



Diversity patterns in Quaternary Large Mammals communities from Italy

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Abstract

The anatomy of large mammals diversity through distinct paleo-communities (PCOMs) spanning across Quaternary Ice Ages was analysed. Diversity counts on previously-established PCOMs have been computed. A rarefaction analysis was accomplished to account for differences in the fossil record quality between PCOMs. Species occupancy (at the PCOMs level) was chosen as a starting point to predict number of taxa expected by the rarefaction model. Large mammals' diversity resulted almost constant despite the overwhelming climatic changes that affected the Italian peninsula during the Ice Ages. Constancy in diversity was discussed in terms of ecological replacements coinciding, perhaps causally, with major extinction events, and predatory-prey dynamics. © 2004 SIe. All rights reserved

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1. Introduction

Quaternary large mammals are well represented by the Italian fossil record and over one hundred papers have been published to describe them (Malatesta 1985; Raia 2003). Different dispersal events changed the composition of Italian faunas starting ca. three million years ago (middle Pliocene) with the *Leptobos event* followed by the arrival of the genera *Equus* and *Mammuthus* (Azzaroli et al. 1988) and by the *Wolf event* (c.ca 2.0 Ma) (Azzaroli 1983; Azzaroli et al. 1988; Torre et al. 1992; Napoleone et al. 2001; Augusti & Antòn 2002). All of these bio-events characterized the Villafranchian stages (early, middle and upper) representative of Pliocene and early Pleistocene mammal epochs in Italy.

The last mammal ages of Pleistocene were defined as Galerian (Ambrosetti et al. 1972; Azzaroli et al. 1988) and Aurelian (Gliozzi et al. 1997). The transition between them was marked by the arrival of the giant Irish elk (*Megaloceros giganteus*), woolly mammoth (*Mammuthus primigenius*) and modern forms such as wolf (*Canis lupus*), chamois (*Rupicapra rupicapra*) and ibex (*Capra ibex*). All of these faunal turnovers have been often correlated with global climate changes whose effects were firstly recorded on plant community (Strasburger 1995; Suc et al. 1995) and, as a consequence, on the mammal assemblages (Kurtèn 1968; Azzaroli et al. 1988; Augusti & Antòn 2002; Lister 2004). In spite of these plain patterns, some questions remain to be clarified on diversity trends during the evolution of large mammals from Italy. Biodiversity trends are, in general, difficult to ascribe in living communities

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(Blackburn & Gaston 2000) and sampling problems are amplified in extinct ones because of taphonomic biases and differences in local assemblages. Recently, Raia (2003) re-elaborated, for Quaternary Italian fossil record, presence-absence matrices in Palombo et al. (2003), and ideated the PCOM concept. PCOMs are taxonomically distinctive units constituted by species coming from Local Assemblages (LAs) of similar age. From a paleontological perspective, the PCOM is comparable to Miller's community model (1993) that considers extinct community at a regional scale, as comprehensive of different local ecosystems whose stability is guaranteed by meta-population dynamics. PCOMs have been demonstrated to represent a quite reliable proxy for 'real' communities as they reproduce some of the characteristics which living communities feat (Raia 2003).

The nine PCOMs identified by Raia (2003) for the Italian Ice Age fossil record allow a quantitative analysis of diversity trends at a macroecological scale. The latter is the main goal of this work.

2. Materials and Methods

Quaternary large mammals whose reconstructed body weight is superior to 5 kg were subjected to diversity analyses. Carnivores, Artiodactyls, Perissodactyls and Proboscideans have been included here. I used the presence-absence matrix for the entire Ice Age fossil record (Palombo et al. 2003) to quantify diversity in the PCOMs recognized - according to Raia (2003)- as: Triversa (2 LAs), Montopoli (5 LAs), Upper Valdarno (14 LAs), Val di Chiana (5 LAs), Pirro (5 LAs), Galerian 1 (6 LAs), Galerian 2 (5 LAs), Galerian 3 (8 LAs), Aurelian (17 LAs).

