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ORIGINAL PAPER

Diversity trends in Neogene European ungulates and rodents: large-scale comparisons and perspectives

Olivier Maridet · Loïc Costeur

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Abstract The ungulate and rodent fossil records are often used independently to understand mammalian evolutionary history. Few studies have directly compared both records over long time periods and large geographic areas. Here, we compiled two datasets of European fossil localities containing rodents and/or ungulates over 20 My (Early Miocene–Early Pliocene) and processed the data with the same methodology. We counted the raw diversity and calculated a measure of evenness (Pielou's index). After controlling for potential biases on diversity estimators, we identify the evenness index as a more reliable estimator bringing interesting insights into the way both mammal groups are structured by biotic or abiotic factors. In this study, we consider that an uneven distribution of the species richness among families, when only some families successfully diversify within the "continental-scale community", represents a lower adaptability of this community to the environmental context. Pielou's index is used to estimate this adaptability through time. The responses of ungulates and rodents to environmental changes are very divergent, especially facing the climatic changes known since the Middle Miocene. The general patterns suggest that rodent broad-scale assemblages are affected by all kinds of perturbations, even short biotic and abiotic events, but show a better adaptability when facing long-term abiotic changes. Unlike rodents, the ungulate assemblages show more stability in periods of relative environmental stability but show less adaptability to long-term climatic changes. Life-history traits of mammals can help explain patterns of diversity and biogeography at different spatial scales and may probably partly explain the opposite patterns evidenced here.

Keywords Ungulates · Rodents · Neogene · Europe · Broad-scale diversity patterns · Life-history traits

Introduction

During the last 20 years, the increasing quality and completeness of the fossil record for European continental Neogene mammals has given the opportunity to carry out broad-scale studies explaining the evolutionary history of European mammalian faunas. Several major biotic events (migration and changes in species distribution; Mein 1999a, b) occurred throughout the Neogene that had major impact on mammalian communities. These events are well known, thanks to several synthetic studies providing an evolutionary overview during the Miocene and the Pliocene (Mein 1999a, b; Fahlbusch 1989; Rössner and Heissig 1999; Agustí et al. 1999).

Most of the time, the fossil diversity of mammals is considered independently through small mammals (mainly rodents) or large mammals (mainly ungulates). However, some studies have compared both the fossil records of large and small mammals. Bernor et al. (1996a) proposed a synthesis of the mammalian fossil record in Eurasia for the Middle and Late Miocene; the authors observed differences between the evolutionary history of large and small mammals. Fortelius et al. (1996) undertook a detailed

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O. Maridet (✉)
Institute of Vertebrate Paleontology and Paleoanthropology,
Chinese Academy of Sciences,
142 Xizhimenwai Dajie, P.O. Box 643, Beijing 100044, China
e-mail: Olivier.Maridet@ivpp.ac.cn

L. Costeur (✉)
Naturhistorisches Museum Basel,
Augustinergasse 2,
4001 Basel, Switzerland
e-mail: Loic.Costeur@bs.ch

analysis of a Eurasian mammalian fossil database, focusing on the Middle and Late Miocene environmental changes in Eurasia. The authors made interesting observations between body-size categories and showed that some size ranges (i.e., between 10 and 100 kg and over 300 kg) presented noticeable opposite trends between Western and Eastern Eurasia and linked the patterns to different climatic contexts although they seemed to interpret the distribution of species within body-size categories as mainly controlled by biases. At the same time, they noticed that dietary guilds and locomotor groups presented large differences depending on the environmental context. Consequently, by considering size categories, dietary guilds, and locomotor adaptations simultaneously, in different provinces of Eurasia, broad-scale patterns in community structure were not clearly resolved.

To date, only Liow et al. (2008) carried out a real comparison between two clearly differentiated datasets of large mammals (including not only herbivorous but also carnivorous and omnivorous mammals) and small mammals (including insectivorous mammals) during all the Neogene of Eurasia. The authors propose that over the whole Neogene of Eurasia, body-size and some linked life-history traits would induce a shorter duration of large mammals' genera as shown by significantly higher per capita rates of origination and extinction. All these previous studies provide interesting clues to further investigate the potential factors that control the pattern of biodiversity in mammalian communities over time and will be compared with our own results.

Unlike previous works, this study substantially diverges in its approach and the method used. Indeed, the purpose of our paper is to carry out a simple comparison in analyzing two datasets of mammal primary plant eaters only (ungulates and rodents) and focusing on the evolution of their diversity through time. The aim is (1) to establish if both datasets present significant differences in their respective patterns and (2) to investigate the processes behind and propose potential factors that could explain the divergent patterns. Both datasets have been compiled identically and processed with the same methods for estimating diversity, paying particular attention to the potential biases that could affect their analysis (Maridet 2003 unpublished Ph.D Thesis; Maridet et al. 2007; Costeur 2005 unpublished Ph.D Thesis; Costeur and Legendre 2008). In the present study, we made the choice to include both periods of climatic stability and of climatic deteriorations in order to fully tackle the question of the climatic influence on the diversity dynamics. Besides classical taxonomic counts, this study pays a particular attention to the structural composition of both faunal assemblages, considering each assemblage as a functional ensemble that can be referred to as a "continental-scale community". We especially focus on two hierarchical ranks: species and families, thus investigating the distribution of species richness within families. Indeed, several ecological studies indicate that species richness alone is not sufficient to understand the evolution of communities (e.g., Qian and Ricklefs 2004; Ricklefs and Renner 2000). Higher taxonomic levels can provide complementary and meaningful information. With regards to this approach, the family level is known both on the extant and fossil records to provide reliable information on biogeographic patterns and evolutionary history (Simpson 1964; Kaufman 1995). Other studies (i.e., Liow et al., 2008) chose the generic level because of statistically non-significant results at the species level.

