from the East to the West (Kostopoulos *et al.* 2002; Spassov 2003). On the other hand, it is generally claimed that at the same time-span the Iberian and Italian peninsulas formed a kind of "cul de sac", where ended most of the Eurasian dispersal events which affected Western Europe (Alberdi *et al.* 1997; Palombo *et al.* 2003). In addition, Southern Europe is considered as a refuge area for northern taxa during the Pleistocene climate worsening.

The quite rich Late Cenozoic mammal record from the North Mediterranean region provides a great opportunity to study the evolution of the ecological features of regional faunas with respect to environmental changes. Alberdi *et al.* (1998), Azanza *et al.* (1999, 2002, 2004), Palombo *et al.* (2003) and Palombo & Valli (2004) already studied the influences of global climatic changes on the structural evolution of southwestern European mammal faunas. In this paper we extend this study eastwards, by comparing the diversity and structural dynamics of the reconstructed Greek palaeocommunities with the SW European ones.

METHODOLOGY

In order to evaluate the possibility of correlating trans-South European faunal renovation with changes in environmental conditions that assumed to have occured at the transition between faunal complexes, we compare the turnover patterns of Greece with those of Spain and Italy from Ruscinian (about 5 Ma BP) to the end of middle Pleistocene (about 175-127 ka BP).

A change in the taxonomical composition between two successive biochrons can be considered as a faunal turnover, when alterations in species composition is provided by the concurrent extinction of existing species (exits) and their replacement through immigration by new ones (entries). An increase or decrease in richness depending on just one of these factors should be regarded as a dispersal or extinction event (see Alberdi *et al.* 1998; Torre *et al.* 1999; Azanza *et al.* 2003; Palombo 2004, 2005 and literature therein). Actually, even if constrained by paleoenvironmental changes, the extinction/emigration and the origination/immigration events were scattered in time. In order to evaluate average trend in ecological structure of extinct faunas, we have to establish a theoretic faunal complex that can be used as a "block of coordinated stasis" during which no turnovers are expected (Brett *et al.* 1996). As local faunal assemblages (LFAs) arranged in biochron units could be regarded as representing not overlapping and "ecologically adjusted groups of animals with specific geographic limits and chronological range" (Tedford 1970), we assume biochrons as "blocks of coordinated stasis"

TABLE 1. — Relative age distribution of Greek, Italian and Spanish local faunal assemblages (LFAs) used in the analyses. Data from Palombo *et al*. (2006) and literature therein.

Mammal ages/ subages	**Greek LFAs**	**Italian LFAs**	**Spanish LFAs**
Aurelian	Petralona, Megalopolis	Montignoso, Casal de Pazzi,Torre in Pietra (lower and upper), Sedia Diavolo	La Carihuella, Los Casares, C. Negra, Valdegoba, Villacastin, Pinarillo-1, Torrejones Congosto, Pinilla del Valle Torralba, Ambrona, Atapuerca 10, La Solana del Zamporino
Galerian	Marathoussa-Megalopolis, Kaiafas, Ravin Voulgarakis, Apollonia	Fontana Ranuccio, Visogliano, Isernia la Pinetta, Valdemino, Slivia, P. Galeria, Redicicoli, Colle Curti	Cullar de Baza, Atapuerca 4, Atapuerca 6, Huescar
Late Villafranchian	Alikes, Pyrgos, Libakos Gerakarou, Vassiloudi	Pirro Nord, Pietrafitta, M. Riccio, Casafrata, Tasso, Olivola, Valdarno superiore, P. Rosso	Venta Micena, Quibas, Ponton de la Oliva, Fonelas
Middle Villafranchian	Volakas, Dafnero, Sesklo, Vatera	C. S. Giacomo, Montopoli	La Puebla de Valverde, Huelago, El Rincón
Early Villafranchian	–	Colle Pardo, Triversa, G. S. Barbara, Barga, Pieve Fosciana	Villaroya
Ruscinian	Apolakkia, Megalo Emvolon Kessani, Maramena	Val di Pugna	La Calera, La Gloria 2, Layna, Alcoy

and we estimate turnover rates between successive biochrons. Consequently, faunal renewals can be extracted from the number of extinctions (last appearances, LA) at the end of a biochron and the new appearances (first appearances, FA) at the beginning of the successive one. Turnover indices (TI = % FA + % LA/2) are calculated using first and last appearance percentages after normalising the LA and FA values (% FA = FA/RM × 100; % LA = LA/RM × 100; RM = N - (FA/2 + LA/2); N = number of taxa) as in Torre *et al.* (1999).

Richness, used as an estimate of faunal diversity, is currently measured by the total number of taxa actually (Nt) or potentially occurring in every biochronological interval. Nevertheless, the richness of a single time interval might be overestimated when first local appearances are considered to occur at the beginning of the interval, and the disappeared taxa thought to persist until its end, whereas they might not actually overlap in time. In order to reduce this bias, it is possible to standardise the number of taxa that potentially occur at a given time interval by considering species richness at its midpoint. Consequently, we calculated standing richness values following Harper's (1975) method: Nrs = Nbda + Nrt + ½ (Nf + Nl - No) (Nrs, number of taxa that potentially occur at a given time interval; Nbda, number of species present before, during and after the faunal unit; Nrt, number of species present before and after but not in the faunal unit; Nf, number of first appearances [FA]; Nl, number of last appearances [LA]; No, number of taxa present only in the faunal unit).

A basic problem remains, however, on how we can ascertain a kind of successive faunal complexes that enable us to correlate among different geographic regions (e.g., Pickford 1990). Actually, correlation among faunal complexes belonging to different geographic areas is not an easy matter because of differences among local fossil records (both by means of taxonomical denomination and completeness), taphonomic biases, endemic phenomena, and differences in the local biochronological/biostratigraphical schemes. Hence, faunal renewals have been calculated at the transition between biochrons (Mammal Ages, MAs, and Mammal subAges, MsAs) according to the biochronological schemes already established for European mammal faunas (e.g., Palombo *et al.* 2006 and literature therein). The following biochronological faunal complexes (BFCs) have been considered: Ruscinian (MN14, MN15), early Villafranchian (MN16a or Italian Triversa faunal unit, FU), middle Villafranchian (MN16b, MN17 or Italian FUs from Montopoli to Costa San Giacomo and MNQ18 *partim*), late Villafranchian (Italian FUs from Olivola to Pirro, MNQ18 [*partim*]-MNQ19), Galerian (Italian FUs from Colle Curti to Fontana Ranuccio, MNQ20-MNQ23), and Aurelian (early Aurelian = Italian Torre in Pietra FU, MNQ24; late Aurelian including late Pleistocene LFAs) (*sensu* Gliozzi *et al.* 1997; Guerin 1990; Mein 1990).

During the last years multivariate techniques have been extensively and successfully applied in the recognition of successive, not overlapping and ecologically adjusted assemblages of taxa, living together in a given space and time (Azanza *et al.* 1997, 1999; Palombo *et al.* 2003; Palombo & Valli 2004 and literature therein). Therefore, we have also analysed the faunal renewals for each geographic area on the basis of large mammal complexes (Table 1) resulting from a similarity analysis based on the common presence of taxa (see Palombo *et al.* 2006). Nineteen Greek faunas ranging from the latest Miocene to the middle Pleistocene, 29 Italian faunas ranging from the earliest Villafranchian to the end of middle Pleistocene and 29 Spanish faunas ranging from the earliest Pliocene to the late Pleistocene have been involved (Palombo *et al.* 2006). According to the results of this analysis, successive groups of LFAs are considered as representing succession of local "biochrons", here named cluster faunal complexes (CFCs).

For ecological purposes, we estimate the percentage of taxa according to the preferred habitat and dietary guild. Carnivores were regarded all together, while the herbivores were separated into grazers (Gr), browsers (Br), and mixed feeders (B-G), including taxa which, on a seasonal, regional or occasional basis, indifferently eat grass, leaves or both. The categories of frugivores (Fr) and omnivores (Om) were also considered. Three major ecological habitat groups were retained: forest dwellers (taxa inhabiting closed woodland, clear woodland, miscellaneous woodland), open land dwellers (taxa inhabiting grassland, steppe or savanna) and mixed dwellers (ubiquitous taxa, which can equally live in forests and open landscape, or at the edge of both).

