



## Diversity and turnover of Plio–Pleistocene large mammal fauna from the Italian Peninsula

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### ABSTRACT

The Plio–Pleistocene large mammal fauna of peninsular Italy has been considered in order to explore diversity and turnover patterns through time. Several diversity metrics and turnover rates were quantified both for the whole mammal community and for large mammalian orders, taken separately. Temporal units of reference were the previously-defined paleocommunities (PCOMs). Rarefaction analysis has been applied to correct for possible sampling biases. The results show that large mammal richness in the Italian fossil record was highly influenced by the number of sites per PCOM. After this bias has been controlled for, no significant variation in species richness was apparent. In spite of the overwhelming climatic changes, species richness remained constant in the mammalian orders and in the whole community as well. In sharp contrast, turnover rates appear guided by major climatic changes (especially at the Villafranchian–Galerian transition) and are highly inconstant. This correlation with climatic change is particularly evident in even-toed ungulates. We argue that diversity dynamics should respond to a larger temporal scale, while ecosystem functioning and structure were sensitive to the strongest climatic oscillations of the Plio–Pleistocene. Our findings agree with previous claims that ecosystem functioning switches to alternative stable states instead of changing continuously.

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### 1. Introduction

There is consistent evidence that climate change affected mammalian community evolution (Alroy et al., 2000; Fortelius et al., 2002, 2006a; Barnosky et al., 2003; Bobe and Behrensmeyer, 2004; Rodríguez et al., 2004; Raia et al., 2005; Barnosky and Kraatz, 2007) although detectable changes in mammalian faunas vary according to the geographical and temporal scale of analysis (Barnosky, 2001; Hadly and Maurer, 2001; Barnosky et al., 2003). In this regard, the evolution of Quaternary mammals is of special interest because Plio–Pleistocene climates repeatedly swung to extremely cold temperatures over short periods of time (Zachos et al., 2001). Consequently, the distribution of many species has been altered by the spread of ice sheets across the Northern Hemisphere (Lister, 2004; Barnosky and Kraatz, 2007) and complex faunal interchanges occurred at the continental scale. As it is common practice in biochronology (Woodburne and Swisher, 1995; Walsh, 1998; Lindsay, 2003) these interchanges characterise continental biochronologic boundaries in Europe, where major dispersal events have been recognized (Azzaroli,

1983; Azzaroli et al., 1988; von Koenigswald and Werdelin, 1992; Agustí and Antón, 2002).

Dispersal modifies the geographic range of a species. If individuals of several species disperse simultaneously, dispersal extends to the macroevolutionary scale producing differences in local faunal associations through time (Tchernov, 1992) even without further effects due to extinction and speciation. Consequently, biochronologic units are regarded as periods of unaltered taxonomic composition intervening between major dispersals and/or extinctions–speciations. However, some important studies cast doubts on the evidence for such co-ordinated dispersals (FAUNMAP, 1996). Moreover, Alroy (1996, 1998) points out that speciation and extinction are non-contemporaneous as well. Thereby, community–taxonomic–evolution would be continuous and, as a consequence, biochronological units (e.g. Land Mammal Ages) would be fleeting. It is unknown if Alroy's findings would actually extend to European fossil faunas. Yet, discrete associations (based on supposedly co-ordinated dispersals) seem to apply in Europe (Mein, 1975). Although this is admittedly conjectural, we guess it is possible that the very method Alroy conceived to align species appearance events in time (maximum likelihood appearance event ordination (ML AEO, Alroy, 2000a)) is unsuited to looking at community patterns (especially at small temporal scale) because it uses pairwise species occurrence record (F/L statements in his terminology) to perform ordination, thereby focusing on taxa, not assemblages. While we have almost no doubts that it is one of the best methods for

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numerical ordination proposed so far (see Fortelius et al.'s 2006b spectral ordering for an alternative candidate) we remain sceptical it could be used to study community-level patterns. For instance, the Plio-Pleistocene Italian fossil record was divided into nine statistically discrete palaeocommunities (PCOMs) which are clusters of Local Assemblages (LAs) (Raia et al., 2005, 2006a). PCOMs allow investigation of the properties of fossil mammalian ecosystems (e.g. species abundance, predator–prey interaction) at the macro scale (Raia et al., 2006b, 2007; Meloro et al., 2007) and how they evolved. These theoretical approaches confirm the validity of PCOMs as discrete and reliable associations of large mammals occurring during the Plio-Pleistocene in the Italian Peninsula.

