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The fossil record of the Neogene Carnivore Mammals from Spain

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Abstract

Carnivore mammals (Carnivora, Mammalia) constitute a significant component of the Spanish Neogene faunas, not so much due to their fossil abundance, which is generally low, but rather because of their high degree of taxonomic diversity. We assessed their evolutionary dynamics from the fossil record of Iberian carnivores using per-taxon rates (origination, extinctions and turnover) combined with a recent approach for removing the sampling signal from diversity curves. Our analysis interval covers most of the Neogene and the early Pleistocene (MN 2 to MN 17), spanning from around 21.6 to 1.8 Ma. We identified six carnivore associations by applying factor analysis to our data. The diversification pattern shows four origination episodes: MN4, MN7/8, MN12 and MN14. We also identified four extinction episodes. The first two are coincident with the onset of the MN 4 and MN7/8 faunas. The last two extinction episodes take place during MN9, coinciding with the Mid Vallesian Crisis (MVC), and MN13, co-occurring with the Messinian Salinity Crisis (MSC).Two major turnover pulses are recognized during MN4 and MN14, the turnover rate remaining moderately high between MN6 and MN13. We suggest that the pattern observed might be primarily triggered by the biogeographic and climatic shifts that took place during the Neogene.

Introduction

The Spanish Cenozoic continental basins have been intensively explored during the last few decades. Consequently, the Spanish mammal fossil record has shown a considerable increase, both in quality and quantity, extending almost continuously throughout the Neogene (Calvo et al. 1993; Daams et al. 1998; Alba et al. 2001; Agustí et al. 2001; Van Dam et al. 2006). These exceptional circumstances have enabled many approaches to the study of both the patterns and the dynamics of the record itself, either based on consideration of discrete temporal ranges (Alberdi et al. 1997; Azanza et al. 1997; Morales et al. 1999; Casanovas-Vilar et al. 2010; Domingo et al. 2014)or on selection of certain taxonomic groups: Rhinocerotidae (Cerdeño and Nieto 1995), Rodentia (Agustí et al. 1999; Van Dam et al. 2006; Van der Meulen et al. 2005), Lagomorpha (Hordijk et al. 2010) and Primates (Marigó et al. 2014).Herein we focus upon the macroevolutionary patterns of the Neogene carnivores from Spain. The carnivore mammals (Carnivora, Mammalia) constitute an important component of the Spanish Neogene faunas, not because of their abundant fossil remains, which is generally low (with exceptions, which usually account for less than 10% of the total identified fossils), but due to their high taxonomic diversity, related to the wide range of dental and locomotor specializations exhibited, which would also imply high ecological diversity (Van Valkenburgh 1985; 1987; 1988; 1989; Taylor 1989; Friscia et al.2006), showing their great capacity to prey upon a wide range of mammals. Approaches to the study of the Spanish carnivore fossil record have been addressed before, from Morales (1996) and Fraile et al. (1997) to the most recent study by Alberdi et al. (2011). Furthermore, Madurell-Malapeira et al. (2014) and Prado et al. (2014) focused on the last 6 Ma, and Abella et al. (2014) tackled the Neogene fossil record of the superfamily Ursoidea.

Material and methods

TEMPORAL FRAMEWORK.

Our analysis covers most of the Neogene in its traditional conception, prior to the definition of the currently recognized Plio-Pleistocene boundary at 2.58 Ma (Cohen et al. 2013), and spans from the beginning of the early Miocene ca. 21.6 Ma to the beginning of the early Pleistocene, ca. 1.8 Ma. We used the biochronological MN units (Mammal Neogene) from MN2 to MN17, with MN7/8 fused (De Bruijn et al. 1992).

FOSSIL DATA.

We included 112 fossil sites selected based on the subsequent criteria; at least one reasonably well-identifiable taxon of the order Carnivora was present, and the site could certainly be included in one of the MN zones. The MN dating of the fossil sites is mainly based on Agustí et al. (2001); Van Dam et al. (2006; 2014); Domingo et al. (2007); Van der Meulen et al. (2011; 2012) and Morales et al. (2013). The selected sites are scattered across all continental Spanish basins (Calvo et al. 1993; López-Martínez 1989), but considering the smaller ones and/or those presenting fewer sites, geographically grouped for practical reasons. Consequently, we considered seven areas, including karst deposits (Table 1, Figure supplementary information). Over 80% of the sites pertain to three areas, the upper part of the Tagus basin or the Spanish Meridional plateau, the Calatayud-Teruel basin and the Catalan coastal basins (the

Vallés-Penedés and Pyrenean basins). In general, all these were endorheic basins for much of the Neogene, particularly the innermost ones (Tagus, Calatayud-Teruel), and with some marine alternation in the Catalan and Southeast basins. There is therefore a high level of homogeneity in the sedimentary facies in most of the fossiliferous deposits. They are generally formed in transition zones between the ephemeral watercourses and very shallow lacustrine areas. Consequently, one can expect no significant biases in the diversity of carnivore species from the Spanish sites.

Both the karst deposits and the pseudo-karstic localities of Cerro de los Batallones (Calvo et al. 2013; Domingo et al. 2013) differ from this general pattern. The pseudo-karstic deposits from Cerro de los Batallones are also important because they constitute natural carnivore traps this gives rise to a biased view regarding the abundance of carnivore remains (with thousands of specimens representing 90% of the total record), but presents a similar diversity of carnivore species to that of the stratified localities. Batallones 3 exhibits the highest diversity of all the Batallones sites (presenting a maximum of 11 species). On the other hand, some karst deposits, such as Layna (Soria), show abundant carnivore remains, but the latter’s diversity is discrete, reaching only eight species. Thus, any bias in diversity based on different sedimentary environments can be ruled out. However, the scarcity of small-sized carnivore species from many localities, practically absent in the Plio-Pleistocene deposits (zones MN14 to MN17) and generally very rare in the rest of the sites (except for those from MN9, see Casanovas-Vilar et al. (2014) for other small mammals), could be interpreted as a widespread negative bias towards small-sized carnivores. Such bias cannot be explained by the palaeontological sampling alone, as sediment washing to obtain micromammals has been common practice over the past 60 years. This negative bias is likely related to the preference of the small carnivores for forest habitats, which are in general more restrictive than those occupied by the larger carnivores (Ginsburg and Morales 1992). The existence of two biogeographic provinces on the Iberian Peninsula during the Late Miocene (Gómez Cano et al. 2011) appears not to have affected the carnivore faunas, and the patterns detected in Vallès-Penedès are similar to those recorded in the rest of the Spanish basins.

In order to construct the database, we considered that the range of a taxon present in at least one locality of a given MN unit would be extended throughout the entire MN unit (Figure 1).

TAXONOMY.

