**Impact of global climate in the diversity patterns of middle Miocene rodents from
the Madrid Basin (Spain)**

Verónica Hernández-Ballarín^{1*} and Pablo Peláez-Campomanes¹

¹*Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC, C/ José
Gutiérrez Abascal, 2 28006 Madrid, Spain.*

E-mail addresses: verohernandez@mncn.csic.es, pablopelaez@mncn.csic.es

*Corresponding author. Email: verohernandez@mncn.csic.es

26 **Abstract**

27 Remarkable palaeoclimatic global changes have been recorded worldwide
28 during the middle Miocene. The Miocene Climatic Optimum (~16.3 to ~15 Ma), one of
29 the warmest phases since the Eocene, was followed by the stepwise cooling trend of
30 the Middle Miocene Climate Transition (~15 to ~13.7 Ma). The entry into an Earth “Ice-
31 house” climate state took place at the end of the latter (~13.76 Ma) marked by one of
32 the major cooling steps in middle Miocene climate recorded at a global scale (Mi3b
33 event). The Madrid Basin, which is part of one of the main Cenozoic basins of the
34 Iberian Peninsula, contains a well-represented small-mammal record from the lower
35 middle Miocene to the upper middle Miocene (middle and upper Aragonian, ~15.9 to
36 12.8 Ma), being an appropriate region to check how these climatic phases influenced
37 the distribution of the mammalian faunas on the center of the Iberian Peninsula.
38 Values of species richness, equitability and heterogeneity of rodents have been
39 calculated for 25 localities of the Madrid Basin and compared to detailed climate
40 isotope records from the marine realm (ODP Site 1146 from the South China Sea and
41 the Mediterranean record of the Ras Il Pellegrin section on the Maltese Islands) and
42 with palaeoprecipitation curves for southwest Europe (Calatayud-Montalbán Basin).
43 The results show that the rodent community during the middle and upper Aragonian in
44 the Madrid Basin was subject to the changing climate conditions imposed in the course
45 of the middle Miocene. The palaeoecological curves witness periods of disturbance of
46 the community during changing climate conditions (marked by important drops in
47 equitability and, in some cases, gradual decreases in heterogeneity and species
48 richness), followed by periods showing a recovery of the community and adaptation to
49 the new climate circumstances (represented by more evenly distributed and diverse

assemblages). The effects of the Miocene Climate Optimum and of three Mi-events (Mi2b, Mi3a and Mi3b) have been related to changes in the small-mammal community. Between ~15.8 to 15.3 Ma, the likely extreme environment (high temperature and low precipitation) of part of the Miocene Climate Optimum may have imposed severe constraints on the fauna, resulting in a community with low values of equitability, heterogeneity and a decreasing number of species. The transition of the Miocene Climate Optimum to the Middle Miocene Climate Transition, reflected by the Mi2b event, have also procured a destabilization of the rodent assemblages, as an important drop in equitability is recorded between ~15 to 14.6 Ma. In this interval, the drop in temperature and increase in rainfall derived from the Middle Miocene Climate Transition promote the southwards migration of northern invaders, leading to an increase in species richness in the Madrid Basin. Starting around 14.4 Ma, the onset of a progressive drop in the rodent equitability and heterogeneity, which also coincides with a major stratigraphic discordance in the basin, is related to the first cooling step of the Middle Miocene Climate Transition (Mi3a event). Finally, the major cooling step in middle Miocene climate recorded at a global scale (Mi3b event) is poorly reflected in the palaeoecological curves. However, the taxonomical study of the rodent faunas of that interval (biozone E) has shown turnover rates and morphometric changes that indicate that this period represents one of the most variable in assemblage composition within the Aragonian. Although the Mi3b event has been correlated for a long time to the substitution of the early-middle Aragonian fauna by a late Aragonian community (E-F boundary), the study of the rodent assemblages of the Madrid Basin may point out that small changes in the small-mammal community started before (within biozone E).

Keywords: Palaeoecology, Mammals, Aragonian, Mi3b event, Middle Miocene Climate Transition, Miocene Climatic Optimum.

1. Introduction

The middle Miocene represents an interval of changing climate conditions within the Cenozoic climate evolution. The Miocene Climatic Optimum (MCO; ~16.3 to ~15 Ma), was a warm phase punctuating the overall cooling trend since the Eocene. Global ice volume during the MCO was low and bottom water temperatures were slightly elevated (Zachos et al., 2001). It was followed by the Middle Miocene Climate Transition (MMCT; ~15 to ~13.7 Ma), which represents the second of three major cooling steps of the Cenozoic. It is characterized by a stepwise cooling trend, in which two different cooling phases can be recognized; a first relatively small step at ~14.2 Ma (Mi3a event) and a second major step between ~13.95 and 13.76 Ma (Mi3b), which marks the end of the MMCT with a sharp and fast drop in temperature marking the entry into an Earth “Ice-house” climate state (Miller et al., 1991; Flower and Kennett, 1994; Miller and Mountain, 1996; Zachos et al., 2001; Shevenell et al., 2004; Abels et al., 2005; Holbourn et al., 2007; Mourik et al., 2011). Apart from temperature shifts, variations in the humidity conditions have also been quantified during this time interval in mid-European latitudes. According to palynological studies, palaeotropical plants along with conifers dominated the subtropical landscapes at the onset of the MCO (Barrón et al., 2010). From the MCO onwards, the palaeotropical flora became scarce, and Arcotertiary plants began to take more importance as seasonality, trend towards lower temperatures and reduction in rainfall became more pronounced (Postigo Mijarra et al., 2009). Grasses became also common from the early Aragonian,

giving rise to great prairies or steppes in the centre of the Iberian Peninsula (Barrón et al., 2010). In accordance with this, the palaeoprecipitation curves obtained for southwest and central Europe from the study of herpetological assemblages indicate a relatively wet interval during the early middle Aragonian, and relatively dry periods during the late middle and late upper Aragonian (Böhme et al., 2008, 2011).

