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Journal of Biogeography (J. Biogeogr.) (2010) **37**, 1079–1093

SPECIAL ISSUE

The European Far West: Miocene mammal isolation, diversity and turnover in the Iberian Peninsula

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ABSTRACT

Aim To analyse the diversity dynamics of Miocene mammalian faunas in the Iberian Peninsula in order to determine whether the patterns are related to the dispersal of taxa from other areas into this region.

Location Mainly the Iberian Peninsula, but two close geographical areas (Central Europe and the Eastern Mediterranean) are also considered in some of our calculations.

Methods Genus-level faunal lists for a total of 299 localities from the Iberian Peninsula, covering 10 successive biochronological units [Mammal Neogene (MN) zones] that span from the latest Early Miocene to the early Pliocene (about 17–4 Ma), were compiled. The dataset was expanded with a further 331 localities in Central Europe and the Eastern Mediterranean for the same time span. Next, a taxonomically standardized database was used to create composite faunal lists of micro- and macromammalian genera present during each MN zone. Separate genera-by-MN-zone matrices for both micro- and macromammals were built for each region. Mean standing diversity as well as origination and extinction rates were calculated for the Iberian Peninsula, and their correlation with preservation rates is discussed. Simpson's coefficient of faunal similarity with Central Europe and the Eastern Mediterranean was calculated in order to evaluate whether diversity patterns were related to changes in the affinity of the Iberian mammalian faunas with those of other regions.

Results Diversity changes in the Iberian macromammalian faunas coincide with periods of increased faunal similarity with other regions, suggesting a relationship to the expansions and contractions of the geographical ranges of the constituent taxa. This pattern is not recognized for micromammals; that is, their diversity trends are not related to changes in geographical ranges.

Main conclusions Climatic shifts result in expansions or contractions in the geographical ranges of macromammals, owing to changes in the distribution of their preferred habitats. The lower dispersal ability of micromammals results in a higher extinction risk when habitat fragmentation confines their populations to relatively small environmental patches. Hence, they are more severely affected by climatic changes. Our results thus emphasize the role of climatic forcing in mammalian biogeography and diversity.

Keywords

Climatic change, diversity, Europe, evolutionary palaeoecology, extinction, geographical range, Iberian Peninsula, Neogene, origination, palaeobiogeography.

www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2010.02286.x

INTRODUCTION

Charles Darwin was one of the first scientists to recognize that geographical patterns not only are the product of agents acting in the present day, but also are the consequence of processes that unfolded during the ancient past. Darwin devoted two chapters of *On the Origin of Species* (Darwin, 1859) to the geographical distribution of organisms. In these chapters he recognized that the differences in the flora and fauna from different regions could not be accounted for by environmental differences alone. As an example, he cited the mammalian faunas from South America, Australia and Africa, which are completely different even though all these continents have regions with similar climates at similar latitudes (Darwin, 1859, p. 349–350). Furthermore, the species found in a particular environment of a given continent are more similar to the species found in other environments of the same continent than they are to the species found in similar environments from other continents. He concluded that 'all the grand leading facts of geographical distribution are explicable on the theory of migration [...] together with subsequent modification and the multiplication of new forms' (Darwin, 1859, p. 408). Darwin was aware that, for a broad analysis of biogeographical patterns, both the temporal and the environmental dimensions must be taken into account. This 'temporal dimension' is provided by the fossil record, which, as Darwin pointed out, was imperfectly known at that time (Darwin, 1859, Chapter IX). The incompleteness of the then-known fossil record may well explain why distinguished contemporaneous palaeontologists, such as Richard Owen, strongly opposed Darwin's evolutionary ideas.

Palaeontology could not be fully reconciled with natural selection and gradualism until the Modern Synthesis of the 1930s and the 1940s. The key palaeontological contribution to the Modern Synthesis was the book *Tempo and Mode in Evolution* by the American palaeontologist George G. Simpson. He clearly demonstrated that natural selection, which many palaeontologists had regarded as a secondary mechanism of evolution, was necessary and sufficient to explain the much longer-term, morphological transformations of skeletal hard parts seen in the fossil record (Simpson, 1944). Simpson was also aware of the contemporaneous achievements of population genetics, so he proposed that the microevolutionary patterns seen at the population level, viewed within an ecological context of these organisms interacting with diversified environments, could account for the macroevolutionary patterns documented by palaeontology.

Today, palaeontologists recognize that the study of evolutionary patterns over long time intervals, when considering an ecological perspective, provides information that is not available to ecologists working with present-day faunas (for some examples see Vermeij, 1977, 1987; Bambach, 1983; Sepkoski & Sheehan, 1983; Vrba, 1985, 1995; Behrensmeyer *et al.*, 1992; Brett & Baird, 1995; Allmon & Bottjer, 2000; DiMichele *et al.*, 2004; Jablonski, 2005; van der Meulen *et al.*, 2005; amongst others). Evolutionary palaeoecology (a term introduced in Valentine, 1973) is an emergent and increasingly popular palaeontological field devoted to the study of these long-term ecological and evolutionary patterns and processes. Obviously, a requirement for any study in evolutionary palaeoecology is a sufficiently well-known fossil record. The latter was lacking when Darwin wrote *On the Origin of Species*, but since then, in some regions, for some taxa, the record has become much more complete. In fact, the availability of data from the fossil record is now such that palaeontologists are faced with a new challenge: they need to recognize patterns in a multitude of data, and be able to explain these patterns in terms of the long-term processes that govern the changes in the biosphere. As a result, palaeontologists are now able to contribute to the study of evolutionary patterns and processes over protracted time intervals.

This paper follows the approach of evolutionary palaeoecology by focusing on the diversity dynamics of Miocene mammalian faunas from the Iberian Peninsula. The Miocene is a crucial epoch, marked by important climatic and physiographic changes. The beginning of the Miocene was characterized by high mean global temperatures, which peaked at the Middle Miocene climatic optimum between 17 and 15 million years ago (Ma) (Zachos *et al.*, 2001). This warm phase was followed by a gradual cooling trend related to the development of Antarctic ice-sheets. The Iberian mammalian record stands out as one of the most complete continental records of the world (Alba *et al.*, 2001) and, therefore, provides a unique opportunity to study how these global changes affected mammalian diversity dynamics. Diversity itself is ultimately regulated by the opposing forces of origination and extinction. In turn, origination has two components (Brown, 1995): *in situ* origination and dispersal. In other words, the diversity of a particular region may increase either because of the evolution of new species locally or as a result of the dispersal of taxa from adjacent areas. Increased speciation rates will obviously result in a more endemic character of the fauna and, therefore, in a decreased faunal similarity with other areas. In contrast, if the incidence of dispersal in diversity dynamics is more important, we would expect a correlation between diversity changes and faunal similarity with other areas. Dispersal may be favoured or made possible by the disappearance of important geographical barriers or simply by the extension of the geographical ranges of taxa owing to climatic changes. As noted above, the Miocene was a time of major climatic changes, which surely affected the geographical ranges of many taxa. As a working hypothesis, we expect that the diversity dynamics of the Iberian Peninsula are determined mostly by the dispersal of taxa from nearby areas as a result of geographical range expansions and contractions. This leads us to make the following testable prediction: if the working hypothesis is correct, then it follows that periods of increased similarity between the Iberian faunas and those from other areas should coincide with times of greater diversity and vice versa. Besides assessing the influence of immigration in the diversity dynamics of the Iberian Peninsula, this study further analyses the tempo and mode of diversity changes, in order to investigate whether they are continuous or whether dramatic turnover pulses sometimes occur.