We identified 147 species belonging to 94 different genera. Only one of these species, *Hyainailourus sulzeri* (Hyaenodontidae, Creodonta), does not belong to the order Carnivora. The remaining 93 genera belong to 13 families (Table 2); four of these are extinct (Amphicyonidae, Hemicyonidae, Percrocutidae and Barbourofelidae). Additionally, only four families have extant representatives in the Spanish faunas (Felidae, Mustelidae, Ursidae and Canidae), while the common genet *Genetta genetta* (Viverridae) and the Egyptian mongoose *Herpestes ichneumon* (Herpestidae) may have been recently introduced by human action (Gaubert et al. 2011). Finally, the members of the Hyaenidae family were geographically extinct in Spain during the Holocene.

Due to the completeness of the mammalian fossil record for the Iberian Peninsula at generic level, which reaches 91% compared to the 77% at specific level (Alba et al.

2001), our analyses were only based on the generic level (Table 1 Supplementary information).

DETRENDED DIVERSITY.

Raw diversity curves usually reflect the collecting effort of palaeontologists. Thus, time-series diversity analyses require sampling bias to be removed (Smith and McGowan 2011). Herein, a recently developed modelling approach for removing the sampling signal in diversity curves was applied to our dataset (Lloyd 2012). This method requires a sampling proxy and the raw diversity values through time, and assumes that the true diversity is constant and the observed diversity is a mere artefact of the sampling proxy. It therefore fits linear and non-linear models to the dataset and chooses the ‘best’ model by calculating the sample size-corrected Akaike Information Criterion (AICc). The model is used to calculate predicted values of diversity, and residuals are estimated by subtracting the predicted diversity from the observed diversity values. By comparing the predicted and observed diversity through time, we identified peaks and troughs of the diversity curve that fall beyond the biased model and potentially reflect the biological signal. We used the number of fossil localities included in the study for each MN unit as the sampling proxy. Lloyd’s (2012) method was applied to the raw diversity of both species and genera separately.

EVOLUTIONARY AND PRESERVATION RATES.

We assessed the evolutionary dynamics from the Iberian carnivore fossil record using per-taxon rates. Both interval span and sampling quality affect the evolutionary rate estimations recovered from the fossil record. For instance, intensifying the sampling in a given time interval may increase the number of rare taxa known exclusively from that interval. Such restricted taxa, also known as singletons (Foote 2000), are especially sensitive to preservation potential and interval length. Therefore, taxonomic and evolutionary metrics usually correct the effect of singletons, or even exclude them from calculations (Van Valen 1984). Furthermore, the total taxonomic diversity within a given interval may also affect the estimation of evolutionary rates. For instance, intervals with higher taxon richness will yield higher evolutionary rates. To avoid this issue, per-taxon rates excluding singletons must be calculated (Foote 2000). We first estimated the mean standing diversity for each MN unit as:

$$N_{sd} = \left(N_b / N_t\right) / 2$$

Where N_b and N_t are the number of taxa crossing the bottom and top boundaries of each time bin.

N_{sd} is then used to estimate origination (p), extinction (q) and turnover (t) rates as follows:

$$p = \left(N_{Ft} / N_{sd}\right) / \Delta t$$

$$q = \left(N_{bL} / N_{sd}\right) / \Delta t$$

$$t = \left(N_{bL} + N_{Ft}\right) / N_{bt} / \Delta t$$

Where N_{Ft} is the number of taxa appearing during the time bin and crossing its upper boundary, N_{bL} is the number of taxa crossing the bottom boundary and disappearing during the time bin and N_{bt} the number of taxa recorded before and after the time bin, but not necessarily in between (Foote 2000). These evolutionary metrics are normalized by the standing diversity (N_{sd}) and the duration of each interval (Δt). Since evolutionary rates may be influenced by the quality of the fossil record, we estimated the preservation rate as follows (Foote 2000):

$$r = -ln(1 - N_{bda}/N_{bt})/\Delta t$$

whereN_{bda} are the taxa recorded before, during and after a given MN unit. We tested for the influence of preservation rates on evolutionary rates using Kendal correlations on their first differences (Domingo et al. 2014).

To test the significance of the evolutionary and preservation rates, we bootstrapped our dataset with replacement 1000 times, using the stratigraphic range of each genus as the sampling unit (Foote 2003). We considered the mean parameter estimation as the best-fit rate, and ± 1 standard deviation of the distribution around each mean was used to define the uncertainty in the corresponding rate estimate (Finarelli and Badgley 2010).

IDENTIFYING CARNIVORE FAUNAS.

Factor analytic descriptions can be applied to the fossil record to identify evolutionary faunas comprising a characteristic association of taxa that share times of origination, diversification and demise (Sepkoski 1981; Figueirido et al. 2012). In order to depict how the turnover and diversification dynamics shaped Spanish Neogene carnivore faunas, we performed *Q*-mode factor analyses (FA) as in Sepkoski (1981). We calculated the diversity of species within each of the MN units. The resulting diversity matrix was constructed with the MN units as columns, and then analyzed using the function *factanal* in R (R Development Core team 2015). We employed the rotation “varimax”, which maximizes the sum of the variances of the squared loadings. We selected those factors with eigenvalues greater or equal to 1, or those conforming a marked slope when plotted against the rank (Sepkoski 1981; Figueirido et al. 2012). The “scree graph” was analyzed using the R package *n Factors*. The genera with scores greater that 1 were retained, since they represent an important contribution to the total diversity of each evolutionary fauna (Sepkoski 1981).

Results

Our results (Figure 2A) show a strong relationship between genera diversity and the number of localities represented in each biozone. A high number of localities included in a biozone would imply more taxa to be recorded. There are evident exceptions in biozones MN5, MN6 and MN9, with few taxa present in a high number of localities in the two first cases (MN 5 and MN 6); however MN9 shows the opposite case, with a high number of taxa, compared with the lower number of localities.

The early Miocene carnivore faunas exhibited low diversity values, even after the palaeontological sampling effort was considered (Figure 2, Figure 3). Nevertheless, genus diversity increased towards MN9, where it reaches a diversity maximum which is not due to pure palaeontological sampling, but rather reflects a true signal (Figure 2C). After the MN9 peak, a sharp decline is evidenced by our analyses, followed by two peaks, detected during the lower Miocene (MN12 and 13) and the late Pliocene (MN 15 and 16) respectively. These trends correlate well with the evolutionary pattern obtained in our analysis (Figure 3). The peak registered during MN 4, subsequent to the initial drop and before the major trough of MN5, agrees with a high turnover pulse. The drastic change in the diversity trend between the MN5-MN6 drop and the MN9 peak took place during the MN7/8 biozone, showing a recovery of the turnover rate. Subsequently, the MN9-MN13 period is characterized by several diversity fluctuations. These results also reveal a turnover maximum at the end of the sequence during the beginning of the Pliocene (MN14). Preservation rates show a heterogeneous pattern, with high positive values during MN14, compared to the lower ones registered for the Miocene/Pliocene boundary biozones (MN13-MN14). Low preservation rate values are also registered in MN4 and MN9.

