

Identification problems of arid environments in the Neogene–Quaternary mammal record of Spain

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Abstract

In this work, we investigate if broadly used methodologies are adequate to detect periods of aridity based on the Spanish fossil record and try to infer which of them were more or less severe. Thus, we present a qualitative statistical approach to two popular palaeoecological methodologies: ecological diversity and cenograms. Discriminant models, derived from modern localities of known biome, determined the probable biomes of Neogene–Quaternary fossil assemblages. Principal component analyses (PCA) provided additional inference on their ordination within an aridity gradient. While models work adequately with modern faunas, the analyses of the palaeocommunities showed that their ecological structure is very different from that of modern faunas, affecting the models' performance. Nevertheless, the PCA was able to establish an aridity gradient. Our results

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suggest that independent tools of palaeoecological analysis are critical when reconstructing palaeoenvironments.

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1. Introduction

In a recent paper [McNeely \(2003\)](#) points out the importance of the biodiversity conservation in arid environments. Since arid regions are characterized by relatively less species than the better-watered biomes, for each species lost from an arid region, the percentage of loss for the region's biodiversity is much higher than in species-rich regions. A palaeontological perspective may provide relevant data concerning the evolution of biotas in these kinds of environments, which is essential to understand the patterns and processes that generated today's diversity in arid environments, and basic for future activities. However, a first step must be to properly identify arid environments along Earth history and to document the diversity of such environments in the past.

In the last decades, numerous palaeoclimatic interpretations have been proposed based on the rich Neogene and Quaternary Spanish fossil record (e.g. [Daams and van der Meulen, 1984](#); [van der Meulen and Daams, 1992](#); [Calvo et al., 1993](#); [Alcalá, 1994](#); [Ruiz Bustos, 1994](#); [Alberdi et al., 1997](#); [Rodríguez, 1997](#); [van Dam, 1998](#); [van Dam and Weltje, 1999](#); [Morales et al., 1999](#); [Alcalá et al., 2000](#); [Amezua et al., 2000](#); [López Antoñanzas and Cuenca Bescós, 2002](#); [Hernández Fernández et al., 2003](#)). Different authors have pointed out periods that are considered as periods with relatively more arid conditions (e.g. the maximum in aridity during the middle Aragonian, the so-called "faunas with *Hispanotherium*", [Morales et al., 1993](#)). Problems have arisen, however, when trying to compare the results of these works because most of them have been only applied to short periods of time and small geographic regions, which generally do not overlap. This makes their correlation and interpretation at larger spatial as well as temporal scales difficult. Additionally, most of the results based on those different approaches are defined on relative terms such as warm/cold and dry/wet, which are somehow vague. Another problem is that most of the methods used have been based on more or less restricted taxonomical subsets of the total fossil assemblage (e.g. rodents, large mammals, etc.). In this sense, it is important to point out that different mammal groups may offer different palaeoecological information. Particularly, macromammals and micromammals usually provide slightly different palaeoenvironmental reconstructions due to disparities in scale of landscape perception and physiological constraints ([Hernández Fernández, 2001](#); [Hernández Fernández and Peláez-Campomanes, 2003, 2005](#)).

The aim of this work is to analyse whether it is possible to recognize periods of aridity on the fossil record using two popular palaeoclimatic methods: ecological diversity analysis ([Andrews et al., 1979](#)) and cenogram analysis ([Legendre, 1986](#)). Both methodologies have the clear advantage of using the nearly whole mammalian association to obtain palaeoenvironmental information. In order to formalize the accuracy of these two methods and to propose models that help to infer palaeoenvironmental conditions we have performed a set of multi-variate analyses applied to modern faunas. Results and models

obtained on the basis of modern faunas have been applied to mammal assemblages from the three most arid periods from the Neogene and Quaternary of the Iberian Peninsula, according to previous works (Calvo et al., 1993; Alcalá et al., 2000). These periods are the middle Aragonian (Middle Miocene, 16.0–13.4 Ma), Turolian (Late Miocene, 8.0–5.3 Ma) and the Lower-Middle Pleistocene (1.8–0.5 Ma).

2. Definition of arid environments

Arid environments are extremely diverse in terms of their landforms, soils, fauna, flora, water balances, or human activities. Because of this variety, no practical definition of arid environments can be derived. Nevertheless, the one binding element to all arid regions is aridity. The concept of aridity used in different scientific fields varies making the literature confuse on this topic (e.g. UNESCO, 1979; Le Houérou and Popov, 1981; McGinnies, 1988). According to the United Nations Convention to Combat Desertification (CCD), aridity can be expressed as a function of rainfall and temperature (FAO, 1989; Findlay, 1996). A common “representation” of aridity is the following climatic aridity index:

$$P/ETP,$$

where P is the mean annual precipitation, and ETP is the mean annual potential evapotranspiration, which is the amount of moisture that, if it were available, would be removed from a given land area by evaporation and transpiration. Using the climatic aridity index, the world is divided into six aridity zones. Drylands include hyperarid, arid, semi-arid, and dry sub-humid areas (other than polar and sub-polar regions) in which this ratio ranges from 0.00 to 0.65. Areas with a ratio greater than 0.65 are considered humid zones. Thus, more than one-third of the total area of the world is arid land (UNSO/UNDP, 1997). These aridity zones spread across all continents, but are found more predominantly in Asia and Africa (UNEP/GRID, 1991).