Although the trigger mechanisms of the climate shifts during the middle Miocene are mostly unknown (Raymo and Ruddiman, 1992; Flower and Kennett, 1994; Shevenell et al., 2004; Shevenell and Kennet, 2004; Holbourn et al., 2005, 2007), profound global effects in mid- to high- latitudes have been recorded worldwide in the marine as well as in the continental record: large fluctuations of sea level, important changes in deep water circulation, variations in the temperature gradient, and changes in the faunal distributions (Flower and Kennett, 1994).

To investigate the influence of the changing climate conditions during the middle Miocene on the distribution of the mammalian faunas on the Iberian Peninsula, we have compiled a small-mammal dataset from the Madrid Basin covering most of the middle Miocene. The Madrid Basin contains a well-represented mammal record between ~15.9 to 13.6 Ma, making it an appropriate region to check how these climatic changes influenced the distribution of the mammalian faunas.

The aims of this work are (1) to establish trends in species richness, equitability and heterogeneity of rodents along the middle Miocene of the Madrid Basin, (2) to compare this record with detailed climate isotope records from the marine realm, ODP Site 1146 from the South China Sea (Holbourn et al., 2005, 2007) and the Mediterranean record of the Ras Il Pellegrin section on the Maltese Islands (Abels et al., 2005; Mourik et al., 2011), as well as with palaeoprecipitation curves for southwest

Europe (Calatayud-Montalbán Basin) (Böhme et al., 2008, 2011) and (3) to identify possible correlations in the trends and events observed.

2. Materials and Methods

2.1. Material, dataset and temporal resolution

The study is based on 25 small-mammals fossil localities from the Madrid Basin (Fig. 1, Table 1) that span most of the middle Miocene. The fossil record shows a high temporal resolution between ~15.9 to ~13.6 Ma, and is less dense between ~13.6 to ~12.8 Ma. Biochronological dating of the localities is established following Hernández Ballarín (2016) and Hernández-Ballarín and Peláez-Campomanes (2017), where localities are arranged and correlated to the local biozones proposed in the Calatayud-Montalbán Basin by Daams et al. (1999a) and modified by Van der Meulen et al. (2012), which are firmly tied to the palaeomagnetic time scale. The dataset used to perform the study comprises specimen counts of first and second molars of the families Sciuridae, Gliridae and Cricetidae from the 25 sites from the Madrid Basin (Table 1). Localities containing low numbers of specimens, having strong taphonomical biases or sites presenting signs of possible sample biases (such as those derived from the use of non-appropriate methodologies in the sample processing) are excluded from the analyses. As not all dental elements are taxonomically identifiable at the species level, and to avoid an over-representation of the taxa that contain premolars in its tooth row, we counted only first and second molars to calculate relative abundances (Van de Weerd and Daams, 1978; Van der Meulen and Daams, 1992; Daams et al., 1999b). Teeth were counted irrespective of whether isolated or in a mandibule, and only if at least half of the tooth was present. The total sample size is of

5841 teeth belonging to nine rodent genera and including 26 species. The calculations are carried out at the species level.

Figure 1. Geological scheme of the Madrid Basin. The Miocene basin filling consists of detritic facies accumulated by alluvial fans in the margins, and carbonatic and evaporitic sediments deposited by lacustrine systems in the central parts of the basin (limit between them marked with a dashed line). The main materials of the sedimentary filling are provided by the alluvial fans coming from the Central System, the Toledo Mountains and the Iberian Range (black arrows). On the upper left corner the Tertiary basins of the Iberian Peninsula; studied area marked with a rectangle.

161

162

Footnote: Table 1 consists in specimen counts of first and second molars of each species in each locality. Localities are arranged and correlated to the local biozones proposed in the Calatayud-Montalbán Basin (Daams et al., 1999a; van der Meulen et al., 1999a; van der Meulen et al., 2012; Hernández-Ballarín and Peláez-Campomanes, in prep.). Inferred ranges of each species are shaded in blue.

2.2. Diversity

We used three indexes to describe the diversity present in the different fossil associations recorded in the Madrid Basin. We followed Peet (1974) and use the three components of diversity he described: Species richness, equitability and heterogeneity.

2.2.1 Species Richness

Species richness of the rodent community is calculated for each locality. Three different measures are taken: observed, rarified and inferred species richness (Fig. 2 and Table 2). The first one, observed richness, comprises the number of species recorded at each site without removing the bias introduced by sampling differences. As expected, this measure is strongly linked to sample size, so that localities with large number of specimens show high number of species. In order to assess species richness independent of sample size we calculated the second measure, rarified richness. We used individual rarefaction, where the sample size is standardized, estimating the number of species in a locality for a particular number of specimens. We have obtained individual rarefaction curves using the software PAST version 1.68 (Hammer et al., 2001) for four different numbers of individuals: 39, 50, 80 and 100. We used the curve obtained with 39 specimens, as it contains the minimum number of specimens which faithfully represents rarified species richness and allows including the maximum number of fossil localities. In applying rarefaction two assumptions are required: 1) samples should be taxonomically similar and taken from comparable sedimentary environments; 2) the collections must have been obtained using standardized sampling procedures. Our dataset meets both requirements. The rodent community is similar at