The diversification pattern depicted in figure 3B shows several origination and extinction episodes. Two faunal turnovers feature high origination and extinction rates (red and blue lines in Figure 3B) during MN4 and MN7/8. Interestingly, however, the diversification pattern is subsequently seen to be diachronic” in the origination and extinction processes. Another two origination events are detected for MN12 and MN14, whereas the last two extinction episodes alternate with the origination peak in MN12. While the origination slowdown during the MN9 matches the Mid Vallesian Crisis (MVC), the MN13 extinction episode coincides with the Messinian Salinity Crisis (MSC). Consequently, the origination rate is usually higher than the extinction rate during the early and middle Miocene, reversing the trend during the beginning of the late Miocene, when extinction and origination show an alternating pattern, but with the former prevailing over the latter.

Therefore, the turnover rates are driven by high origination during the early and middle Miocene and are interchanged with extinction-dominated replacement in the late Miocene and early Pliocene (Figure 3C). The maximum diversification rate occurs during MN4, followed by another positive peak in biozone MN7/8. The diversity decline with extinction-driven turnover began in the Late Miocene (MN9). This trend was reversed during MN12. The last turnover pulse is detected in MN14 (Early Pliocene), following the sharp drop in diversity of MN13 (with the above mentioned precautions resulting from the low preservation rate).

Our FA yielded six carnivore evolutionary faunas, which explained 77.2 % of the original variance (Figure 4).

CARNIVORE ASSOCIATION I (MN2-3).Prior to MN2 there are no localities with carnivores in the Spanish Miocene, resulting in an important gap in the record of the group since the Late Oligocene. The early Miocene carnivore association is relatively close to the contemporary associations registered in Western/Central Europe, with a predominance of primitive Hemicyonidae and Amphicyonidae (Dehm 1950; Ginsburg and Morales 1998; Fejfar et al. 2003). There is, however, a significant difference in the

Spanish associations regarding those of western Europe, due to the absence of Ursidae (Abella et al. 2014).

CARNIVORE ASSOCIATION II (MN 4-7/8).This period is characterised by a significant increase in origination, occurring during MN4. Some of the genera can be considered as immigrants from Africa or the southern areas. This is the case of *Afrosmilus*, the first European Barbourofelidaea (Morales et al. 2001) and *Hyainailourus*, the only creodont recorded in the Miocene faunas from Spain (Ginsburg 1980; Morales et al. 1998), and probably for *Sivanasua,* because of its Viverridae affinities (Fejfar and Schmidt-Kittler 1997). From biozones MN5 to MN6 a significant drop in diversity arises (Figure 2 b, C; Table 2). But the most remarkable event involves the first appearance of the true Ailuridae, with *Magerictis* (Ginsburg et al. 1997). The faunas from both these biozones were homogeneous, with a dominance of Hemicyonidae and Amphicyonidae. Finally, during MN 7/8 the first ursids appear in the Spanish record, a family absent in previous faunas (Crusafont and Kurtén 1976; Abella et al. 2014); this coincided with the beginning of the Hyaenidae cladogenesis, with a significant increase in its diversity (Table 2), and with the extinction of Hemicyonidae at the end of the biozone. Interestingly, most of the localities of this biozone involve the Catalan coastal basins. However, the remaining scarce sites from other basins show a remarkable similarity to those of the Vallès-Penedès basin (Abella et al. 2011; 2013).

CARNIVORE ASSOCIATION III (MN 9). During this biozone the overall maximum diversity rate is reached. The emergence of the Machairodontinae (Ginsburg et al. 1981; Salesa et al. 2010), together with the extinction of their ecological counterparts, the Barbourofelids, constitute two of the most significant phenomena during this biozone. This diversity increase is largely caused by the presence of singleton taxa, many of which almost exclusively occur in localities of the Vallés-Penedés. Indeed, the maximum total diversity reached during MN9 coincides with a low preservation time lapse, which, in some way, accentuates the singularity of this great diversity pulse.

CARNIVORE ASSOCIATION IV MN (MN 10-11).This period is marked by a progressive decline in diversity. The extinction of the Amphicyonidae is among the most important events to occur during MN 10 (Peigné et al. 2008), implying the loss of one of the most iconic groups of the Miocene record. This gradual decrease in diversity continues until the end of MN 11, resulting in one of the lowest diversity records of the whole Miocene.

CARNIVORE ASSOCIATION V (MN 12-13).During biozone MN12 two important immigrants arrived on the Iberian Peninsula: *"Canis" cipio* (Crusafont 1950; Pons and Crusafont 1978), the first Canidae with the oldest unequivocally American origin, and of the mostprobable Asian *Percrocuta gigantea* (Soria 1980). During this period, eastern immigrants such as *Eucyon* and *Agriotherium* have their first record. This biozone has even been postulated to record a faunal exchange event between the Iberian Peninsula and North Africa (Van der Made et al. 2006; Gibert et al. 2013; Morales et al. 2013), with a major extinction episode, which particularly affected two dominant groups of carnivores: the Hyaenidae and the Machairodontinae, which had been representative of Vallesian and Early Turolian faunas.

CARNIVORE ASSOCIATION VI (MN 14-17).This evolutionary fauna is characterized by a low diversity at all taxonomic levels, with the presence of no more than five families. Nevertheless, a new association of carnivores emerges throughout Eurasia. In Spain, new forms of hyaenids, felids and canids, clearly related to the current representatives of these families (Alcalá 1994; Morales et al. 2003), are recorded. Additionally, the presence of the modern bear *Ursus* in North America emphasizes the Holarctic character of this association (Hunt 2004). During MN 16-17 Villafranchian carnivore faunas show a very low diversity level, even lower than during the middle and late Miocene. Towards the end of this period, a significant extinction event occurred in the Iberian basins, affecting some of the typical genera of this age, such as *Nyctereutes*, *Caracal* and *Chasmaportetes*. The latter was the only member of the hyaenids to migrate across the Bering Strait to North America during the Pliocene (Antón et al. 2006).

Discussion

During the Neogene and early Pleistocene, significant fluctuations in the taxonomic diversity of carnivores occurred in Spain. In general terms, synchronic origination and extinction events took place during the first part of the Neogene (between 20-10 Ma). Subsequently, both processes alternate successively. Biases in the fossil record resulting from preservation rate fluctuations could explain part of this alternation between originations and extinctions. Indeed, the macromammal diversity crisis during MN13, also detected by Casanovas-Vilar et al. (2010), might be magnified by a low preservation rate. The long duration of the MN13 unit, together with its relative scarcity of fossil sites recording large mammals (including carnivores, Morales et al. 2013), may be responsible for such low preservation rates. Nevertheless, the drop in diversity after MN 9 appears to be caused by a continuous phase of subsequent extinctions, rather than by low preservation rates. Notably, our analyses would appear to indicate that preservation is not biasing estimates of origination and extinction rates. Additionally, our results are highly congruent with those reported by Casanovas-Vilar et al. (2010), whose study encompasses faunas from MN5 to MN13. Therefore, our general pattern of turnover rates is close to the one described by these authors (Casanovas-Vilar et al. 2014 Fig. 2A), with the exception of the Turolian, in which different diversity values were obtained. By contrast, we found extinction-driven and origination-driven replacements during MN11 and MN12, respectively. Minor differences exist on comparing our results with those of Domingo et al. (2014), regardless of the different biochronological frameworks used in the two studies (MN units vs Maximum Likelihood Appearance Event Ordination). From 12 to 5.5 Ma, the turnover rate curve shows a “W” pattern with the three peaks corresponding respectively to MN7/8, MN10 and MN13 and two moderate troughs drops during MN9 and MN11. The turnover curve published by Domingo et al. (2014), whose analysis also includes herbivores, shows a similar pattern, with three peaks during the 11.7 Ma, 9.7-8.7 and 5.7 Ma, and two slowdowns at 11.3-9.7 and 7.2 Ma.