Ricklefs and Renner (1994, 2000) evidenced the broad-scale relationship between familial species richness and the ability of species or lineages to diversify into different ecological roles. Based on this theoretical ground, one can assume that the proportion of species in each family will illustrate the "flexibility" (sensu Ricklefs and Renner 1994) or functional adaptation of the community facing environmental perturbations. In our study at the European spatial resolution, we assume that an uneven distribution of species richness in a community (low Pielou's index values) overall reflects the success of few families to occupy a variety of ecological niches as opposed to all the other families, demonstrating a generally lower ability of adaptation of the whole community to resist environmental stress (Wittebolle et al. 2009). Such a general assumption does not mean that the structure of a community is homogeneous as is well-known that each family composing a community also has its own dynamics depending on its ecological features. However, we propose here to examine whether it is possible to point out some main opposite patterns between rodent and ungulate communities that would reveal a specific aspect of each community. In order to do so, we consider the Pielou's index as an indicator of communities' adaptability. The interpretation of this index is relevant at a continental spatial resolution where it can point to deep functional evolutionary changes in both ungulate and rodent assemblages, whereas familial species richness considered at a smaller resolution would rather reflect distribution discrepancies of taxa facing local environmental contexts.

Material and methods

Data sets

This study uses published faunal lists and individual systematic studies of European mammal localities in order to compile a dataset as complete as possible. The data used in this study come from two datasets already used in studies dealing with the biogeography of small and large mammals, respectively (Maridet et al. 2007; Costeur et al. 2004). This compilation is a five-year-long work of database construction carried out from 1999 to 2004, including 1,622 localities. Among these localities, 564 localities have provided small mammals and 747 large mammals with a good and controlled systematic record. Both lists have been uniformly treated giving two comparable datasets of ungulates and rodents. Of the localities, 545 localities are included in both lists; the rest only yielded either small or large mammals. In the following analyses, both datasets have been processed identically. The complete lists of the localities are available on request to the authors. The number of species, families, and localities for both ungulates and rodents and for each biochronological unit used in this study are summarized in Table 1.

Classification of mammals

The classification followed is that of Wilson and Reeder (2005). As far as rodents are concerned, Muroidea is a super-family sensus Wilson and Reeder (2005), including Spalacidae, Cricetidae, and Muridae. Murinae, Arvicolinae, and Gerbillinae are subfamilies of the higher Muridae.

Nonetheless, the classification usually used in the Neogene fossil record presents some peculiarities that have to be taken into account. Thus, the three subfamilies Murinae, Arvicolinae, and Gerbillinae are considered here as equivalent to families (e.g., Rössner and Heissig 1999). Indeed, even if Murinae, Arvicolinae, and Gerbillinae are not considered as families in the recent classification because of close genetic affinities, the strong morphological differences, the size disparity, as well as their abundance in the Neogene fossil record implies very different ecological demands and thus, a priori, noticeably different ecological niches. Consequently, in order to follow the structural adaptation of rodent assemblages through time, these family-like features justify the use of these subfamilies as equivalent to families.

As far as ungulates are concerned, much lesser problems occur. The Neogene fossil and recent classifications are almost identical so that the families present in the European Neogene (Rössner and Heissig 1999) are either also found in Wilson and Reeder (2005) or no real arguments against the validity of extinct families used hereafter has been raised so far.

Biochronological timescale

The temporal framework used in this study and commonly employed in diversity analyses in the European Neogene is the Mammal Neogene (MN) Biochronological Continental Scale defined by Mein (1975) and later refined by many authors (Mein 1989, 1999a, b; Agusti and Moya Sola 1991; De Bruijn et al. 1992). They are defined at the European level on the basis of associations of diagnostic mammal species with large geographical ranges. For each biochronological unit, a reference locality provides the typical association of evolutionary stages observed in phyletic lineages. These associations allow the relative dating of other faunas. Thus, biochronological units are characterized at the European level by faunal assemblages without

Table 1 Taxonomic richness (number of species and families) in both datasets used in this study (ungulates and rodents) and for each biochronological interval. The number of localities which have yielded ungulate and rodent material is listed in the two last columns

	European ungulate species richness	European ungulate family richness	European rodent species richness	European rodent family richness	Number of localities bearing ungulates	Number of localities bearing rodents
MN 15	84	13	84	13	21	32
MN 14	83	13	83	13	33	48
MN 13	71	14	71	14	47	50
MN 12	39	9	39	9	32	15
MN 11	50	11	50	11	24	25
MN 10	54	10	54	10	30	36
MN 9	58	9	58	9	82	32
MN 7-8	68	8	68	8	110	38
MN 6	66	8	66	8	74	52
MN 5	77	11	77	11	87	62
MN 4	92	11	92	11	76	62
MN 3	68	8	68	8	49	42
MN 2	52	7	52	7	51	37
MN 1	44	8	44	8	31	33

marked phases of origination, extinction, or migration events, whereas such events are used to define their limits. Consequently, each taxonomical assemblage here analyzed for each biochronological unit can reasonably be considered as a stable pool of species coexisting throughout the corresponding time span.