the generic level in all the sites included in the analyses, with some first appearances and last occurrences that give rise to the addition or absence of species in some localities. The facies where the localities were found are also similar; the bulk of the sites correspond to distal, middle and transitional facies of alluvial fans (Hoyos et al., 1985; López-Martínez et al., 1987; López Olmedo et al., 2004; Cuevas González, 2005), and only two localities (El Cañaveral and Casa Montero) could be linked to lacustrine facies (Barrón, 2007). All the samples were recovered using the screen-washing method described by Daams and Freudenthal (1988). Finally, the third measure, inferred richness, allows determining the species richness in a given locality taking into account the inferred range of each species. It is expected to be less influenced by sample size. To estimate the inferred range of a given species we have used an approach that calculates the probability of finding a given taxon taking into account its abundance and the sample size. Here we followed the method devised by Barry et al. (2002) and modified by Van der Meulen et al. (2005):

$$P_i = 1 - (1 - p_i)^r, \quad (1)$$

Where P_i is the probability of finding the taxon i in the localities adjacent to those containing the observed first or last occurrence, p_i is the relative abundance of the taxon i in the locality where it was first or last recorded, and r is the number of specimens in the localities for which the probability of taxon i being there is estimated; r is cumulative. Thus, P_i is here calculated for each locality. In the cases where a species disappears from the record and re-appear after some time, we used the lower frequency found in the localities adjacent to the gap to calculate P_i . Following Barry et al. (2002), a species is considered to be absent when the calculated P_i is greater than 0.8. In a few cases, when the taxon is very rare in the locality where it was first or last

recorded, its inferred range will usually be long, unless the sample size of the succeeding or preceding localities is large enough to reject that it was actually present. We closed all gaps caused by absence in a single intermediate locality (because they may result from chance), and only then we closed remaining gaps if the time span in-between is $\leq 200,000$ years (Van der Meulen et al., 2005).

Most of the published studies involving calculations of sampling probability and inferred taxon ranges require assigning an absolute age to each locality. Then, the time span studied is divided in 0.1 or 0.5 Myr bins, assigning each locality to a single interval (Barry et al., 2002; Van Dam et al., 2006; Casanovas-Vilar et al., 2014). However, the lack of magnetostratigraphic data in the Madrid Basin (only the localities of Paracuellos and Villaluenga are placed in magnetostratigraphical sections) does not allow us to establish an accurate relative age for each locality. Despite this, the inferred ranges obtained seem to be consistent enough. The inferred ranges of each species are shaded in blue in Table 1.

Besides the three richness measures (observed, rarified and inferred richness), percentages of each genus in each site are calculated (Table 2) and represented for localities whose sample size is larger than 50 specimens (Fig. 3).

Figure 2. Biochronological position of the localities included (Hernández Ballarín, 2016; Hernández-Ballarín and Peláez-Campomanes, 2017), showing its sample size (grey bar-chart), richness measures (observed, rarified and inferred), equitability and heterogeneity values. Grey horizontal lines in the equitability and heterogeneity indices represent maximum and minimum values for each locality. Due to the lack of magnetostratigraphical data (only available for PA5, PA3 and VLL), black rectangles to the left of the localities represent the age range in which the locality is situated.

Table 2. Values of species richness, equitability, heterogeneity and the relative abundances of the rodent genera for each locality.

			Absolute age (Ma)	Sample size	Observed richness	Rarefied richness (n=39)	Inferred richness	Equitability (D/Dmax)	Heterogeneity (1/Simpson)								
										% <i>Megacricetodon</i>	% <i>Democricetodon</i>	% <i>Arvantomys</i>	% <i>Microdromys</i>	% <i>Simplomys</i>	% <i>Pseudodromys</i>	% <i>Heteroxerus</i>	% <i>Atlantoxerus</i>
Upper Aragonian	G2	Paracuellos 3	12.8	217	6	4,33	7	0,28	1,66	76,0	3,7	14,7	1,4	-	-	4,1	-
	G1	Villaluenga	13.4	25	6	-	9	0,37	2,19	64,0	20,0	4,0	8,0	-	-	4,0	-
	F	Alhambra-Túneles	-	103	6	5,19	9	0,26	1,59	81,6	7,8	4,9	-	-	-	5,8	-
		Paracuellos 5	13.7	39	5	5	9	0,41	2,06	71,8	-	7,7	2,6	-	-	17,9	-
Middle Aragonian	E	Henares 1	-	21	5	-	9	0,46	2,31	66,7	19,0	4,8	-	-	-	9,5	-
		Carpetana	-	354	8	5,39	9	0,27	2,20	65,8	16,9	9,3	1,4	-	-	6,5	-
		Casa Montero	-	1232	8	4,14	8	0,27	2,17	62,4	25,4	4,9	6,5	-	-	0,8	-
		Somosaguas Sur	-	340	8	5,87	9	0,32	2,58	57,6	22,1	5,6	11,2	-	-	3,5	-
	Dd	El Cañaveral	-	1431	9	5,65	10	0,27	2,45	59,6	20,0	8,7	5,5	2,0	-	4,2	-
		Las Musas 7	-	162	7	4,29	8	0,41	2,87	47,5	20,4	1,9	0,6	0,6	-	29,0	-
		Torrijos 2	-	65	7	6,02	8	0,54	3,80	26,2	33,8	6,2	1,5	3,1	-	29,2	-
		Henares 2	-	68	7	6,46	9	0,50	3,48	45,6	10,3	10,3	1,5	8,8	-	23,5	-
	Dc	O'Donnell	-	386	8	6,46	9	0,45	3,60	35,2	38,3	6,0	5,4	2,3	-	12,7	-
		La Alameda	-	457	9	4,71	9	0,25	2,30	58,6	30,0	1,1	7,7	0,2	-	2,4	-
Lower Aragonian		Estación Imperial	-	39	8	8	10	0,46	3,65	15,4	7,7	48,7	2,6	7,7	-	15,4	2,6
		Paseo de las Acacias	-	96	9	7,1	10	0,36	3,21	46,9	3,1	29,2	7,3	7,3	-	5,2	1,0
		Gasómetro 6	-	48	7	6,56	10	0,30	2,13	66,7	2,1	14,6	4,2	2,1	-	10,4	-
		Los Nogales	-	130	9	6,89	10	0,51	4,61	33,8	20,0	23,1	5,4	1,5	-	15,4	0,8
		Paseo de la Esperanza 7	-	17	6	-	10	0,50	2,98	52,9	5,9	29,4	5,9	-	-	5,9	-
		Moratines	-	18	4	-	8	0,86	3,45	27,8	-	22,2	-	11,1	-	38,9	-
		Puente de Segovia 9	-	50	6	5,73	8	0,57	3,44	40,0	2,0	18,0	-	8,0	-	32,0	-
		Atocha-Pedro Bosch	-	30	5	-	8	0,31	1,53	80,0	3,3	10,0	-	3,3	-	3,3	-
	Db	By Pass Sur Tunel Sur	-	339	9	4,43	9	0,18	1,64	77,0	7,7	4,1	0,3	0,6	0,3	9,7	0,3
		Puente de Praga 92	-	39	7	7	11	0,27	1,87	82,1	10,3	-	2,6	-	2,6	2,6	-
		Puente de Praga 16	-	135	7	5,33	9	0,47	3,27	74,8	4,4	0,7	0,7	-	14,8	4,4	-