By using PCOMs, it is also possible to look at the course of mammal species diversity through time. Diversity trends are related to changes in community composition (i.e. temporal turnover) through time. Although several metrics for calculating turnovers have been proposed so far (Foote, 2000), they share the rationale of counting new occurrences (immigrants plus speciations) and last occurrences (emigrants plus extinct taxa). Only if the two counts cancel each other out does diversity go unchanged. Raia et al. (2005) investigated turnover of Italian Plio-Pleistocene mammalian communities using both the classic biochronologic units (Faunal Units, FUs, Gliozzi et al., 1997) and PCOMs. They found a large influence of climate change on turnover rates. Recently, Kostopoulos et al. (2007) confirmed such an influence for the Galerian Mammal Age of the Mediterranean area, by comparing diversity and turnover trends in large Plio-Pleistocene mammals in Greece, Italy and Spain. Sardella et al. (1998) had already computed diversity trends for Italian Plio-Pleistocene mammals using Faunal Units, and found that diversity varied dramatically over time.

Unfortunately, these analyses did not correct for sampling biases, which can severely alter the interpretation of paleodiversity curves (Alroy, 2000b; Bush et al., 2004). Statistical techniques can be used to correct for sampling biases (Alroy, 2000a; Foote, 2000; Bush et al., 2004; Lane et al., 2005; Barnosky et al., 2005). It is therefore important that they are applied to diversity counts in order to get reliable estimates of trends. In addition, species diversity can be influenced by the scale (local, regional) of investigation (Whittaker et al., 2001), and this should be considered as well, especially in the light of possible stasis in diversity observed in different organisms at different time scales (Brown et al., 2001). In fact, if diversity is unlikely to change it is relevant to understand what aspect of diversity has been considered. In the ecological literature, different metrics and aspects of diversity have been considered. Peet (1974) reviewed different quantification approaches to species diversity which span from simple richness (the raw count of species in a certain place or stratigraphic interval) to the complex indices (e.g. Simpson, Margalef etc.). Palaeontological investigations mostly rely on species counts (richness) and usually seek explanation of richness alteration via correlation to changes in the climatic regime, at different time scales (Rosenzweig, 1995), although biotic factors should be considered as well (Jablonski, 2003).

It is noteworthy that almost all the previous approaches to the quantification of species diversity and turnover applied to mammal communities as a whole (e.g. Stucky, 1990; Prothero and Heaton, 1996; Behrensmeyer et al., 1997; Alroy, 2000b; Bobe et al., 2002; Bobe and Behrensmeyer, 2004) have not taken into account possible differences between taxonomic groups. For instance, Werdelin and Lewis (2005) found little evidence of turnover pulse in Plio-Pleistocene carnivores from East Africa (contra bovids, see Vrba, 1995a,b). This fact suggests possible differences of climate change effect on different kinds of mammals.

The aim of the present study is to explore diversity and turnover trends, in the whole large mammal community as well as in major mammalian orders, to get evidence for possible differences among taxonomic groups and how they combine to give the community-level pattern. After correcting for sampling biases, we analysed diversity and turnover trends in Italian Plio-Pleistocene PCOMs, and look at the possible relationship of both with climate changes.

## 2. Materials and methods

### 2.1. The fossil record

The Italian Plio-Pleistocene large mammal fossil record described in Raia et al. (2005, 2006a,b) and Meloro et al. (2007) is used here to investigate species richness (*sensu* Peet, 1974).

The record includes 73 Local Assemblages (LAs) partitioned among 9 succeeding palaeocommunities (PCOMs) that range in age from 3.2 Ma until 0.3 Ma. Eighty-nine species recognized as large mammals (that is, their estimated body weight is higher than 5 kg) are distributed in a total of 620 Local Occurrences (LO). Only members of the orders Artiodactyla, Carnivora, Perissodactyla and Proboscidea were included in the order-level analyses (see Raia et al., 2005, 2006a for further details on the record and species selection criteria).

Species richness was quantified as the number of species occurring together in each PCOM. The latter comprises a distinct number of Local Assemblages covering different periods of time: Triversa PCOM (2 LAs, 3.2 Ma), Montopoli PCOM (5 LAs, 2.6 Ma), Upper Valdarno PCOM (14 LAs, 1.9 Ma), Val di Chiana PCOM (5 LAs, 1.5 Ma), Pirro PCOM (5 LAs, 1.1 Ma), Galerian 1 PCOM (6 LAs, 0.8 Ma), Galerian 2 PCOM (5 LAs, 0.6 Ma), Galerian 3 PCOM (8 LAs, 0.45 Ma), Aurelian PCOM (22 LAs, 0.3 Ma). Some time periods are better represented than others (Fig. 1). In particular, both Upper Valdarno and Aurelian appear oversampled in comparison with other PCOMs.

### 2.2. Computing species diversity

Several biases are likely to alter the quantification of species richness per PCOM. Firstly, the species richness at the PCOM level ( $D$ ) may be underestimated because of either discontinuous species distribution in the fossil record and variable study intensity (Bush et al., 2004). To correct for discontinuity, we applied range-throughs (Barry et al., 1995; Maas et al., 1995; Foote, 2000): consider a species  $x$  and three continuous (in time) PCOMs A, B, C. If  $x$  is present in A and C, its absence from PCOM B may be caused by a preservation bias, consequently we can assume that  $x$  is still present in B. Even if the range-through does not allow correction for the last (Aurelian) diversity count, it is important to note that this PCOM has the greatest number of localities. Consequently, it is conceivable that no sample bias occurs in this PCOM.