Even if MN zone boundary dates are still debated, this temporal division appears to be relevant and precise enough when dealing with long-term mammalian evolutionary patterns throughout the Neogene (Maridet et al. 2007).

Diversity dynamics descriptors

Three different diversity estimators have been used: species richness, family richness, and evenness index. Species and family richness are basic counts of the number of species and families known from the fossil record for a particular time interval. Evenness indices are usually used in ecology to quantify diversity through the distribution of abundances across species (Magurran 1988). In this study, we propose to use an evenness index at a higher taxonomic level to assess how even or uneven species richness is distributed within families. The Pielou's index has been chosen because of its weak correlation to the number of categories (Clarke and Warwick 1998), in this case, family richness. Nevertheless, this index is theoretically not independent to sampling effort (Clarke and Warwick 1998), and potential bias needs to be further tested (see below). The computation of this index for each biochronological unit is:

$$J = \frac{-\sum pi \ln pi}{\ln N}$$

with, pi the proportion of species in one family; N the number of families, and i, from 1 to N. In order to get a graphical illustration of this species richness distribution, two diagrams with the proportion of species per family have been given as a complementary describing tool (Fig. 3).

Sampling effort

Dealing with diversity at such a broad scale, encompassing all the European territory from the western border to the Dead Sea and from the early Miocene to the mid-Pliocene implies inequality of the fossil record. Before any analysis, even preliminary, the potential impact of sampling effort (independent variable: number of localities known for each biochronological unit) on our diversity estimates had to be tested. Both data sets of ungulates (Fig. 1a–c) and rodents (Fig. 1d–f) were tested separately due to the fact that not all localities are common to both groups.

For each relationship to be tested, because the classic coefficient of correlation is likely to be biased by the low number of values (14 pairs of values matching the 14 biochronological units), we provide the non-parametric Spearman's rank correlation coefficient (ρ) and the non-parametric test of Mantel is performed to test the significance (P; based on 9,999 permutations).

European species richness (dependant variable) is not significantly correlated with number of localities for the ungulate data set (Fig. 1a, Spearman $\rho=0.169$, $P=0.334$) whereas it is significantly and strongly correlated for the rodent data set (Fig. 1d, Spearman $\rho=0.661$, $P<0.001$). Family richness is significantly correlated with number of localities for ungulates (Fig. 1b, Spearman $\rho=0.771$, $P=0.008$) but not for rodents (Fig. 1e, Spearman $\rho=0.127$, $P=0.365$). Based on these observations, the raw number of species or families should be used with caution for any comparison.

In the same way, the Pielou's index has also been tested against sampling effort. For both ungulates and rodents, the index shows a noticeable high correlation coefficient but no significant correlation (Fig. 1c, 1f: $P=0.146$ for ungulates and $P=0.064$ for rodents), demonstrating a lower sensitivity to sampling effort than the raw diversity descriptors. For this reason, in the following discussion, particular attention will not only be paid to the number of species and families but also to the distribution of species richness within families and thus to the Pielou's index. This will allow us to pinpoint relevant similarities or dissimilarities in the functional adaptation of both continental-scale communities.

Evolutionary history compared for ungulates and rodents

The broad composition of Miocene ungulate and rodent faunas change from faunas dominated by Oligocene-inherited groups to faunas dominated by newly appeared groups. Nevertheless, the distribution of small and large mammals' diversity within communities is markedly different. For ungulates, the very Early Miocene (MN1-2) shows a situation where few families [rhinocerotids (*Aceratherium*, *Diaceratherium*, *Protaceratherium*), moschids (*Dremotherium, Amphitragulus),* and cainotheriids (*Cainotherium*)] are composed of numerous species, just like during the Late Oligocene (Hugueney 1997; Sudre and Legendre 1992; Legendre et al. 1991; Erfurt and Métais 2007). At the same time, rodent family richness is also very low (Fig. 2) with almost half of the species belonging to family Gliridae resulting in a very uneven overall distribution (Fig. 3b-1). The evenness index (Fig 2c) for rodents is thus very low whereas ungulate species richness is much more evenly distributed within families yielding a higher value.