Figure 3. Relative abundances of rodent genera for the middle and upper Aragonian from the Madrid Basin. Only localities with sample size larger than 50 specimens are shown.

2.3.2 Heterogeneity

Heterogeneity is a diversity concept that measures the functional number of species in a community (Peet, 1974). According to the latter author, heterogeneity is the result of the contribution of two components: the number of species (species richness) and the distribution of individuals among those species (equitability). We have used Simpson's Inverse Index of Diversity [equivalent to N_2 of Hill (1971) and 2D the 'true diversity' of order 2 of Jost (2016)] to estimate the values of heterogeneity of the rodent assemblages of the Madrid Basin (Fig. 2, Table 2). In contrast to other heterogeneity indices (e.g, Shannon's index), Simpson's Index of Diversity is less sensitive to rare species, the dominant taxa contributing more to the final value of heterogeneity (Peet, 1974; Jost, 2006). As in the fossil record rare species are less probable to be recorded, Simpson's Index is one of the most appropriate in this case. The inverse of Simpson's index has the advantage of a very intuitive interpretation since it can be understood as the number of equally abundant species needed to produce the same heterogeneity present in the sample. In addition, since it is strongly dependent on dominant species, it is less correlated to sample size than other indexes based on entropy (Kempton, 1979). We use for the calculation of the calculation of the Simpson's inverse index the correction for finite samples proposed by Pielou (1969):

$$D = 1 / \sum [(n_i (n_i - 1)) / (N(N - 1))]$$

Being D the inverse of the Simpson's index, n_i the number of specimens of species i and N the total number of specimens. It ranges from one (lowest diversity, for a community of only one species) to the number of species in the community analyzed (highest diversity, for a community composed of species equally present).

2.4.3 Equitability

Equitability measures the evenness with which individuals are divided among the species present. Here it is calculated by taking the Simpson's Inverse Index and divided it by the maximum value possible if individuals in the community were completely evenly distributed:

$$\text{Evenness} = D / D_{\text{max}} \quad (2)$$

(Peet, 1974). In this work D_{max} is represented by the number of inferred species in each locality, instead of the observed number of species, as the latter is strongly influenced by sample size and would give biased values of equitability. Faunas with equitability close to one contain species with evenly distributed abundances, while faunas with equitability close to zero have generally one predominant species. The results of equitability estimated for the small-mammal assemblages from the Madrid Basin are shown in Figure 2 and Table 2.

3. RESULTS

3.1. Influence of sample size on the diversity indexes

Figure 2 shows an overview of the number of species calculated for each site with the three measures of species richness (observed, rarified and inferred), the equitability and heterogeneity values, and a bar-chart representing the number of specimens found in each locality.

A visual approach immediately shows that there is a clear correlation between sample size and observed richness; localities with larger sample sizes show higher numbers of species, while sites with low numbers of specimens show lower values of

observed species. Statistical analyses confirm the correlation of sample size with observed richness (Pearson value of correlation $p = 0.009$).

The curves of species richness based on the other two richness measures, rarefaction and inferred ranges, have no correlation with sample size, as can be seeing in Figure 2 and corroborated by statistical analyses (Pearson values of correlation: $p = 0.488$ for rarified richness and $p = 0.927$ for inferred richness).

The values of heterogeneity and equitability calculated are also independent of sample size (Pearson values of correlation: $p=0.429$ and $p=0.445$ for the heterogeneity and equitability indexes, respectively)

3.2 Species richness

As stated in the previous paragraph, observed richness is highly influenced by sample size. Fossil sites as El Cañaveral, of which the number of specimens is higher than 1000, show some of the maxima of species observed. However, it stands out other localities where the sample is smaller and where a relatively high number of species is collected (By Pass Sur Tunel Sur, Los Nogales, Paseo de las Acacias). The minimum of species observed is from the Moratines site, where the sample size is one of the smallest, with only 18 specimens.