Diversity has been quantified as the number of species recognized in each single PCOM. This index, called species richness (Peet 1974), has been calculated for all species included and for different orders separately. For an accurate quantification of species richness in time, I corrected diversity data by including range-through (Barry et al. 1995; Maas et al. 1995): consider a continuous distribution - in time - of three PCOMs, say A, B, C. If a species x is

present in PCOMs A and C it was assumed that its absence in PCOM B may be attributed to either chance or taphonomy, so x were actually considered as present in PCOM B. This correction is useful in paleontology to avoid any bias caused by different preservation probability (Foote 2000).

The inhomogeneous distribution of the number of Local Assemblages per PCOM posits a further possible bias. Locality-poor PCOMs are prone to miss species (particularly rare species) because of sampling. I accounted for sampling differences between PCOMs applying the rarefaction method (Sanders 1968). This technique permits to calculate the expected number of species derived from an hypergeometric distribution (Heck et al. 1975) assuming that species richness, in samples of different size, is a function of number of individuals. Rarefaction has been widely used in ecology and paleontology (Koheller et al. 2004; Westrop et al. 1998; Adrain et al. 2000; Alroy 2000) and its statistical robustness has been confirmed in comparison with other techniques (Gotelli & Colwell 2001). Of course, the number of individuals of any species is quite uncertain in fossil assemblages. Individuals number has to be inferred by bone counts and even corrected for species' body size (Damuth 1982). I overcame this problem assuming that the number of individuals for every species in any single PCOM is directly related with its occupancy (=number of presences per PCOM). The relationship between abundance and occupancy is very robust, as confirmed in modern ecosystem studies on birds and mammals (for a review: Blackburn & Gaston 2000) and indicates that rarity and abundance are comparable at local and regional scale. The cause of this relationship still matter of controversy (Holt & Gaston 2003) yet it represents one of the most widely held pattern in macro-ecology. Further, it has been demonstrated that large mammals species richness is comparable with a good percentage of similarity (superior than 60%) among living and extinct communities (Kidwell & Flessa 1995). Thus, the distribution of species occupancies in the largest sample (Aurelian PCOM with 17 LAs) has been quantified to perform the rarefaction curve. I calculated rarefaction curves for all large mammals and at the order level.

The results have been compared with the empirical quantification of species richness (all species together and the number of species per order) for every PCOM.

The program PAST has been used to quantify species richness at empirical level (with range through correction) and with rarefaction methodology. Chi-square statistics together with Spearman correlation index have been applied to compare the results obtained.

3. Results

Species richness appears to change little across PCOMs (Fig.1) and chi-square confirms the pattern of no variation of diversity among them ($\chi^2=8.58$, $df=8$, $p=0.38$).

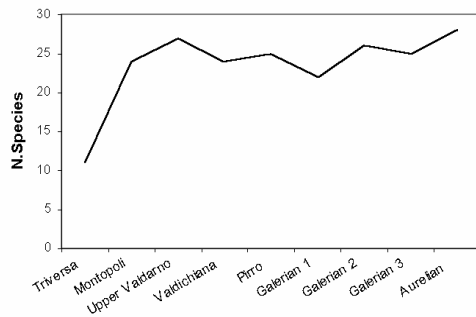


Fig. 1: Variation of species richness among PCOMs.

Similar results are identifiable for the orders separately (Fig.2; Tab.1). The great diversity difference between Triversa PCOM and the others thus depends on sample size. In fact, Triversa PCOM represents the poorest in Local Assemblages ($n=2$) and as a consequence the poorest as for species richness.

The influence of number of LAs on PCOMs is evidenced by a positive correlation among mammals richness/PCOM and number of Local Assemblages/PCOM ($N=9$, $r_s=0.698$; $p=0.037$). Other significant correlation stressed for the great influence of carnivores diversity on the entire mammals species richness ($N=9$, $r_s=0.678$, $p=0.045$). Interestingly, there is a positive relationship among

carnivores and artiodactyls diversity ($N=9$, $r_s=0.690$, $p=0.040$). Even if not surprising (see the intro section), these results confirm the importance of controlling for sampling biases.