The situation drastically changes in MN3-4 for ungulates with an increase of both species and family richness (Fig. 2a, b). Even if the larger number of localities known for this period can partially bias this observation (see

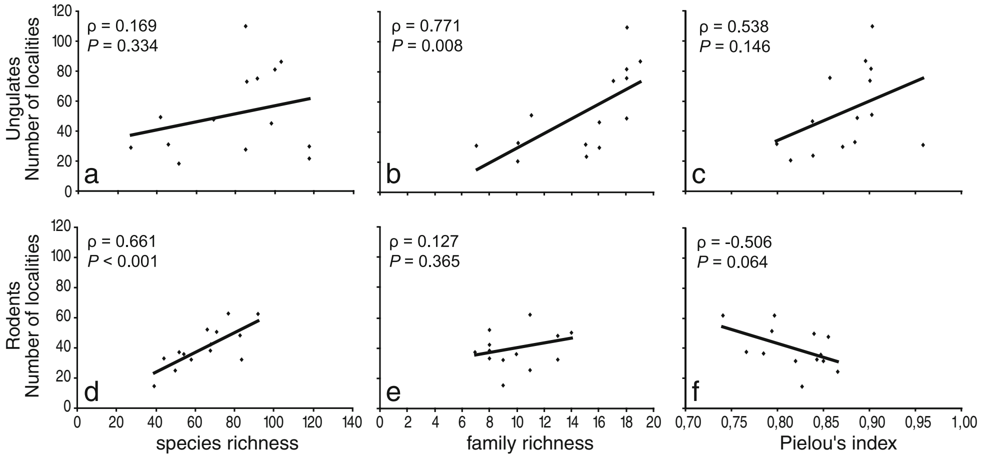

Fig. 1 Relationship between species richness, family richness, and the number of localities at the European resolution. Both ungulates and rodents fossil records are compared for each biochronological unit throughout the Neogene (MN 1 to MN 15). For each regression, the non-parametric Spearman's rank correlation coefficient (*ρ*) and the significance of the relationship (*P*) are provided, the significance being given by the Mantel non-parametric test, based on 9,999 permutations

previous paragraph "Sampling effort"), the appearance (Fig. 3a-1) of many new taxa either coming from Africa (Proboscideans such as *Gomphotherium*) or from Asia (e.g., equids [*Anchitherium*], cervids [*Lagomeryx*, *Procervulus*], and bovids [*Eotragus*]) through the land connection between Eurasia and Africa (i.e., "*Gomphotherium* landbridge", Rögl 1999) comforts this interpretation. The change, although well-recorded, does not seem to be as drastic for rodents at the end of the Early Miocene in MN4. Family richness remains low compared with ungulates, but species richness increases rapidly (Fig. 2a, b). The increasing number of localities known for this period is likely to influence this result. However, the change is also directly related to the replacement of Oligocene-inherited cricetids (e.g., *Pseudocricetodon* and *Eucricetodon*) by new immigrants of the same family (e.g., *Megacricetodon*, *Democricetodon*, and *Cricetodon*) leading to an increase in species number (Fig. 2a). By then, almost 70% of rodent species are only restricted to two families (glirids and cricetids) producing lower values of the Pielou's index (Fig. 2c). Pielou's values for rodents are clearly lower than for ungulates during the Early Miocene, but the trend toward unevenness is similar.

From the Middle Miocene onwards, both fossil records begin to show opposite evenness trends (Fig. 2c) in a generally similar evolutionary context: a progressive decline of the Oligocene-inherited taxa occurs for both groups. For instance, cainotheriids disappear (Fig. 3a-2), and modern ruminants such as cervids and bovids increase in number. For rodents, the proportions of newly immigrated cricetids increase in the communities while glirid proportions quickly decrease.

The early Late Miocene (MN9) is marked by the rapid immigration of hipparionine horses (Bernor et al. 1996b; Agustí and Oms 2001; Fig. 3a-3) as well as of murines (Michaux et al. 1997; Fig. 3b-3). But, this immigration event is marked by totally different patterns for rodent and ungulate communities. Species richness increases rapidly for "new ruminants" (especially cervids and bovids) at the expense of other families leading to a rapid decrease of the Pielou's index (Fig. 2c). Rodent species richness appears much more evenly distributed within each families and subfamilies as opposed to the Middle Miocene trend. For the first time in the Neogene, a clearly opposite trend occurs between ungulates and rodents.

Later in the Late Miocene (MN11) one of the most important components of the Late Oligocene and Early Miocene faunas, the family Moschidae, finally disappears (Fig. 3a-4). Bovids and cervids continue to increase and dominate the faunas all over Europe (with mainly cervids in Northern Europe and bovids and giraffids in South-Eastern Europe, Costeur and Legendre 2008; Fig. 3a-5, 6). Hipparionine horses also progressively increase in number while the diversity of rhinocerotids and other perissodactyls (chalicotheres and tapirs) slightly decline. The Early Pliocene continues these trends, and cervids have a large place in the European faunas (Fig. 3a-7). On the other side, the increase of rodent diversity can clearly be attributed to the diversification taking place among murids with the appearance of new subfamilies (Fig 3b-3, 4). This reflects the rapid morphological adaptation and ecological diversification of murid lineages in the corresponding communities. The Pielou's index for both data sets again presents a similar decreasing trend (Fig. 2c).

At the end of the Miocene and in the Early Pliocene, both rodent and ungulate records show obvious opposite dynamics (Fig. 2a, b). But the low number of localities recording ungulates compared with the richer rodent locality representation prevents any firm conclusion concerning this contrast.

Pielou's index shows a quite similar trend for both fossil records, fitting the known evolutionary history of both groups. Rodents become much more diversified in morphology, especially with morphological specializations occurring in muroid rodents (see Michaux et al. 1997; Renaud et al. 1996 for murines; Mörs and Kalthoff 2004 for cricetids; and Wessels 1999 for gerbillines), and a similar evolution is observed for bovids and cervids (Gentry et al. 1999).