MATERIALS AND METHODS

Geographical and temporal setting

The studied time span includes 10 Mammal Neogene (MN) zones, from MN4 to MN14, that is, from the latest Early Miocene to the early Pliocene (*c.* 16.6 to 4.2 Ma, after Agustí *et al.*, 2001). We focus on this time interval because it covers the Miocene stepwise global cooling that began just after the Middle Miocene climatic optimum (Zachos *et al.*, 2001). The Mammal Neogene zones were introduced by Mein (1975) as a division of the European Neogene mammalian record based mainly on the association of certain diagnostic mammal taxa. MN zones have been widely used since their definition, with only minor modifications. Recent reviews (Mein, 1999; Agustí *et al.*, 2001) have redefined the MN zones mainly on the basis of the first and/or last occurrence of various mammalian taxa.

Our dataset for the Iberian Peninsula includes 265 micromammal and 94 macromammal localities. The Portuguese record is rather sparse, so most of the localities in our database are from Spain. The records from different Spanish basins are not all of the same quality: for example, the Calatayud-Daroca and Teruel basins (east central Spain) are particularly well sampled, whereas others, such as the Cerdanya basin (Catalan Pyrenees), are not. Furthermore, the micromammal record is much more complete than the macromammal one, and includes more than double the number of sites. This is particularly true in the case of the east central basins (Calatayud-Daroca and Teruel), which proportionally include very few macromammal sites (Alcalá *et al.*, 2000; van Dam *et al.*, 2001). However, this problem is of minor significance in this paper because the faunas from the different basins are lumped together in order to carry out the calculations at the level of the whole Iberian Peninsula. Unfortunately, this masks some biogeographical differences between several Iberian basins, which have been emphasized by some previous studies (Agustí, 1990; Casanovas-Vilar & Agustí, 2007).

In order to evaluate the faunal similarity between the Iberian Peninsula and other regions, we built another database comprising 326 localities from the Mediterranean regions of Europe, including Turkey and extending into Central Europe. The sites from Russia, Belarus and the Baltic countries are excluded because of the paucity of localities and their insufficiently studied faunas. During most of the studied time span, Italy was isolated from mainland Europe and fragmented into different islands that together housed a characteristic endemic mammalian fauna (Moyà-Solà *et al.*, 1999; Rook *et al.*, 1999). We therefore excluded Italy from the calculations because its faunas have very few taxa in common with the other regions until the latest Miocene, when a connection with the European continent was established. For the sake of simplicity, the data from different countries are lumped into three great geographical divisions: the Eastern Mediterranean, Central Europe and the Iberian Peninsula (Fig. 1). This subdivision of Europe is based on what is known of Miocene mammal biogeography. The existence of two distinct provinces occurring synchronously in the Eurasian Miocene was first recognized by Tobien (1967) and has been confirmed by subsequent studies (e.g. Bernor *et al.*, 1979, 1996; Bernor, 1983, 1984; Fortelius *et al.*, 1996; Casanovas-Vilar *et al.*, 2005). Tobien (1967) noted that, during the Late Miocene, a fauna with a prevalent woodland character is recorded in Central Europe, whereas a fauna with a steppe and/or savanna character is recorded in the Eastern Mediterranean. Subsequent studies have shown that this oriental province extended as far as Iran (Bernor *et al.*, 1979; Bernor, 1983, 1984), so it is often referred to as the 'Greek–Iranian' province (de Bonis

Figure 1 Map of the study area. The different shades indicate the main divisions of Europe employed in the analysis: the Iberian Peninsula, Central Europe and the Eastern Mediterranean.

et al., 1992). It has also been shown that this division of Europe into two distinct major biogeographical provinces can also be extended back to the Middle Miocene (Bernor, 1984; Bernor *et al.*, 1996; Fortelius *et al.*, 1996; Casanovas-Vilar *et al.*, 2005). The Late Miocene open-country faunas of the Greek–Iranian province are usually referred to as Pikermian faunas (Crusafont Pairó, 1950; Solounias *et al.*, 1999), after the Turolian site of Pikermi near Athens, one of the richest localities discovered. These faunas are characterized by the dominance and great diversity of antelopes, giraffes and horses, and a scarcity of deer (see, for example, Bernor *et al.*, 1996; Solounias *et al.*, 1999). Such faunas are often treated as a rather uniform mammal community (see, for example, Solounias *et al.*, 1999; Eronen *et al.*, 2009). However, it has been recently proposed (Kostopoulos, 2009) that these 'Pikermian faunas' are an oversimplification, and that two provinces can be recognized in south-eastern Europe during the Late Miocene: Anatolia and the southern Balkans. Although these two areas show clear affinities, the faunal similarity at the species level indicates important differences during particular time intervals (Kostopoulos, 2009). Nevertheless, merging these two bioprovinces in just one Eastern Mediterranean province seems justified in our case, considering the scale of the analysis and the need for simplification of the data outside the study area.

Data preparation

We built a database combining data taken from several publications, and from our own unpublished notes on certain Spanish sites and from the Neogene of the Old World database of fossil mammals (NOW) (Fortelius, 2009). During this process the NOW database was reviewed and some errors were emended; these corrections, as well as our additions, have been submitted to the coordinators of the NOW. Macromammals and micromammals were separated into two databases because in most of the sites they were recovered using different methods (that is, surface excavation for macromammals and screen washing for micromammals). This implies that a given locality containing both macro- and micromammals appears in both databases. Only the localities that included at least five genera (treating macro- and micromammals separately) were selected. Taxa identified at a suprageneric level were not considered to represent an additional genus. Uncertain determinations of genera, such as 'cf. genus', were treated as if these taxa had been confidently identified and, hence, were taken into account. Taxonomy was standardized on the basis of recent reviews (primarily Rössner & Heissig, 1999).

Concerning the localities in the database, synonymies, resulting from the use of different names for the same locality, were removed. We also removed the localities for which the sample was not homogenous, consisting of a mixture of faunas of clearly different ages. Unfortunately, this is a rather common situation in the case of karstic sites and has resulted in the deletion of certain rich localities. As discussed above, the analysis was carried out at the temporal scale of the MN zones, so we have excluded all those localities for which dating at this level was uncertain. The list of localities used to build our raw database is reported in Appendix S1 in Supporting Information.

Composite faunal lists of micro- and macromammals for each geographical region were used to build genera-by-MN-zone matrices (see Appendix S2). The calculations of taxonomic diversity and per-capita rates were carried out on these matrices.