Table 1

Chi square statistics for species richness distribution in different orders.

	df	χ^2	p
Artiodactyla	8	5.54	0.70
Perissodactyla	8	4.63	0.80
Carnivora	8	6.66	0.57
Proboscideans	8	1.20	0.99

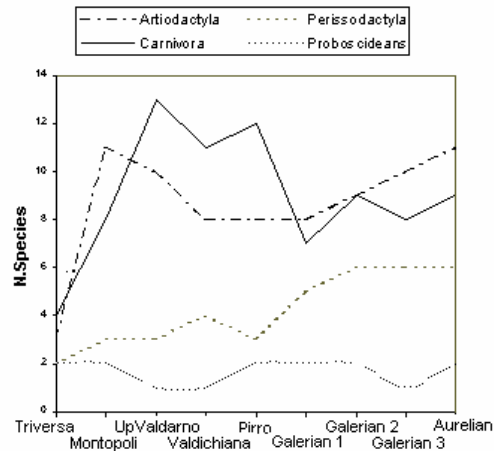


Fig. 2: Species richness variation in different mammalian orders.

Rarefaction allows to comprehend if such major diversity changes were 'real' or driven by the effect of LAs number. The number of species expected is comparable to the observed one at either global and order scale. Chi-square analysis shows no differences between rarefied and observed samples (see Tab.2). Triversa, Upper Valdarno and Aurelian represent the PCOMs that better follow the rarefaction model; the other PCOMs are pooled together because of their similarity in number of Local Assemblages (Fig.3). For Proboscideans it wasn't possible to calculate rarefaction curves because of little sample size, but

the constancy of diversity for this group is evident (Fig.2).

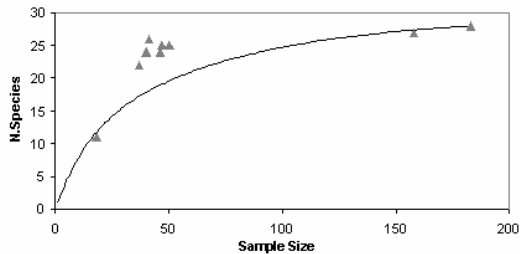


Fig. 3: Species richness obtained from rarefaction (solid line) and observed (grey triangles).

Table 2

Chi square statistics for differences between observed and rarefied number of species.

	df	χ^2	p
All Mammals	7	11.74	0.11
Artiodactyla	7	1.91	0.96
Perissodactyla	7	7.66	0.36
Carnivora	7	6.98	0.43

4. Discussion

The constancy observed for Italian mammals diversity during Ice Age is not unexpected trend. Several authors (for a review: Rosenzweig 1995) founded out similar results for mammals as well as for other groups and, recently, Brown et al. (2001) confirmed that diversity changes a little, in spite of different time scale (from one to 10,000 years) and different taxonomical assemblages they analysed.

An explanation for the pattern observed should involve different hypotheses because of the complex interplay between biotic and abiotic factors that shape diversity trends: resilience, spatial scale, productivity, habitat heterogeneity, potential evapotranspiration (Peterson et al. 1998; Fraser 1998; Barnosky et al. 1999; Schwartz et al. 2000; Whittaker et al. 2001;

Ruggiero & Kitzberger 2004) are just few representative variables claimed to influence diversity. Unfortunately, it is difficult to precisely reconstruct environmental parameters for extinct ecosystems.

However, the history of large mammals in Italy is indicative. A poor speciation rate was observed in this peninsula over the Ice Ages (Kotsatkis et al. 2002). Coupling this latter fact with the well known phenomenon of dispersal events (quoted above), the whole picture is of punctuated and somewhat massive faunal substitutions. As diversity changed little, species incomes at the events must be counterbalanced by similar-sized extinction events. Quaternary large mammals diversity thus represents an equilibrium point between inconstant arrivals and extinctions. Niche incumbency (Rosenzweig & McCord 1991) could well explain this pattern. In this view, massive arrivals (here dispersal events) are causally linked to niche substitution bolstered by extinctions of the incumbents. This signal is captured by the incidence of the two numerous taxonomic groups - Carnivores and Artiodactyls - on the Italian mammals richness. Intriguingly, the positive relationship between these orders' diversity could be plainly dependent on LAs richness difference among PCOMs. Raia (2003) found out substantial evidence for uneven distribution of predator/prey ratios across PCOMs. This indicates that structural changes accompanied, to some degree, species turnover in spite of diversity constancy. The other taxonomic groups representative of Italian herbivore guild may be poorly implicated in this process because they evolve forms with large body size (such as rhinos or elephants) that possibly escaped predator control (Owen Smith 1990).