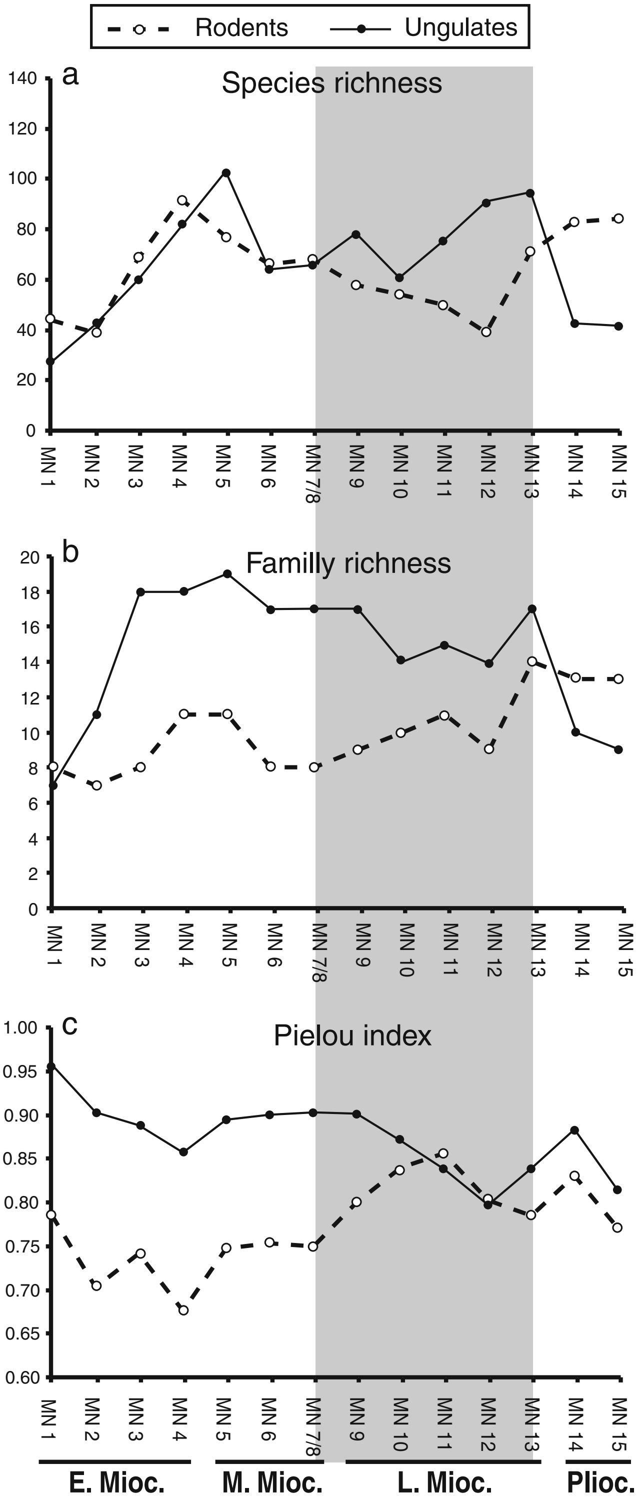

Fig. 2 Comparison of ungulate and rodent diversity dynamics throughout the Neogene of Europe. Three different estimators are used: **a** number of species, **b** number of families, and **c** Pielou's evenness index based on number of species per families. In *gray* is indicated the period of long-term climatic deterioration (from MN7/8 to MN13); see the text for detailed explanation

Broad-scale diversity patterns and environmental context

Three main phases in the structure of rodent and ungulate communities can be deduced from the diversity estimators.

The first phase covers the whole Early Miocene and the beginning of the Middle Miocene (MN 1 to MN 6). This period has been described by different studies as a period of relative environmental stability, with especially the Miocene Climatic Optimum, one of the warmest episodes in the Cenozoic history, as illustrated by isotopic data (e.g., Miller et al. 1991; Zachos et al. 2001) or palynological studies (e.g., Utescher et al. 2000; Jiménez-Moreno et al. 2005). This period seems to be characterized by weaker climatic limitations. Nevertheless, it is also punctuated by successive short abiotic events such as short positive oxygen isotope excursions, interpreted as glaciation events, at the very beginning of the Miocene (Naish et al. 2001), short climatic cyclic variations during the early Miocene (Jiménez-Moreno et al. 2007), and also episodic land connection between Eurasia and Africa (*Gomphotherium* Landbridge, Rögl 1999; MN4) allowing for the immigration of many African and Asian species and/or families. For this period, both datasets present clearly different diversity levels probably directly related to the hierarchical structure inherited from the Oligocene. Both datasets display a similar evolution in the Early Miocene, characterized by a slight decrease of the evenness values. However, this trend is inverted at the end of the Early Miocene. An increase in family richness occurs for ungulates, as well as an increase in species richness for both groups. Both Pielou's curves are still largely separated but follow a parallel path, suggesting similar controlling factors.