The value  $D$  was then separated into its  $\alpha$  (local) and  $\beta$  (regional) components.  $\alpha$  is the diversity computed for each Local Assemblage. The algebraic mean of  $\alpha$  ( $\bar{\alpha}$ ) across LAs was then taken for each PCOM. The parameter  $\beta$  is obtained as the ratio between  $D$  and  $\bar{\alpha}$  (Whittaker, 1960; Bush et al., 2004). Both of these parameters allow predictions on whether species diversity among PCOMs varies as an artefact of increasing sample size. If sample size affects the calculation of  $D$  it is likely that the  $\beta$  parameter increases, with mean  $\alpha$  being relatively constant through time (cfr. Bush et al., 2004). The parameters  $D$ ,  $\bar{\alpha}$  and  $\beta$  were independently assessed for large mammal community in each PCOM.

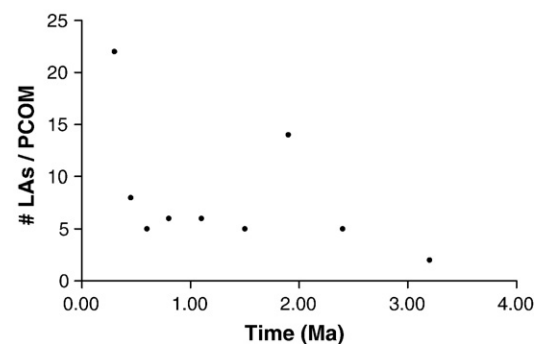


Fig. 1. Scatter plot of the relationship between estimated time (in Ma) and number of LAs for each PCOM.

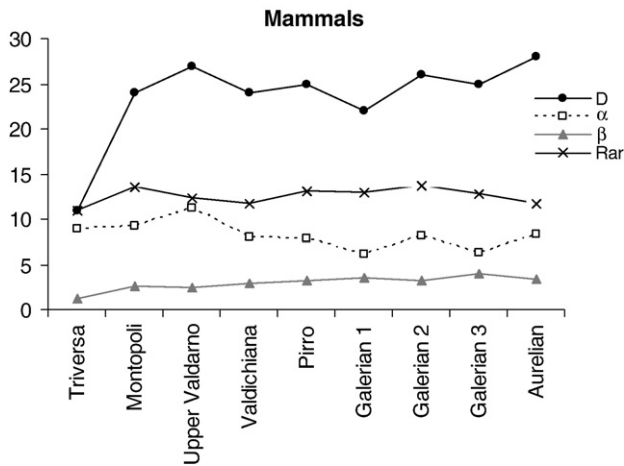


Fig. 2. Trends of species diversity (partitioned in  $D$ , mean  $\alpha$ ,  $\beta$  and rarefied at 18 LOs) computed for all large mammalian community toward PCOMs.

The orders Artiodactyla, Carnivora and Perissodactyla were considered for taxonomically nested calculations of these diversity parameters. Proboscideans were excluded because of the small sample size, as no more than two proboscideans occur in the same PCOM.

### 2.3. Correcting diversity values

In a previous study (see Raia et al., 2005, p. 300) we computed the number of species described per year in a two-centuries record of paleontological work on Italian Plio-Pleistocene large mammals. We demonstrated that the number of described species did not increase significantly for more than a century despite a great increase in the number of paleontologists involved. Thereby, we argued any sampling bias occurring in our data is likely to depend on the number of fossil sites sampled and not on the study effort. In order to obtain sample size-free diversity values, rarefaction (Sanders, 1968) was applied for each PCOM. This technique has been widely used in ecology (Peet, 1974; Siegel and German, 1982; Koellner et al., 2004) and paleontology (Siegel and German, 1982; Westrop and Adrain, 1998; Hadly, 1999; Adrain et al., 2000; Alroy, 2000a). Gottelli and Colwell (2001) caution rarefaction should be applied carefully because of some possible pitfalls in quantification. Bush et al. (2004) point out that rarefaction is most appropriate if species rarity/commonness distribution is likely to change over time or space. We demonstrated elsewhere (Raia et al., 2006b) that species commonness varies across PCOMs. Thereby, rarefaction is appropriate to correct for sampling biases here. The rarefaction method calculates the expected number of species at a given sample size analysing species number distribution of real samples of variable size. If we assume that species number is an hypergeometric function of number of individuals (Heck et al., 1975), expected species richness is calculated applying the algorithm reported in Sanders (1968) and Krebs (1989). Consider  $N$  as the total number of individuals in a sample,  $s$  the total number of species and  $N_i$  the number of individuals of species  $i$ , the expected number of species  $E(S_n)$  in a sample of size  $n$  is given by:

$$E(S_n) = \sum_{i=1}^s \left[ 1 - \frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right]$$

In our case, PCOMs are the sample unit while the number of individuals is quantified as the number of Local Occurrences of each species present in the PCOM considered (cfr. Miller and Foote, 1996; Alroy, 1996; Markwick, 1998). Rarefaction curves were obtained for each PCOM, and diversity values were recomputed as the values predicted by each curve at a standard sample size.