Taxonomic diversity and per-capita rates

Taxonomic diversity measures cannot simply count the total number of taxa present in a given time interval, as this number is affected by several factors, of which the two most important are interval duration and sampling quality. A comparatively better record in a certain time unit will normally imply that many rare taxa are known exclusively from this unit (singletons). The number of singletons will also logically increase with the duration of time units, because the probability of the first and last appearances of a particular taxon occurring within the same unit is directly proportional to the duration of the latter. Accordingly, most metrics of taxonomic diversity correct for the effect of the singletons, sometimes by excluding them from the calculations. This is the case for Van Valen's mean standing diversity (N_{st}; Van Valen, 1984), which estimates standing diversity at a point in time and best expresses the number of taxa susceptible to origination or extinction. It is calculated by the formula

$$N_{st} = (N_b + N_t)/2,$$

where N_b and N_t are the number of taxa that cross the lower and upper boundaries of this time unit, respectively. N_b results from the sum of (1) the taxa that cross the lower boundary and go extinct during this interval (N_{bL}), and (2) range-through taxa, that is, those known from before and after the interval (N_{bt}). Similarly, N_t is calculated as $N_{bt} + N_{Ft}$, where N_{Ft} is the number of taxa that first appear during this interval and cross its upper boundary. In the calculation of N_{bt}, a taxon is assumed to be present in the time span between its first and last occurrence even if not recorded. The main advantage of N_{st} is that singletons simply become irrelevant. The calculation of origination and extinction rates is affected not only by the presence of singletons, but also by the total taxonomic diversity within an interval. The higher the number of taxa during an interval, the higher these rates will be. Therefore, when comparing time units containing a different total number of taxa, per-capita rates must be calculated. Estimated per-capita origination (p) and extinction (q) rates are calculated as follows (Foote, 2000):

$$p = -\ln(N_{bt}/N_t)/\Delta t,$$

$$q = -\ln(N_{bt}/N_b)/\Delta t.$$

These metrics are independent from one another and normalized by interval duration (Δt). Furthermore, they are expected not to be very sensitive to variation in preservation rates because singletons are irrelevant for their computation. In our analysis, these rates include not only true originations and extinctions, but also immigrations and regional disappearances of taxa. As in the case of N_{st}, and by definition, these rates cannot be calculated for our first and last intervals (MN4 and MN14). It is also possible to calculate a fundamental growth rate $p-q$ that gives the proportional change in diversity throughout an interval and can be used as an estimate of turnover (Foote, 2000).

Although singletons are excluded from their computation, this does not mean that origination and extinction rates are completely independent of variation in preservation rate (r). A singular increase in r in one interval will cause an increase of both rates during this interval (Foote, 2000, figure 15). The number of genera that would have made their last appearance in preceding intervals is reduced because they now appear last in the interval with better preservation. The same is true for first appearances in succeeding intervals. The metrics underestimate extinction before the pulse in preservation and underestimate origination afterwards. A singular decrease in the preservation rate affects the measures in the opposite way. Therefore, we have assessed to what extent the apparent variation in taxonomic rates might be attributable to variation in preservation rates by testing their correlation (Table 1). The preservation rate r_i for an interval i is calculated as (Foote, 2000)

$$r_i = -\ln(1 - R_i)/\Delta t,$$

where R_i is the preservation probability, which is calculated using gap analysis (Paul, 1998) as

$$R_i = X_{\mathrm{bt,samp}}/X_{\mathrm{bt}},$$

where X_{bt} is the number of known range-through genera and $X_{\mathrm{bt,\,samp}}$ is the number of these genera that have actually been sampled during this interval. If variations in apparent taxonomic rates were primarily dominated by variation in preservation rates, then the correlation between the two kinds of rates would be high and positive.

Faunal similarity

Originations (p) result from both the local evolution of new genera within the Iberian Peninsula and immigration from other European regions. Faunal similarity would be expected to decrease if the recorded diversity changes were accounted for mainly by *in situ* origination, whereas the opposite would be true if immigration was more important. In order to assess which one of these two components of p is more important, we calculated Simpson's coefficient of faunal similarity (Simpson, 1960) between the Iberian Peninsula and both Central Europe ($S_{\mathrm{IB,CE}}$) and the Eastern Mediterranean ($S_{\mathrm{IB,EM}}$) during each time unit. In doing so, we used a range-through approach, assuming that a genus was present in a region during the interval between its first and last occurrence there. Singletons were excluded from these calculations for the sake of consistency with the other analysis, and to remove the effects of different duration and/or preservation quality between the time units. Simpson's coefficient of similarity (S) for two samples i and j, with a total number of taxa N_i and N_j, respectively, and providing that $N_i > N_j$, is simply calculated as (Simpson, 1960)

$$S_{i,j} = M/N_i,$$

where M is the number of taxa that are common to both samples. This coefficient is insensitive to the size of the larger sample, because it normalizes by the size of the smaller one. As such, it is highly recommended when sampling is considered to be incomplete (Simpson, 1960). For the sake of comparison we have also calculated the Jaccard (1912)) and Dice (1945) coefficients of similarity, which are given in Appendix S3. These coefficients are more sensitive to differences in sample size, but they show the same patterns as the Simpson's coefficient. It is worth noting that the number of sites from a particular area, Central European or Eastern Mediterranean, can affect the values of similarity. Consider what happens if there is a marked increase in the number of localities from the Eastern Mediterranean for a particular interval. Because many more records are introduced, there are good chances that the similarity with this area will increase just because the probability of sharing taxa increases with the addition of new records. Therefore, faunal similarity is potentially dependent on the quality of the record. If variations in the coefficient of similarity were mainly the product of variations in the number of sites in different areas, one would also expect to find a significant positive correlation between the similarity values with a particular area and its number of sites. We assessed this possible source of bias using Kendall's correlation tests between these two variables for each region, and treating micro- and macromammals separately (Table 2).

Table 1 Correlation tests between mean standing diversity (N_{st}), origination (p), extinction (q) and preservation (r) rates for Miocene Iberian micro- and macromammals. Correlation is evaluated using Kendall's correlation test. Kendall's τ, the probability of no correlation and the permutation probability of correlation (1000 replicates) are given. Significant values are indicated as follows: *$P < 0.1$.

	Micromammals				Macromammals			
	N_{st} and r	p and r	q and r	p and q	N_{st} and r	p and r	q and r	p and q
τ	0.33	0.14	0.28	0.28	0.40	0.57	0.07	0.36
P (uncorrelated)	0.26	0.62	0.32	0.32	0.16	0.05*	0.80	0.22
Permutation P	0.33	0.74	0.38	0.38	0.21	0.07*	0.90	0.28

Table 2 Correlation tests between Simpson's coefficient of faunal similarity between the Iberian Peninsula and Central Europe ($S_{IB,CE}$) and the Eastern Mediterranean ($S_{IB,EM}$) and the number of Central European sites (n_{CE}) and the number of Eastern Mediterranean sites (n_{EM}) for both micro- and macromammals. Correlation is evaluated using Kendall's correlation test. Kendall's τ, the probability of no correlation and the permutation probability of correlation (1000 replicates) are given. Significant values are indicated as follows: $^{**}P < 0.05$; $^{*}P < 0.1$.