The role climate played in shaping the evolution of mammal communities is still controversial (Alroy et al. 2000), partly because of different methods for diversity quantifications (Peet 1974; Shepherd 1998; Barker 2002). It is worth noting that Palombo & Mussi (2001) pointed out for a significant effect of humans on the Italian large mammals diversity since the Middle Pleistocene. Present results don't leave out the latter hypothesis but emphasize for structural changes in Italian faunas as been empirically shown by Torre et al. (2001) for Plio-Pleistocene large mammal assemblages.

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References

- Adrain J.M., Westrop S.R., Chatterton B.D.E. & Ramsköld L. (2000) Silurian trilobite alpha diversity and the end-Ordovician mass extinction. *Paleobiology*, **26**, 4, 625-646.
- Agustí J. & Antón M. (2002) *Mammoths, sabretooths, and hominids: 65 million years of mammalian evolution in Europe*. Columbia University Press.
- Alroy, J. (2000) New methods for quantifying macroevolutionary patterns and processes. *Paleobiology*, **26**, 707-733.
- Alroy, J., Koch, P.L. & Zachos, J.C. (2000) Global climate change and North American mammalian evolution. *Deep Time. Paleobiology* supp. **26**, 4 (eds. Erwin, D.H., Wing, S.L.) pp. 259-288.
- Ambrosetti P., Azzaroli A., Bonadonna F.P. & Follieri M. (1972) A scheme of Pleistocene chronostratigraphy for the Tyrrhenian side of Central Italy. *Bollettino della Società Geologica Italiana*, **91**, 169-84.
- Arita H.T. & Rodriguez P. (2004) Local-regional relationships and the geographical distribution of species. *Global Ecology Biogeography*, **13**, 15-21.
- Azzaroli, A. (1983) Quaternary mammals and the "end-Villafranchian" 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.
- Barker G.M. (2002) Phylogenetic diversity: a quantitative framework for measurement of priority and achievement in biodiversity conservation. *Biological Journal of the Linnean Society*, **76**, 165-194.
- Barnosky A.D., Hadly E.A., Maurer B.A. & Christie M.I. (1999) Temperate terrestrial vertebrate faunas in North and South America: interplay of ecology, evolution, and geography with biodiversity. *Conservation Biology*, **15**, 3, 658-674.
- Barry, J.C., Morgan M.E., Flynn L.J., Pilbeam D., Jacobs L.L., Lindsay E.H., Raza S.M. & Solounias N. (1995) Patterns of faunal turnover and diversity in the Neogene Siwaliks of Northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **115**, 209-26.
- Brown J.H., Morgan S.K.E., Parody J.M. & Haskell J.P. (2001) Regulation of diversity: maintenance of species richness in changing environments. *Oecologia*, **126**, 321-332.
- Caley M.J. & Schluter D. (1997) The relationship between local and regional diversity. *Ecology*, **78**, 1, 70-80.
- Damuth J. (1982) Analysis of the preservation of community structure in assemblages of fossil mammals. *Paleobiology*, **8**, 4, 434-446.
- Foote, M. (2000) Origination and extinction components of taxonomic diversity: general problems. *Deep Time. Paleobiology* supp. **26**, 4 (eds. Erwin, D.H., Wing, S.L.) pp. 74-102.
- Fraser R.H. (1998) Vertebrate species richness at the mesoscale: relative roles of energy and heterogeneity. *Global Ecology and Biogeography Letters*, **7**, 215-220.
- Gaston K.J. & Blackburn T.M. (2000) *Patterns and processes in macroecology*. Blackwell Science Ltd.
- 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. & D. Torre, (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.
- Gotelli N.J. & Colwell R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.
- Koellner T., Hersperger A.M. & Wohgemuth T. (2004) Rarefaction method for assessing plant species diversity on a regional scale. *Ecography*, **27**, 532-544.
- Heck K.L.Jr, Van Belle G. & Simberloff D. (1975) Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology*, **56**, 1459-1461.
- Holt A.R. & Gaston K.J. (2003) Interspecific abundance-occupancy relationship of British mammals and birds: is it possible to explain the residual variation? *Global Ecology and Biogeography*, **12**, 37-46.
- Kidwell S.M. & Flessa K.W. (1995) The quality of the fossil record: populations, species and communities. *Annual Review of Ecology and Systematics*, **26**, 269-99.
- Kotsakis, T., Petronio, C., Angelone, C., Argenti, P., Barione, G., Bedetti, C., Capasso Barbato, L., Di Canzio, E., Marcolini, F. & Sardella, R. (2002) Endemisms in Plio-Pleistocene Vertebrate faunas of Italian peninsula and their palaeobiogeographical meaning. *1st International Paleontological Congress* Sydney, Australia.
- Kurtén B. (1968) *Pleistocene mammals of Europe*. Aldine Publishing Company, Chicago.
- Lister A. M. (2004) The impact of Quaternary Ice Ages on mammalian evolution. *Philosophical Transactions of Royal Society of London B*, **359**, 221-241.
- Maas M.C., Anthony M.R.L., Gingerich P.D., Gunnell G.F. & Krause D.W. (1995) Mammalian generic diversity and turnover in the Late Paleocene and Early Eocene of the Bighorn and Crazy Mountains basins, Wyoming and Montana (USA). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **115**, 181-207.