Since the Triversa PCOM has the lowest number of Local Occurrences and the lowest number of LAs, sample size was standardised at Triversa LO level. Rarefied diversity values were then computed for the other PCOMs and used to evaluate diversity trends through time. This correction is applied to the sample of all large mammals but also to nested, order-level, samples.

### 2.4. Turnover and climate data

The computation of turnover index is central to test for the effect of climate change on mammal fauna. In fact, Raia et al. (2005) already showed a significant relationship between climate data and turnover of large mammal fauna, in Italy. In keeping with that result, here we applied similar equation to compute turnover index on PCOMs, quantified as:

$$TR = \frac{(FO_t + LO_{t-1})}{[D_t * (t - (t-1))]}$$

TR was computed for each PCOM interval ( $t$ ) with  $FO_t$  being the First Occurrences for the PCOM considered,  $LO_{t-1}$  the Last Occurrences of the preceding PCOM ( $t-1$ ) and  $D_t$  corresponding to total richness for the PCOM interval  $t$  (including range-through data) (see Raia et al., 2005 for further details). This metric was assessed for all the large mammal community as well as for Artiodactyla, Carnivora and Perissodactyla, separately. Proboscideans were not analysed separately because of the small sample size.

Climatic data were taken from the oxygen isotopic record in Kroon et al. (1998). Again, Raia et al. (2005) have previously evaluated the oxygen isotopic data set as proxy for climatic changes in keeping with Alroy et al. (2000; see also Barnosky and Kraatz, 2007). The  $\delta^{18}O$  record was extracted by pooling the data of ODP site 967 A and B, in the Eastern Mediterranean. The sequences A and B show a continuous record from 3.2 until 0.13 Ma. Data were clustered in order to cover the time interval of each PCOM. Because of the different scale of analyses (if compared to the Faunal Units, FUs in Raia et al., 2005), we used the absolute mean isotopic value for each time period in order to look at the possible relationship with species diversity and turnovers obtained for each PCOM. The nature of such relationship is assessed also at order level with non-parametric linear correlation tests (Zar, 1984).

## 3. Results

### 3.1. Diversity trends

A number of range-through has been applied to the PCOMs Val di Chiana, Galerian 2 and Galerian 3 (6; 4; and 3, respectively) but this does not alter species richness consistently (comparison of raw and

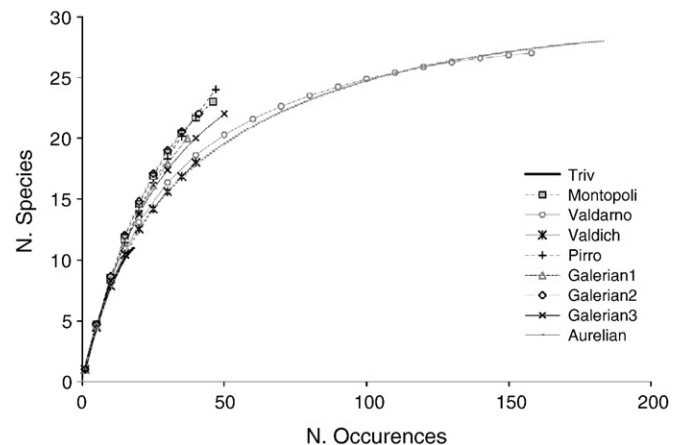


Fig. 3. Rarefaction curves for each PCOMs.

range-through corrected data:  $\chi^2=2.74$ ;  $df=8$ ;  $p=0.97$ ). There is a net increase in large mammal species diversity between the Triversa and Montopoli PCOMs (Fig. 2). The value of  $D$  is relatively unaltered throughout the other PCOMs and no significant changes of  $D$  occur through time ( $\chi^2=5.51$ ;  $df=8$ ;  $p_{\text{montecarlo corrected}}=0.704$ ).

Mean  $\alpha$  values describe a different trend. Middle/Upper Villafranchian PCOMs (Triversa up to and including Upper Valdarno) have significantly higher values than other PCOMs (Fig. 2; Mann–Whitney