	Micromammals		Macromammals	
	$S_{IB,CE}$ and n_{CE}	$S_{IB,EM}$ and n_{EM}	$S_{IB,CE}$ and n_{CE}	$S_{IB,EM}$ and n_{EM}
τ	−0.72	−0.05	0.42	0.48
P (uncorrelated)	0.004**	0.85	0.11	0.05*
Permutation *P*	0.002**	0.93	0.13	0.07*

Limitations of the methods

Species identification in many localities is uncertain, thus precluding an analysis at a finer (infrageneric) taxonomic level. As a result, our analyses cannot detect patterns occurring below the genus level. However, Alroy (1996) compared the genus- and species-level results of his diversity analysis of North American mammalian palaeofaunas, concluding that the genus-level data are more taxonomically robust and preserve much of the same signal as the species-level data. This claim is supported by several observations: the genus to species ratio is usually very low (Alroy, 1996), and the median genus duration is merely twice as long as the median species duration (Foote & Raup, 1996).

Another important methodological difficulty is related to the criteria used to define the time intervals. As usual in the definition of biozones, the diagnosis of the various MN zones is commonly based on the first and/or last appearance of certain taxa. Obviously this implies that origination and extinction rates will be noticeably high in all the MN zones. This seems to be an insurmountable difficulty of the analysis, although we can recognize taxonomic pulses by focusing on those MN zones in which taxonomic rates are clearly above the mean. Furthermore, our analyses cannot determine the point within a time unit at which an observed event occurred because rates are computed for the whole interval; therefore, it is impossible to know whether extinction and origination events are clustered at a certain point.

Finally, another drawback arises from the treatment of the gaps in the range of the taxa. We assume that a taxon is present throughout all the time units between its first and last occurrences, even though it has not been recorded in between. This range-through approach is conservative, in the sense that it assumes that the fossil record is incomplete, but unfortunately masks true short-lasting absences of the taxon from a certain geographical area. Therefore, our methods are unable to detect short-lasting range shifts, although they will still unravel major changes related to long-lasting trends in climatic change.

RESULTS

Diversity and taxonomic rates

Macromammals

Mean standing diversity (N_{st}) in the Iberian Peninsula shows a gradual increase starting by MN6 that culminates by MN9 (Fig. 2a). From then on, N_{st} decreases moderately until the latest Miocene (MN13), when there is a sharp decline resulting from the loss of more than the 30% of the existing genera. p and q are not constant during the studied time interval, showing important variations and pulses that are clearly above the mean 'background' rates (Fig. 2a). The correlation tests (Table 1) cannot reject the null hypothesis of no correlation between r and N_{st}, and between r and the taxonomic rates (p, q) at the 0.05 significance level. Even though correlation tests do not indicate that the general trends are affected by the quality of the record, singular variations in preservation may overemphasize some patterns. There is a pronounced extinction pulse during the Vallesian (MN9 and MN10) that coincides with a high r (Fig. 3). However, this extinction pulse may be somewhat overemphasized, particularly in the case of MN10, because r in MN11 is much lower. In contrast, r is lower during MN9 than in MN7+8, which would underestimate q, even though the results show that q is considerably higher than in the previous unit. Therefore, we can be quite confident about the existence of this Vallesian extinction peak. A second, more important extinction peak is observed during the Middle to Late Turolian (MN12 and MN13), with q taking a value close to 0.8 by MN13. Again, this extinction peak coincides with a rather high r during MN12 (Fig. 3), whereas during MN13 r is not above the mean. r cannot be calculated for MN14, which shows a comparatively lower number of localities as compared to MN13, so that this extinction peak may also be somewhat overemphasized by a singular increase in preservation.

The origination rate is usually lower than the extinction rate, except for the Middle Miocene. The higher values of both p and q tend to coincide (Figs 2a & 3). Accordingly, p and q are high during the Vallesian (MN9 and MN10) and the Middle Turolian (MN12). Both maxima coincide with high r, as already discussed in the case of q. As we have seen, we can be confident about the existence of the Vallesian peak on p during MN9 because r is higher in the neighbouring intervals. In contrast, the MN12 peak coincides with a singular increase in preservation that may overemphasize p during this interval.

Micromammals

Micromammal trends in N_{st} parallel those of macromammals until the Late Vallesian, with a gradual increase until an MN9 peak is reached (Fig. 2b). From this point on, the evolution of N_{st} is somewhat different in the two groups of mammals. Micromammal N_{st} shows a marked decline in the Late Vallesian (MN10), and this trend continues during the Early