Hereinafter, we will place our findings within a broad climatic and biogeographic context at different scales and discuss their potential role in the patterns described (Figure 5). If compared with the European record (Ginsburg 1999), the MN2 and MN3 Spanish carnivore associations show a similar abundance of Hemicyonidae and

Amphicyonidae, and also present some members of the Felidae and Hyaenidae families. However, slight differences are found, such as, for example, the absence of Ailuridae, Mustelidae, and Ursidae. Some of these differences may be due to biases in the fossil record. Nevertheless, the persistent absence of Ursidae until the end of the middle Miocene could be associated with broad-ranging environmental conditions (Abella et al. 2014). High temperatures and variable relative humidity were recorded for mostof the MN2 and MN3 association. Pulses of high humidity, markedby the presence ofcrocodiles andtapirs, have been detected throughout biozone MN2 and much of MN3 (Pickford and Morales 1994; Cerdeño and Ginsburg 1988). However, the insectivore and rodent associations indicate a change towards lower humidity and temperature close to the end of MN3 (Van der Meulen and Daams 1992; Daams et al. 1997; Alcalá et al. 2000; Van Dam 2006).

During the MN4 we found a major turnover pulse. It is characterized by high temperatures, starting with the Middle Miocene Climatic Optimum (MMCO) (Zachos et al. 2001; 2008), which includes all the MN4. High temperatures and humidity have been inferred for the Iberian basins based on rodent associations. However, beavers disappear after the MN3 localities (Van der Meulen and Daams 1992), and MN 4 appears to show an initial opening of the landscape, with the appearance of the first bovids. Humidity was definitely greater than in the Middle Miocene (Daams et al. 1997; Alcalá et al. 2000).During this first Aragonian biozone, the Iberian Peninsula was located at the northern limit of the boundary zone between the Proto-Ethiopic and Proto-Palearctic biogeographic regions (LBZBR), implying greater ease in the faunal exchanges between both domains, and enabling the development of biogeographic corridors (Pickford and Morales 1994). In Spain,the appearance of the first Barbourofelidae, *Afrosmilus*, and the creodont *Hyainailourus*, or the dispersal events of *Sivanasua*, support this conclusion.

Through most of the MN5 biozone, high temperatures still prevailed, and the carnivore association shows a remarkably low diversity level. Rodent associations are interpreted as indicators of very arid environments (Daams et al. 1997; Alcalá et al. 2000), and maximum aridity was reached ca. 13.5-14.5 (Van Dam 2006). Close to the end of MN5 a short episode of cooling occurred, known as the Middle Miocene Cooling (MMC), which can be recognized in the Madrid Basin faunas (Van der Meulen and Daams 1992; Hernández Fernández et al. 2006; Domingo et al. 2009; 2012). Nonetheless, the carnivore associations show no major changes during MN6, having apparently been unaffected by this fluctuation. However, an increase in both humidity and temperature is detected throughout this biozone, although the MMCO values are not reached. Why there are almost no changes in the carnivore associations remains unclear, particularly when considering the significant change in composition of the grazing associations between the so-called “*Hispanotherium* faunas”, which characterized the MN5 biozone, and the “*Alicornops* faunas”, established since MN6 (Sanisidro et al. 2012; Cerdeño and Iñigo 1997; Cerdeño and Nieto 1995; Peláez-Campomanes et al. 2003).

An increase in the turnover rate took place during MN7/8. Although mean temperatures remained virtually unchanged, precipitation levels showed a substantial increase during MN7/8 compared to the previous biozone (Van Dam 2006). At this time, the LBZBR returns to a very northern position, thus favouring new faunal exchanges both in the N-S and the E-W axes (Pickford and Morales 1994). The first ursid appearance in the Spanish record may result from this increase in humidity, related to a subsequent development of closer environments, which would also have affected the Hemicyonidae extinction (Abella et al. 2014). Interpretation of the Hyaenidae origination recorded in this association is much more complex, but it might also be favoured by the position of the LBZBR. The appearance of primates and giraffes in the Spanish basins also supports the latter argument (Crusafont 1952; Marigó et al. 2014)

At the beginning of the Vallesian, a long period of turnover fluctuation rates was installed, which lasted until the end of the Miocene. During the first part of this interval (MN 9) a gradual decrease in temperature coincided with an increase in humidity, which reached very high scores at the beginning of late Miocene (10-9Ma). Diversity in the carnivore associations remained high, reaching maximum absolute values, and coinciding with a general increase in the biodiversity of other groups of large mammals (Morales et al. 1999; Casanovas-Vilar et al. 2010). The first appearance of Machairodontinae in the region characterises these carnivore associations. This subfamily coexisted in some localities with Barbourofelidae (Ginsburg et al. 1981; Robles et al. 2013), its ecological counterparts; this family became locally extinct during this period. Van Dam (2006) postulated the existence of a large humid zone presenting a homogeneous environment extending from northern Spain to Ukraine, the European Wet Temperate Zone (ETWZ), which favoured the immigration of *Hipparion* and *Sinohippus* (Garcés et al. 2003; Salesa et al. 2004).

During this period, a decrease in the diversity of carnivore associations is also detected; this is much more pronounced in the Catalan coastal basins. This decline in diversity has been termed the Mid Vallesian Crisis (MVC) (Moyà-Solà and Agustí 1987; Agustí and Moyà-Solà 1990), and involves the removal of most of the middle Miocene elements adapted to the warm and wet subtropical conditions in Western Europe (Agustí et al. 1999) as the result of a continued drop in temperature and humidity (see Casanovas-Vilar et al. 2014 for a critical opinion regarding the intensity of the crisis). The prevalence of arid conditions between 10-8 Ma, named by Van Dam (2006) as the Subtropical High Pressure Zone (SHPZ), could be one of the causes of this decline in diversity. The presence of the last members of the Amphicyonidae during MN 10 is one of the most important events in the Spanish carnivore associations, these being particularly abundant in the localities of Cerro de los Batallones (only represented by two species). The temperature and humidity fall persisted during MN 11, affecting the carnivore associations, which remained similar to those recorded during MN 10, dominated by large-sized species such as the Machairodontinae and Hyaenidae, but without Amphicyonidae, extinct in Eurasia and North America (Hunt 2004).

The MN12 carnivore fauna association experienced a moderate diversity recovery, and was dominated by the Machairodontinae and Hyaenidae and showing the oldest record of Canidae in Eurasia. The temperature is close to those recorded during MN 10/11, but the rodent associations indicate an increase in humidity, with the gradual re-establishment of the ETWZ, which continues during the first part of MN13 (Van Dam 2006).