- Malatesta A. (1985) *Geologia e Paleobiologia dell'Era Glaciale*. La Nuova Italia Scientifica, Roma.
- Miller W. III (1993) Models of recurrent fossil assemblages. *Lethaia*, **26**, 182-183.
- Napoleone G., Albanelli A. & Mazzini M. (2001) The fossil rhinoceros found by Nesti on 1811 dated in the final Pliocene by magnetostratigraphy of the Upper Valdarno sequence. *Bollettino della Società Paleontologica Italiana*, **40**, 2, 249-56.
- Owen Smith N. (1990) *Megaherbivores*. Cambridge University Press.
- Palombo M.R., Azanza B. & Alberdi M.T. (2003) Italian mammal biochronology from latest miocene to middle Pleistocene: a multivariate approach. *Geologica Romana*, **36** (2000-2002), 335-368.
- Palombo M.R. & Mussi M. (2001) Large mammals guilds and human settlement in the Middle Pleistocene of Italy. *Bollettino della Società Paleontologica Italiana*, **40**, 2, 257-267.
- Peet R.K. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics*, **5**, 285-307.
- Peterson G., Allen C.R. & Holling C.S. (1998) Ecological Resilience, Biodiversity, and Scale. *Ecosystems*, **1**, 6-18.
- Raia P. (2003) *The evolutionary ecology of Ice Ages large mammals from Italy*. Phd thesis. Università del Molise, Italia.
- Rook L. & Torre D. (1996) The wolf-event in western Europe and the beginning of the Late Villafranchian. *Neuse Jahrbuch Geologie und Paläontologie Mh H*, **8**, 495-501.
- Rosenzweig, M.J. (1995) *Species diversity in space and time*. Cambridge University Press.
- Rosenzweig, M.L. & McCord, R.D. (1991) Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology*, **17**, 202-213.
- Ruggiero A. & Kitzberger T. (2004) Environmental correlates of mammal species in South America: effects of spatial structure, taxonomy and geographic range. *Ecography*, **27**, 401-416.
- Sanders H.L. (1968) Marine benthic diversity: a comparative study. *American Naturalist*, **102**, 243-82.
- Shepherd U. (1998) A comparison of species diversity and morphological diversity across the North American latitudinal gradient. *Journal of Biogeography*, **25**, 19-30.
- Strasburger E., Noll F., Schenck H. & Schimper A.F.W. (1995) *Trattato di botanica per le università*. A. delfino Ed., Bologna.
- Suc J.P., Bertini A., Combourieu-Nebout N., Diniz Filomena, 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 cracovia*, **38**, 1, 3-16.
- Torre D., Abazzi L., Bestini A., Fanfani F., Ficarelli G., Masini F., Mazza P. & Rook L. (2001) Structural changes in Italian Pliocene-Pleistocene large mammal assemblages. *Bollettino della Società Paleontologica Italiana*, **40**, 2, 303-306.
- Westrop S.R. & Adrain J.M. (1998) Trilobite alpha diversity and the reorganization of Ordovician benthic marine communities. *Paleobiology*, **24**, 1, 1-16.
- Whittaker R.J., Willis K.J. & Field R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453-470.