TURNOVER ANALYSIS

GREECE

The BFCs and CFCs analyses results are almost identical (Fig. 1). The main problem concerns the paucity of Greek early Villafranchian LFAs and the consequent inability to establish a distinct faunal complex for this mammal stage, based on the selected data. Following the results of the cluster analysis (Palombo *et al.* 2006), we decide to join the Ruscinian and the early Villafranchian faunal complexes, admitting an a-priori distortion, which causes an overestimation of the turnover between the Ruscinian and the Villafranchian, characterised by high rates of extinction and much more first appearances (Fig. 1). Although fictitious, these results broadly reflect reality, especially regarding the extinction phase at the Ruscinian-Villafranchian boundary and the richness increase after Ruscinan. Both in the BFCs and CFCs analyses, the middle-late Villafranchian transition is characterized by the predominance of first appearances over extinctions, even with a low turnover index, leading to the increase of richness, which reaches its maximum during the late Villafranchian. An important renewal event occurs at the boundary between the late Villafranchian and the Galerian, in the BFCs analysis, or at the transition between the early and middle Galerian, in CFCs analysis (Fig. 1). In both cases, the turnover index reaches its maximum values, whereas the phase is characterised by an important increase of extinctions and a rather decline of first appearances (CFCs analysis), providing a richness reduction, especially during the middle Galerian (CFCs analysis). At the Galerian-Aurelian transition, last appearances are minimized and rates of new appearances slightly rise, leading together to a significant richness increase (Fig. 1).

ITALY

During the early and the middle Villafranchian, diffusion phases have occurred, characterised by the predominance of first appearances (Fig. 2). This

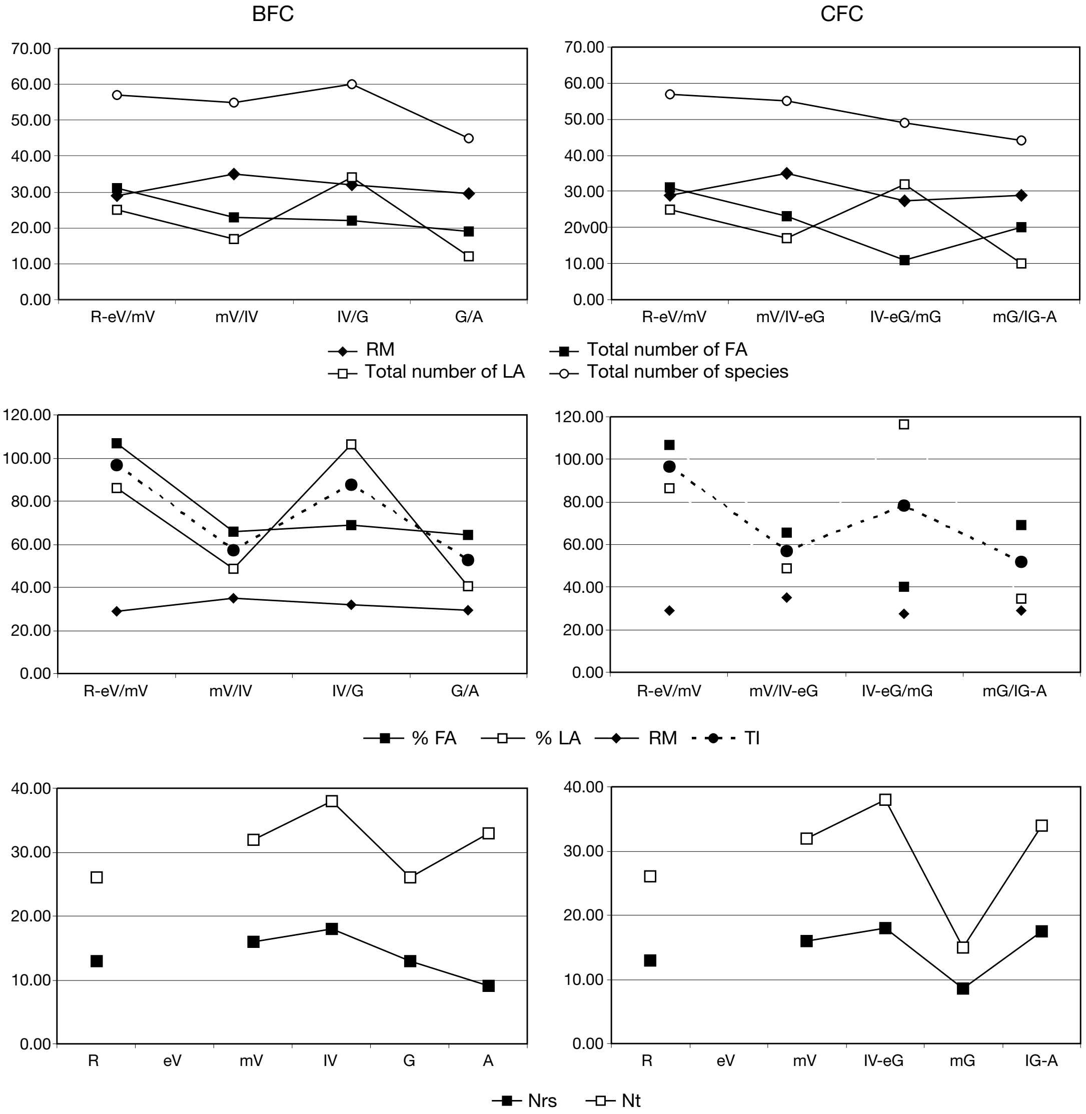

FIG. 1. — Turnover pattern analysis of Greek biochronological (BFC) and cluster (CFC) faunal complexes. Abbreviations: **FA**, first appearances; **LA**, last appearances; **Nrs**, standing species richness; **Nt**, species richness; **RM**, running mean; **TI**, turnover index; **A**, Aurelian; **G**, Galerian; **R**, Ruscinian; **V**, Villafranchian; **e**, early; **l**, late; **m**, middle.

trend allows richness to reach its maximum at the beginning of the late Villafranchian, while according to CFCs analysis (Fig. 2), richness decreases during the latest Villafranchian and at the transition between Villafranchian and Galerian. The end of early Pleistocene marks the major faunal renewal, documented either at the boundary between the late Villafranchian and the Galerian in the BFCs analysis or during the transition from the early to the middle Galerian in the CFCs analysis (Fig. 2). In the first case, the passage is characterised by an increase of extinctions whereas rates of appear-