The appearance of taxa from Asia and North America (the latter migrating via the Bering Strait), such as *Agriotherium* and *Eucyon,* is recorded during MN13 (Van der Made et al. 2006; Montoya et al. 2006; Montoya et al. 2009; Morales et al. 2013). The LBZBR returns to very northern position (Pickford and Morales 1994) and the establishment of a land bridge between the Iberian Peninsula and North Africa is recorded ca. 6.2 Ma (Gibert et al. 2013). This scenario, also favoured by the development of the ETWZ, enabled a global increase in faunal exchanges (Morales et al. 2013). Once again, the carnivore associations maintained the same features as in MN12, and were dominated by the Hyaenidae and Machairodontinae, the latter reaching their maximum diversity during MN13. The humid conditions started to change during a complex period culminated in the Messinian Salinity Crisis (MSC). This event has previously been recognised to deeply influence the mammalian faunas (Azanza et al. 2000; Domingo et al. 2013; Gibert et al. 2013; Gómez Cano et al. 2014). Unfortunately, the carnivore record for this period is too scarce on the Iberian Peninsula to relate both factors. The apparent disappearance of many carnivore taxa recorded during MN13 is likely the result of a shortage of sites between 6.2-5.1 Ma. In any case, the decline both in Hyaenidae and in Machairodontinae occurred during MN13.

At the beginning of the Pliocene (MN14-15) the Carnivore fauna underwent a profound change in composition and, although Machairodontinae and Hyaenidae are still abundant, they are represented by different lineages. Additionally, neither group constituted the dominant carnivores any longer, and they came to share this roll with the Canidae (*Canis*, *Nyctereutes*) and Felinae (*Caracal*, *Acinonyx*), thus lowering the diversity of the large carnivores (Alcalá 1994). Temperatures decreased progressively and the Spanish rodent associations indicate relatively arid conditions (Van Dam 2006; Hernández Fernández et al. 2007). Finally, during MN16-17 the Machairodontinae became rare, and new felines such as *Panthera* appeared. This carnivore association could be described as a typically "Villafranchian" fauna, presenting a wide-ranging geographical distribution throughout Eurasia and also indicating several faunal exchanges with both North America and Africa. Although it is beyond our temporal scope, it should be noted that during MN17 there was a significant period of extinction in the carnivore faunas (see Gómez Cano et al. 2013 for rodent assemblages),with the local demise of such representative forms as *Caracal*, *Chasmaportetes* and *Nyctereutes*, among other taxa.

Final remarks

Apparently, there is a relationship between diversity patterns and abiotic factors, i.e. local and global climatic shifts during the Neogene. However, researchers tend to use *ad hoc* explanations to link biotic and abiotic events. It is true that we mentioned the synchrony between, for instance, the MN4 turnover event and the MMCO, as well as the concomitancy between the deterioration of the carnivore assemblages during MN13, and the MSC. By highlighting such temporal connections we attempt to provide an environmental context rather than identifying the true and only drivers of the waxing and waning of these associations. Turnover pulses of carnivore faunas during the Neogene were most likely driven by several multi-layer and multi-scale factors.

Nevertheless, our results and those of previous researchers suggest that the pattern observed might have its primary trigger in the biogeographic and climatic shifts during the Neogene (Van Dam 2006; Pickford and Morales 1994). During MN4 and MN7/8, origination bursts took place when the Iberian Peninsula was located within a transition zone between the Proto-Palearctic and Proto-Ethiopian realms, the so-called Boundary Zone (Pickford and Morales 1994). This situation would have promoted the enrichment of the Iberian carnivore faunas through a wide array of biotic (e.g. migrations form Eurasia and Africa) and abiotic (e.g. a warmer climate) connections. After 11 Ma, origination bursts are recorded when the Iberia Peninsula was included in the Palearctic realm due to climatic fluctuations (MN9 to MN12). This reversed trend implies that the immigrants that enriched the Spanish carnivore faunas were mainly of Eurasian or American origin, as the ecological connections with Africa were not operating during such pulses. Additionally, more temperate environments could not have supported the diversity observed from 12.5 to 10 Ma. In general terms, this new climatic and biogeographic scenario at the broader scale brought about a marked impoverishment of the Spanish carnivores as from MN9. Indeed, future research addressing the macroevolutionary patterns of other Neogene mammalian groups of the Spanish basins, together with more detailed information on the local physical changes in their terrestrial environments (e.g. isotopic information), will shed valuable light on these connections, confirming or discarding our interpretations.

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Figures and tables caption

Figure 1 Chart of the Neogene-Early Pleistocene ranges and absolute diversity of carnivores families thorough time. Data source the same as the Table 2. MA= Mammals Age. MN Mein zones (De Bruijn et al. 1992). Extending data in the Suplementary Information.

Figure 2. A) Scatterplot of the number of localities against raw genera richness of each MN unit. B) Comparison of the observed (black) and estimated (grey) genera richness through time based on Lloyd's approach (see methods). C) Detrended diversity, this is, time series of residuals derived from our modelling approach. This method assumes true taxonomic richness is constant and apparent richness is rendered by sampling intensity (Lloyd 2012). In B and C dashed line indicates 1.96 standard errors and dashed–dotted line 1.96 standard deviations of the model.

Figure 3. A) Mean standing diversity (black) and preservation rate (orange) through time. B) origination (blue) and extinction (red) rates estimated for each MN unit. Their Kendall correlation with the preservation rate (p-values and taus) are shown. C) Faunal Turnover through time. Shadowed areas in (B) and (C) represent ± 1 standard deviation from the bootstrapped distribution. Note that, unlike raw diversity in Figure 2, mean standing diversity exclude singletons from the calculations.

Figure 4. Succession of carnivore associations through the Neogene according to our factor analysis. MN units are assigned to one of the associations based on the higher loading factor they obtain. Bellow, the three genera with the highest contribution (based on their scores) to each of the association is depicted.

Figure 5. Originations and extintions of significative taxa at the carnivore associations. MA, Mammals Age. MN Mein zones (De Bruijn et al. 1992). Black bars, turnover peaks (big asteric* denote maximums). White bars, turnover troughs. Temperature curve from Zachos et al. (2008). Humidity curve, from 2-13 Ma, modified from Vam Dam (2006), from 13 to 21 Ma, modified from Van der Meulen and Daams (1992); Daams et al. (1997; 1999) and Alcalá et al. (2000). The carnivore associations (I to VI) from the FA are also shown.

Table 1. Distribution of carnivores localities and genera per MN zones and basin. Time is the estimated duration for each zone. See López-Martínez (1989) and Calvo et al. (1993) for additional information about the Neogene Spanish continental basins. Extending data in the Supplementary Information.

Table 2. Number of family genera per MN Zones. Extending data in the Supplementary Information.

Supplementary information

Figure 1. Cenozoic basins from the Iberian Peninsula with carnivore fossil sites used in this study.