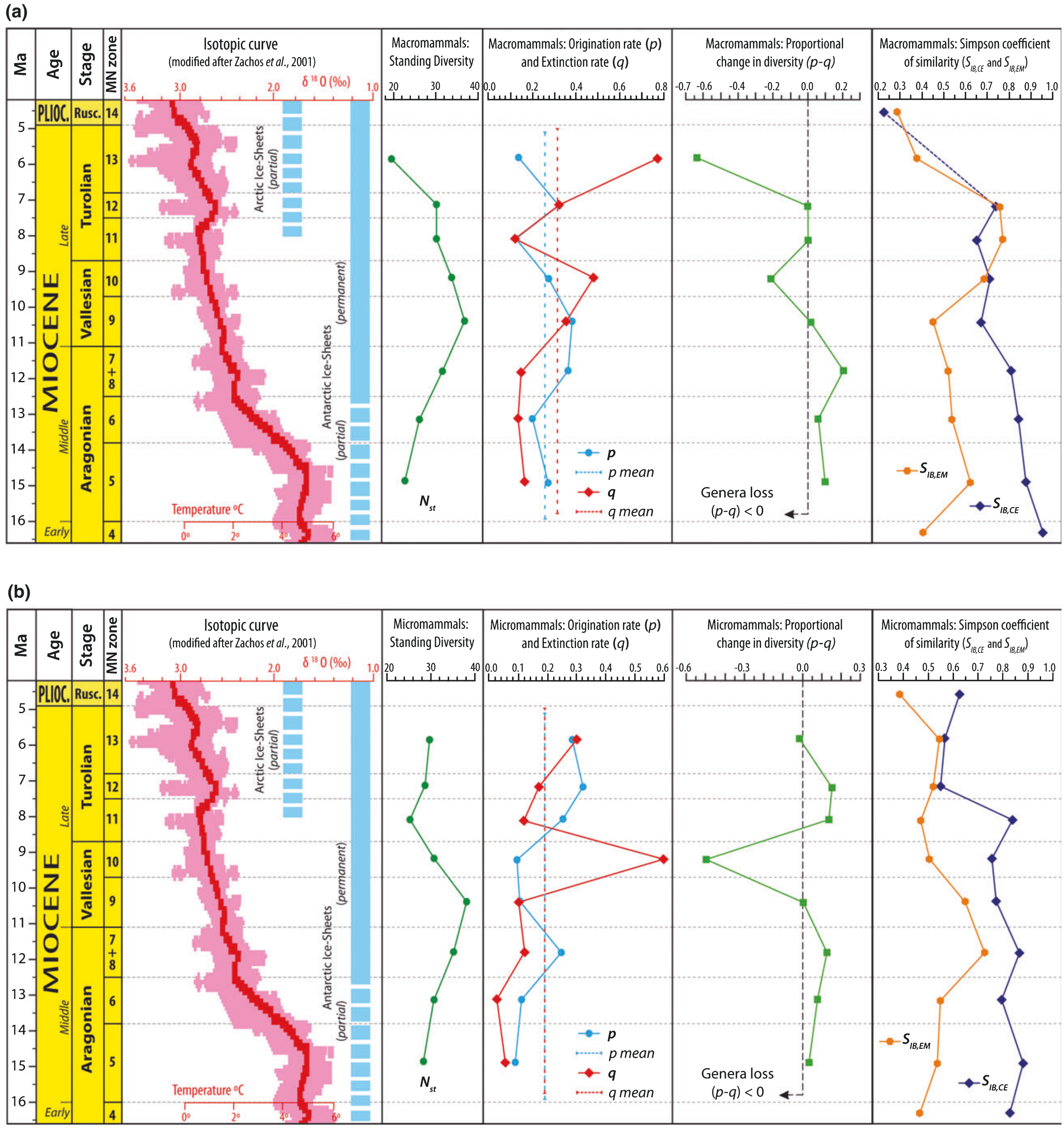

Figure 2 Changes in standing diversity, taxonomic rates and proportional changes in diversity in Middle to Late Miocene (a) macro- and (b) micromammalian faunas from the Iberian Peninsula. The similarity of Iberian mammalian faunas to those of Central Europe and the Eastern Mediterranean is also indicated. The global oxygen isotope record and the development of the polar ice-sheets are included so that the observed diversity patterns can be discussed in the light of Miocene climatic changes (see text for discussion).

Turolian, when the standing diversity reaches its lowest values. Nearly 40% of the micromammalian genera found during MN9 went extinct during the Late Vallesian and the Turolian. A moderate recovery occurred by the Middle and Late Turolian (MN12 and MN13), although N_{st} remains low as compared with the Early Vallesian. This major extinction event may be somewhat overemphasized, however, because r is particularly high in MN10 as compared with MN11 (Fig. 3).

After this peak, q markedly decreases during the Early Turolian and rises again by the end of the Miocene. Again, although the correlation tests cannot reject the null hypothesis of no correlation between r and q (see Table 1), this increase in q may be partly accounted for by the high r during MN13. Concerning the origination rates, p shows a peak in MN7+8 (Fig. 2b) that does not coincide with a particularly high r (Fig. 3). After this peak, during the Vallesian, p remains low.

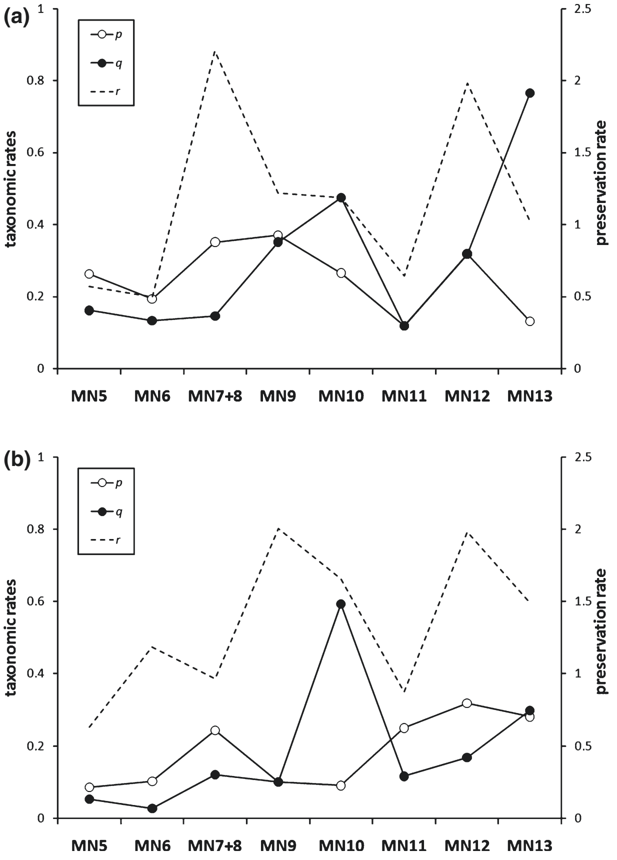

Figure 3 Changes in origination (p), extinction (q) and preservation (r) rates from Mammal Neogene zone 5 (MN5) to MN13 for both (a) macro- and (b) micromammals in the Iberian Peninsula. A singular increase in r may cause an apparent increase in the other two rates during the same time unit.

A new increase is seen in the Early Turolian, and high p values are recorded until the end of the Miocene. p may be somewhat exaggerated during MN12 and MN13, when r is particularly high (Fig. 3).

Faunal similarity and proportional change in diversity

Faunal affinities with other areas are generally high, Simpson's coefficient of similarity being well above 0.5 during most of the time interval (Fig. 2). The correlation tests between the similarity values and the number of sites in each area (Table 2) could reject the null hypothesis of no correlation at the 0.05 significance level in just one case, that of $S_{\mathrm{IB,CE}}$ for the micromammals. However, if changes in $S_{\mathrm{IB,CE}}$ were dictated by a change in the number of Central European localities one would expect a positive correlation – the result is exactly the opposite. Thus, singular decreases in $S_{\mathrm{IB,CE}}$ in the micromammals are not related to the smaller number of Central European sites than in adjacent time intervals. Regarding the macromammals, there is a positive correlation between the number of sites and $S_{\mathrm{IB,EM}}$ that is significant at $P = 0.1$. This indicates that the similarity with the Eastern Mediterranean is influenced to some degree by the number of macromammal localities from that area for a particular time interval. The higher the number of sites, the higher the similarity values will be. Therefore, the high similarity between the Iberian and the Eastern Mediterranean faunas during certain periods (the Early–Middle Turolian, see below) might be overemphasized.

The values of S are generally comparable between micro- and macromammals, and overall $S_{\mathrm{IB,CE}}$ is higher than $S_{\mathrm{IB,EM}}$. Nevertheless, the temporal trends in S compared with diversity changes deserve a detailed description. During the Middle Miocene, the balance between p and q is slightly positive (Fig. 2), resulting in a gradual increase in N_{st} that peaks during the earliest Late Miocene (Early Vallesian, MN9). $S_{\mathrm{IB,CE}}$ is very high during the whole interval, whereas $S_{\mathrm{IB,EM}}$ is much lower, showing merely a marked increase in the micromammal record during MN7+8–MN9, which coincides with an important origination peak. The Vallesian macromammal record is characterized by somewhat higher extinction rates, particularly during MN10. This is correlated with a sharp decline in $S_{\mathrm{IB,CE}}$. In contrast, $S_{\mathrm{IB,EM}}$ has started increasing by MN10. This marked decrease in $S_{\mathrm{IB,CE}}$ results in a negative balance between p and q, implying a moderate decrease in N_{st}. The micromammal record shows a major extinction peak during MN10, associated with a moderate decline in $S_{\mathrm{IB,CE}}$ and $S_{\mathrm{IB,EM}}$, although the decrease in $S_{\mathrm{IB,EM}}$ is much more important.

