Diversity of mammals in the Neogene of Europe: Comparing data quality of large and small mammals in the NOW database*

Pablo Peláez-Campomanes[1] & Albert J. van der Meulen[2]

[1]*Department of Paleobiology, National Museum of Natural History, CSIC, c/José Gutierrez Abascal 2, Madrid 28006, Spain*
e-mail: mcnp177@mncn.csic.es
[2]*Faculty of Earth Sciences, Utrecht University, Budapestlaan 4, 3584 CD Utrecht, the Netherlands*
e-mail: avermeul@geo.uu.nl

ABSTRACT: This work intends to analyze the effects of the differences in nature between small and large mammal records for paleoecological studies using the Neogene of the Old World Database (NOW). Several variables at generic taxonomic level and MN unit as temporal scale have been used for the diversity comparisons. The results obtained indicate the necessity to evaluate the database quality used, in order to avoid artificial results and interpretations resulting from insufficient and/or heterogeneous data through time and space. Our evaluation of the NOW database seems to indicate, that the set of localities included represent a heterogeneous sampling for large mammals while homogeneous for small mammal (except for MN12).
Key-words: *mammals, Neogene of the Old World Database (NOW), Europe.*

ΠΕΡΙΛΗΨΗ: Η εργασία αυτή έχει σκοπό την ανάλυση της επίπτωσης των διαφορών μεταξύ του αρχείου μικρών και μεγάλων θηλαστικών στις παλαιο-οικολογικές μελέτες με την χρήση της Βάσης Δεδομένων του Νεογενούς του Παλαιού Κόσμου. Για της συγκρίσεις ποικιλότητας χρησιμοποιήθηκαν πολλές παράμετροι σε επίπεδο γένους καθώς και μονάδες MN σε χρονική κλίμακα. Τα αποτελέσματα δείχνουν ότι είναι αναγκαία η αποτίμηση της ποιότητα της Βάσης Δεδομένων που χρησιμοποιούμε, ώστε να αποφύγουμε αποτελέσματα και ερμηνείες λόγω ατελειών και ετερογενών πληροφοριών μέσα στον χρόνο και τον χώρο. Η αποτίμησης μας της Βάσης Δεδομένων δείχνει ότι οι θέσεις που περιέχονται εκπροσωπούν ένα ετερογενές δείγμα όσον αφορά τα μεγάλα θηλαστικά ενώ το δείγμα είναι ομογενές για τα μικρά (εκτός της MN12).
Λέξεις-κλειδιά: *Θηλαστικά, Βάση Δεδομένων του Νεογενούς του Παλαιού Κόσμου, Ευρώπη*.

INTRODUCTION

Computers have revolutionized the world of calculation, data storage, and communication (internet). With the NOW (Neogene of the Old World) database, fossil mammal specialists follow this trend. The database, maintained and coordinated at the University of Helsinki by Mikael Fortelius (http://www. helsinki.fi/science/now/) contains information about Eurasian Miocene to Pleistocene land mammal taxa and localities. Several publications (see the website) have used the database, and it played a central role in the ESF EEDEN project. Of course, it needs constant updating and correction of errors of determination and stratigraphic assignments, to which end an advisory board is responsible. However, in spite of these (relatively few) errors, the database has already generated remarkable and new results, especially after the introduction of the concept of "locality coverage" as a proxy for commonness by JERNVAL & FORTELIUS (2004).

FORTELIUS *et al*. (1996) published the first paleobiological synthesis of late Miocene large and small mammals using the combined Karlsruhe (rodents and insectivores) and NOW (large mammals) databases. They thoroughly discussed the general problem of sampling bias (e.g. correlation between number of taxa and localities) and investigated the data-sampling quality (with completeness indices), but did not analyse the effects of the differences in nature between micro- and macromammal data. The latter analysis is the subject of this paper, in order to evaluate differences of taxon richness (either counts or indexes) between large and small mammals. We specifically address the consistency and uniformity of the data of the two categories throughout the successive MN units.

MATERIAL AND METHODS

We use NOW database, version 030717, the interval MN 3-MN 16, and the European localities west of 20 degrees longitude. This subset contains 589 localities, and the number of taxon-locality occurrences is 5654. Genera rather than species are employed to measure richness and diversity, because there exists supposedly more consensus on genus assignments than on species determinations, for which, in addition, open nomenclature may have been

* Ποικιλότητα των θηλαστικών του Νεογενούς της Ευρώπης: Σύγκριση της ποιότητας των δεδομένων μικρών και μεγάλων θηλαστικών στη Βάση Δεδομένων του Νεογενούς του Παλαιού Κόσμου

used. In addition, for this analysis we have used only the land mammals (excluding marine mammals and Chiroptera). The basic data used are:

1) number of localities per MN unit (**Nloc**),
2) average number of genera per locality per MN unit (**Ngenloc**),
3) number of genera per MN unit (**Ngen**),
4) genus occurrences per MN unit (**Occ**), and
5) age determination in terms of MN units (**MNspan**).

For the study of the mammal diversity of the western European Miocene we have set the temporal scale at MN units, following earlier studies. Given that we want to compare species counts from the different MN units, we distinguish between two sources of sampling heterogeneity. The first one is the sampling effort at each locality (the better sampled a locality is, the higher the number of taxa occurrences), and the second is the number of samples per MN (i.e. the number of localities sampled in each MN unit).

Estimates on the number of genera present at any given time slice are thwarted by the fact, that neither the number of localities nor the number of specimens are equivalent between the MN units. Thus, biodiversity results could be no more than the reflection of sampling effort. To avoid this undesirable correlation one needs to transform the raw data either to standardized counts (e.g. by means of the rarefaction techniques), or to indexes insensitive to variations in sample size (e.g. Fisher alpha). The rarefaction method proposed by (SANDERS, 1968) and corrected by (HURLBERT, 1971) allows the reduction of samples of different sizes to an equal smaller one, based on the relative abundances of the taxa. It assumes that the abundance distributions are similar in all studied samples, which may not be the case when one compares assemblages produced under different taphonomic conditions, and/or originated from different periods or geographic areas (DAAMS *et al*., 1999c; TIPPER, 1979). Nevertheless, while it is true that the use of rarefaction methods as a tool to compare species counts has its problems, it is a powerful method to analyze taxon diversity (richness and relative abundances) (OLSZEWSKI, 2004).