When rarefaction is used to avoid biases caused by sample size, a different trend in the species richness turns up. The maximum value of species richness for a sample of 39 individuals is reached in Estación Imperial, while several localities show minimum values: By Pass Sur Tunel Sur, La Alameda, Las Musas 7, Casa Montero and Paracuellos 3. It stands out the sites By Pass Sur Tunel Sur and Casa Montero, which in

the observed richness showed relatively high values, and are among the lowest when rarefaction is applied. The whole curve of rarefaction does not show a clear general trend; it is an alternation of high and low values. However, it seems that a decrease in the number of species starts from the beginning of local zone Dd (~14.8 Ma) onwards.

When the probability of sampling is taken into account and the inferred ranges of the species are calculated, the gaps within the ranges of most of the species become continuous, with only a few showing an intermittent distribution (*Armantomys jasperi* or *Microdyromys* aff. *monspeliensis*) (Table 1). The latter species, when appears, is found in very low percentages, indicating that it is rare. It is important to note, that the number of inferred species in the localities of biozones F and G is higher due to the nature of the method. In this case, the species *Heteroxerus* nov.sp. is very rare in the locality where it was last recorded (Casa Montero site), and its inferred range is longer, as the sample size of the succeeding localities (biozones F and G1) are not large enough to reject that it was present (Table 1). Therefore, despite the graph (Fig.2) remains at nine species at the end of the sequence, we can safely assume that the actual number of species is lower. Taking this into account, the curve of species richness obtained from the inferred ranges represents a general trend of species loss along the sequence. The number of species is variable during the middle Aragonian, in which the curve fluctuates between low and high values, and starts diminishing from the end of the middle Aragonian (~14 Ma) onwards, reaching its minimum at the end of the sequence. More in detail, the species richness is high during local zone Db, decreases rapidly and remains low in the low and middle part of local zone Dc, peaking in the upper part. During biozone Dd a trend of species loss is visible, with low values

at the end of it, after which starts rising and peaking in El Cañaveral site. From there onwards a gradual decrease starts, with some periods of stabilization.

3.3 Equitability

The graph representing equitability (Fig. 2) is a series of low values (that reflect periods of disturbance for the community) followed by gradual rises (which represent a recovery and stabilization of the community). The oldest part of the record starts with a peak around 15.8 Ma of relatively high equitability, followed by a period with low values (~15.8 to ~15.3 Ma), where the genus *Megacricetodon* is the predominant species and represents almost 80% of the fauna (Fig. 3). After that, a gradual recovery in the equitability curve is observed and an interval with stable values is recorded (~15.3 to ~15 Ma). The species are almost evenly distributed along this time frame (Fig. 3). A period of destabilization occurred from 15 Ma to ~14.8 Ma (with an alternation of low and high values), resulting in a drop in equitability and a restoration of its values up to 14.4 Ma. The remaining part of the sequence, ~14.4 to 12.8 Ma, represents a gradual decrease in equitability, *Megacricetodon* becoming again the predominant genus, increasing from almost 50% to 80% of the fauna in the youngest part of the sequence.

3.4 Heterogeneity

The curve of heterogeneity estimated with the Simpson's Inverse Index of Diversity shows a similar pattern to that of equitability (Fig. 2). The oldest part of the record shows a peak of high heterogeneity (~15.8 Ma), followed by an interval of low values (~15.8 to ~15.3 Ma). A recovery is observed thereafter, and during most of the

middle Aragonian (~15.2 to ~14.4 Ma) heterogeneity values remain relatively high (just with two peaks of low heterogeneity in Gasómetro 6 and La Alameda sites). The last and most important step occurs from ~14.4 Ma onwards: a continuous decrease in heterogeneity starts and its values keep diminishing up to the end of the late Aragonian.

3.5 Relative abundances

The relative abundances of each species are shown in Table 2 and Figure 3. The genus *Megacricetodon* is predominant in all the record, comprising 80 % of the fauna at the beginning of the middle Aragonian, and going from 50% to 80% from ~ 14.2 Ma to the end of the late Aragonian. *Democricetodon* appears in low percentages during the first part of the middle Aragonian, but from ~14.6 Ma onwards it constitutes between 20-30% of the fauna. Among the glirids, *Armantomys* has been recorded during all the sequence, but shows its higher percentages in the central part of the middle Aragonian (~15.3 to ~14.8 Ma), where it represents 20-50% of the rodents. The other genera of glirids (*Simplomys*, *Microdyromys* and *Pseudodryomys*) occur in lower proportions, never exceeding 15%. Representatives of *Simplomys* are found continuously almost up to the end of the middle Aragonian. *Microdyromys* shows a most discontinuous record presenting higher percentages, but not exceeding 8% during part of the middle Aragonian (~15 to ~14.4 Ma), reaching ~12% at the end of it (14.1 to 13.8 Ma) and reappearing in the upper Aragonian (Villaluenga site). The genus *Pseudodryomys* is only found at the beginning of the middle Aragonian (biozone Db, ~15.8-15.7 Ma). The sciurids, which are represented by the genera *Heteroxerus* and *Atlantoxerus*, show very variable percentages. *Atlantoxerus* is only sporadically

recorded; it only appears between ~15.6 to ~14.8 Ma and always with percentages lower than 3%. *Heteroxerus* has a very continuous record, with two maxima during the middle Aragonian (between ~15.3-15.1 Ma and between ~14.6-14.2 Ma).