From the end of the Middle Miocene to that of the Early Pliocene (MN 7/8 to MN 13), the diversity dynamics of both groups then diverge. As opposed to the previous one, this period of time shows strong environmental perturbations in Europe. The climatic context is indeed different in Europe since the late Middle Miocene, with a decrease in temperatures and increase in aridification following the well-known mid-Miocene climatic event (Flower and Kennett 1994). This climatic change induced a deep modification of environments all along the Late Miocene, characterized by a general opening of the landscapes and a drastic change in vegetation types (e.g., Suc et al. 1999; Favre et al. 2007). At the end of this period, a main environmental event also occurred: the Messinian event (during the biozone MN13). This environmental change mainly affected the peri-Mediterranean area. During this time

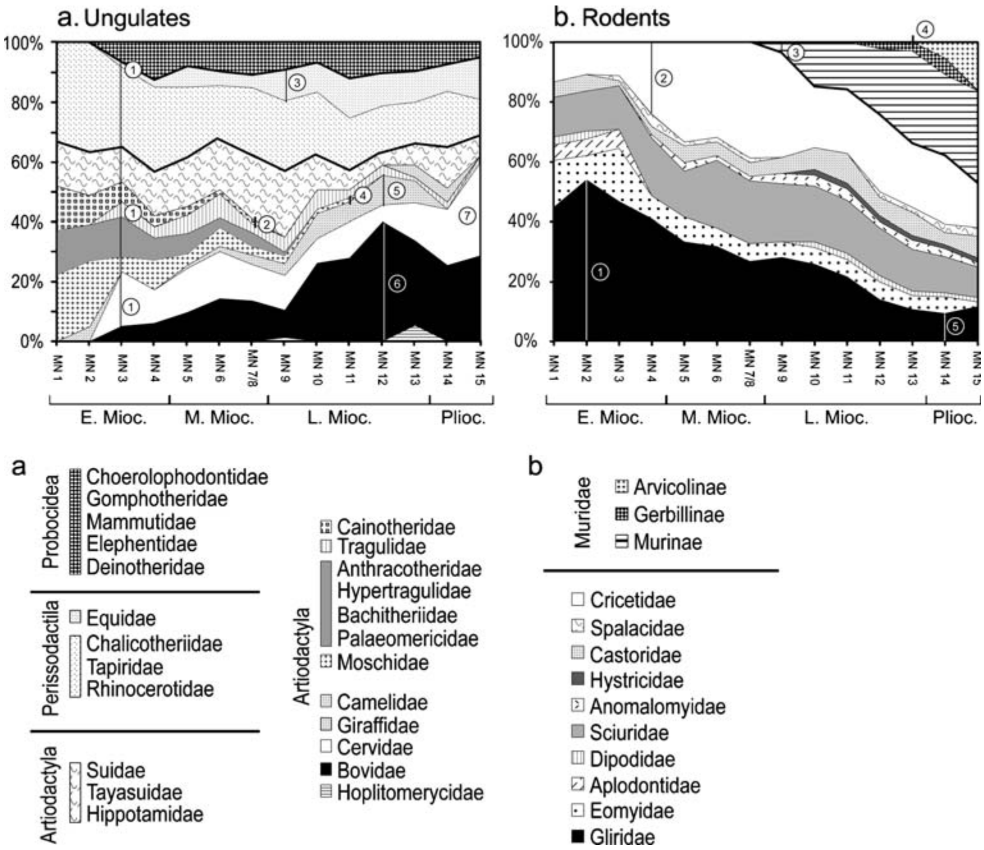

Fig. 3 Proportions of species per family throughout the Neogene (MN1 to MN 15) for **a** ungulates and **b** rodent. For ungulates : [*1*]First occurrence of proboscideans, equids, tragulids, bovids, and cervids; [*2*] Last occurrence of cainotherids; first occurrence of hipparion; [*4*] Last occurrence of moshids; [*5*] maximum species richness of giraffids; [*6*]maximum species richness of bovids; [*7*]maximum species richness of cervids. For rodents: [*1*]maximum species richness of glirids; [*2*]replacement of Oligocene-inherited cricetids by immigrant cricetids, decrease of diversity for Gliridae and Eomyidae; [*3*]first occurrence of murines; [*4*]First occurrence of arvicolines; [*5*] minimum species richness of glirids

interval, the interruptions of the Atlantic–Mediterranean connection, due to sea level fall and tectonic activity in the Betic and Rifian corridors, led to a Mediterranean drawdown (Clauzon et al. 1996; Meulenkamp and Sissingh 2003). As a consequence of this perturbation, land connections were then established, and faunal exchanges occurred between the European and African continents (van der Made 1999).

Along with this period of deep environmental changes, a drastic reorganization takes place in the communities: the composition of communities as inherited from the Oligocene finally totally disappears and the new families which arrived during the Miocene fully diversify. This faunal transition is similar for both groups, but is expressed by a completely different pattern. Rodent species richness, previously largely unevenly distributed within families (mainly in glirids and cricetids) is redistributed among the newly immigrated murines, gerbillines, and arvicolines. Families that were dominant in the Early Miocene (Eomyidae, Gliridae) are now less diversified but not extinct. This leads to a much more even distribution of species within families suggesting an overall better adaptability of rodents facing this long-term environmental modification. As opposed to this pattern, ungulate species richness becomes more uneven and concentrated within two families (bovids and cervids). It is also worth noting that the onset of these changes is not synchronous for ungulates and rodents. Indeed, Pielou's values for rodents show a rapid increase right at beginning of the Late Miocene (MN9) while they decrease for ungulates, later in the early Late Miocene (MN10). The same type of observation can be made at the end of the Miocene with an earlier reaction for rodents (MN12) than for ungulates (MN13), indicating that rodent community structures were already modifying before the Messinian event, supporting also the assumption that the entry of African micro-mammals preceded the Messinian event (Krijgsman et al. 2002).