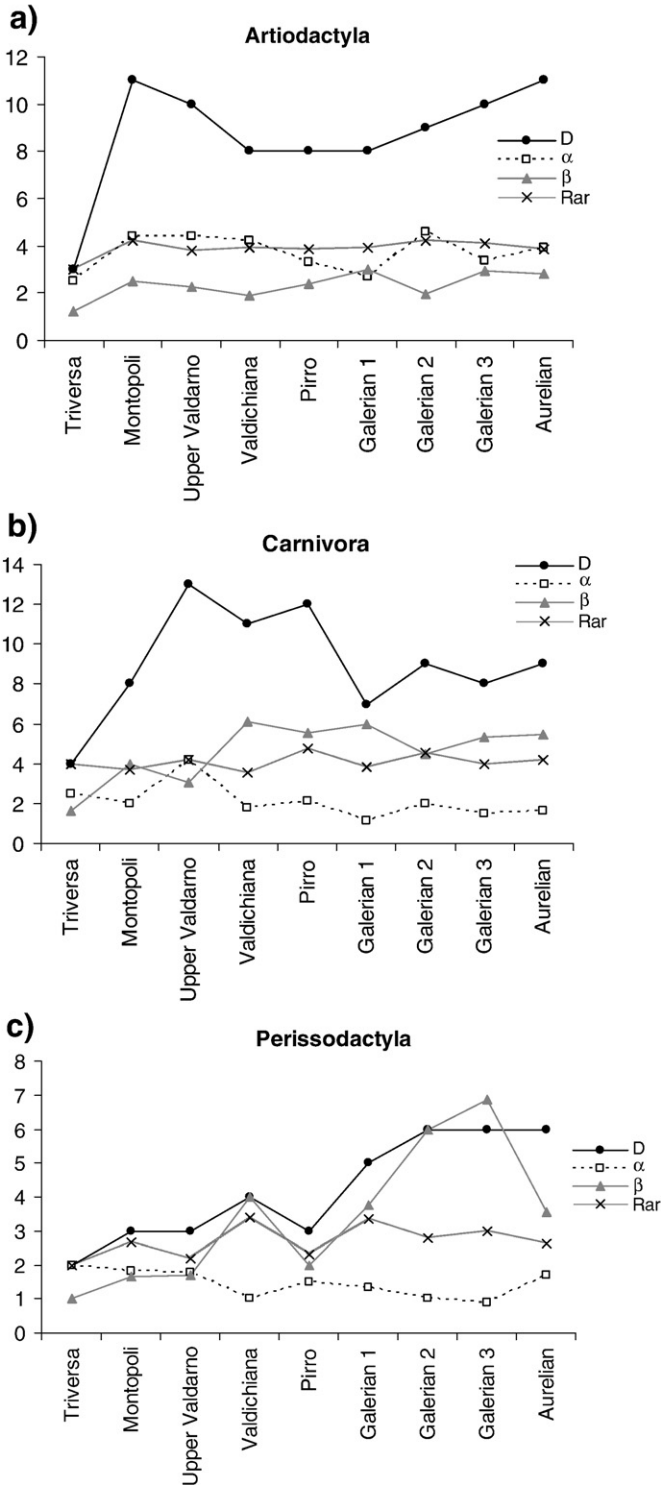


Fig. 4. Trends of species diversity (partitioned in  $D$ , mean  $\alpha$ ,  $\beta$  and rarefied at 18 LOs) computed for Artiodactyla, Carnivora and Perissodactyla toward PCOMs.

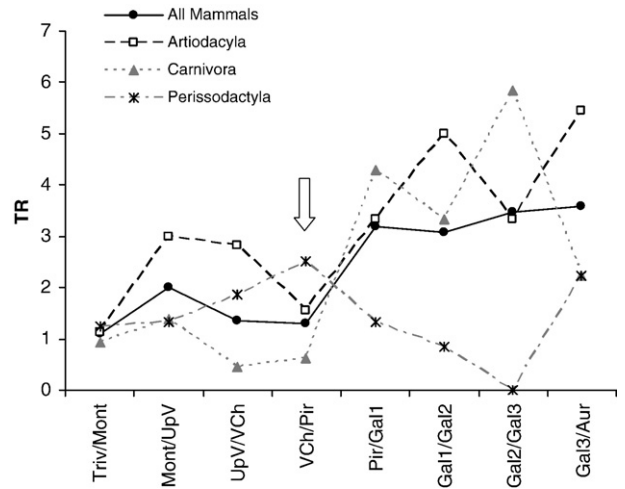


Fig. 5. Turnover trends computed for all mammals and at order level.

$U < 0.0001$ ;  $Z = -2.324$ ,  $n_{1,2} = 3, 6$ ;  $p_{\text{montecarlo corrected}} = 0.032$ ). This runs contrary to the basic taphonomic expectation of lower  $\bar{\alpha}$  in older lists (as the probability of destruction of fossil remains increases with time). On the other hand, there is a significant increase of  $\beta$  values through time as expressed by the negative relationship with the absolute PCOMs age estimates ( $n=9$ ;  $r_s = -0.867$ ;  $p=0.002$ ).

Rarefaction curves were computed separately for each PCOM (Fig. 3) with all sample sizes standardised at Triversa LO level. Again, species diversity went unaltered through PCOMs, after correcting for different sample sizes (Fig. 2).