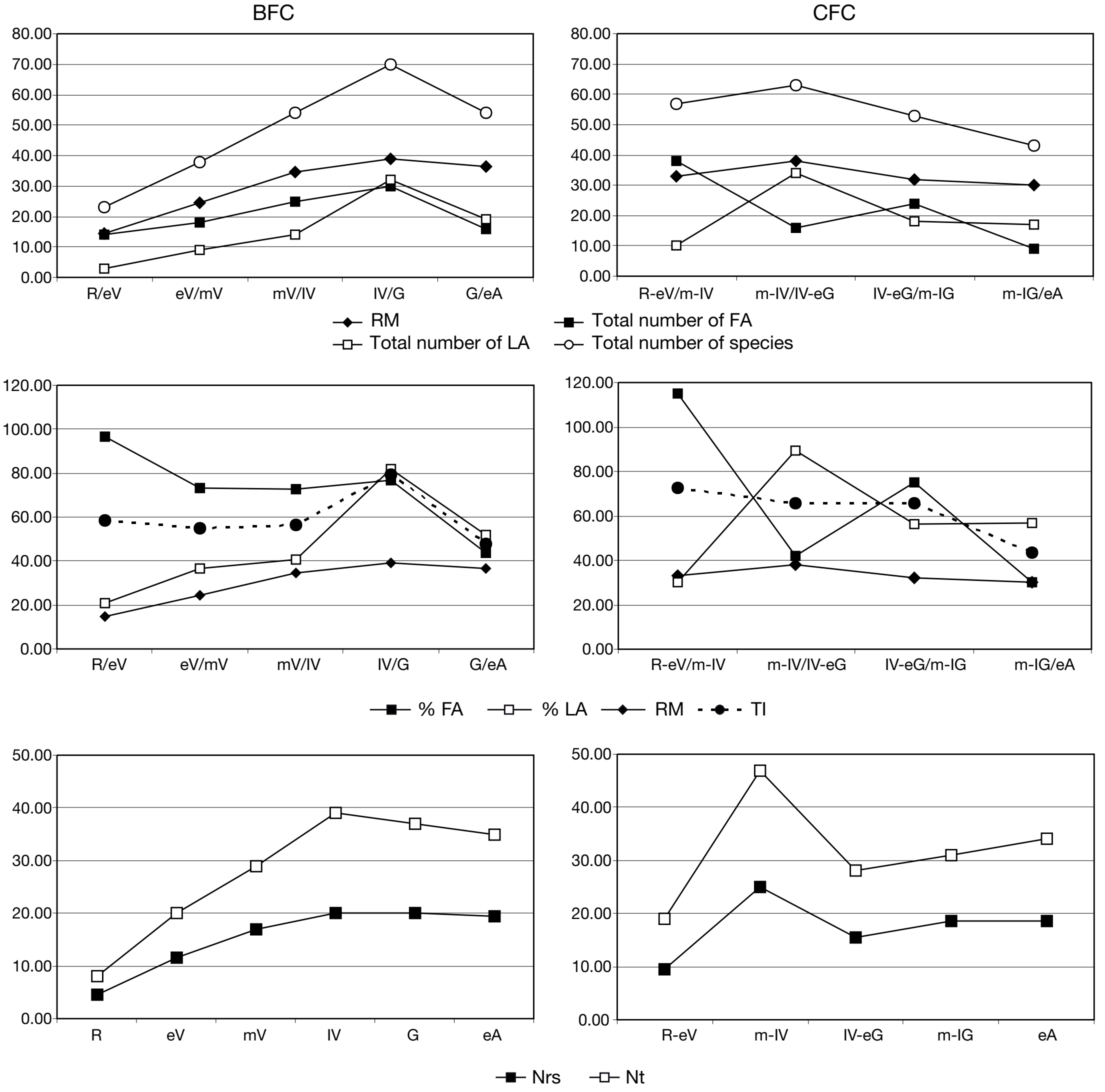

FIG. 2. — Turnover pattern analysis of Italian biochronological (BFC) and cluster (CFC) faunal complexes. Abbreviations as in Fig. 1.

ances show just a slight increase compared to the preceding phases, while in the CFCs analysis, it is characterised by the predominance of first appearance data.

SPAIN

The BFCs analysis shows a turnover at the Ruscinian-early Villafranchian boundary, followed by an extinction phase and a richness decline (Fig. 3). Afterwards, a progressive renewal takes place, reaching its apex at the late Villafranchian-early Galerian transition (at *c.* 1 Ma). This renewal, already evident at the middle-late Villafranchian boundary (Fig. 3), is firstly characterised by a predominance of new appearances over extinctions and allows richness to increase. Then, extinctions exceed new appearances (BFCs analysis) causing a progressive drop in the richness. At the Galerian-Aurelian transition

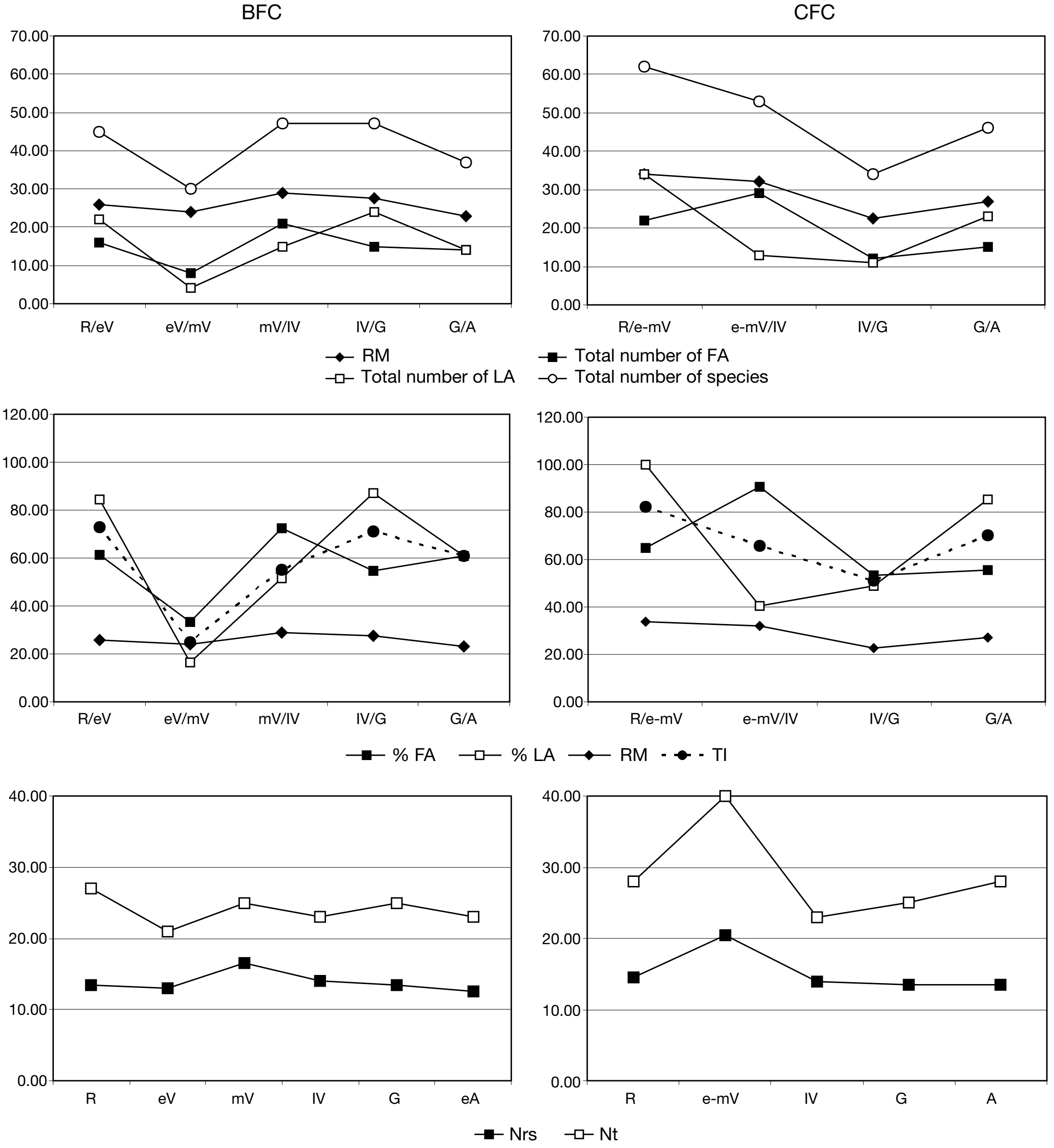

FIG. 3. — Turnover pattern analysis of Spanish biochronological (BFC) and cluster (CFC) faunal complexes. Abbreviations as in Fig. 1.

extinctions still prevail, but the progressive uplift of new appearances leads to a bend in richness. The CFCs analysis (Fig. 3) indicates both the dispersion phase at the middle-late Villafranchian transition and the extinction increase from the late Villafranchian to the Galerian-Aurelian.

PALAEOECOLOGICAL ANALYSIS

In the absence of data, early Villafranchian complex is excluded from Greek BFCs calculations. Greek carnivores number is rather stable during Villafranchian but it decreases in Galerian, recovering during Aurelian (BFCs analysis; Fig. 4). Omnivorous and frugivorous species show a gradual decline from the Ruscinian to the late Villafranchian/early Galerian, but they increase afterwards (Fig. 4). From the Pliocene to the early middle Pleistocene herbivores remain stable with a significant increase during Galerian (Fig. 4). Nevertheless, browsers gradually decrease from the Ruscinian to the late Villafranchian/early Galerian and then they slightly recover, whereas grazers show a general increase throughout this period, interrupted by a reversal in Galerian, when mixed feeders predominated over them (Fig. 5). During Aurelian, grazers reach their maximum, while mixed feeders and browsers are in balance (Fig. 5).

Comparison of the Greek data with those taken from the analysis of the Italian and Spanish faunal complexes (Figs 6-9) shows that Ruscinian faunal complex is characterized by a clearly distinct faunal structure (even on taxonomic level), whereas differences are less pronounced during the successive Plio-Pleistocene complexes.

As far as the carnivores are concerned, it seems that they are always more abundant in Spain than in Italy and even more in Greece (Figs 4; 6; 8). The Spanish complexes show that carnivores are almost as much numerous as herbivores (early and late Villafranchian) or exceed them (Aurelian), reaching (but not dramatically) their minimum percentage during Galerian (Fig. 6). In Italy, carnivores were more abundant than herbivores only during the early Villafranchian and then their number decreases towards the Galerian, recovering slightly in the Aurelian (Fig. 8). Apart from the general reduction of carnivore percentage during Galerian, the three regions were also characterised by a less evident decline during the middle Villafranchian that has been followed by a more or less marked increase during the late Villafranchian, corresponding grosso modo to the "wolf event" of Azzaroli (1983).