Data on relative abundances of taxa (needed for diversity measures) are not available for many of the studied localities, either because they have not been recorded or, because they are not comparable due to different sampling methods (especially important when using data on small and large mammals together). Only in studies at local scale with a priori isotaphonomic conditions and focused on restricted taxonomical groups, relative abundances may be reliable (DAAMS *et al*., 1999c). To remedy the lack of data on relative abundances for taxa from the Miocene of Western Europe, we follow JERNVALL & FORTELIUS (2004) using taxa occurrence as a proxy (=locality coverage). They assume a positive abundance-occupancy correlation, regardless of the existence of underlying biological causes behind this correlation (GASTON, 2000; HARTE *et al*., 2001; HARTLEY, 1998; WRIGHT, 1991). JERNVALL & FORTELIUS (2004), who studied Neogene large mammals only, calculated locality coverage as the proportion of the total number of fossil localities that are occupied by a taxon. Here, studying both large and small mammals, we follow the same procedure using total locality numbers per mammal category. A taxon that occurs in 30 out of 50 possible localities has a standard occurrence (**Sdocc**) (= locality coverage, occupancy) of 60. In this way we avoid differences in frequencies due to differences in number of sampling units (localities). Once the standard occurrences have been calculated, and assuming the positive correlation between abundance and occupancy, we calculate the distribution of relative abundances for each of our temporal units (Fig. 1).

RESULTS

Taxonomic richness

Richness indexes: Several richness indexes have been proposed (PEET, 1974), but for each of them we have to assume that all our samples show a similar and known species/specimens relationship, which *a priori* may not be the case (see above). According to (BUZAS *et al*., 1982) the number of species and the number of occurrences fit a log series distribution. Therefore, for our study Fisher's *alpha* is considered to be the most adequate richness index. Table 1 shows the results for some of the richness indexes calculated with the PAST program using the actual and standard occurrences

Taxon counts: Fig. 2 shows the calculated rarefaction curves for all mammals, large mammals and small mammals from each MN unit. It shows both the expected richness for a given sample size and the relative abundances per MN unit. Comparing, for example, the curves for MN 10 and MN 13 (Fig. 2A), it appears, that both have a similar number of species for a sample of 1200 specimens, while for smaller samples the richness of MN 10 is much higher. The explanation of this phenomenon is that the sample from MN 10 shows a more even relative-abundance distribution (fewer taxa with high and very low abundances, see histogram of Fig. 1) than that of MN 13. Figure 2 also shows that the relative richness among MN units does not change significantly for samples of more than 500 specimens, and that most of the curves have zero slope around sample size of 1000. To compare the taxon counts obtained by rarefaction techniques for each of the tree mammals categories studied, we have chosen a sample size of 800 for the whole land-mammal fauna, and of 400 for small and large mammals, since they are the maximum number of standard occurrences in some of the MN units. In addition, the rarified counts have been compared in figure 3 with the Fisher alpha index calculated also for each of the three groups.