4. Discussion

The main palaeoecological changes in the small-mammal community from the Madrid Basin inferred by the palaeoecological curves coincide with the large climatic events and trends evidenced by the marine stable isotope record and the continental palaeoprecipitation curve (Fig. 4). The lowest part of the Madrid faunal succession (~15.8 to ~15 Ma) corresponds to the Miocene Climate Optimum (MCO) and correlates with light values of $\delta^{18}\text{O}$ (Holbourn et al., 2005, 2007; Mourik et al., 2011), where according to ectothermic vertebrates from Central Europe the lower limit for mean annual temperature (MAT) was 17.4°C (Böhme, 2003) and even as high as ~22°C according to palaeobotanical data and bauxite records (Price et al., 1997). Two local biozones based on small mammals (biozones Db and Dc) are defined during the interval that spans the MCO (Van der Meulen et al., 2012). The boundary between both zones is dated at 15.6 Ma and coincides with a temperature shift where a peak of light values in $\delta^{18}\text{O}$ is recognized in the marine stable isotopes record from benthic foraminifera from ODP site 1146 in the South China Sea (Holbourn et al., 2005, 2007; Mourik et al., 2011). The small mammal community during the oldest part of the MCO (~15.8 Ma) is represented by a relatively stable rodent community with high number of species, which are evenly distributed, and with heterogeneity values relatively high. The elevated rates of precipitation pointed out by Böhme et al. (2011) around 15.8 Ma along with the warm temperatures inferred by the oxygen isotope curves (Holbourn et

al., 2005, 2007; Mourik et al., 2011) may have created favourable conditions that lead to that stable community. Thereafter (~15.8 to ~15.3 Ma), the assemblages suffered a sudden drop in equitability and heterogeneity and a gradual decrease in the number of species, among which *Megacricetodon* dominates the community. This disturbance on the fauna coincides with an important drop in precipitation, which shows extreme low values in this interval (Böhme et al., 2011). Domingo et al. (2012) also indicate dry conditions in the Madrid Basin between ~15.6 to ~15 Ma based on carbon and oxygen isotope analyses on mammalian fossil tooth enamel. The likely extreme environment inferred by the climate proxies (high temperature and low precipitation) may have imposed severe constraints on the fauna, so that only the species able to cope with these harsh conditions were able to persist, resulting in a community with low values of equitability, heterogeneity and decreasing number of species between 15.8 to 15.3 Ma.

The community organized and adapted to this new climatic and environmental conditions, and as a result, a considerable increase in the equitability and heterogeneity values took place between ~15.3 and ~15 Ma. The relative abundances of the genera also reflect those changes (Fig. 3); middle part of biozone Dc show the most evenly distributed assemblages, with the genera *Heteroxerus*, *Megacricetodon* and *Armantomys* being the most abundant. Around 15 Ma, the end of the MCO and the transition to the MMCT started, being recorded worldwide as an oxygen isotope excursion (Mi2b event, after John et al., 2011). In shallow marine carbonates of the Central Apennines (Decontra Section in the Maiella Platform, Italy), this interval is clearly expressed by important peaks in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ and the occurrence of an extensive phosphatic hardground, thus reflecting changes in the palaeoenvironmental

conditions at the end of the MCO and the onset of the MMCT (Auer et al., 2015, Fig. 4). In the Madrid Basin, those changing climate conditions have procured a destabilization of the rodent community, as the small-mammal assemblages became less evenly distributed (drop in equitability between ~15 to 14.6 Ma). The increase in the number of species in the upper part of biozone Dc (~ 15 to ~14.85 Ma) could be related to the improvement of the local environment caused by a drop in temperatures (onset of the MMCT) and an increase in rainfall (Böhme et al., 2011). These changes were probably beneficial for northern invaders, which were able to move southwards again after a long time of non-invasibility due to the extreme conditions on the Iberian Peninsula during the MCO. The entrance of new species could be also in part responsible for the changing equitability values in this interval. A gradual recovery of the community took place as the MMCT progressed, being reflected by an increase in the equitability and heterogeneity values between ~14.6 to 14.4 Ma. Domingo et al. (2012) noted wetter conditions during local zone Dd in the Madrid Basin; also Böhme et al. (2011) recorded in Calatayud-Montalbán, which could provide favourable conditions for the assemblages. On the other hand, Hordijk et al. (2010) demonstrated an immigration phase in local zone Dd in the Calatayud-Montalbán Basin, not recorded in Madrid. Most of the taxa that enter the Calatayud-Montalbán Basin in that time interval compromise species with complicated dental pattern related to more humid environments. The lack in Madrid of most of these taxa could represent differences in the local environments between the Madrid and Calatayud-Montalbán basins, indicating more open or drier conditions for the former (as previously suggested by Pelaéz-Campomanes et al., 2003; Hernández-Ballarín et al., 2011; Hernández-Ballarín,

2016; Hernández-Ballarín and Peláez-Campomanes, 2017), and be also the reason for the no record of this immigration event in Madrid.