Herbivore guild presents quite different trends in the Greek, Italian and Spanish succession of faunal complexes (both in the CFCs and BFCs analyses; Figs 5; 7; 9). Similarly to Greece, a progressive increase of grazers, emphasized in the CFCs analysis (Fig. 7), characterizes all the Villafranchian faunal complexes of Italy, interrupted by a weak Galerian decrease. In Spain the highest herbivore percentage corresponds to the Ruscinian, followed by a decrease of grazers in the following Pliocene, an increase during the late Villafranchian and the Aurelian and by a drop during the Galerian (also similarly to the Greek trend; Fig. 9). Browsers are differently represented in the three peninsulas, being much more abundant in Spain than in Italy and very low in Greece (Figs 5; 7; 9). However, they show a relatively uniform trend in the three peninsulas, decreasing towards the late Villafranchian-early Galerian and then recovering towards the middle Pleistocene, in association with a reduction of mixed feeders.

Habitat analysis shows that mixed dwellers were always poorly represented in Spain in comparison with Greece and Italy, whereas forest dwellers were much less frequent in Greece that in Italy and Spain (Figs 10; 11). From the Ruscinian to the late Villafranchian open inhabitants predominate in Spain, interrupted perhaps by a more forestrial phase during the early Villafranchian (Fig. 11). On the contrary, at the same time in Greece and Italy forest and mixed dwellers are rather gradually displaced by open land dwellers, reaching a maximum during the Galerian (Figs 10; 11). From Galerian to Aurelian the entire area shows the same decreasing tendency of open landscapes associated with an increase of mixed dwellers, as a result of the climatic mildness and the fragmentation of the environment (Figs 10; 11).

DISCUSSION

Evidently, major faunal renewals and reconstructions do not always correspond to "true turnover phases" (i.e. the complete or almost complete replacement of a mammal fauna by a new one) but as the renewal often allows to a change in diversity, we have to deal with an extinction phase or a dispersion event. Moreover, a faunal renewal usually marks the beginning of a more or less long period of richness increase, which is followed by a period of decreasing richness. Accordingly, it seems that in some cases an environmental change encourages a more efficient exploitation of resources, which gives rise to an increase in mammal diversity and richness.

Our results show that at the transition from the Ruscinian to the Villafranchian the marginal parts of the studied area (Spain, Greece) are rather affected by a true turnover. At the West, this event is followed by a distinction phase while in Italy and Greece a diffusion phase occurs, associated with a predominance of new appearances. Although based on insufficient data, the obtained results confirm the relevance of the so-called *Equus-Elephant* dispersal event (Aguirre *et al.* 1976; Azzaroli 1983; Steininger *et al.* 1985; Azzaroli *et al.* 1988; Aguirre & Morales 1990) that signified a marked increase in diversity due to the high number of first appearances. This event should be related to the double seasonality caused by the 3.5 Ma establishment of cool winters that generated a thermic seasonality, superimposed on the pre-existing North hydric seasonality (Shackleton 1995; White 1995; Suc *et al.* 1995 and literature therein).

From the early to the late Villafranchian, carnivores decrease in Greece and Italy but remain balanced with herbivores and quite abundant in Spain, where browsers and grazers decrease with a simultaneous increase of mixed feeders. At the same time in Italy and Greece, grazer's participation gradually raises together with an elimination of browsers. While open land dwellers predominate in Spain during this period, forest and mixed dwellers are progressively displaced by open land dwellers taxa toward the East.

The apparent – less dramatic – reorganization of the faunal structure from 3.5-2.6 Ma seems to be related to the occurred onset of bi-polar glaciations, followed by glacial-interglacial cycles of moderate amplitude, sustained at the orbital periodicity of 41 ka (Williams *et al.* 1988; Suc *et al.* 1995; Shackleton 1995). During this time the Mediterranean region experienced a modern climate, which allowed the establishment of the current floral assemblage. Furthermore, the glacial-interglacial cycles starting at 2.6 Ma permitted the institution of alternations between open vegetation of steppe type and deciduous broad-leaved forests (plus *Taxodium*/*Glyptostrobus* type during the Pliocene) (Bertini 1994; Pontini & Bertini 2000). The increasing extension of grassy areas indicates highly arid conditions, though it is possible that, due to latitudinal and altitudinal differences, the development of a mosaic vegetation-cover furnishes new available niches.

Around 1.9-1.7 Ma the so-called "wolf event" (Azzaroli 1983) differently affected Greek, Italian and Spanish faunal complexes. In the Italian and Greek peninsulas, most Pliocene species disappeared, particularly among herbivores, and the percentage of ruminant taxa reached lower levels. Consequently, the dispersal phase was essentially related to the progressive appearance of carnivores. The hypothesis that the increase in carnivore diversity and their predatory pressure might have contributed to herbivore decrease cannot be ruled out, even if an important role might have been played by changes in vegetation structure and the consequent presence of more monotonous environments (Torre *et al.* 2001). Although herbivore standing richness dwindled during the latest Pliocene, the increase in large-sized species suggests that the environment could sustain a quite large biomass. Moreover, the dominance of mixed feeders might also imply minimal specialisation in restricted ecological niches.

During the early Pleistocene the climatic trend was characterised by a progressive decrease in mean temperatures, even if climatic oscillations were not accentuated. Indeed, the establishment of 40 ka climate cyclicity permitted the alternation of "warm" steppes under xeric cool temperate climates and deciduous forests under humid and warm-temperate climates (Suc *et al.* 1995; Bertini 2000 and references therein). Climate changes are fully reflected on the mammal assemblage as a broadly simultaneous early-middle Galerian renewal phase documented in the entire region. During or little after this period, carnivores and browsers reach their minimum values, whereas open landscapes predominate and grazers prevail over other herbivore categories. This faunal renewal represents an essential community reorganization that shows a total rejuvenation of the fauna, and a general trend towards larger body size, reduction in the number of medium-sized herbivores, and increase of large herbivores and megaherbivores. At that moment, a great part of the lineages that constitute the living mammal communities appears, including humans (Thouveney & Bonifay 1984; Lister 1992; Foley 1994; Turner 1995; Eronen & Rook 2004).

The faunal renewal was speeded up by significant climatic variations with cooler temperatures and lower humidity, starting around the Jaramillo submagnetozone, and possibly corresponding to the Menapian of the Duct palynilozones (Zagwijn 1992a, b). The peaks of last occurrences around 1 Ma coincide with low sea levels and cooler-drier conditions, representing the so-called "Glacial Pleistocene". This event is fairly well documented in the isotope record that changes from low amplitude (40-50 ka quasiperiodic cycles, orbital obliquity) to lower frequency (100 ka cycles, orbital eccentricity) and the higher amplitude nature of the signal (Williams *et al.* 1988). This cyclic change resulted in exceptional shifts of seasonal pattern in precipitation and temperature across a range of latitudes. The change in vegetation prolonged global drought and increased seasonal variation; the Italian faunal record suggests a consistent decrease in temperature and humidity (Torre *et al.* 2001; Palombo 2005).

The early-middle Pleistocene faunal renewal takes its origin in two distinct trends: 1) the progressive reduction in richness characterising late early Pleistocene faunas (during which last appearances prevailed); and 2) the subsequent dispersal related, above all, to the progressive diffusion of taxa from Eastern and Central Europe that led to the important and relatively rapid increase in diversity (due firstly to immigration and secondly to local origination bioevents) occurring at the beginning of the middle Pleistocene.

From the middle Galerian to the Aurelian an increase in extinctions and richness occurs, associated with an increase in carnivore taxa. Browsers recover in Greece and Italy while in Spain grazers enhance again. In a general way, open landscape dwellers decline with a contemporaneous increase of ubiquitous large mammals. Italian, Greek and Spanish faunal complexes, belonging to the early Aurelian show that the most flexible species became the predominant groups, browser percentage increased and the fauna progressively acquired modern characteristics. Moreover, after the decrease of herbivore standing richness due to the extinction of the Galerian taxa, diversity slightly increased because of the appearance of new carnivores and herbivores, including small or medium sized forms. Furthermore, some new medium-sized taxa appeared possibly at the beginning of MIS 6, when more severe, arid climatic oscillations facilitated the spread of some "mountain" bovids along with the dispersion of the "steppe horse" *Equus hydruntinus*, and the appearance of a primitive representative of *Mammuthus primigenius* (Palombo 2005).

CONCLUSION

Our inferences are in good agreement with those of previous works in the same line (Alberdi *et al.* 1998; Azanza *et al.* 1999, 2003, 2004; Torre *et al.* 2001; Palombo 2004, 2005) and complement the study of the Plio-Pleistocene North Mediterranean faunal diversity with respect to time and space. The succession of local faunal complexes groups, provided by cluster analysis (CFCs), is characterised by chronological ranges that slightly differ between geographic areas (Palombo *et al.* 2006). This could suggest that time and pattern of renewal phases also differ for each region. However, differences in the LFA richness, diversity of localities in local scale and disparity of localities per cluster might affect the analysis, consenting to overestimation of differences in time and overall pattern.