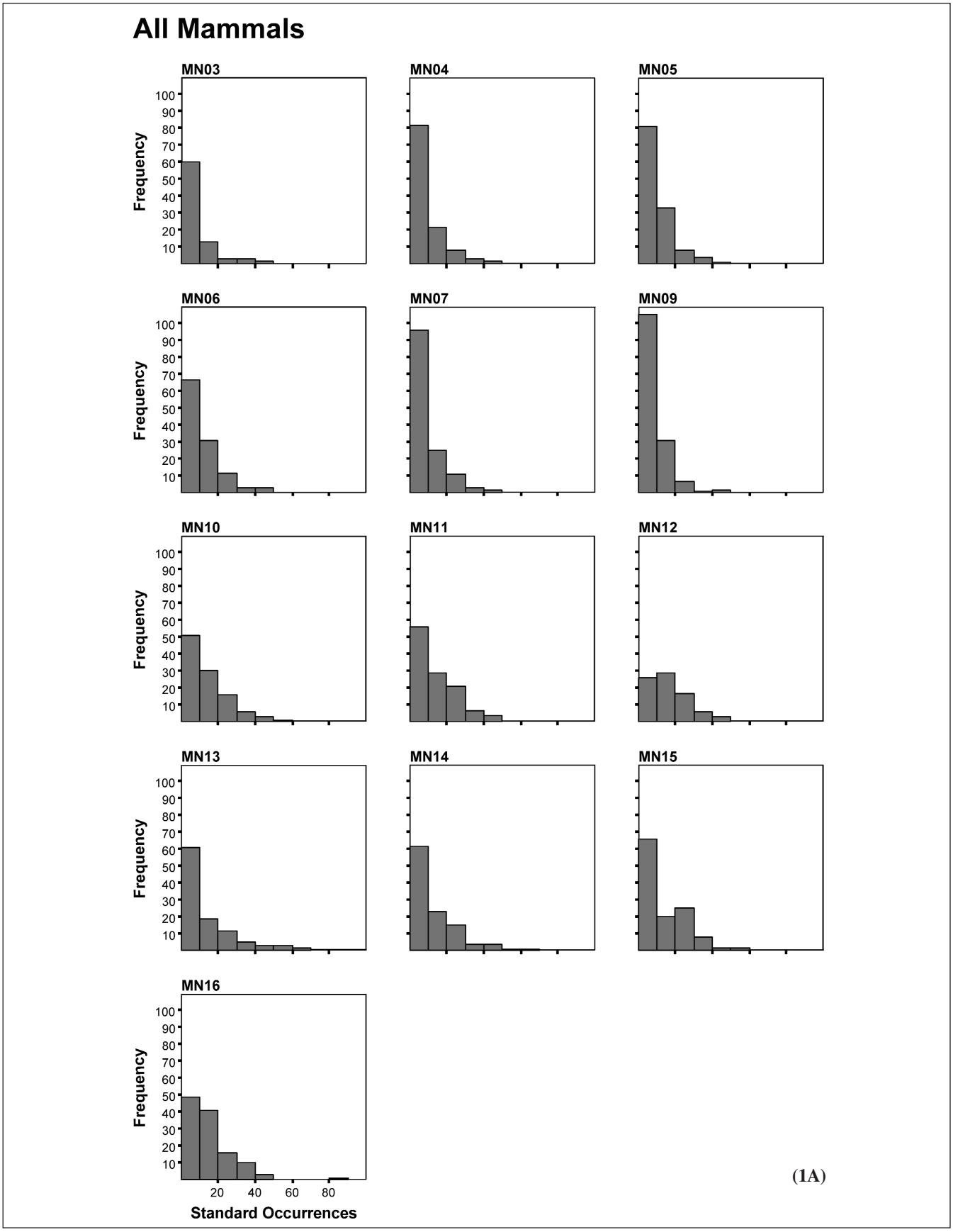
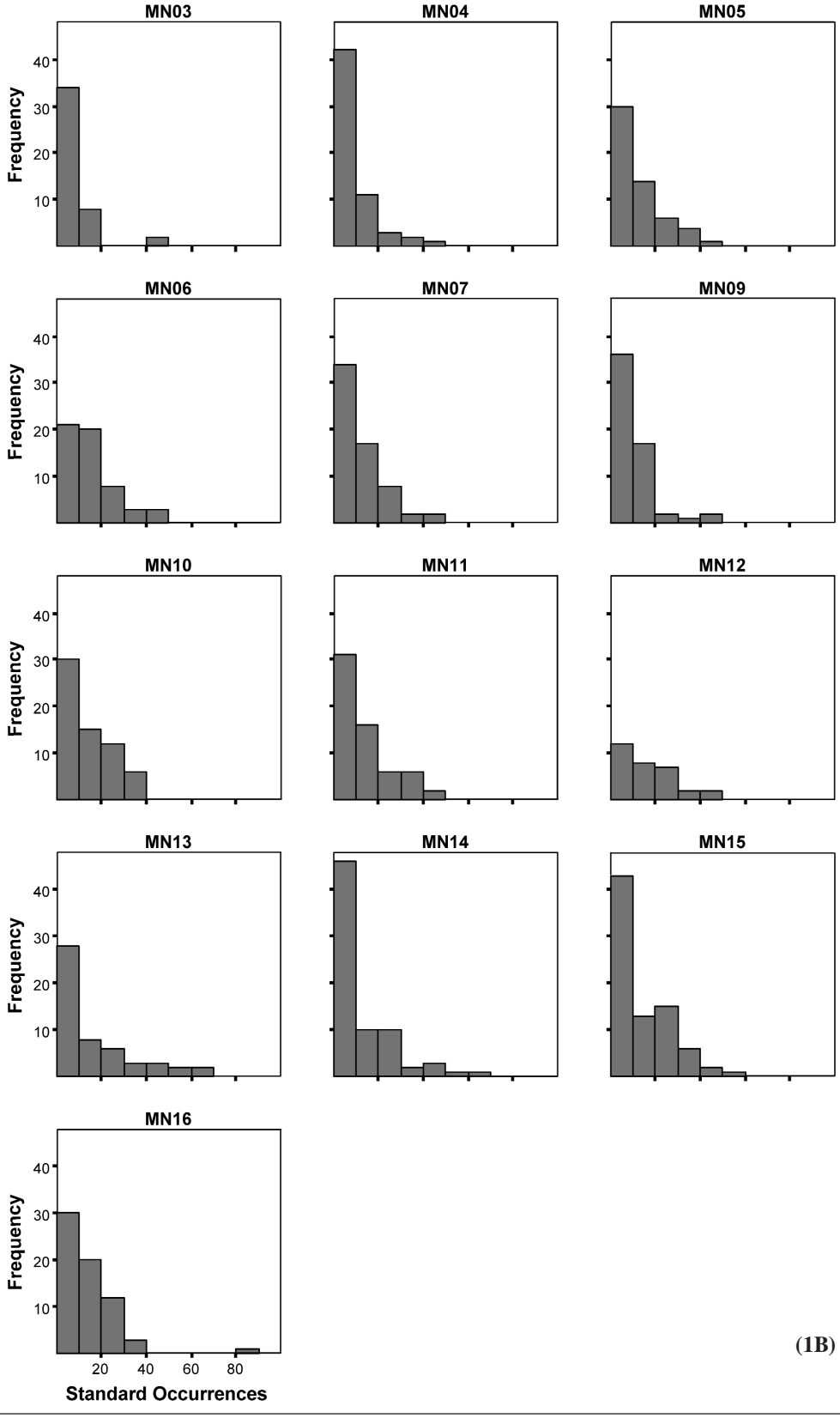
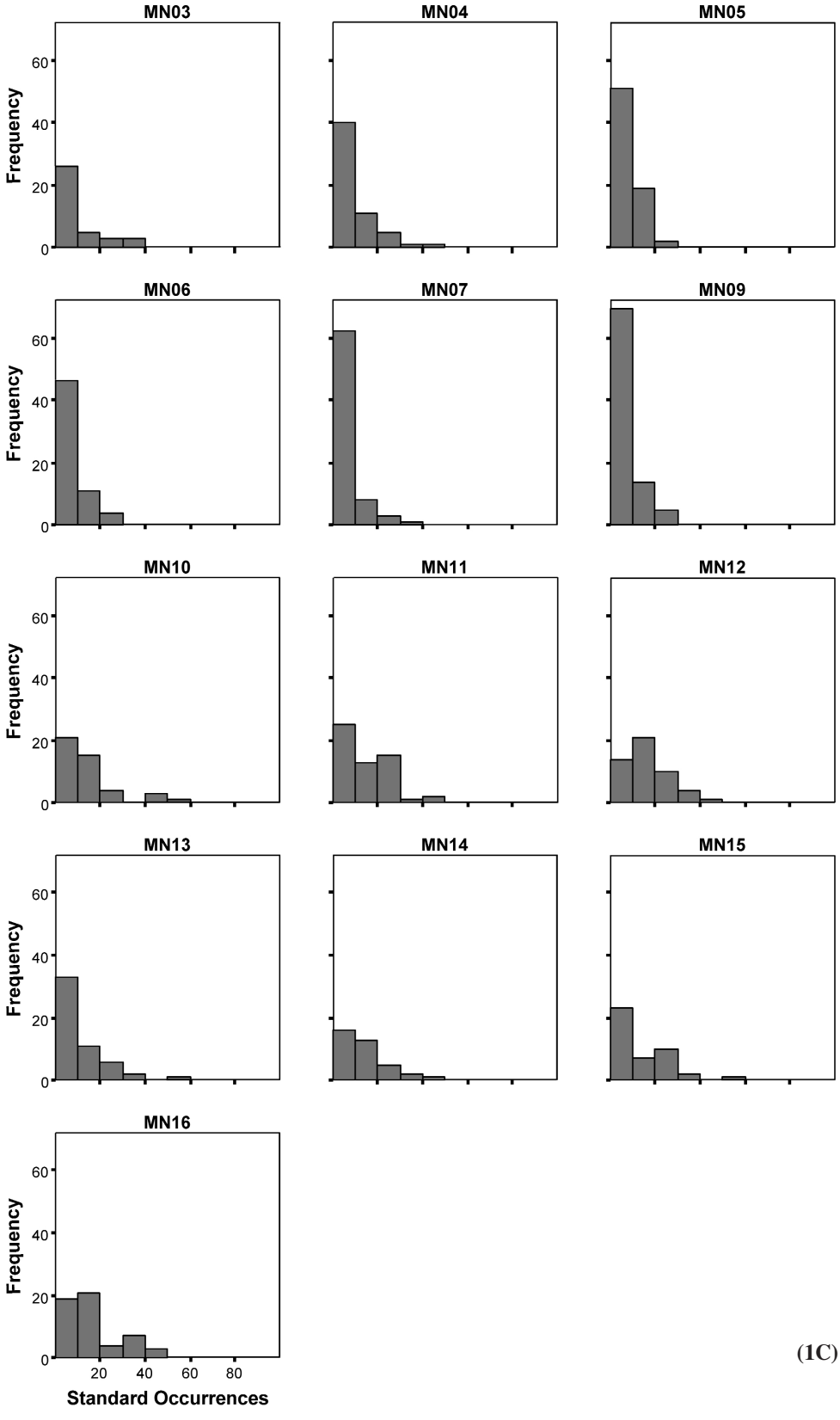