In the remaining faunal succession of the Madrid Basin, a major faunal change starting around 14.4 Ma is observed. It represents the onset of a progressive drop in the rodent equitability and heterogeneity, and could be related to a major stratigraphic discordance in the basin. The Intermediate Unit I, which contains a predominance of carbonatic sediments in central parts of the basin and detritical deposits on the rest, lies unconformably above the Lower Stratigraphic Unit, which mainly consists of clayey sediments and evaporites in the central parts and detritic sediments to the north and northwest, showing a detritical arkose and sandstones progradation (Montes et al., 2006). Although the causes of the arrangement of the sequential units from the Madrid Basin are enigmatic, two alocyclic factors can be pointed out: tectonics, as it controls the available space for sedimentation (accommodation), and climate, as it influences the water flows that move the sediment (Calvo et al., 1989, 1996; Montes et al., 2006). The fact that a change in the trend of heterogeneity and equitability in the faunal succession occurred synchronously with a change in the stratigraphical units in the Madrid Basin could correlate to the first cooling step of the MMCT (Mi3a event; Miller et al., 1991; Miller and Mountain, 1996). The Mi3a event is poorly defined in the pelagic records of the Mediterranean and in the ODP $\delta^{18}\text{O}$ records (Mourik et al., 2011). However, it has been dated at ~14.2 Ma from Southern Ocean planktonic foraminifera (Shevenell et al., 2004) and around 14.3 Ma in shallow marine carbonates in the Mediterranean (Auer et al., 2015), ages which agree with the changes observed in the Madrid Basin. The palaeoprecipitation curve also shows changes in its trend around this age; a

decrease and thereafter stabilization in the mean annual precipitation is observed (Böhme et al., 2011). Shifts in the relative abundances of small-mammals are also recognized during this event: maximum values of *Heteroxerus* are recorded and the percentage of *Megacricetodon* starts increasing gradually from there onwards (Fig. 3).

Finally, the major cooling step in middle Miocene climate recorded at a global scale, the Mi3b event (Miller et al., 1991; Miller and Mountain, 1996), is poorly represented in the palaeoecological curves of the Madrid Basin. The pattern only reflects an increase on species richness around 14 Ma followed by a gradual decline. The Mi3b event, which has been related to a major cryogenic expansion of Antarctica marking the entry into an Earth “Icehouse” climate state (Flower and Kennet, 1994; Zachos et al., 2001; Shevenell et al., 2004), is clearly visible in all benthic $\delta^{18}\text{O}$ records, in contrast to the poorly defined Mi3a event (Abels et al., 2005; Holbourn et al., 2005, 2007; Mourik et al., 2010, 2011). It has been accurately dated magnetostratigraphically in the Mediterranean area. Abels et al. (2005) carried out an astronomical age model to a bulk carbonate oxygen isotope record on Malta, which indicates an age of $13.82\text{Ma} \pm 0.003$ for this major event. However, Mourik et al. (2011) argued that part of the section that the former authors used was subject to uncertainty, so that they constructed a high resolution benthic and planktic oxygen isotope records giving an age between ~ 13.95 and 13.76 Ma to the Mi3b event. This event is also associated with a shift to heavier $\delta^{13}\text{C}$ values in benthic foraminiferal carbonate and labeled CM6 (Woodruff and Savin, 1991). Oxygen isotopic analysis on large mammal tooth enamel in the Somosaguas site in the Madrid Basin also show high values of $\delta^{18}\text{O}$ between 14 and 13.8 Ma, pointing out a sudden drop in temperatures calculated between 9.6° and 10.6° (Domingo et al., 2009, 2012). Analyses on rodent faunas in the Calatayud-

Montalbán Basin also emphasize a decrease in temperatures starting at the beginning of biozone E (Van der Meulen and Daams, 1992). Therefore, the remarkable increase on species richness in the rodent community from Madrid at around 14 Ma could be linked to northern immigration because of the low temperatures in northern areas, a model that is corroborated by the entrance in Madrid of species typical of Central Europe (*Heteroxerus grivensis*). As the effects of the Mi3b event strengthened the species richness in Madrid started dropping gradually. This gradual decrease in the number of species (that is even more pronounced if we take into account the lower number of species in biozones F and G1 due to the long inferred range of *Heteroxerus* nov.sp.), is also accompanied by the origination of less diverse communities (Fig. 2). Although the palaeoecological curves from Madrid do not reflect important changes during that time span (probably due to the high deterioration of the community before the event), the taxonomical study of the rodent assemblages of this time frame (biozone E) has shown turnover rates and morphometric changes that indicate that this period represents one of the most variable in assemblage composition in both the Madrid and the Calatayud-Montalbán basins (Van der Meulen et al., 2005; Van Dam et al., 2006; Hernández-Ballarín et al., 2011; Hernández-Ballarín, 2016; Hernández-Ballarín and Peláez-Campomanes, 2017). In Madrid, the bulk of faunal changes are concentrated between the localities of El Cañaveral and Somosaguas Sur, thus coinciding with the ages given for the onset of the Mi3b event in the Mediterranean area (~13.95, Mourik et al., 2011). The relative proportions of the rodent assemblages also highlight changes in the structure of the community: the genus *Megacricetodon* begins to constitute the most abundant taxon, giving rise to low equitable assemblages. A shift in the palaeoprecipitation curve in the Calatayud-Montalbán

Basin is also detected; a relatively dry interval takes place between ~13.9 and ~13.6 Ma according to herpetological assemblages (Fig. 4, Böhme et al., 2011). Analyses applied to rodent faunas in the Calatayud-Montalbán Basin emphasize dry conditions during local zone E (Van der Meulen and Daams, 1992), and an aridity phase is also recorded in Madrid based on large mammals (Domingo et al., 2012).

The Mi3b event has been correlated for a long time to the substitution of the early-middle Aragonian fauna by a late Aragonian community, which is formally defined by the E-F boundary (Van der Meulen and Daams, 1992; Krijnsman et al., 1996; Van der Meulen et al., 2005; Van Dam et al., 2006). However, the results obtained from the rodent assemblages from the Madrid Basin point out that small changes in the small-mammal community started before (within biozone E).