Since the particular composition of a regional faunal complex is the result of multiple ecological parameters, as well as, of historical factors, some minor differences can be discerned between the West and the East of the North Mediterranean region. From this point of view, the Greek Ruscinian and Villafranchian turnover and diversity patterns and the large mammal guilds are more closely related to the Italian that to the Spanish ones. During this time-interval, open country taxa gradually substitute forest dwellers in the Greek and Italian faunal complexes, while in Spain, open land mammals prevailed since the beginning of the Villafranchian, at least. The present work stresses out, however, that significant faunal renewals and reorganizations, already recognized in Spain and

Italy at the transition from the Villafranchian to the Galerian (according to BFCs analysis) or between the early and the middle Galerian (according to CFCs analysis) (Azanza *et al.* 1999, 2004; Palombo 2004), are well reflected on the Greek faunal complex either. This early Galerian faunal renovation seems, therefore, to affect more or less simultaneously the entire North Mediterranean region, which responds rather uniformly to the establishment of cooler-dryer climatic conditions around Jaramilo magnetochron (1 Ma).

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REFERENCES

AGUIRRE E. & MORALES J. 1990. — Villafranchian faunal record of Spain. *Quartärpaläontologie* 8: 7-11.

AGUIRRE E., LOPEZ N. & MORALES J. 1976. — Continental faunas in Southeast Spain related to the Messinian, *in* Messinian Seminar, 2: *Il significato Geodinamico della crisi di Salinità del Miocene terminale nel Mediterraneo. Messinian Seminar, Gargnano, September 5-12, 1976*: 62-63.

ALBERDI M. T., AZANZA B., CERDEÑO E. & PRADO J. L. 1997. — Similarity relationship between Mammal faunas and biochronology from latest Miocene to Pleistocene in the Western Mediterranean area. *Eclogiae Geolica Helvetiae* 90 (1): 115-132.

ALBERDI M. T., CALOI L., DUBROVO I., PALOMBO M. R. & TSOUKALA E. 1998. — Large mammal faunal complexes and palaeoenvironmental changes in the late middle and late Pleistocene: a preliminary comparison between the Eastern European and the Mediterranean areas. *Geologija* 25: 8-19.

AZANZA B., ALBERDI M. T., CERDEÑO E. & PRADO J. L. 1997. — Biochronology from latest Miocene to middle Pleistocene in the Western Mediterranean area. A multivariate approach. *Mémoires et Travaux de l'EPHE*, Montpellier 21: 567-574.

AZANZA B., ALBERDI M. T. & PRADO J. L. 1999. — Large mammal diversity and turnover patterns during the Plio-Pleistocene in Western Mediterranean Area. *Revista de la Sociedad Geológica de España* 12 (1): 113-122.

AZANZA B., PALOMBO M. R. & ALBERDI M. T. 2002. — Mammalian biochronological framework of the European Plio-Pleistocene: some remarks. *Third French Symposium on Stratigraphy*, Lyon: 25-26.

AZANZA B., PALOMBO M. R. & ALBERDI M. T. 2003. — Similarity relationships between large mammal faunas of Spanish and Italian peninsulas from the latest Miocene to the middle Pleistocene. *Neues Jahrbuch für Geologie und Paläontologie, Abh.* 229 (1): 95-127.

AZANZA B., PALOMBO M. R. & ALBERDI M. T. 2004. — Large mammal turnover and diversity from the Pliocene to the Pleistocene in Italian peninsula. *Rivista Italiana di Paleontologia e Stratigrafia* 110 (2): 531-545.

AZZAROLI A. 1983. — Quaternary mammals and the "End-Villafranchian" dispersal event – A turning point in the history of Eurasia. *Palaeogeography Palaeoclimatology Palaeoecology* 44: 117-139.

AZZAROLI A., DE GIULI C., FICCARELLI G. & TORRE D. 1988. — Late Pliocene to early Mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. *Palaeogeography Palaeoclimatology Palaeoecology* 66: 77-100.

BEHRENSMEYER A. K., TODD N. E., POTTS R. & MCBRINN G. E. 1997. — Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science* 278: 1589-1594.

BERTINI A. 1994. — Palynological investigations on upper Neogene and lower Pleistocene sections in central and northern Italy. *Memorie della Società Geologica Italiana* 48: 431-443.

BERTINI A. 2000. — Pollen record from Colle Curti and Cesi: early and middle Pleistocene mammal sites in the Umbro-Marchean Apennine Mountains (central Italy). *Journal of Quaternary Science* 15: 825-840.

BRETT C. E., IVANY L. C. & SCHOPF K. M. 1996. — Coordinated stasis: an overview. *Palaeogeography Palaeoclimatology Palaeoecology* 127: 1-20.

ERONEN J. & ROOK L. 2004. — The Mio-Pliocene European primate fossil record: dynamics and habitat tracking. *Journal of Human Evolution* 47: 323-341.

FOLEY R. A. 1994. — Speciation, extinction and climatic change in hominid evolution. *Journal of Human Evolution* 26: 275-289.

FORTELIUS M., ERONEN J., LIU L., PUSKINA D., TESAKOV A.,VISLOBOKOVA I. & ZHANG Z. 2006. — Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeography Palaeoclimatology Palaeoecology* 238: 219-227.

GLIOZZI E., ABBAZZI L., AMBROSETTI P., ARGENTI P., AZZAROLI A., CALOI L., CAPASSO BARBATO L., DI STEFANO G., ESU D., FICCARELLI G., GIROTTI O., KOTSAKIS T., MASINI F., MAZZA P., MEZZABOTTA C., PALOMBO M. R., PETRONIO C., ROOK L., SALA B., SARDELLA R., ZANALDA E. & TORRE D. 1997. — Biochronology of selected mammals, molluscs, ostracods from the middle Pliocene to the late Pleistocene in Italy. The state of the art. *Rivista Italiana di Paleontologia e Stratigrafia* 103 (3): 369-388.

GUERIN C. 1990. — Biozones or mammal units? Methods and limits in biochronology, *in* LINDSAY E. H., FAHLBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 119-130.

HARPER C.W. JR. 1975. — Standing diversity of fossil group in successive intervals of geologic time: a new measure. *Journal of Paleobiology* 4: 181-207.

KOSTOPOULOS S. D., VASSILIADOU K. & KOUFOS G. D. 2002. — The beginning of Pleistocene in the Balkan area according to the mammal record; palaeozoogeographic approach. *Annales géologiques des Pays hélleniques* 39 A: 253-278.

LISTER A. 1992. — Mammalian fossils and Quaternary biostratigraphy. *Quaternary Science Reviews* 11: 329-344.

MEIN P. 1990. — Updating of MN zones, *in* LINDSAY E. H., FAHLBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 73-90.

PALOMBO M. R. 2004. — Guilds of large mammals from the Pliocene to the late Pleistocene in the Italian peninsula, *in* BAQUEDANO E. & RUBIO S. (eds), *Homenaje a Emiliano Aguirre.* Museo Archeologico Regional, Madrid, Zona Archaeologica 4 (2 Palaeontologia): 20-29.

PALOMBO M. R. 2005. — Middle Pliocene-late Pleistocene herbivore guilds of Italy, *in* CRÉGUT-BONNOURE E. (ed.), Les ongulés holarctiques du Pliocène et du Pléistocène. *Quaternaire*, hors série 2: 123-136.

PALOMBO M. R. & VALLI A. M. F. 2004. — Similarities between large mammal faunas of the Italian Peninsula and France from the Pliocene to the middle Pleistocene. *Neues Jahrbuch für Geologie und Paläontologie, Abh.* 233 (1): 69-102.

PALOMBO M. R., AZANZA B. & ALBERDI M. T. 2003. — Italian mammal biochronology from latest Miocene to middle Pleistocene: a multivariate approach. *Geologica Romana* 36: 335-368.

PALOMBO M. R., VALLI A. F. M., KOSTOPOULOS D. S., ALBERDI M.T., SPASSOV N. & VISLOBOKOVA I. 2006. — Similarity relationships between the Pliocene to middle Pleistocene large mammal faunas of Southern Europe from Spain to the Balkans and the North Pontic region, *in* KAHLKE R.-D., MAUL L. C. & MAZZA P. P. A. (eds), Late Neogene and Quaternary biodiversity and evolution: regional developments and interregional correlations. *Courier Forschungsinstitut Senckenberg* 256: 329-347.

PICKFORD M. 1990. — Dynamics of Old World biogeographic realms during the Neogene: implications for biostratigraphy, *in* LINDSAY E. H., FAHLBUSCH V. & MEIN P. (eds), *European Neogene Mammal Chronology*. Plenum Press, New York: 413-442.