The Early Turolian (MN11) sees a slight diversity recovery. Although micromammal N_{st} reaches its minimum values, the balance between p and q is positive. The faunal affinities with Central Europe increase again, whereas those with the Eastern Mediterranean remain low. Concerning the macromammals, the decline in N_{st} stops, and p and q both attain similar, and also very low, values. $S_{\mathrm{IB,CE}}$ remains approximately the same, $S_{\mathrm{IB,EM}}$ shows a substantial increase, and the affinities with the Eastern Mediterranean are greater than those with Central Europe for the first time. However, this increase in similarity may be somewhat overemphasized because of the markedly higher number of Eastern Mediterranean sites as compared with preceding periods. This situation does not change during the Middle Turolian (MN12), when high macromammal $S_{\mathrm{IB,EM}}$ coincides with a maximum in p (although it is probably overemphasized because of a singular increase in r). The latest Miocene (MN13) records the most important extinction peak for macromammals, which coincides with a pronounced decline in N_{st}. In contrast to the situation seen during the Vallesian, this marked increment in q is not accompanied by a similar, less important increment in p. In fact, p declines from MN12 to MN13, resulting in a markedly negative balance between the two rates. This extinction event coincides with a sharp decrease in $S_{\mathrm{IB,EM}}$, which reaches its lowest value (0.34). Unfortunately, the Central European record during MN13 is too poor to evaluate whether a similar decrease in $S_{\mathrm{IB,CE}}$ occurred. $S_{\mathrm{IB,EM}}$ as well as $S_{\mathrm{IB,CE}}$ can be calculated for the next interval (MN14, Early Pliocene), when they are very low (S slightly above 0.20 in both cases), thus indicating the continuation of the trend towards lower faunal similarity, which can be also recognized in the Central European faunas.

Regarding micromammals during MN12 and MN13, a slight increase in $S_{\mathrm{IB,EM}}$ occurs in parallel to a very pronounced decline in $S_{\mathrm{IB,CE}}$, so that this parameter takes approximately the same value for both Central Europe and the Eastern Mediterranean. In any case, the overall similarity of the Iberian micro-mammal faunas with those of other areas of Europe is low, particularly with Central Europe. This coincides with rather high q that are partly balanced by similar (although lower during MN13) p, resulting in more or less stable and characteristically low N_{st}. However, this pattern may be exaggerated because of the impoverishment of the Central European record during this time.

DISCUSSION

Tempo and mode of diversity changes

The taxonomic rates for both micro- and macromammals are generally low, being above 0.3 only in particular intervals of high origination and/or extinction. The maxima of both rates tend to coincide, implying the replacement of part of the existing fauna by a new set of elements. This is particularly true for macromammals, so that the extinction pulses seen in the Vallesian (MN9–MN10) and the Middle Turolian (MN12) are accompanied by similar, albeit somewhat lower, origination rates (Fig. 2a). In contrast, this correlation is rare in the case of micromammals, being observed only during the Late Turolian (MN13; Fig. 2b). The occurrence of singular periods of concurrent increases in origination and extinction rates is predicted by models that advocate punctuational trends at the level of ecosystems or species aggregates, namely coordinated stasis (Brett & Baird, 1995) and turnover pulse (Vrba, 1985, 1995) models. These can be simply viewed as an extension of the punctuated equilibrium theory to ecology, in the sense that they advocate long periods of stasis for taxonomic richness, composition and abundance pattern, which are abruptly disrupted by dramatic turnover pulses (Gould, 2002). Both models rely on physical disturbances as an explanation for the turnover events, but differ in the mechanism hypothesized to provide stability: ecological locking plays a major role in the case of the coordinated stasis (Brett & Baird, 1995); in contrast, stability is mainly a collateral effect of the expectation of punctuated equilibrium for individual species in the turnover pulse model (Gould, 2002). Even though there are differences concerning the mechanisms of stasis, both models make testable predictions with regard to the nature of faunal turnovers (Alroy, 1996): (1) origination and extinction rates should be correlated; and (2) turnover should be a composite function of very low background rates and singular major pulses. In the case of the Iberian mammal record, these predictions do not seem to hold, as origination and extinction rates are not correlated (Table 1). Even though many pulses in p and q coincide, there are important exceptions, such as the important extinction event affecting the micromammals in MN10 and the major diversity crisis seen in the macromammal record during MN13. Furthermore, the intervals in which the two rates coincide are not marked by a major restructuring of the fauna. On the contrary, they merely represent the replacement of some taxa, as the faunal assemblage retains from 60% to 80% (or more) of the genera from the previous unit.

Geographical range shifts and diversity dynamics

The affinities of the Iberian faunas with those of other European regions are generally high at the generic level, thus suggesting that the presence of endemic genera restricted to the Iberian Peninsula is quite rare. The occurrence of endemic Iberian species, particularly for micromammals, is more common, although it may derive in great part from the better Spanish fossil record when compared to other areas of Europe. Genera of Iberian origin consist mostly of rodents of the families Gliridae (such as *Armantomys* and *Tempestia*) during the Aragonian, and Muridae (such as *Stephanomys*, which is also recorded from southern France) during the Turolian (Agustí, 1990).

Major diversity changes coincide with important changes in the affinity of the Iberian faunas with those of other areas, particularly in the case of macromammals. In this way, the Vallesian increase in extinction rates coincides with a decrease in similarity with Central European faunas, suggesting that a contraction of the geographical ranges of macromammals can explain this extinction event. During the Early and Middle Turolian (MN11–MN12) the affinities with the Eastern Mediterranean increased and became more important than those with Central Europe. Certain taxa of eastern origin (such as *Machairodus*, *Microstonyx* and *Adcrocuta*) are known to have dispersed into the Iberian Peninsula during the Late Vallesian (MN10; Agustí *et al.*, 2001). However, the most important entry of Eastern immigrants occurred during the Turolian (mainly during MN11–MN12) and concerned several antelopes (such as *Hispanodorcas*, *Gazella* and *Palaeoryx*) as well as giraffes (*Birgerbohlinia*) (see Agustí *et al.*, 2001; van der Made *et al.*, 2006). These events reflect the maximum geographical extension of the so-called 'Pikermian' fauna (Crusafont Pairó, 1950; Solounias *et al.*, 1999), a rather homogenous (but see Kostopoulos, 2009), savanna-like macromammal assemblage that collapsed soon after, during MN13 (Eronen *et al.*, 2009; Kostopoulos, 2009). The Pikermian macromammal faunas are characterized by a great diversity of horses (including *Hipparion*, *Hippotherium* and *Cremohipparion*), grazing rhinos (*Acerorhinus*, *Chilotherium* and *Ceratotherium*), giraffes (*Bohlinia*, *Samotherium* and *Helladotherium*) and antelopes (*Tragoportax*, *Prostrepsiceros*, *Nisidorcas*, *Hispanodorcas*, *Urmiatherium*, *Plesiaddax*, *Palaeoryx* and many others), and a poor representation of cervids and other forest-dwelling herbivores. The felids (such as the sabre-toothed cats *Machairodus* and *Paramachairodus*) and the hyaenids (*Hyaenictitherium*, *Hyaenotherium*, *Adcrocuta*, *Plioviverrops* and *Thalassictis*) characterize the carnivore guild. The collapse of the Pikermian fauna is recorded as a major extinction event in MN13 that coincided with a dramatic decline in the affinities of the Iberian macromammalian faunas with those of other areas of Europe.