Figure 4. Overview of the trends and events observed during the middle Miocene in the small mammal community from the Madrid Basin and the main climate proxies for this time interval in the marine and the continental realm. (A) Species composition curves calculated for the rodent assemblages of the Madrid Basin (inferred species richness, equitability and heterogeneity indexes). (B) Palaeoprecipitation curve for the Calatayud-Montalbán Basin obtained from herpetological assemblages therein (Böhme et al., 2008, 2011). (C) Marine stable oxygen and carbon isotope records from benthic foraminifera from ODP site 1146 in the South China Sea (Holbourn et al., 2005, 2007; Mourik et al., 2011). (D) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data of the Decontra section (Maiella Platform, central Apennines, Italy) (Auer et al., 2015). Pink box in the $\delta^{13}\text{C}$ indicates the extent of the Monterey Excursion, and the pink bars in the $\delta^{18}\text{O}$ show the relative position of the Mi-events and their correlation with marked changes on the lithology of the Decontra section.

5. Conclusions

The small mammal assemblages from the Madrid Basin (~15.9 to 12.8 Ma) have proved to be an appropriate record to check how middle Miocene climate changes influenced the distribution of the mammalian faunas on the Iberian Peninsula. A close relationship between changes in global climate (evidenced by marine stable isotope records and continental palaeoprecipitation curves) and changes in the composition and evolution of the local small-mammal community from the Madrid Basin is observed. The palaeoecological curves show periods of disturbance in the rodent assemblages (reflected by drops in equitability, and in some cases in heterogeneity and species richness), that have been related to changing climate

conditions, such as during part of the MCO and at the Mi2b and Mi3a events. A recovery and adaptation of the community to the new climate circumstances is recorded thereafter, being reflected by more evenly distributed and diverse assemblages.

The major cooling step in middle Miocene climate recorded at a global scale (Mi3b event) is poorly represented in the palaeoecological curves from Madrid. However, the taxonomical study of the rodent faunas of that interval (biozone E) has shown turnover rates and morphometric changes that indicate that this period represents one of the most variable in assemblage composition within the Aragonian. Although the Mi3b event has been correlated for a long time to the substitution of the early-middle Aragonian fauna by a late Aragonian community (E-F boundary), the study of the rodent assemblages of the Madrid Basin may point out that small changes in the small-mammal community started before (within biozone E).

Acknowledgments

We thank all the people who participated in the fieldwork and the processing of the samples. We acknowledge editors of the journal, as well as Lars W. van den Hoek Ostende and an anonymous reviewer for their constructive suggestions that considerably improved the manuscript. This work was supported by the Spanish MICINN projects CGL-2008-04200/BTE and CGL2011-28877. VH-B was supported by a FPI pre-doctoral contract.

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FIGURE CAPTIONS

Figure 1. Geological scheme of the Madrid Basin. The Miocene basin filling consists of detritic facies accumulated by alluvial fans in the margins and carbonatic and evaporitic sediments deposited by lacustrine systems in the central parts of the basin (limit between them marked with a dashed line). The main materials of the sedimentary filling are provided by the alluvial fans coming from the Central System, the Toledo Mounts and the Iberian Range (black arrows). On the upper left corner the Tertiary basins of the Iberian Peninsula; studied area marked with a rectangle.

Figure 2. Biochronological position of the localities included (Hernández Ballarín, 2016; Hernández-Ballarín and Peláez-Campomanes, 2017), showing its sample size (grey bar-chart), richness measures (observed, rarified and inferred), equitability and heterogeneity values. Grey horizontal lines in the equitability and heterogeneity indices represent maximum and minimum values for each locality. Due to the lack of

magnetostratigraphical data (only available for PA5, PA3 and VLL), black rectangles to the left of the localities represent the age range in which the locality is situated.

Figure 3. Relative abundances of rodent genera for the middle and upper Aragonian from the Madrid Basin. Only localities with sample size larger than 50 specimens are shown.

Figure 4. Overview of the trends and events observed during the middle Miocene in the small mammal community from the Madrid Basin and the main climate proxies for this time interval in the marine and the continental realm. (A) Species composition curves calculated for the rodent assemblages of the Madrid Basin (inferred species richness, equitability and heterogeneity indexes). (B) Palaeoprecipitation curve for the Calatayud-Montalbán Basin obtained from herpetological assemblages therein (Böhme et al., 2008, 2011). (C) Marine stable oxygen and carbon isotope records from benthic foraminifera from ODP site 1146 in the South China Sea (Holbourn et al., 2005, 2007; Mourik et al., 2011). (D) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data of the Decontra section (Maiella Platform, central Apennines, Italy) (Auer et al., 2015). Pink box in the $\delta^{13}\text{C}$ indicates the extent of the Monterey Excursion, and the pink bars in the $\delta^{18}\text{O}$ show the relative position of the Mi-events and their correlation with marked changes on the lithology of the Decontra section.

Table 1. Frequency of fossil rodent occurrences by locality. It consists in specimen counts of first and second molars of each species in each locality. Localities are arranged and correlated to the local biozones proposed in the Calatayud-Montalbán Basin (Daams et al., 1999a; Van der Meulen et al., 2012; Hernández Ballarín, 2016; Hernández-Ballarín and Peláez-Campomanes, 2017). Inferred ranges of each species are shaded in blue.

830 **Table 2.** Values of species richness, equitability, heterogeneity and the relative
831 abundances of the rodent genera for each locality.

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