PONTINI M. R. & BERTINI A. 2000. — Late Pliocene vegetation and climate in central Italy: high resolution pollen analysis from the Fosso Bianco succession (Tiberino basin). *Geobios* 33 (5): 519-526.

SHACKLETON N. J. 1995. — New data on the evolution of Pliocene climatic variability, *in* VRBA E. S., DENTON G. H., PARTRIDGE T. C. & BURCKLE L. H. (eds), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven: 242-248.

SPASSOV N. 2003. — The Plio-Pleistocene vertebrate fauna in South-Eastern Europe and the megafaunal migratory waves from the east to Europe. *Revue paléobiologique* 22 (1): 197-229.

STEININGER F. F., RABETER G. & ROEGL F. 1985. — Land mammal distribution in the Mediterranean Neogene: a consequence of geokinematic and climatic events, *in* STANLEY D. J. & WEZEL F. C. (eds), *Evolution of the Mediterranean Basin*. Raimondo Selli Commemoratio, Springer Verlag: 559-571.

SUC J.-P., BERTINI A., COMBOURIEU-NEBOUT N., DINIZ F., LEROY S., RUSSO-ERMOLLI E., ZHENG Z., BESSAIS E. & FERRIER J. 1995. — Structure of West Mediterranean vegetation and climate since 5.3 Ma. *Acta Zoologica Cracoviensia* 38: 3-16.

TEDFORD R. H. 1970. — Principles and practices of mammalian geochronology in North America. *American Paleontological Convention*, Chicago 1969, *Procceedings* F: 666-703.

TORRE D., ROOK L. & FICCARELLI G. 1999. — The mammal fauna turnover in Italy at the early to middle Pleistocene transition, *in* GIBERT G., SANCHEZ F., GIBERT L. & RIBOT F. (eds), *The Hominids and their Environment During the Lower and Middle Pleistocene of Eurasia*. Museo de Prehistoria y Paleontologia “J. Gibert”, Orce: 541-548.

TORRE D., ABBAZZI L., BERTINI A., FANFANI F., FICCARELLI G., MASINI F., MAZZA P. & ROOK L. 2001. — Structural changes in Italian late Pliocene-Pleistocene large mammal assemblages, *in* ROOK L. & TORRE D. (eds), Neogene and Quaternary continental stratigraphy and mammal evolution. *Bollettino della Società Paleontologica Italiana* 40 (2): 303-306.

TURNER A. 1995. — Plio-Pleistocene correlations between climatic change and evolution in terrestrial mammals. The 2.5 Ma event in Africa and Europe. *Acta Zoologica Cracoviensia* 38: 45-58.

THOUVENEY N. & BONIFAY E. 1984. — New chronological data on European Plio-Pleistocene faunas and hominid occupation sites. *Nature* 308: 355-358.

VAN VALEN L. 1973. — A new evolutionary law. *Evolutionary Theory* 1: 1-30.

VRBA E. S. 1985. — Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *South African Journal of Sciences* 81: 229-236.

VRBA E. S. 1993. — Turnover pulse, the Red Queen, and related topics. *American Journal of Science* 293:

418-452.

VRBA E. S. 1995. — On the connections between paleoclimate and evolution, *in* VRBA E. S., DENTON G. H., PARTRIDGE T. C. & BURCKLE L. H. (eds), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven: 24-48.

WHITE T. D. 1995. — African omnivores: global climatic change and Plio-Pleistocene hominids and suids, *in* VRBA E. S., DENTON G. H., PARTRIDGE T. C. & BURCKLE L. H. (eds), *Paleoclimate and Evolution with Emphasis on Human Origins*. Yale University Press, New Haven: 369-384.

WILLIAMS D. F., THUNELL R. C., TAPPA E., RIO D. & RAFFI I. 1988. — Chronology of the Pleistocene oxygen isotope record: 0-1.88 m.y. B.P. *Palaeogeography Palaeoclimatology Palaeoecology* 64: 221-240.

ZAGWIJN W. H. 1992a. — The beginning of the Ice Age in Europe and its major subdivisions. *Quaternary Science Review* 2: 538-591.

ZAGWIJN W. H. 1992b. — Migration of vegetation during the Quaternary in Europe. *Courier Forschungsinstitut Senckenberg* 153: 9-20.

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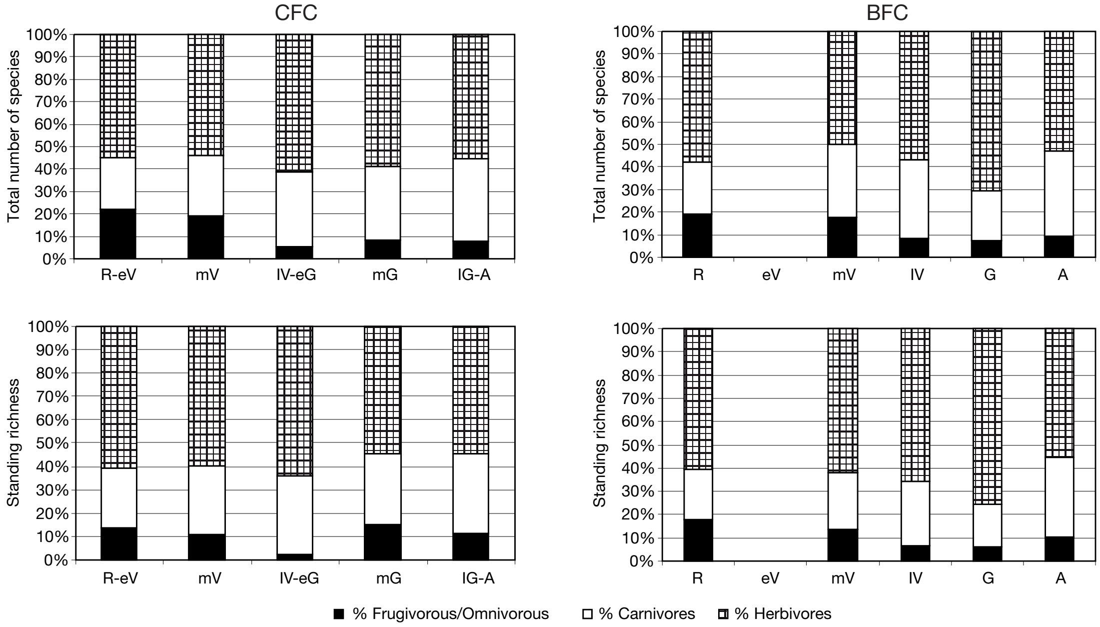


FIG. 4. — Distribution of all large mammal diet categories in Greek cluster (CFC) and biochronological (BFC) faunal complexes. Abbreviations as in Fig. 1.

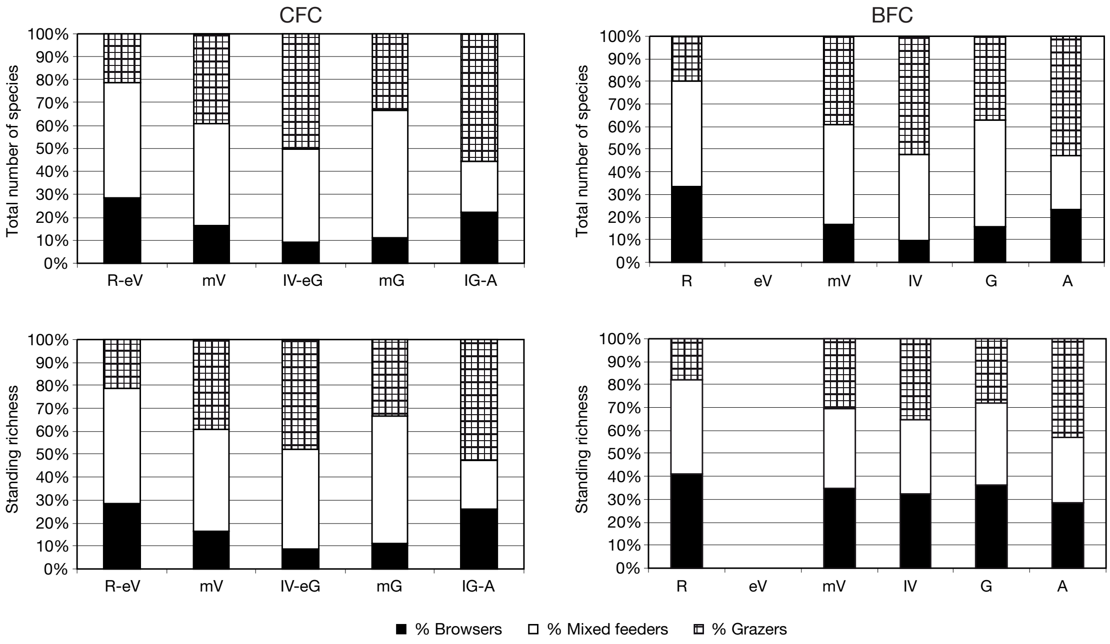


FIG. 5. — Distribution of large mammal herbivore categories in Greek cluster (CFC) and biochronological (BFC) faunal complexes. Abbreviations as in Fig. 1.