The third and last phase occurs after the Messinian event (MN14-MN15). A new environmental context sets up around the Mediterranean Sea leading to the "Early Pliocene climatic optimum" (Bertini 2001; Kovar-Eder et al. 2006). As for the first phase, the period is characterized by a relatively less limiting climate and shows once again higher Pielou values for ungulates compared with rodents. Finally, at the end of the early Pliocene (MN15), Pielou values show a noticeable decrease for both ungulates and rodents. This new change in the diversity dynamics seems synchronous and coeval with the end of the early Pliocene climatic optimum, and this is best illustrated by the appearance of the first sigmodont-like cricetids. This last diversity change could be related to the first climatic deterioration towards coolness and dryness, indicating the onset of glacial cycles. The new trend toward uneven diversity observed in both datasets indicates that both communities probably present a low adaptability to this new unprecedented worldwide climatic regime.

Discussion

Our study analyzes the evolution of mammalian assemblages through evolutionary times. Scale-related mechanisms that explain how populations, species, and, in turn, larger ecological levels adapt and evolve over smaller timescales are interesting to recall and yield potential clues to understanding the patterns identified over millions of years and continental areas.

Body size and populations dynamics

Body size is actually well known to drive several mammalian life-history attributes, physiology, and ecological characteristics (Blueweiss et al. 1978; Brown et al. 2004). It is linked to individual metabolic rates (e.g., White and Seymour 2003), species geographic ranges, and the potential for species to disperse (e.g., Brown 1995; Gaston 2003), as well as to life-history traits such as mortality, lactation period, and digestion ability (e.g., Langer 2003). All this indicates that the lifestyle of each mammalian species is strongly dependant on its body size (for a review, see also McNab, 1990 and Eisenberg 1990). Consequently, mammalian population dynamics also depends on the body size of the constituting species (Jetz et al. 2004). Large and small mammal populations seem to be both mainly driven by extrinsic environmental factors (Beckerman et al. 2002), but large mammals usually present more stable population dynamics showing better resistance to limiting environmental factors (Erb et al. 2001). Specific life-history traits such as high potential for dispersion, better resistance to disease, or lack of food resources play a crucial role in their resistance and better stability (Erb et al. 2001). Such traits buffer the effect of environmental factors and eventually lead to delayed responses of the populations compared with small mammals (Beckerman et al. 2002). In other words, resistance to environmental stress seems to be enhanced through the interplay of specific life-history traits correlated to body size.

As opposed to large mammals and mainly because of their size and shorter generation time, rodent populations seem to respond with much less delay to many extrinsic environmental stresses (such as fluctuation of food resources or variation in climatic parameters, e.g., Ergon et al. 2001; Turchin and Batzli 2001; Lima et al. 2002; Moshkin et al. 2002). This high potential of rodent populations to react quickly to environmental perturbations has evolutionary implications: their body size evolution seems to be directly linked to the climatic conditions prevailing, probably also accounting for more rapid adaptation of their life-history traits (e.g., Millien and Damuth 2004; Yom-Tov and Yom-Tov 2004).

From populations to broad-scale diversity patterns

At the continental scale, we investigate here that the broad ensemble dynamics are likely partly controlled by the set of smaller-scale processes, i.e., the diversity dynamics of the mammalian assemblage is the result of the interactions between all European communities for each period of time considered. Therefore, the dynamics of populations that compose each community and consequently, the associated traits and interactions at the individual level can possibly affect the diversity dynamics at the broader scale. However, this influence is difficult to assess as many intermediate scale-bounded mechanisms are involved from the individual to the broad scale assemblage.

With respect to this hypothesis, our results on mammalian communities at the whole European scale actually display a striking similarity in their dynamics when compared with the population dynamics of both rodents and ungulates. Indeed, either at population or communities scales, rodents are affected by all kind of environmental stress (biotic and abiotic, short- and long-term), whereas ungulates display more stability, seem to be buffered from smaller scale perturbations, and react mainly to long-term abiotic perturbations. Unlike ungulates, when facing long-term perturbations, rodents' community shows a high potential for adaptation.

This simple comparison of the patterns between the different ecological levels and the cascade effects between them suggests that mammalian life-history traits may also largely be involved in the structuring process of communities and broad-scale diversity patterns on evolutionary timescales. Although the impacts of life-history attributes on population dynamics are now well known and their implication on evolutionary processes also well investigated (e.g., Magnanou et al. 2005; Sibly and Brown 2007; Liow et al. 2008), their potential long-term influence on the structure of communities has only recently been proposed (e.g., Beckerman et al. 2002; Jernvall and Fortelius 2004) and never deeply been investigated.

Long-term control of diversity: evidences from the rodent and ungulate Neogene fossil records

Along with the associated life-history traits, body size is deeply involved in the diversity regulation processes at the level of communities. Our results seem to imply a general "evolutionary flexibility" of rodent communities as opposed to an "evolutionary inertia" of ungulate communities.