However, definitional problems increase considerably both in the attempts to put boundaries encompassing areas described as arid and to categorize areas by degrees of aridity. Several issues should be pointed out. First, there is a continuous gradient in aridity, which spans several biomes (e.g. from tropical rainforest to tropical deciduous woodland, to savanna, to desert). This makes it difficult to recognize discrete limits between humid and arid regions. Second, there are differences in the rainfall seasonal regime. The landscape and ecological interactions in regions with similar drought length and intensity can be very different depending on the timing of the precipitations. For example, while the vegetation in Mediterranean areas with winter rainfall is mainly woodlands, the East African savannas with a summer humid period are regarded as grasslands with scattered trees. Finally, even under the same seasonal regime, the relationship between temperature and precipitations greatly influences the vegetation and its allied fauna. This is related to the association between hydric and thermal stresses, which determines the length of the vegetative activity period. Moreover, many other factors may also condition the degree of aridity within a climatic zone. Local characteristics such as wind, which removes the air moisture, or the presence of major mountain ranges that disrupt the structure of cyclones passing over them, creating “rain shadow” effects, may increase the degree of aridity. In a different way, soil characteristics may contribute to increase or decrease the effects of aridity by means of the variation in the water-holding capacity of the soils, which depends

on their structure (internal arrangement of soil particles), texture (relative distribution of different-sized particles), composition and depth.

A clear-cut distinction that may be fruitfully used in ecological studies is the one between open-lands and forested-lands. This division is easily noticed in the landscape and has major consequences for the fauna. Nevertheless, three potential problems are associated with the linkage of open-lands and arid-lands, and their detection in the Iberian Neogene–Quaternary. First, while the drought is the main obstacle for the growth of trees, this is not always the case (e.g. in the tundra this is impeded by the extremely low temperatures). This dissociates the association between open-landscape and aridity. Second, regions affected by natural disturbances (e.g. fire-prone areas, regularly flooded plains, etc.) may be defined as open-lands although they are under climatic conditions that theoretically favour the forest. Yet usually the scale of the disturbance is small, which allows the coexistence of open-land and forest species. Further, the succession process regenerates the forest. In a similar way, closed environments and their allied faunal elements may be linked to water available from sources other than rainfall, i.e. watercourses and freatic resources. Riparian environments may be of particular importance in analysing the fossil record, since a large amount of fossil localities are found in fluvial deposits. Finally, most of the time the Iberian landscapes were mainly woodlands due to the existence of a moderated aridity and actual open-land biomes were developed only in very punctual moments of greater aridity (van der Meulen and Daams, 1992; Barrón et al., 1996; Hernández Fernández et al., 2003; Hernández Fernández, 2005).

Therefore, in order to overcome all these problems it is needed to refer our definition of arid lands to a concrete climate classification. During the twentieth century, with the development of climatology as scientific discipline, the division between climate and vegetation classifications have become more pronounced. Climate classifications range from simple annual precipitation classes to those that incorporate precipitation and its variability, length of humid and growing seasons, precipitation–temperature relationships, evaporation, and precipitation–evaporation relationships, and even weather mechanisms (e.g. Köppen and Geiger, 1928, 1954; Budyko, 1958; Strahler, 1969). Vegetation classifications are geographically based using local characteristics of flora, ecology, or physiognomy such as rainforest, grassland, savanna, and desert scrub (e.g. Diels, 1908; Brockmann-Jerosch and Rübél, 1912; Mueller-Dombois and Ellenberg, 1974). Vegetation-based classifications are especially useful for identifying arid environments when extreme climatic variability is not captured by climatic classifications.

While precipitation data and various derived climatic indexes define aridity with precision, the type of vegetation might more conveniently define aridity for ecological studies, which frequently describe the landscape based on plant adaptive strategies. Therefore, in this work we define arid lands according to the climatic classification provided by Walter (1970), which complementarily combines both vegetation and climatic information (Table 1). Additionally, this climatic typology has been selected as opposed to other possibilities (e.g. Thornthwaite, 1931, 1948; Holdridge, 1967; Viers, 1975; Rivas Martínez, 1994) because it has a simple nomenclature and coincides with traditional biomes (Odum, 1971; Lacoste and Salanon, 1973; Lieth, 1975; Strahler and Strahler, 1987). Walter (1970) defines aridity as a function of the relation between the mean monthly precipitation and temperature values. Drought is considered present when the monthly mean temperature (measured as °C) is higher than twice its mean precipitation (mm). The ratio $1\text{ }^{\circ}\text{C} = 2\text{ mm}$ of rain has been found to agree well with the actual weather conditions

Table 1
Climatic typology used in this paper and its correspondence with world vegetation types

Climate zone		Zonobiome ^a	
I	Equatorial	I	Evergreen tropical rain forest
II	Tropical with summer rains	II	Tropical deciduous woodland
II/III	Transition tropical semiarid ^b	II/III	Savanna ^b
III	Subtropical arid	III	Subtropical desert
IV	Winter rain and summer drought	IV	Sclerophyllous woodland-shrubland
V	Warm-temperate	V	Temperate evergreen forest
VI	Typical temperate	VI	Nemoral broadleaf-deciduous forest
VII	Arid-temperate	VII	Steppe to cold desert
VIII	Cold-temperate (boreal)	VIII	Boreal coniferous forest (taiga)
IX	Arctic	IX	Tundra

^a*Sensu* Walter (1970), mainly vegetation type.