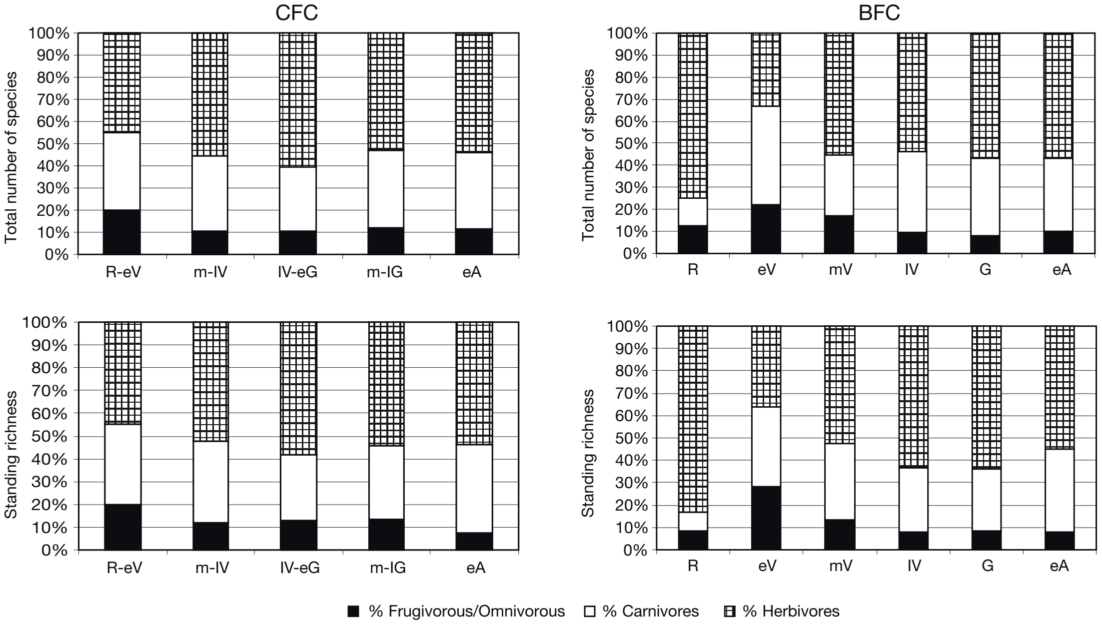


FIG. 6. — Distribution of all large mammal diet categories in Italian cluster (CFC) and biochronological (BFC) faunal complexes. Abbreviations as in Fig. 1.

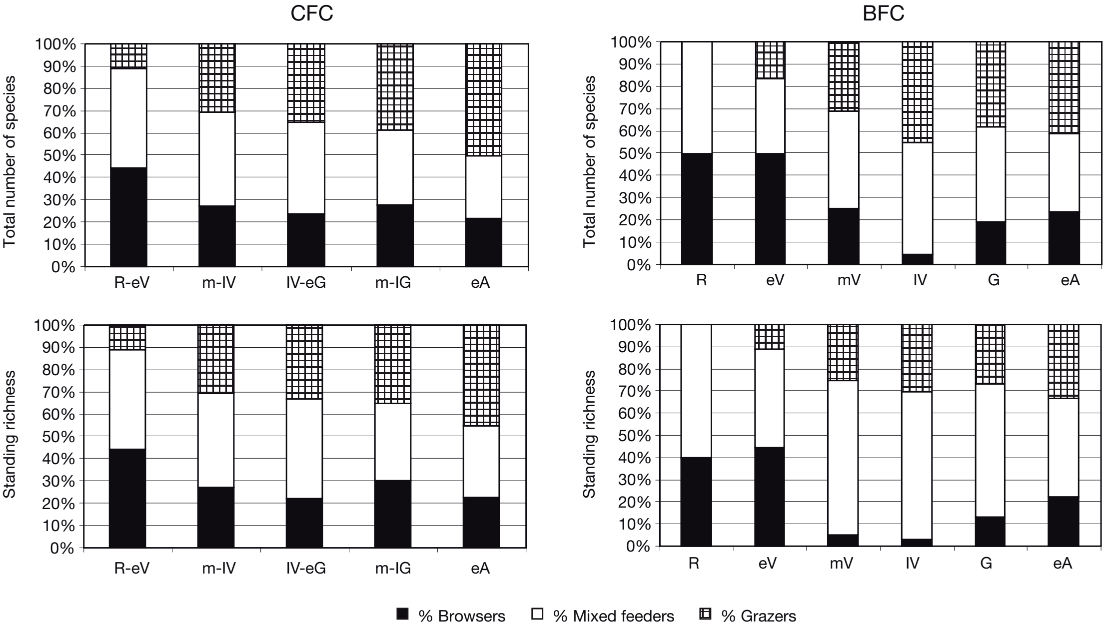
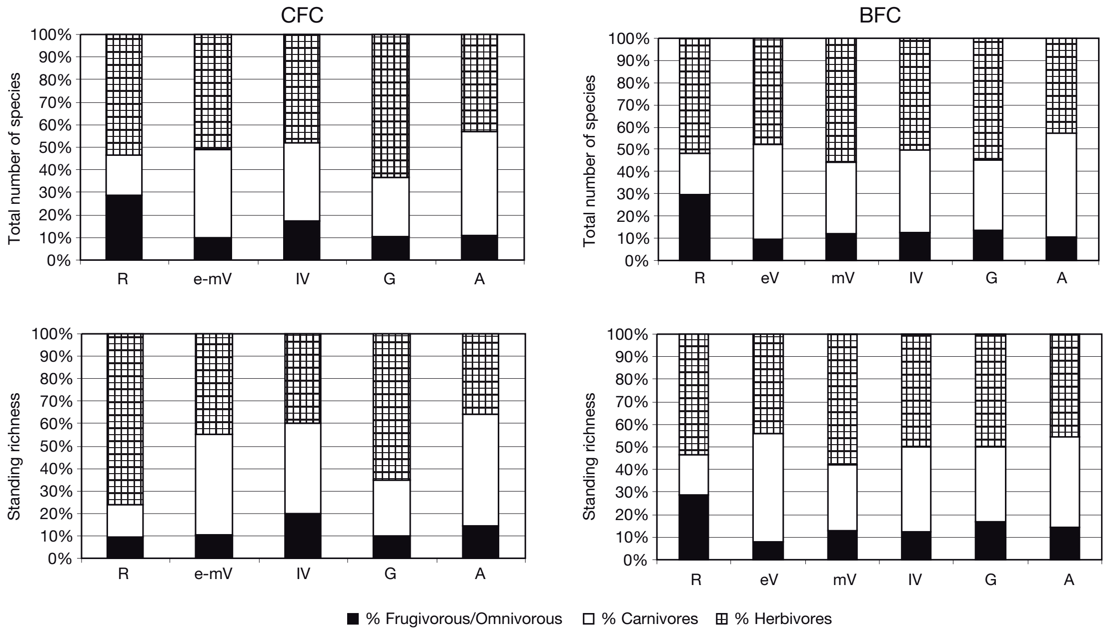


FIG. 7. — Distribution of large mammal herbivore categories in Italian cluster (CFC) and biochronological (BFC) faunal complexes. Abbreviations as in Fig. 1.