Fig. 1. Histograms showing the variation of the standard occurrences per MN unit for all land mammals (1A), large mammals (1B), and small mammals (1C). See text for further explanation.


Small Mammals
MN03
MN04
MN05
MN06
MN07
MN09
MN10
MN11
MN12
MN13
MN14
MN15
MN16
Frequency
10
20
30
40
20
40
60
80
Standard Occurrences

(1B)


Large Mammals
MN03
MN04
MN05
MN06
MN07
MN09
MN10
MN11
MN12
MN13
MN14
MN15
MN16
Frequency
0
20
40
60
20
40
60
80
Standard Occurrences

(1C)

The taxonomic richness per MN unit of all land-mammal taxa shows a first small drop at MN 6, and two later strong drops at MN 10 and MN 12 (Fig. 3). Several *ad hoc* hypotheses could be proposed to explain the observed pattern such as:

1) the decrease observed at MN 6 may be related to the climatic changes occurred during MN 5 (mid-Miocene cooling event at the end of the middle Aragonian). DAAMS *et al*. (1999c) indicated a significant local change in community composition in this period;
2) the low richness in MN 10 may be interpreted as the result of the mid-Vallesian crisis occurring around that period (AGUSTÍ & MOYÀ-SOLÀ, 1990; CASANOVAS-VILAR *et al*., 2005).
3) the low diversity of MN 12 may be due to sampling bias, since the localities MN unit are more restricted geographically. Thus its low diversity could be the result of a smaller area (and/or a lower number of habitats) sampled.

The independent analysis of small and large mammals

TABLE 1
Calculated Fisher's alpha diversity index for each MN unit, using the standard occurrences (occurrences per 100 localities).

		Standard Occurrences (All taxa)	
	Nbr. of Taxa	Strd. Occur.	Fisher Alpha
MN 16	120	1861	28.65
MN 15	123	2035	28.79
MN 14	110	1478	27.48
MN 13	105	1407	26.25
MN 12	81	1244	19.39
MN 11	117	1740	28.29
MN 10	107	1610	25.78
MN 9	146	1148	44.36
MN 7+8	137	1287	38.79
MN 6	116	1269	31.07
MN 5	127	1146	36.52
MN 4	117	1128	32.81
MN 3	81	781	22.71
		Standard Occurrences (Large Mammals)	
	Nbr. of Taxa	Strd. Occur.	Fisher Alpha
MN 16	54	912	12.56
MN 15	43	730	9.99
MN 14	37	469	9.42
MN 13	53	576	14.23
MN 12	50	756	12.03
MN 11	56	848	13.47
MN 10	44	620	10.82
MN 9	88	585	28.75
MN 7+8	74	455	25.06
MN 6	61	503	18.18
MN 5	72	547	22.19
MN 4	58	544	16.43
MN 3	37	407	9.89
		Standard Occurrences (Small Mammals)	
	Nbr. of Taxa	Strd. Occur.	Fisher Alpha
MN 16	66	948	16.14
MN 15	80	1305	18.81
MN 14	73	1009	18.07
MN 13	52	831	12.30
MN 12	31	488	7.37
MN 11	61	892	14.83
MN 10	63	990	14.98
MN 9	58	563	16.22
MN 7+8	63	832	15.82
MN 6	55	766	13.58
MN 5	55	599	14.75
MN 4	59	584	16.38
MN 3	44	375	12.94