Table 1. Distribution of genera per MN zones. 1= Creodonta; 2= Amphicyonidae; 3= Canidae; 4= Ailuridae; 5= Hemicyonidae; 6= Ursidae; 7= Mustelidae; 8= Mephitidae; 9= Herpestidae+Viverridae; 10= Hyaenidae+Percrocutidae; 11= Barbourofelidae; 12= Felidae

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Figure1

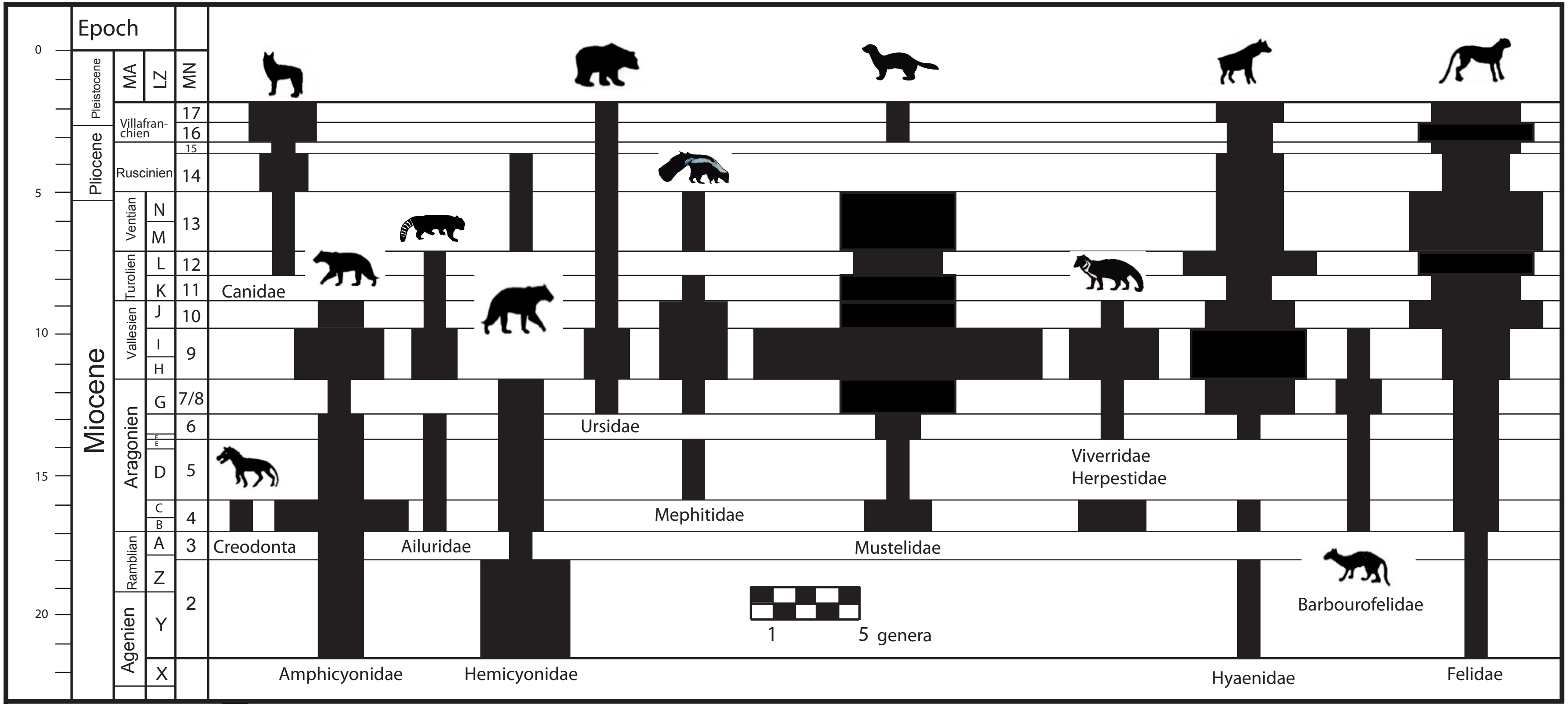

Epoch
0
5
10
15
20
Pleistocene
Pliocene
Miocene
MA
LZ
MN
Villafranchien
Ruscinien
Ventian
Turolien
Vallesien
Aragonien
Ramblian
Agenien
N
M
L
K
J
I
H
G
F
E
D
C
B
A
Z
Y
X
17
16
15
14
13
12
11
10
9
7/8
6
5
4
3
2
Canidae
Creodonta
Amphicyonidae
Hemicyonidae
Ailuridae
Ursidae
Mephitidae
Mustelidae
Viverridae
Herpestidae
Barbourofelidae
Hyaenidae
Felidae
1
5 genera

Figure2

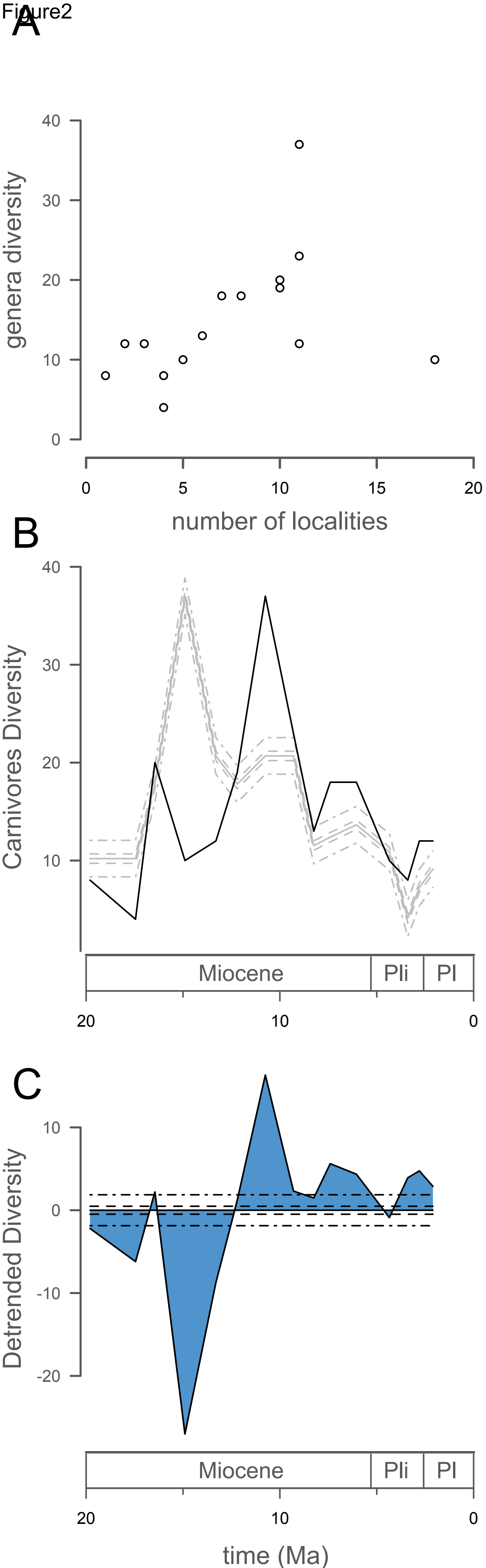

A
genera diversity
0
10
20
30
40
0
5
10
15
20
number of localities
B
Carnivores Diversity
10
20
30
40
Miocene
Pli
Pl
20
10
0
C
Detrended Diversity
10
0
-10
-20
Miocene
Pli
Pl
20
10
0
time (Ma)