This pattern has been reported by other authors (Costeur *et al.*, 2004; Costeur & Legendre, 2008; Eronen *et al.*, 2009), who recognized high levels of provinciality in all the European regions during MN13 and MN14, with very few species showing wide geographical ranges.

The pattern shown by micromammals is somewhat different. The Late Vallesian (MN10) diversity crisis did not coincide with a comparatively sharp decline in the affinities with the Central European faunas. The similarity with the Eastern Mediterranean faunas decreased markedly, but this range contraction could account for only some of the recorded extinctions (about 35%). The explanation for this diversity crisis is more probably related to a major extinction event that affected the mammal faunas of (at least) the whole of Western and Central Europe. This event, the Vallesian Crisis (also cited as the 'Mid' or 'Late Vallesian Crisis') was first recognized by Agustí & Moyà-Solà (1990) on the basis of the mammalian record from the Vallès-Penedès Basin (Catalonia, Spain). This implied the extinction of many taxa of Middle Miocene origin, including both macro- and micromammals. Our results confirm previous studies (Casanovas-Vilar *et al.*, 2005) showing that micromammals were more severely affected. Regarding the geographical range of the Vallesian Crisis, it has been suggested that it was a continent-wide event (Agustí *et al.*, 1999; Fortelius & Hokkanen, 2001). In contrast, Casanovas-Vilar *et al.* (2005) concluded that the extinction pulse seen in Central Europe was probably related to the poorer quality of the Turolian record in this area as compared to that of the Vallesian. A recalculation of the diversity and taxonomic rates for Central Europe, considering a wider area than in Casanovas-Vilar *et al.* (2005), shows that the diversity started declining prior to the Vallesian, during MN7+8 (authors' unpublished data).

The major decrease of micromammal faunal similarity with Central Europe occurred after the Vallesian Crisis, during the Middle Turolian (MN12), and coincided with an increase in the affinities with the Eastern Mediterranean faunas that resulted in high origination rates. A surprising result is the low faunal similarity of the micromammal faunas of the Mediterranean regions during MN13. This contrasts with the results of Geraads (1998) and Maridet *et al.* (2007), who found a relatively high faunal homogeneity. Nevertheless, our results are in accordance with the pattern shown by the macromammals, which shows high levels of provinciality during the latest Miocene and the Early Pliocene.

Our hypothesis, linking geographical range shifts to diversity changes in the Iberian mammal record, seems to hold for the macromammals, but not for the micromammals. This suggests a relationship between range size and the characteristics of the organisms, such as body size. In most cases, there are highly significant positive correlations between range size and body mass (Brown, 1995, 1996; Gaston, 1996), so that smaller species tend to have smaller range sizes. In its turn, body size covaries with many other biological characteristics of organisms, including their life history and demographic attributes, which have a significant influence on range sizes (Brown, 1996). The limited dispersal ability of the micromammals would result in a higher sensibility to local climatic conditions and an increased extinction risk. This prediction has recently been challenged by Liow *et al.* (2008), who reported higher origination and extinction rates for macromammals. Our rates were calculated using the same methods as Liow *et al.* (2008), but instead show that the results are generally comparable between Iberian macro- and micromammals in the Miocene, although the extinction rates for micromammals are clearly higher in particular time intervals (the Vallesian Crisis). The differences may result from (1) the different areas and time intervals considered by the two studies; (2) some errors detected in the data used by Liow *et al.*, which were taken from the NOW, so that the temporal ranges for some micromammal genera cited as examples of longer duration are wrong (the dormice *Armantomys* and the mice *Parapodemus*); (3) thus, even though certain micromammals actually have very long temporal ranges (as is the case for some squirrel and dormice genera such as *Spermophilinus, Miopetaurista*, *Glis*, *Muscardinus* or *Glirulus*), this is not generally the case.

The meaning of it all: relationships with global and regional palaeoclimatic records

The Middle Miocene cooling event (Zachos *et al.*, 2001) caused an increase in seasonality in Central European regions. The palaeobotanical data show a significant decrease of the mean temperature during the coldest month, whereas mean annual precipitation rates remained high and mostly unchanged (Mosbrugger *et al.*, 2005). Central Europe was covered by warm-temperate evergreen forests during the Middle Miocene. These were progressively replaced by mixed mesophytic forests, and finally by deciduous broad-leaved forests during the Late Miocene (Kovar-Eder, 2003). This high-latitude cooling was accompanied by lower-latitude drying and the development of open landscapes in Mediterranean regions, such as the inner Iberian basins (Rivas-Carballo, 1991) and Turkey (Strömberg *et al.*, 2007). Although all these changes had already started by the Middle Miocene (*c.* 14 Ma, at about the MN5/MN6 boundary), the Iberian mammal faunas do not show major changes until much later, around 10 to 9 Ma, during the early Late Miocene (MN9–MN10, Vallesian). The global deep-sea oxygen isotope record does not show a significant break at this time (Fig. 2), but 10 Ma (approximately the MN9/MN10 boundary) coincided with the time that major ice-sheets were re-established in Antarctica and the oxygen isotope ratios again reached the high levels that were attained during the Early Oligocene Glaciation (Zachos *et al.*, 2001). On the basis of these data, it has been previously suggested that some critical climatic threshold may have been crossed by the Vallesian (van Dam, 2006).