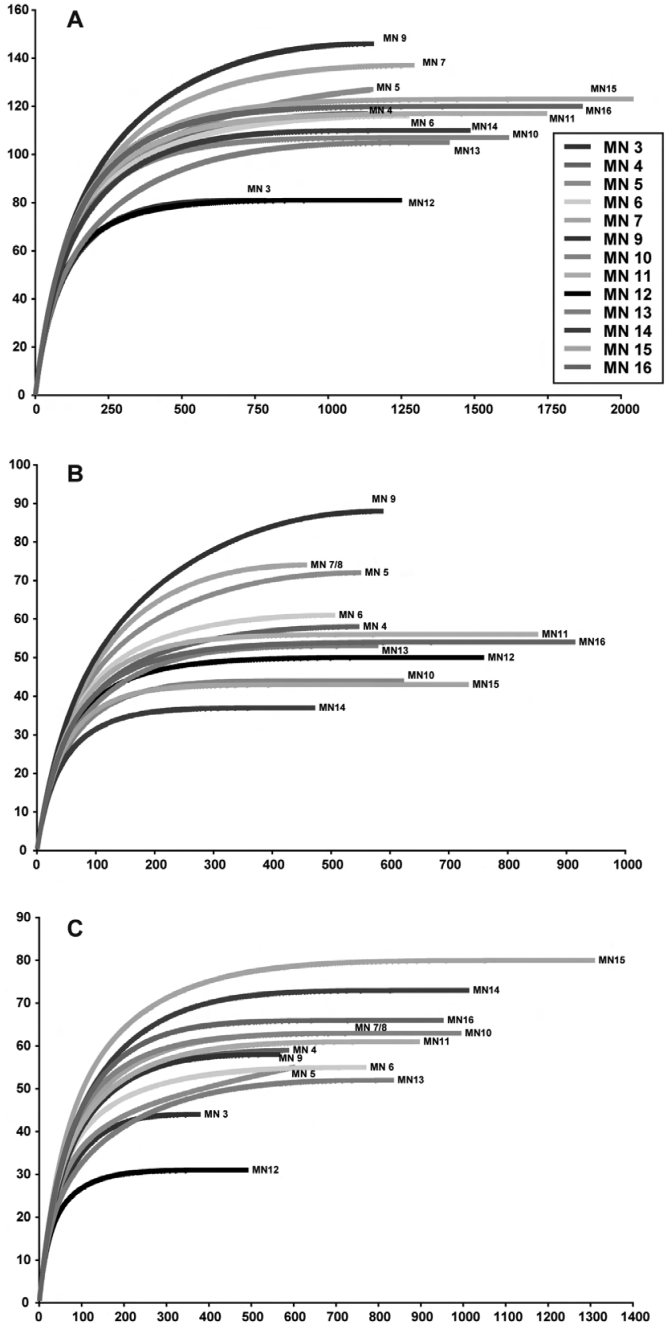


Fig. 2. Calculated rarefaction curves for all mammals (2A), large mammals (2B), and small mammals (2C) per MN unit. See text for further explanation.

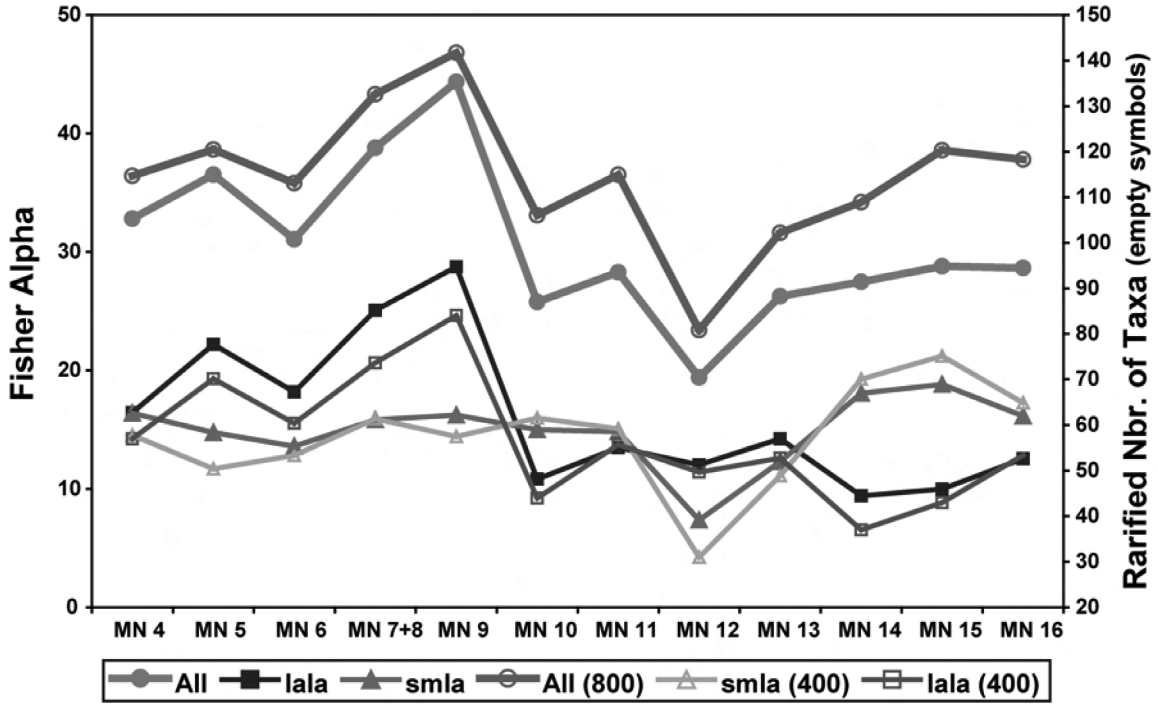


Fig. 3. Genus richness (rarified) and diversity (Fischer Alpha) for all mammals (All), large mammals (lala), and small mammals (smla) per MN unit. See text for further explanation.

(Fig. 3) shows that the richness pattern of large mammals contributes strongly to the pattern of all mammals between MN 4 and MN 11, while the small mammals contribute strongly to the pattern between MN 12 and MN 16. Large mammals show higher diversity during Aragonian and early Vallesian while the small mammals during the Ruscinian and Villafranchian.

In order to check the consistency of those patters one has to study the relationships of the number of genera per MN unit with other factors, as discussed before. We will focus mainly on the relationship between number of genera per MN unit (Ngen), number of localities (Nloc) and number of genera per locality (Ngenloc).

The number of genera per locality depends on two main factors: a) the sampling effort at the locality, and b) the local diversity of the fossil assemblage (alpha diversity). In order to determine which of the two is the main factor influencing Ngen, we will compare Ngenloc, mean number of genera per locality per MN unit (separately for large and small mammals), with **Ngenloc>5**, the mean number of genera per locality considering only localities in which there are at least five genera, and with **Maxgenlo**c, the maximum number of genera recorded in one locality per MN unit. We use Ngenloc>5 as a means to investigate sampling effort at the localities, because poorly sampled localities and isolated finds are excluded. Our working hypothesis is that Ngenloc, Ngenloc>5 and Maxgenloc must be correlated, if the main factor determining the variation in Ngenloc among MN units is local diversity. No correlation amongst them is expected if the sampling effort varies between MN units affecting Ngenloc of each MN unit in a different way.

Ngen versus Nloc (Fig. 4)

There is no clear relationship between Ngen of all mammals and Nloc ($p=0.058$), no relationship at all between Ngen of small mammals and Nloc ($p=0.55$), while Ngen of large mammals and Nloc are significantly correlated ($p<0.01$). The latter relationship indicates that the metacommunity sampling effort (as the number of localities sampled per MN unit) may be considered as a main factor driving the observed large-mammal richness (particularly for the period between MN 3 to MN 10). Thus, the sampling for large and small mammals, as recorded in the NOW database, is not equivalent implying, that the richness pattern for all mammals probably depends more on the proportion of localities of the two subcategories than on environmental conditions.