Figure3

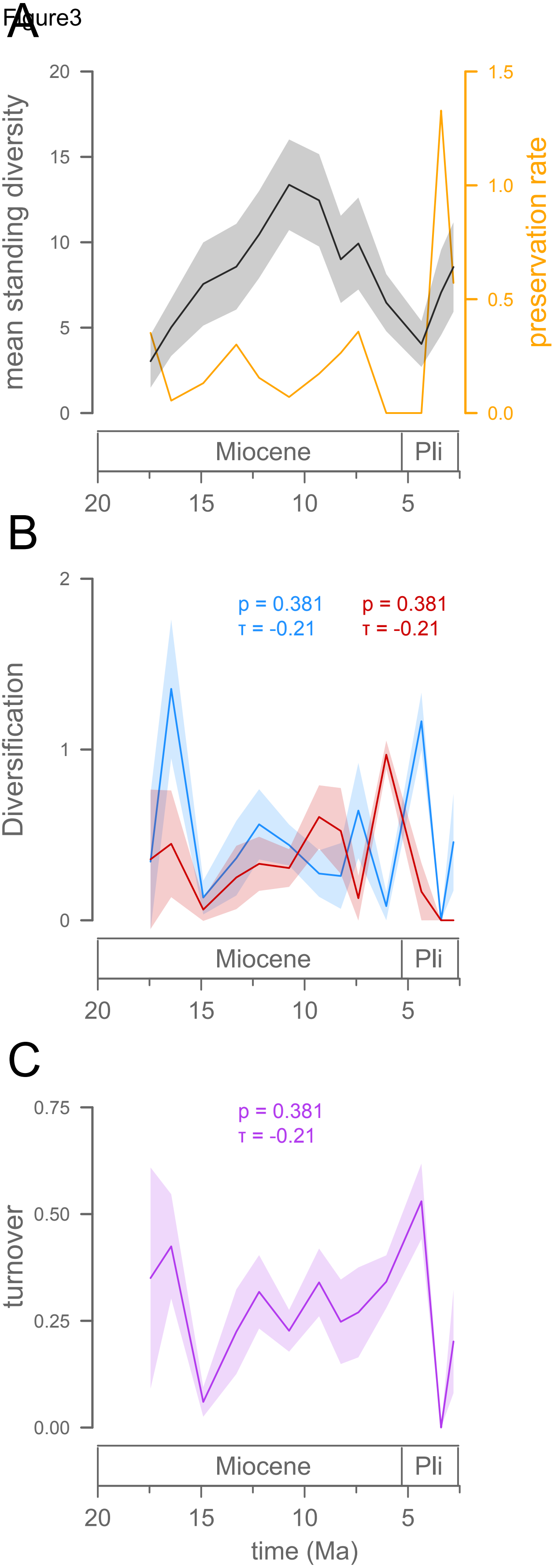

A
mean standing diversity
20
15
10
5
0
preservation rate
1.5
1.0
0.5
0.0
Miocene
Pli
20
15
10
5
B
Diversification
2
1
0
p = 0.381
τ = -0.21
p = 0.381
τ = -0.21
Miocene
Pli
20
15
10
5
C
turnover
0.75
0.50
0.25
0.00
p = 0.381
τ = -0.21
Miocene
Pli
20
15
10
5
time (Ma)

Figure4

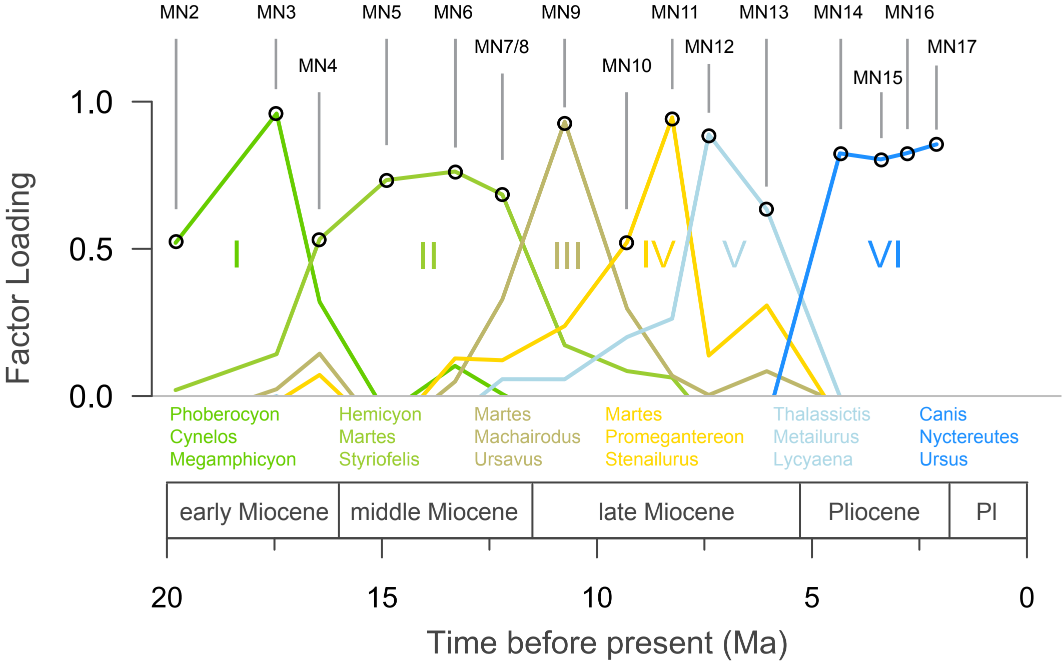
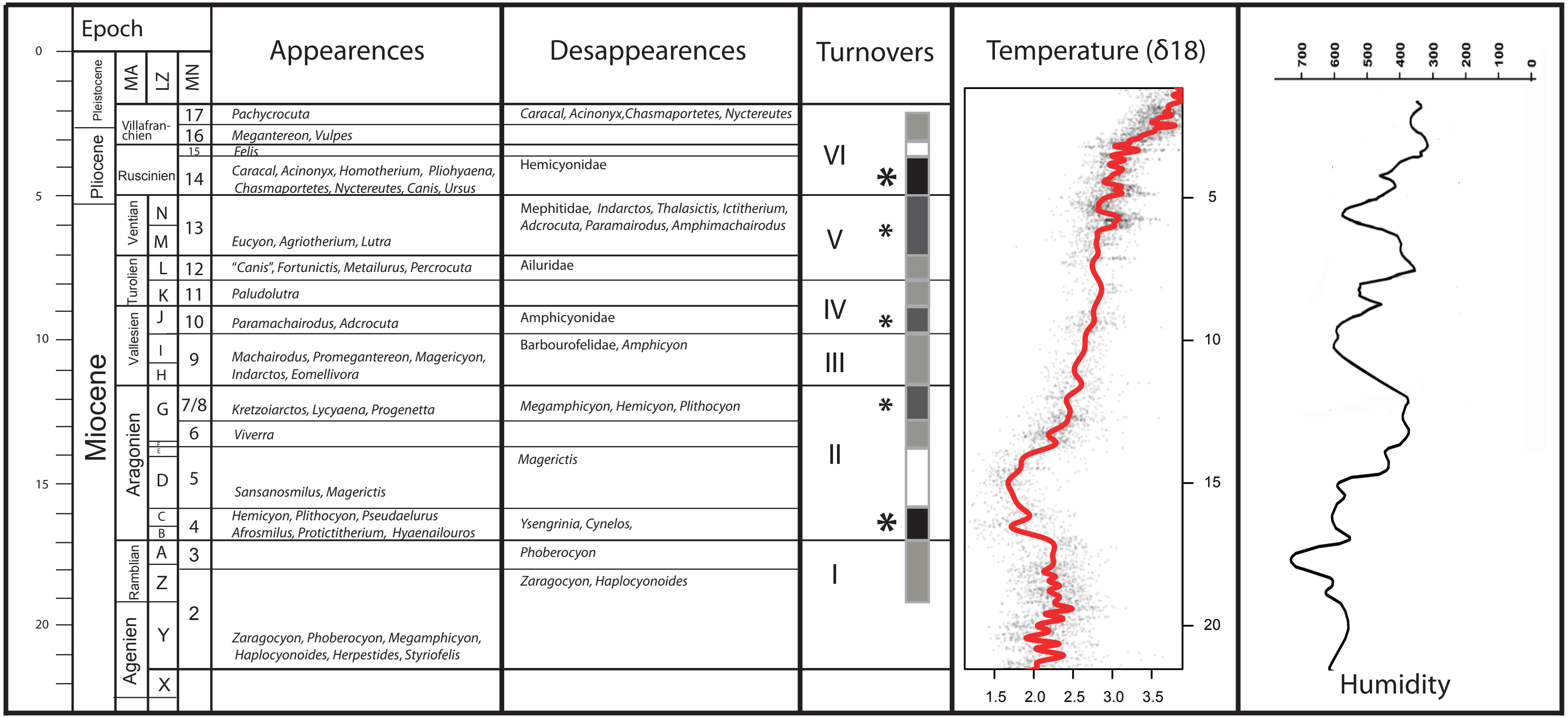