Our results show that macromammals suffered a significant range contraction during the Vallesian. By the Late Vallesian–Early Turolian (MN10–MN11) many forest-adapted taxa went extinct in the Iberian Peninsula. Amongst the macromammals these included, for example, the suid *Conohyus*, the cervid *Amphiprox*, the rhinos *Dicerorhinus* and *Lartetotherium* and hominoid primates of the genus *Hispanopithecus* (Agustí *et al.*, 1999, 2003). Some of these taxa survived until the Turolian (MN11) in Central Europe (Franzen & Storch, 1999). At the same time, many forest-adapted taxa, such as the dwarf deer *Cervavitulus*, the small tapir *Tapiriscus* and the small ursid *Ursavus*, are known to have migrated into Central Europe from the Mediterranean regions (Franzen & Storch, 1999). In contrast, other forest-dwelling mammals that could not tolerate the temperature seasonality existing in the northern regions, such as hominoids, were confined to the Mediterranean area and ultimately vanished from the study area by the Late Vallesian (Fortelius & Hokkanen, 2001). The peculiar hominoid *Oreopithecus* would survive in isolation in the Tusco-Sardinian archipelago until the Messinian (MN13). Micromammal diversity was severely affected during the Late Vallesian (MN10), with many taxa disappearing from both the Iberian Peninsula and Central Europe. These included the cricetid genera that characterized the Middle Miocene (*Eumyarion*, *Democricetodon*, *Megacricetodon*) and that disappeared at the same time as the first murids dispersed into Western Europe. Again, the forest-adapted taxa were major victims of the extinction event. The flying squirrels *Albanensia* and *Miopetaurista* are last recorded in the Iberian Peninsula in MN10. The same is true for the presumably arboreal dormice of the genera *Paraglis*, *Paraglirulus* and *Myoglis*, and for the minute eomyid rodents of the genera *Keramidomys* and *Eomyops*. However, similarly to what occurred in the case of the macromammals, some of these genera did survive until the Early Turolian (MN11) in Central Europe. As already discussed, it is expected that micromammals show a higher extinction risk than macromammals because of the more restricted geographical ranges in the former. That the Vallesian Crisis was much more important for micromammals than for macromammals supports this prediction. Initially, climatic changes would have fragmented the preferred habitats of many micromammal taxa. As climatic deterioration continued, these environmental patches would have become too restricted to sustain a viable population, and the micromammals confined to these areas would ultimately have disappeared, given their lower dispersal ability as compared to macromammals.

The situation seen during the latest Miocene (the Messinian, MN13) is somewhat puzzling. This time coincided with the interruption in the Atlantic–Mediterranean connection, mainly as a result of tectonic events that led to the complete desiccation of the Mediterranean (Hsü *et al.*, 1973). This allowed a few, short-lasting incursions of African taxa into the Iberian Peninsula (gerbils, crested rats, the hippo *Hexaprotodon* and the cercopithecine monkey *Macaca*; Agustí *et al.*, 2006; van der Made *et al.*, 2006) and of Iberian elements into northern Africa (many rodents, including *Eliomys*, *Apodemus*, *Apocricetus*, *Ruscinomys* and *Stephanomys*; Agustí *et al.*, 2006). However, our results show that the Messinian coincided with a major macromammalian diversity crisis and with the lowest levels of similarity. This diversity crisis is apparently explained by the collapse of the so-called Pikermian faunas. Eronen *et al.* (2009) provided evidence for a geographical range contraction of the Pikermian faunas during MN13, with the Iberian faunas showing very low levels of similarity to the eastern ones. For example, MN13 records the last occurrence of the horse *Cremohipparion*, the bovids *Turiacemas* and *Hispanodorcas*, the large suid *Microstonyx*, and the hyaenids *Adcrocuta* and *Thalassictis* in the Iberian Peninsula. The Pikermian faunas would ultimately vanish (even from the Eastern Mediterranean) by the Early Pliocene (MN14), presumably because of environmental reversal towards increased humidity and forestation. The palaeobotanical data have shown that the Early Pliocene was a relatively warm and humid period, with evergreen/warm mixed forests present in northern Spain and southern France (Suc *et al.*, 1999). This shift towards warmer and more humid conditions may have started by the Messinian (MN13), when a number of forest dwellers appeared, such as the cervids *Croizetoceros* and *Pliocervus*. However, the palaeobotanical data show that no major changes occurred during the Messinian in the terrestrial environment (Fauquette *et al.*, 2006; Kovar-Eder *et al.*, 2006). The Mediterranean area was characterized by a dry and open landscape before, during and after the Messinian event (Fauquette *et al.*, 2006), whereas more forested areas existed northwards (Kovar-Eder *et al.*, 2006). Increased environmental humidity and forestation does not seem to have occurred until the Pliocene.

CONCLUSIONS

The diversity changes seen in the Miocene mammalian record of the Iberian Peninsula are partly related to geographical range modifications, particularly in the case of macromammals. Climatic changes resulted in expansions or contractions of the geographical ranges of macromammals, as a result of changes in the distribution of their preferred habitats. The lower dispersal ability of micromammals resulted in a higher extinction risk because of the tendency of their populations to be confined to excessively small environmental patches. Hence, they were more severely affected by climatic changes. The results presented here are in accordance with other studies that have explained mammalian turnovers in relation to climatic forcing (for recent examples see van Dam *et al.*, 2006; Badgley *et al.*, 2008; Eronen *et al.*, 2009).

ACKNOWLEDGEMENTS

This collaborative project was possible thanks to the support of the Generalitat de Catalunya (Grup de Recerca Consolidat 2009 SGR 754 of the AGAUR), the Spanish Ministerio de Ciencia e Innovación (CGL2008-00325/BTE; CGL2008-04200/BTE) and the National Science Foundation (project RHOI-Hominid-NSF-BCS-0321893). I.G-P. acknowledges the support, in the form of a post-doctoral contract, given by the Fundación Española para la Ciencia y la Tecnología (FECYT) and the Spanish Ministerio de Ciencia e Innovación. The authors also acknowledge the interest of organizers and attendants of the symposium *Evolutionary islands: 150 years after Darwin* held in Leiden in February 2009, which offered us the opportunity to take part in this important event. We gratefully acknowledge the remarks and comments of the editors (H.P. Linder and R.J. Whittaker) and the two referees of this paper, R.L. Bernor (Howard University, Washington) and D. Kostopoulos (University of Thessaloniki, Thessaloniki), which greatly improved the final version. We are indebted to our colleague H. de Bruijn (University of Utrecht, Utrecht) for kindly providing substantial information on the age of certain Turkish sites. Similarly, G.D. Koufos (University of Thessaloniki, Thessaloniki) kindly sent us his personal database of Greek Neogene mammals. The remarks and interesting discussions provided by Victoria Quiralte (Museo Nacional de Ciencias Naturales–CSIC, Madrid), and J.A. van Dam and R. Minwer-Barakat (Institut Català de Paleontologia, Cerdanyola del Vallès) are acknowledged. We also thank S.K. Donovan (Naturalis, Leiden), who reviewed our manuscript and added several comments and corrections that improved the English. Finally, this paper would have not been possible without the efforts of the large team of European palaeontologists who have devoted a great amount of time to creating, improving and expanding the NOW database.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 List of localities used to build our raw database for (a) micromammals and (b) macromammals.

Appendix S2 Genera-by-MN-zone matrices for each geographical region considered for (a) micromammals and (b) macromammals.

Appendix S3 Jaccard, Dice and Simpson similarity coefficients between the Iberian micro- and macromammal faunas and those of Central Europe and the Eastern Mediterranean.

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Editor: Peter Linder

The papers in this Special Issue arose from the symposium *Evolutionary islands: 150 years after Darwin* (http://science.naturalis.nl/darwin2009), held from 11 to 13 February 2009 at the Museum Naturalis, Leiden, The Netherlands. The theme of the symposium was to explore the contribution of islands to our understanding of evolutionary biology and to analyse the role of island biological processes in a world in which the insularity of island and mainland ecosystems is being drastically altered.