Nonetheless, when species counts are repeated at the order level some distinct trends become apparent.  $D$  values increase in both Artiodactyla and Carnivora in the middle/Upper Villafranchian PCOMs (Fig. 4), as confirmed by a positive relationships between the  $D$  values for these orders ( $N=9$ ;  $r_s = 0.690$ ;  $p=0.040$ ).  $\bar{\alpha}$  and  $\beta$  values are trendless in Artiodactyla. Yet,  $\bar{\alpha}$  diversity of Carnivora achieves an unusually high value during the Upper Villafranchian while the trend in  $\beta$  diversity goes in the opposite direction: values were significantly lower in the Triversa, Montopoli and Upper Valdarno PCOMs than in others (Mann–Whitney  $U < 0.001$ ;  $Z = -2.324$ ,  $n_{1,2} = 3, 6$ ;  $p_{\text{montecarlo corrected}} = 0.032$ ). Diversity values in Perissodactyla increase towards Galerian/Aurelian boundary (some 0.3 Ma). This increase in species number is recorded for both  $D$  and  $\beta$  values while the increase in  $\bar{\alpha}$  happens to be an artefact of sample size.

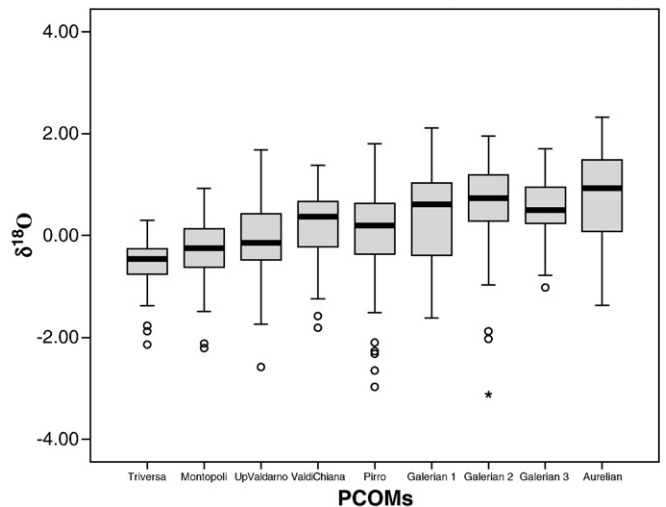


Fig. 6. Box plot of  $\delta^{18}\text{O}$  toward PCOMs.

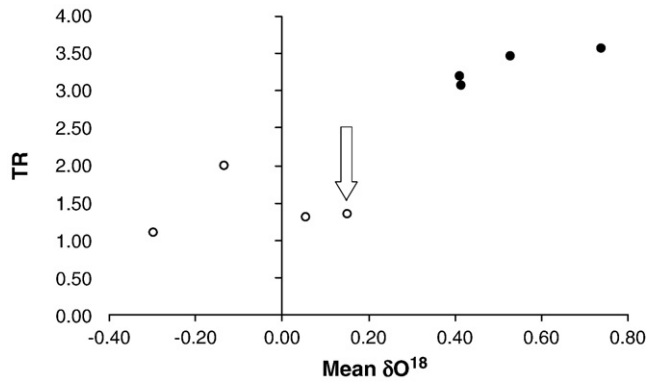


Fig. 7. Scatter plot between mean  $\delta^{18}\text{O}$  and TR for all mammals. White circle are Villafranchian PCOMs, Black are Galerian and Aurelian.

### 3.2. Turnover rate

Although species diversity at the community level showed few changes during Plio-Pleistocene, turnover rates vary a lot. In fact, turnover changes consistently between PCOMs, with a significant decrease in the ValdiChiana/Pirro interval (Fig. 5). This low peak is recorded for the whole mammal assemblage as well as for Artiodactyla and Carnivora taken separately.

From that period on, there is a net increase in turnover rates toward the Galerian for all groups except perissodactyls.

### 3.3. The role of climate

To test for possible effects of climatic changes on mammal fauna, we tested for correlation between mean oxygen isotope data and diversity and TRs. The oxygen isotope record comprises 441 data points covering a period between 3.2 and 0.3 Ma. Jonckheere–Terpstra evidenced a significant increase of  $\delta^{18}\text{O}$  through time (Observed  $J-T=57759.50$ ; Mean  $J-T=42360.50$ ; Std Deviation of  $J-T=1531.58$ ; Std.  $J-T=10.154$ ;  $p$  (2 tailed) $<0.0001$ ) (Fig. 6).

In this regard mean oxygen values can be used as proxy to describe the mean climatic condition for each PCOM.