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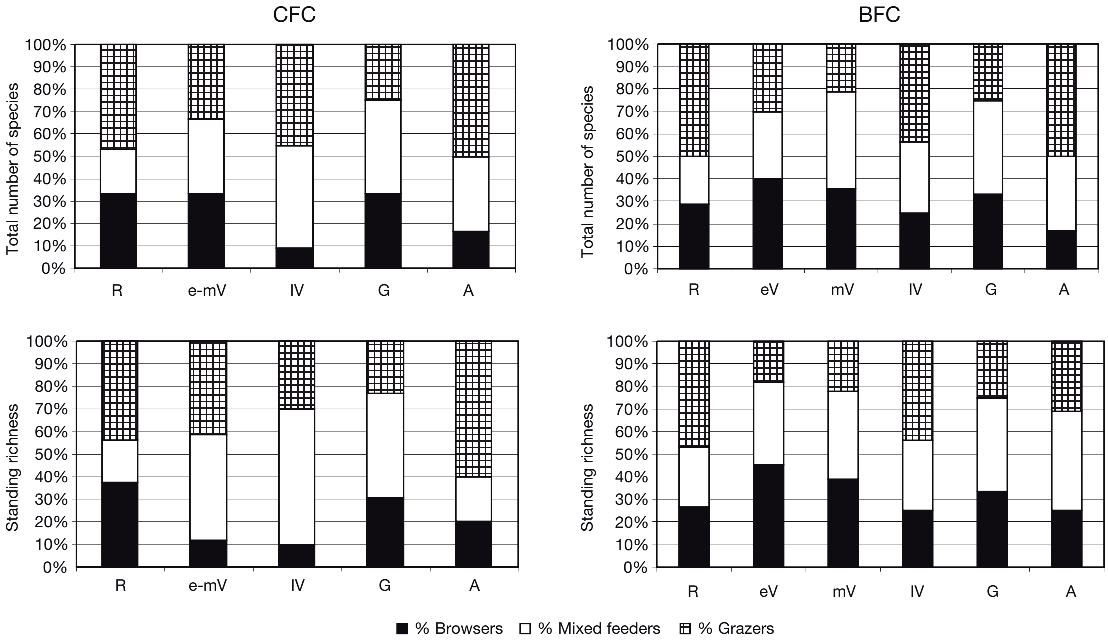

FIG. 9. — Distribution of large mammal herbivore categories in Spanish cluster (CFC) and biochronological (BFC) faunal complexes. Abbreviations as in Fig. 1.

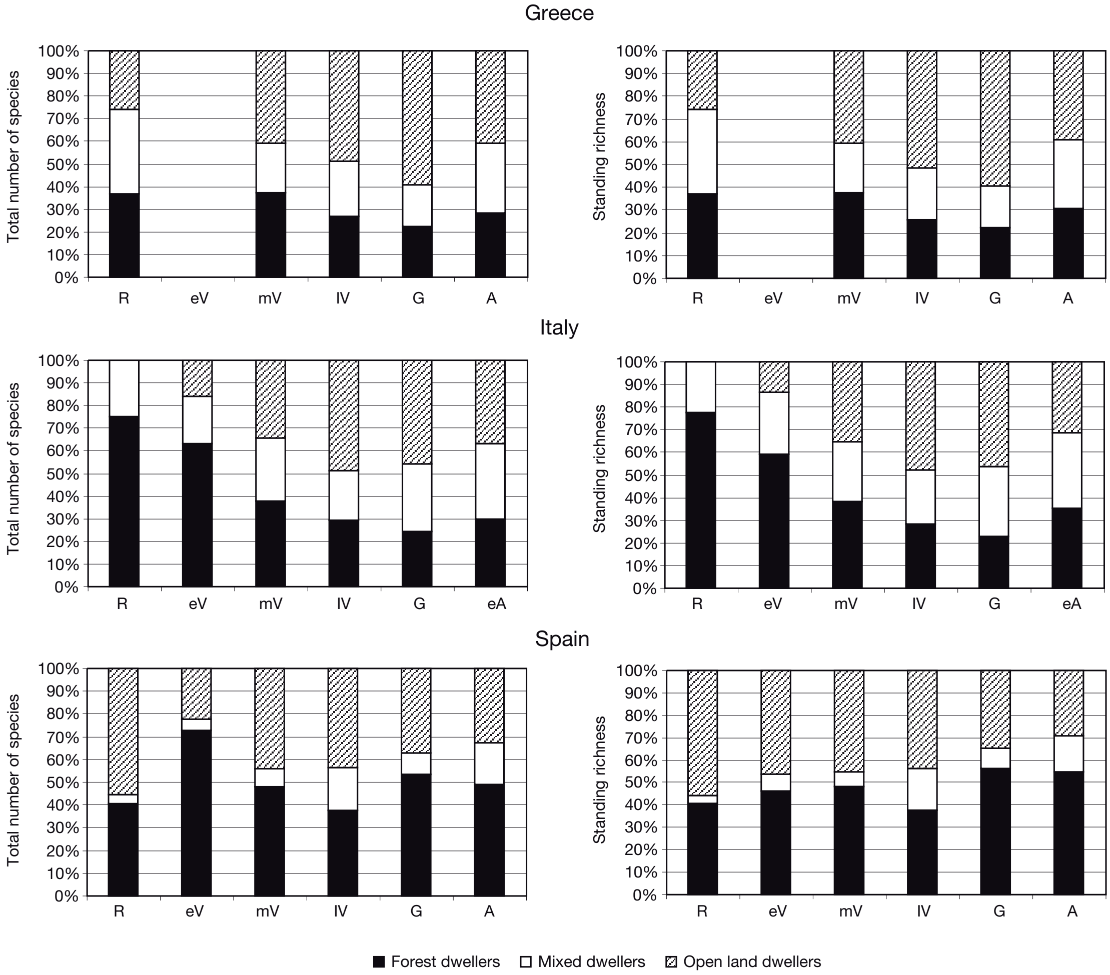

FIG. 10. — Distribution of large mammal categories according to their habitat type in Greek, Italian and Spanish biochronological faunal complexes. Abbreviations as in Fig. 1.

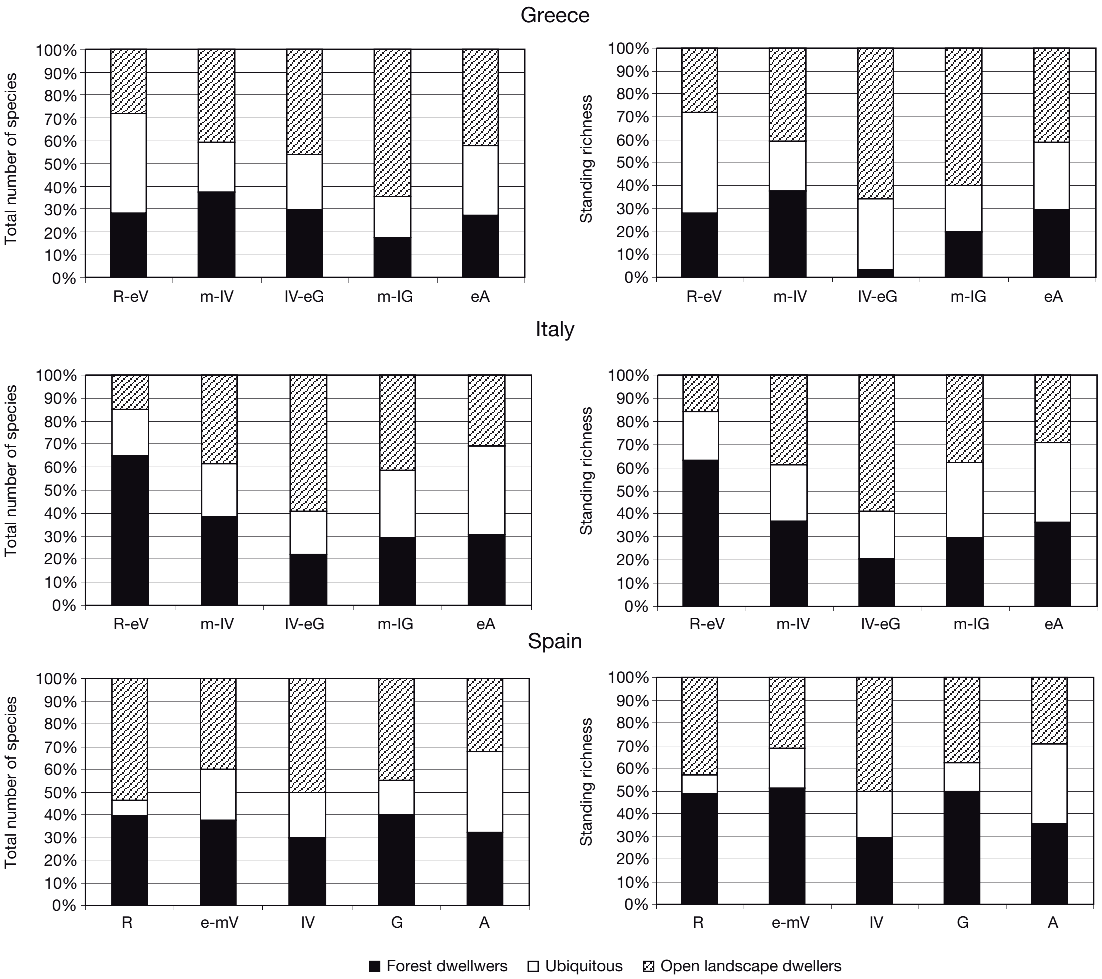

FIG. 11. — Distribution of large mammal categories according to their habitat type in Greek, Italian and Spanish cluster faunal complexes. Abbreviations as in Fig. 1.