This confirms what Holliday (2005) expressed as: "fluctuating environments are more likely to promote the evolution of small species whereas the evolution of larger species may be favored in periods of constant environmental conditions", i.e., "when mortality is decreased and reproductive success enhanced" (Brown and Sibly 2006) or again "if the environment changes, for whatever the reason, small rapidly breeding species are able to adapt and survive much more easily than large slow breeding species" (Holliday 2005). Even if the present study did not focus on the body size structure within each dataset, it is noteworthy that the largest ungulates (Proboscidea, Perissodactyla) and the largest rodents (Castoridae, Hystricidae) also show a lower species richness and a more stable familial species richness through times compared with the communities they belong to, suggesting that our observations are not only true at taxonomical levels, but that generally, large sizes may induce more "evolutionary inertia".

Fortelius et al. (1996) undertook different analyses of mammal communities' composition compared between Europe and Asia; in one of those, they tried to follow the distribution of species richness within size categories through time (Fortelius et al. 1996: fig. 31.30, p. 433 and fig. 31.29., p. 434). Although they firstly interpret their results as indicators of bias by comparing with extant communities, they noticed clear differences between European and Asia datasets mainly due to the diversity of species less than 100 kg. Considering the different environmental conditions between Europe and Asia from the Middle Miocene onward (Fortelius et al. 2003), this apparent contradiction between both datasets may actually reflect the opposition of adaptability of large and small mammals to different environments, as also suggested by our results. Moreover, the reading of their results clearly shows in both the European and Asian datasets that large categories (more than 50 kg) tend to be less species-rich but also more stable, whereas small species (less than 10 kg) present much more variability in their richness. Although they do not take the taxonomic level into account, this opposition between largest and smallest categories dynamics tends to confirm the general "evolutionary inertia" of large mammals suggested by our results.

Based on an updated version of the same database, the higher origination and extinction rates observed for ungulates by Liow et al. (2008) could be expected to induce more adaptability in periods of strong environmental perturbations for ungulate communities. However, a high origination and extinction rates driving ecological species replacements within families do not necessarily imply a change in structure of the community. Moreover, the choices of Liow et al. (2008) to analyze all the Eurasian Neogene dataset assuming constant environmental conditions in time and space, mixing different dietary guilds whereas dietary specialization can also play a crucial role in addition to body size (e.g., Van Valkenburgh et al. 2004) and not taking into account the strong differences between the European and Asian environments as noticed before by Fortelius et al. (2003), render direct comparisons of their results to ours rather difficult.

As stated by Blackburn and Gaston (1994), many studies observe different relationships between body size and extinction risk, partly due to the fact that these concern taxa with different dietary needs and at different spatial scales which imply different processes of originations and extinctions. With respect to the different communities' dynamics observed here through time, it is indeed highly likely that the question of the ungulates and rodents communities' compositions as well as their respective origination–extinction rates at broad scale have no definitive answer and depends on the environmental context (either characterized by short and limited environmental perturbations or by deep long-termed climatic changes). The key to tackle this problem in the future will probably be to undertake multi-approach comprehensive studies including turnover rates, size, and taxonomic structures of communities.

Conclusions

This study is a one of the first attempts to compare both the fossil records of small and large primarily herbivorous mammals over more than 20 My and over a large geographic area (Europe) using a standardized method. As a main result, we show that both diversity dynamics of ungulates and rodents present noticeable differences, when looking at long-term changes of species and family richness (based on the unbiased Pielou index). While the evolutionary context of increasing presence of newly appeared families and decreasing dominance of Oligocene-inherited families seems to be identical in both small and large mammals, the distribution of species within families is largely diverging.

Indeed, even though the individual variations in diversity can be correlated to well-known biotic or abiotic events throughout the Neogene for both groups, the patterns are clearly different, especially during periods of climatic change, as observed during the Late Miocene. During this period of climatic change, the ungulate communities usually showing more stability actually present a lower adaptability, with only few families succeeding to diversify at the expense of the others. Three observations can be made following our results: (1) the diversity dynamics of rodents can be coined as an "evolutionary flexibility" as opposed to a somewhat "evolutionary inertia" for ungulates. (2) The simple comparison of our results with the processes known to regulate the population dynamics of both extant ungulates and rodents confirms the implication of life-history traits in evolutionary processes but also calls for a strong implication in long-term community structuring and broad-scale diversity control. (3) In order to explain these different patterns between both datasets, we assume that the environmental context plays a differential role in structuring the herbivorous mammal assemblages depending on their size; large herbivorous mammal communities being favored in periods of relative climatic stability when only limited environmental perturbations occur, whereas small herbivorous mammals seem to adapt more successfully under deep long-termed climatic changes.

Concerning the untangling processes driving the structure of broad-scale mammalian assemblages, more synthetic comprehensive studies analyzing fossil mammals diversity dynamics in the light of their extant relatives' life-history traits are needed in the future to better understand the overall evolutionary history of mammals and its relationships to paleoenvironmental changes. In order to tackle this question, further studies based on other groups (e.g., Erinaceomorpha, Soricomorpha, Carnivora) will be necessary to test the inferences made here on the diversity dynamics of primary plant eaters.

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