Diversity values  $D$  are not significantly correlated with mean oxygen data except in perissodactyls with a positive significant relationship ( $N=9$ ;  $r_s=0.97$ ;  $p<0.0001$ ). Rarefied  $D$  values are equally never related with oxygen isotope in all groups ( $p>0.10$ ). Interestingly, a negative relationship occurs between Carnivora  $\bar{\alpha}$  and isotopes ( $N=9$ ;  $r_s=-0.73$ ;  $p<0.026$ ). A similar negative association is recorded with  $\bar{\alpha}$  in perissodactyls ( $N=9$ ;  $r_s=-0.72$ ;  $p=0.03$ ) yet opposite trends occur with  $\beta$  values ( $N=9$ ;  $r_s=0.82$ ;  $p<0.007$ ). The  $\beta$  diversity is positively related to mean  $\delta^{18}\text{O}$  data in all mammals as well ( $N=9$ ;  $r_s=0.83$ ;  $p<0.005$ ).

A positive association between turnover rates and climate changes is apparent with PCOMs record ( $N=9$ ;  $r_s=0.904$ ;  $p<0.002$ ) although no significant associations occur when we take orders separately, except for Artiodactyla ( $N=9$ ;  $r_s=0.886$ ;  $p<0.014$ ).

It is noteworthy that, even if the relationship between TRs and  $\delta^{18}\text{O}$  record is generally positive, it could be interpreted as a temporal stepwise trend (Fig. 7).

## 4. Discussion

In spite of the striking changes in climate, it is evident that diversity of Italian Plio-Pleistocene large mammals was constant through time. Interestingly, Brown et al. (2001) emphasize that species diversity is usually constant through time irrespective of the scale and organisms considered. This model basically reflects island diversity theory (MacArthur and Wilson, 1967), where immigrations

and extinctions control island species richness around an equilibrium point. The same mechanism could apply to the evolution of Italian large mammal communities, where species diversity was controlled by major dispersal events (von Koenigswald and Werdelin, 1992; Torre et al., 2001), and local extinctions, while speciation is numerically negligible (Kotsakis et al., 2002). In this perspective, the record we dealt with here is different from others used in comparable studies on mammals, where diversity was quite inconstant (Stucky, 1990; Alroy, 1998) and turnover rate was quite insensitive to both climatic and tectonic upheavals (Prothero, 1999, 2004).

Nonetheless, we found not all components of species diversity to go without significant trends. In fact,  $\bar{\alpha}$  and  $\beta$  changed. For  $D$  to be constant,  $\bar{\alpha}$  values should be high when  $\beta$  is low and vice versa (Bush et al., 2004). Both of these factors reflect ecosystem functioning at different spatial scales (Whittaker et al., 2001).

In this study, we found high  $\bar{\alpha}$  in Villafranchian faunas (older than 1 Ma) and high  $\beta$  in younger lists (aged less than 1 Ma). A possible, ecological, interpretation is that low regional ( $\beta$ ) diversity of Villafranchian PCOMs depends on the more constant climate, and habitat homogeneity. During the Villafranchian, climatic variability, as evidenced by the  $\delta^{18}\text{O}$  record, was less intense (Imbrie et al., 1993). On the other hand, the regional diversity of Galerian/Aurelian PCOMs was higher because glacial/interglacial alternations were more intense, then. It is important to note that LAs are not coeval in the strict sense. As a consequence, if climate affects faunas, a low  $\beta$  component of diversity (taxonomic difference among LAs) should reflect climatic evenness.

This theory is borne out of considering trends observed for the mammalian orders taken separately. The mean  $\alpha$  of Carnivora for the Upper Valdarno PCOM is unusually high and this could be an artefact of taphonomy (e.g. sites are mostly represented by carnivore dens). Yet, Meloro et al. (2007) found evidence of nestedness for this PCOM. Basically, nestedness occurs in a PCOM when only species abundance is responsible for species presence at sites. In keeping with that, Raia et al. (2007) demonstrated an unusually high predator/prey ratio during the whole Upper Villafranchian.

Among herbivores,  $\beta$  values of perissodactyls increased between the Villafranchian/Galerian transition and this could depend on the effect of habitat complexity (either spatial or temporal or both). During most of the Middle Pleistocene, rhinos were either browsers (e.g. *Stephanorhinus kirchbergensis*) or steppe inhabitants (e.g. *S. hemitoechus*) and their distribution was probably more influenced by habitat heterogeneity at regional scale (Owen Smith, 1990). The same applies to horses. Although all of them were grazers, the caballine horse (*Equus ferus*) lived along with stenonian remnants (*E. altidens*, *E. suessenbornensis*) for some time. These horses have been claimed to show adaptation to different habitats, on the basis of their postcranial anatomy (Caloi and Palombo, 1988). For Artiodactyla, no significant changes in  $\bar{\alpha}$  and  $\beta$  occurred even if a very high  $\beta$  is recorded at Galerian 1.

In the light of such changes, the constancy of diversity through time is striking. Species richness seems not to be indicative of mammalian community dynamics. We argue diversity should reflect the effect of evolutionary changes (e.g. radiations, major clade-level substitutions) occurring at a much larger temporal scale (e.g. all the Cenozoic, cfr. Fortelius et al., 1996; Van Valkenburgh, 1999; Alroy et al., 2000).