Ngen versus Ngenloc (Fig. 5)

Ngen of the small mammals is significantly correlated with Ngenloc ($p< 0.001$), while for the large mammals Ngen and Ngenloc are correlated ($p< 0.012$) from MN 10 till MN 16 only.

Table 2 shows the calculated Pearson correlation coefficient for large and small mammals. As regards the large

mammals, Ngenloc is neither correlated with Ngenloc>5 nor with Maxgenloc. As pointed out above, Ngen is correlated with Nloc, and the latter is also correlated with Maxgenloc (p=0.002). Therefore, the large mammal record seems to be biased by the sampling effort at the

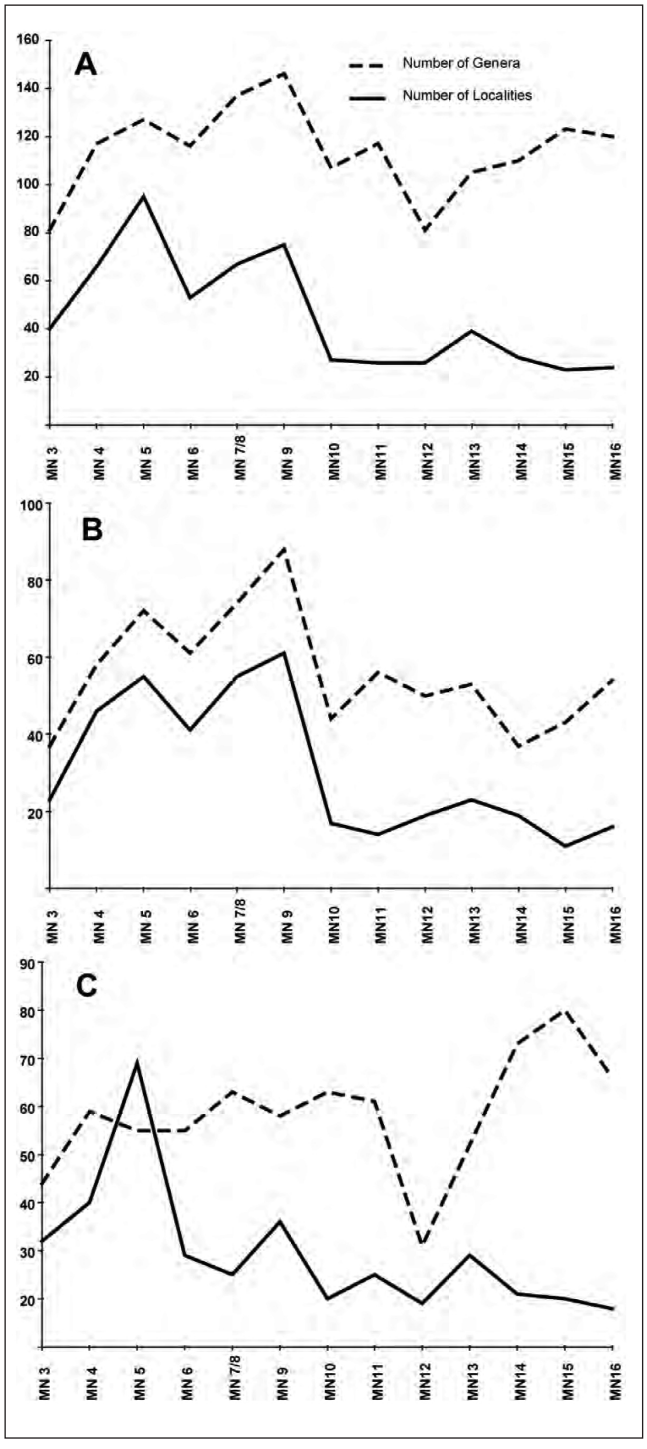


Fig. 4. Comparisons between genus richness and number of localities per MN unit for all mammals (4A), large mammals (4B), and small mammals (4C). See text for further explanation.

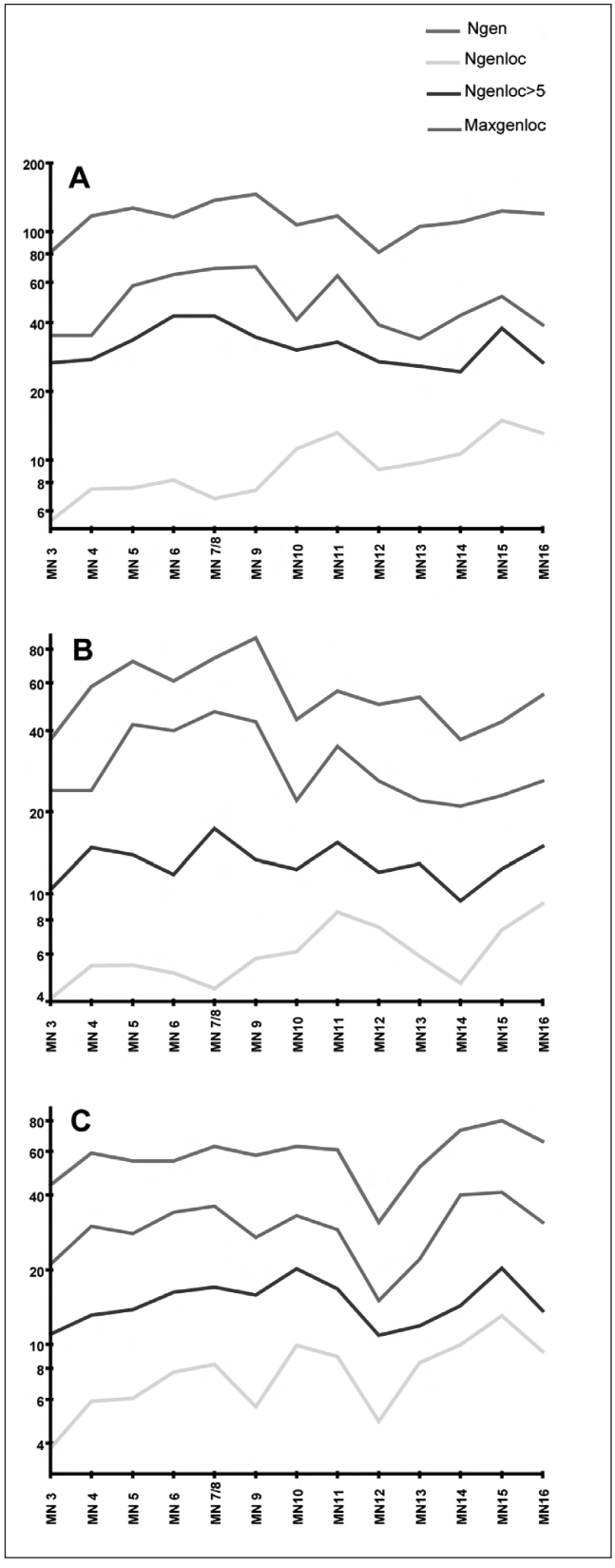


Fig. 5. Comparisons between average number of genera per MN unit (Ngen), average number of genera per locality, per MN unit (Ngenloc), idem for localities with five or more genera (Ngenloc>5), idem for localities with highest number of genera (Maxgenloc); all mammals (5A), large mammals (5B), and small mammals (5C).