MN2
MN3
MN4
MN5
MN6
MN7/8
MN9
MN10
MN11
MN12
MN13
MN14
MN15
MN16
MN17
1.0
0.5
0.0
Factor Loading
I
II
III
IV
V
VI
Phoberocyon
Cynelos
Megamphicyon
Hemicyon
Martes
Styriofelis
Martes
Machairodus
Ursavus
Martes
Promegantereon
Stenailurus
Thalassictis
Metailurus
Lycyaena
Canis
Nyctereutes
Ursus
early Miocene
middle Miocene
late Miocene
Pliocene
Pl
20
15
10
5
0
Time before present (Ma)

Figure5


Epoch
MA
LZ
MN
Appearences
Desappearences
Turnovers
Temperature (δ18)
Humidity
0
5
10
15
20
Pleistocene
Pliocene
Miocene
Villafran-chien
Ruscinien
Ventian
Turolien
Vallesien
Aragonien
Rambian
Agenien
N
M
L
K
J
I
H
G
F
E
D
C
B
A
Z
Y
X
17
16
15
14
13
12
11
10
9
7/8
6
5
4
3
2
Pachycrocuta
Megantereon, Vulpes
Felis
Caracal, Acinonyx, Homotherium, Pliohyaena, Chasmaportetes, Nyctereutes, Canis, Ursus
Eucyon, Agriotherium, Lutra
"Canis", Fortunictis, Metailurus, Percrocuta
Paludolutra
Paramachairodus, Adcrocuta
Machairodus, Promegantereon, Magericyon, Indarctos, Eomellivora
Kretzoiarctos, Lycyaena, Progenetta
Viverra
Sansanosmilus, Magerictis
Hemicyon, Plithocyon, Pseudaelurus Afrosmilus, Protictitherium, Hyaenailouros
Zaragocyon, Phoberocyon, Megamphicyon, Haplocyonoides, Herpestides, Styriofelis
Caracal, Acinonyx,Chasmaportetes, Nyctereutes
Hemicyonidae
Mephitidae, Indarctos, Thalasictis, Ictitherium, Adcrocuta, Paramairodus, Amphimachairodus
Ailuridae
Amphicyonidae
Barbourofelidae, Amphicyon
Megamphicyon, Hemicyon, Plithocyon
Magerictis
Ysengrinia, Cynelos,
Phoberocyon
Zaragocyon, Haplocyonoides
VI
V
IV
III
II
I
*
*
*
*
*
5
10
15
20
1.5
2.0
2.5
3.0
3.5
700
600
500
400
300
200
100
0

Basin / MN	MN2	MN3	MN4	MN5	MN6	MN7/8	MN9	MN10	MN11	MN12	MN13	MN14	MN15	MN16	MN17
Vallès-Penedès-Pirenaicas		1	5			3	7	3	1						
Ebro				1										1	
Duero-Almazán	1			1		3	1								
Calatayud-Teruel		1	1	2	3	4	3	2	2	7	3	2			1
Tajo-Meseta Meridional	3	2	3	15	8		1	6	1		2	2	1	1	
Levante/Andalucia			1						1	1	3	1			2
N. Localities	4	4	10	19	11	10	12	11	4	8	8	5	1	2	3
N. Genera	8	4	20	10	12	19	37	23	13	18	18	10	8	12	12
Time	3.6	1.1	0.9	2.2	1.0	1.2	1.7	1.2	0.9	0.8	1.9	1.5	0.4	0.8	0.6

Table2

Genera	MN2	MN3	MN4	MN5	MN6	MN7/8	MN9	MN10	MN11	MN12	MN13	MN14	MN15	MN16	MN17
Creodonta	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Amphicyonidae	2	2	6	2	2	1	4	2							
Canidae										1	1	2	1	3	3
Ailuridae			1	1	1		2	1	1	1					
Hemicyonidae	4	1	2	2	2	2					1	1			
Ursidae						1	2	1	1	1	1	1	1	1	1
Mustelinae			3	1	2	2	8	2	3	2	3				
Leptarctinae						1	1								
Melinae						2	2	2		1					1
Lutrinae							2	1	1	1	2			1	
Mephitinae				1		1	3	3	1		1				
Herpestidae/Viverridae			3		1	1	4	1							
Hyaenidae/Percrocutidae	1		1		1	4	5	4	2	6	3	3	2	2	3
Barbourofelidae			1	1	1	2	1								
Felidae	1	1	2	2	2	2	3	6	4	5	6	3	4	5	4
Total	8	4	20	10	12	19	37	23	13	18	18	10	8	12	12

Supplementary Material
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