It is unclear to what extent climatic changes did influence mammalian community evolution. Some studies validated turnover pulse for the whole large mammalian community, and for artiodactyls in particular. Some other studies point to quite the opposite, even on the same fossil records. Here we found support for turnover pulse, in keeping with a previous study (FUs of Raia et al., 2005). As with diversity, we argue community evolution here is properly framed in the context of large-scale dispersal, while many other studies involve mainly speciation.

Climate changes seem to have affected TR in artiodactyls in particular, as an intimate association of this group with habitat

conditions is revealed. Being herbivorous, perissodactyls should be considered a “sensible” group as well, yet several taxonomic and evolutionary arguments could help explain their low responsiveness to the turnover pulse. In this group, an “eco-morphological” pre-adaptation to open environments had been already achieved all over Europe by the beginning of middle Villafranchian, with the spread of the genus *Equus* (Azzaroli et al., 1988). Furthermore, artiodactyls were much more diverse, with the spread and extinction of several evolutionary lineages (e.g. the Villafranchian/Galerian boundary is characterised by the disappearance of the genera *Eucladoceros*, *Galligoral*, *Leptobos*). Consequently, any trend would be more apparent in artiodactyls than in odd-toed ungulates by numbers alone.

The intensity of species turnover suggests massive ecosystem rearrangements should have occurred at least during the Villafranchian/Galerian boundary (cfr. Rodríguez et al., 2004). This trend is consistent with general finding of Kostopoulos et al. (2007) who recognise a similar phenomenon for all Mediterranean Europe. It seems apparent that turnover dynamics were accelerated during the Galerian and Aurelian. This was expected because of the faster rates of climate changes (cfr. Lister, 2004). Interestingly, ecological arguments justify the trend in turnover co-ordinated with a stasis in species diversity. Peterson et al. (1998) noted ecosystems have some ecological resilience which allows them to rearrange around new sets of conditions even when massive disturbance take place. This resilience depends on the cross-scale interaction of species within functional groups, and scale is commanded by body size. In evolutionary time, the rearrangement of ecosystem functioning should occur with incomers (immigrant species) filling new niches and resident species depopulating to the extinction. This is exactly what we found for the Italian Plio-Pleistocene large mammals. A similar dynamic has been described for the evolution of the Atapuerca fossil site mammal community (Rodríguez, 2004). The steady-state observed for turnover is consistently supported by previous findings where we suggest a switch in ecosystem functioning between Villafranchian and Galerian (cfr. Rodríguez, 2006; Meloro et al., 2007; Raia et al., 2007).

Changes in productivity can be considered another possible argument for diversity stasis and turnover pulse. Intuitively, the increasingly colder and drier climate in the Late Pleistocene could have decreased diversity via lower productivity. More or less the same situation exists along the latitudinal gradients from the tropics to the poles at the present day. Albeit attractive, this line of reasoning is potentially misleading. Janis et al. (1994) and Guthrie (2001) cautioned against direct comparison of apparently similar past habitats with modern ones. For instance, there were many species of Ice Age ‘mammoth steppes’ (Guthrie, 1984, 2001) at very high latitudes. Without productivity information on hand, ecological theories on the control of diversity (e.g. Rosenzweig, 1995; Tilman, 1996) are mostly inapplicable. Interestingly, Brown et al. (2001) argued their theory is applicable when productivity does not change significantly.

## 5. Conclusion

Mammal faunas certainly underwent (and they are undergoing) times of dramatic diversity crisis. One of such massive extinction crises occurred at the end of Pleistocene, when many large mammals went extinct almost simultaneously (Barnosky et al., 2004; Cardillo and Lister, 2002). In spite of extremely intense climate changes, the Plio-Pleistocene species richness of large mammals remained (at least in Italy) unaltered. We found empirical agreement with a recent ecological theory of diversity regulation presented in Brown et al. (2001). In addition, we posit that consistent taxonomic changes occurred in coincidence with the largest climatic oscillation (cfr. Raia et al., 2005, this study). The latter drove transcontinental dispersal, local extinction, and ecosystems rearrangement. These rearrange-

ments left diversity unaltered. It is noteworthy that mammalian diversity changes were tracked at larger time scale (e.g. all over Cenozoic Stucky 1990; Alroy, 2000b; Fortelius et al., 1996; Prothero, 1999) most notably when speciation was a factor. Our scale of analysis is probably too short, and speciation all too negligible, to detect such a change.

Jablonski (2003) illustrated the determinants of life change on Earth should be framed out into a biotic and abiotic component affecting organisms at various scales (e.g. individuals, populations, ecosystems). The biotic component includes both intrinsic (e.g. body size, geographical range) and extrinsic (predation, competition) factors. Here we found an extensive role for an abiotic factor (climate change) to control the rate of community turnover. Elsewhere, we had shown it altered predation regimes (Meloro et al., 2007; Raia et al., 2007) as well. Yet, diversity goes beyond that control, and, more likely, could correlate to larger-scale evolutionary phenomena.

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