TABLE 2
Pearson correlations.

All Mammals		**Ngen**	**Nloc**	**Ngenloc**	**Ngenloc>5**	**Maxgenloc**
Ngen	Pearson Correlation	**1**	**0.538**	**0.073**	**0.580**	**0.723**
	Sig. (2-tailed)	.	0.058	0.813	0.038	0.005
	N	13	13	13	13	13
Nloc	Pearson Correlation	**0.538**	**1**	**-0.692**	**0.372**	**0.457**
	Sig. (2-tailed)	0.058	.	0.009	0.211	0.116
	N	13	13	13	13	13
Ngenloc	Pearson Correlation	**0.073**	**-0.692**	**1**	**-0.075**	**-0.077**
	Sig. (2-tailed)	0.813	0.009	.	0.807	0.802
	N	13	13	13	13	13
Ngenloc>5	Pearson Correlation	**0.580**	**0.372**	**-0.075**	**1**	**0.833**
	Sig. (2-tailed)	0.038	0.211	0.807	.	0.000
	N	13	13	13	13	13
Maxgenloc	Pearson Correlation	**0.723**	**0.457**	**-0.077**	**0.833**	**1**
	Sig. (2-tailed)	0.005	0.116	0.802	0.000	.
	N	13	13	13	13	13
Large Mammals		**Ngen**	**Nloc**	**Ngenloc**	**Ngenloc>5**	**Maxgenloc**
Ngen	Pearson Correlation	**1**	**0.857**	**-0.078**	**0.615**	**0.861**
	Sig. (2-tailed)	.	0.000	0.800	0.025	0.000
	N	13	13	13	13	13
Nloc	Pearson Correlation	**0.857**	**1**	**-0.528**	**0.390**	**0.773**
	Sig. (2-tailed)	0.000	.	0.063	0.187	0.002
	N	13	13	13	13	13
Ngenloc	Pearson Correlation	**-0.078**	**-0.528**	**1**	**0.296**	**-0.188**
	Sig. (2-tailed)	0.800	0.063	.	0.326	0.537
	N	13	13	13	13	13
Ngenloc>5	Pearson Correlation	**0.615**	**0.390**	**0.296**	**1**	**0.545**
	Sig. (2-tailed)	0.025	0.187	0.326	.	0.054
	N	13	13	13	13	13
Maxgenloc	Pearson Correlation	**0.861**	**0.773**	**-0.188**	**0.545**	**1**
	Sig. (2-tailed)	0	0.002	0.537	0.054	.
	N	13	13	13	13	13
Small Mammals		**Ngen**	**Nloc**	**Ngenloc**	**Ngenloc>5**	**Maxgenloc**
Ngen	Pearson Correlation	**1**	**-0.182**	**0.833**	**0.705**	**0.926**
	Sig. (2-tailed)	.	0.553	0	0.007	0
	N	13	13	13	13	13
Nloc	Pearson Correlation	**-0.182**	**1**	**-0.471**	**-0.238**	**-0.174**
	Sig. (2-tailed)	0.553		0.104	0.434	0.569
	N	13	13	13	13	13
Ngenloc	Pearson Correlation	**0.833**	**-0.471**	**1**	**0.725**	**0.767**
	Sig. (2-tailed)	0	0.104	.	0.005	0.002
	N	13	13	13	13	13
Ngenloc>5	Pearson Correlation	**0.705**	**-0.238**	**0.725**	**1**	**0.737**
	Sig. (2-tailed)	0.007	0.434	0.005	.	0.004
	N	13	13	13	13	13
Maxgenloc	Pearson Correlation	**0.926**	**-0.174**	**0.767**	**0.737**	**1**
	Sig. (2-tailed)	0.000	0.569	0.002	0.004	.
	N	13	13	13	13	13

metacommunity level, as well as at the locality level. In order to eliminate the bias due to the number of localities sampled we have performed partial correlations controlling for Nloc (Table 3). It appears, that Ngen is strongly correlated to Ngenloc ($p<0.01$), while the correlation coefficients with Ngenloc>5 and Maxgenloc are lower. In addition we see a change in the significance of the correlation between Ngen and Maxgenloc, being signifi cantly lower than when controlled by Nloc, thus indicating that the correlation observed in table 2 is artificially high. In conclusion, we propose that for large mammals the main factor affecting Ngenloc is the sampling effort, rather than the actual alpha diversity of the localities.

Ngenloc, Ngenloc5 and Maxgenloc of the small mammals, on the contrary, show significant correlations amongst each other. We assume, therefore, that bias due to sampling effort is not the main factor affecting Ngenloc. Instead we think that local diversity (alpha diversity) is the main factor determining Ngenloc, and thus the values of Ngen (gamma diversity). This is confirmed by the coefficients of partial correlations controlling for Nloc (Table 3): they are similar to the zero order correlations indicating that there is no influence of Nloc on the correlations among the studied variables.

TABLE 3
Partial correlations controlling for number of localities (Nloc).

All Mammals				
	Ngen	**Ngenloc**	**Ngenloc>5**	**Maxgenloc**
Ngen	1	0.732	0.485	0.636
		10	10	10
		0.007	0.110	0.026
Ngenloc	0.732	1	0.272	0.373
	10		10	10
	0.007		0.393	0.232
Ngenloc>5	0.485	0.272	1	00.802
	10	10		10
	0.110	0.393		0.002
Maxgenloc	0.636	0.373	0.802	1
	10	10	10	
	0.026	0.232	0.002	
Large Mammals				
	Ngen	**Ngenloc**	**Ngenloc>5**	**Maxgenloc**
Ngen	1	0.855	0.592	0.609
		10	10	10
		0.000	0.043	0.036
Ngenloc	0.855	1	0.643	0.408
	10		10	10
	0.000		0.024	0.188
Ngenloc>5	0.592	0.643	1	0.416
	10	10		10
	0.043	0.024		0.178
Maxgenloc	0.609	0.408	0.416	1
	10	10	10	
	0.036	0.188	0.178	
Small Mammals				
	Ngen	**Ngenloc**	**Ngenloc>5**	**Maxgenloc**
Ngen	1	0.861	0.693	0.923
		10	10	10
		0.000	0.013	0.000
Ngenloc	0.861	1	0.716	0.789
	10		10	10
	0.000		0.009	0.002
Ngenloc>5	0.693	0.716	1	0.727
	10	10		10
	0.013	0.009		0.007
Maxgenloc	0.923	0.789	0.727	1
	10	10	10	
	0.000	0.002	0.007	

CONCLUSIONS

The main conclusion obtained with this analysis is the necessity of evaluation of the quality of the database used, in order to avoid artificial results and interpretations resulting from insufficient and/or heterogeneous data through time and space.

Our evaluation of the NOW database seems to indicate, that the set of localities included does not represent an homogeneous sampling for large mammals. On the other hand, the small mammal database is homogeneous (except for MN 12). We do not wish to imply that any part of the database is better than the other, we only demonstrated that paleoecological studies, using the NOW database including the large mammals, should be carried out with caution since some results could be artifacts due to the unbalanced sampling through time.

ACKNOWLEDGEMENTS

We acknowledge the ESF for participation in the EEDEN project. We thank M. Fortelius for fruitful discussions on, and the use of the NOW database. This work was partly funded by the Spanish projects GL2007-65208, CGL2008-04200/BTE.

REFERENCES

AGUSTÌ, J. & S. MOYÀ-SOLÀ (1990). Mammal extinctions in the Vallesian (Upper Miocene). *Lecture Notes in Earth Sciences*, Springer-Verlag, Germany, 30, 425-432.

BUZAS, M.A., KOCH, C.F., CULVER, S.J. & N.F. SOHL (1982). On the Distribution of Species Occurrence. *Paleobiology*, 8(2), 143-150.

CASANOVAS-VILAR, I., MOYÀ-SOLÀ, S. AGUSTÌ, J. & M. KÖHLER (2005). The geography of a faunal turnover: tracking the Vallesian Crisis. *In:* ELEWA, A. (*Ed*.), *Migration in organisms: climatology, geography, ecoology*, Springer-Verlag Publishers, Heidelberg, 247-301.

DAAMS, R., ALCALA, L., ÁLVAREZ-SIERRA, M.A., AZANZA, B., DAM, J.A. VAN, MEULEN, A.J. VAN DER, MORALES, J., NIETO, M., PELÁEZ-CAMPOMANES, P. & D. SORIA (1998). A stratigraphical framework for Miocene (MN 4-MN 13) continental sediments of Central Spain. *Comptes Rendus de L' Academie Des Sciences Serie Ii Fascicule a-Sciences De La Terre Et Des Planetes*, 327(9), 625-631.

DAAMS, R., MEULEN, A.J. VAN DER., ÁLVAREZ-SIERRA, M.A., PELAEZ-CAMPOMANES, P., CALVO, J.P., ALONSO ZARZA, M.A. & W. KRIJGSMAN (1999a). Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North-Central Spain). *Newsletters on Stratigraphy*, 37(3), 103-139.

DAAMS, R., MEULEN, A.J. VAN DER, ÁLVAREZ-SIERRA, M.A., PELÁEZ-CAMPOMANES, P. & W. KRIJGSMAN (1999b). Aragonian stratigraphy reconsidered, and a re-evaluation of the middle Miocene mammal biochronology in Europe. *Earth and Planetary Science Letters*, 165, 287-294.

DAAMS, R., MEULEN, A.J. VAN DER, PELÁEZ-CAMPOMANES, P. & M.A. ÁLVAREZ-SIERRA (1999c). Trends in rodent assemblages from the Aragonian (Early Middle Miocene) of the Calatayud-Daroca Basin (Aragón, Spain). *In:*

AGUSTÌ, J., ROOK L. & P. ANDREWS (*Eds*), *Hominoid Evolution and Climate Change in Europe. 1 The Evolution of Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, 127-139 pp.

DAAMS, R., MEULEN, A.J. VAN DER, ÁLVAREZ-SIERRA, M.A., PELÁEZ-CAMPOMANES, P. & W. KRIJGSMAN (1999d). Aragonian stratigraphy reconsidered, and a re-evaluation of the middle Miocene mammal biochronology in Europe. *Earth and Planetary Science Letters*, 165(3-4), 287-294.

FOOTE, M. (2000). Origination and extinction components of taxonomic diversity: general problems. *Paleobiology*, 26(4), 74-102.

GASTON, K. (2000). Global patterns in biodiversity. *Nature*, 405, 220-227.

HARTE, J., BLACKBURN, T. & A. OSTLING (2001). Self-similarity and the relationship between abundance and range size. *American Naturalist*, 157(4), 374-386.

HARTLEY, S. (1998). A positive relationship between local abundance and regional occupancy is almost inevitable (but not all positive relationships are the same). *Journal of Animal Ecology*, 67(6), 992-994.

HURLBERT, S. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, 52(4), 577-586.

JERNVALL, J. & M. FORTELIUS (2004). Maintenance of trophic structure in fossil mammal communities: Site occupancy and taxon resilience. *American Naturalist*, 164(5), 614-624.

OLSZEWSKI, T.D. (2004). A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos*, 104(2), 377-387.

PEET, R.K. (1974). The measurement of species diversity. *Annual Review of Ecology and Systematic*, 5, 285-307.

SANDERS, H.I. (1968). Marine benthic diversity: a comparative study. *American Naturalist*, 102, 243-282.

TIPPER, J. (1979). Rarefaction and rarefiction-the use and abuse of a method in paleoecology. *Paleobiology*, 5(4), 423-434.

TUKEY, J.W. (1962). The Future of Data Analysis. *The Annals of Mathematical Statistics*, 33(1), 1-67.

WRIGHT, D.H. (1991). Correlations between Incidence and Abundance Are Expected by Chance. *Journal of Biogeography*, 18(4), 463-466.