^bModified from Walter (1970); Walter considers II/III as a zoneocotone between tropical forests and deserts, but we consider it as a zonobiome.

(Gaussen, 1954; Walter, 1970). The drought length, in combination with the seasonality regime, allows the definition of the different biomes (Walter, 1970; Allué Andrade, 1990). Thus, the tropical deciduous woodland (II), savanna (II/III), subtropical desert (III), sclerophyllous woodland-shrubland (IV) and steppe (VII) biomes are characterized by the existence of aridity, which is essentially seasonal but it can be much more prolonged in tropical and cold deserts. Of these, savannas, subtropical deserts and steppes are the biomes characterized by largely treeless vegetation.

3. Material and methods

Fossil sites: 16 localities, distributed among three arid periods (Middle–Late Aragonian, Turolian and Lower–Middle Pleistocene) of the Iberian Peninsula record, were selected for this analysis. Only localities with large and small mammal fossil record have been included on the analysis.

All the localities used in the analysis of Aragonian faunas come from the Madrid basin and the data are from Peláez-Campomanes et al. (2003). The period represented by them is Middle and early Late Aragonian, including the supposed maximum of aridity at the end of the Middle Aragonian (van der Meulen and Daams, 1992). These localities are: Estación Imperial, Paseo de las Acacias and Puente de Vallecas+Arroyo del Olivar (MN5), Paracuellos 5 and Paracuellos 3 (MN6). All these localities were preserved in marginal alluvial fan systems that graded to palustrine–lacustrine environments.

The selected Turolian localities come from several Neogene basins (Alfambra-Teruel basin, Vinalopó-Alicante basin, and Cabriel River basin) and their data are mainly from Alcalá (1994) and Montoya and Morales (2004). These localities are: Crevillente 2 (MN11, Vinalopó-Alicante basin), Puente Minero (MN11, Alfambra-Teruel basin), Cerro de la Garita and Los Mansuetos (MN12, Alfambra-Teruel basin), El Arquillo (MN13, Alfambra-Teruel basin) and Venta del Moro (MN13, Cabriel River basin). The Upper Miocene sediments in the area of Crevillente were deposited in a delta with alternating marine and continental conditions (Martín Suárez et al., 2001). The mammal assemblages

from Alfambra-Teruel basin where preserved mainly in palustrine–lacustrine environments and towards the margin of the basin in the terrigenous deposits of alluvial fans (Alcalá et al., 2000). The fossiliferous levels of Venta del Moro belong to a lacustrine sequence with several flooding and desiccation cycles (Mathisen and Morales, 1981).

The localities used in the analysis of Pleistocene faunas come from the Guadix-Baza basin and the karstic system of the Sierra de Atapuerca and data are mainly from Palmqvist et al. (1996), Alberdi et al. (2001), van der Made et al. (2003), Hernández Fernández (2005), and Laplana (personal com.). These localities are: Venta Micena and Huéscar 1 (Lower Pleistocene, Guadix-Baza basin), Atapuerca TD4 and TD6 (Lower-Middle Pleistocene, Sierra de Atapuerca), and Cúllar de Baza 1 (Middle Pleistocene, Guadix-Baza basin). The localities from the Guadix-Baza basin were preserved in lake-margin settings. Hydraulic factors greatly controlled the selective skeletal composition, except at Venta Micena site where short-faced hyenas (*Pachycrocuta brevirostris*) acted as collecting agents of bones (Palmqvist et al., 1996; Alberdi et al., 2001). The two units (TD4 and TD6) of Gran Dolina section belong to a sedimentary infilling in a gallery originated by karstification of the host Cretaceous limestones of Sierra de Atapuerca. Upper TD6 was interpreted as a space that man used for animal processing (van der Made et al., 2003).

We included fossil assemblages originated on different taphonomical conditions since the methodologies we wanted to test have been used for all of them, thus assuming that the original communities show a high degree of functional redundancy and therefore the structure shown by the fossil assemblages could be a good representation of the extinct community. Although it is true that modern mammal communities show a high degree of functional redundancy we do think that taphonomical processes have a strong influence on the resulting structure exhibited by the fossil assemblages. What we do not know is whether the resulting assemblage structure is more dependant on the different taphonomical processes at work or on the original mammal community, in which the relative abundances of the constituent taxa may strongly determine the resulting structure. As results of this uncertainty we have preferred to include localities of very different taphonomy and check if all of them behave in a similar way when compared to modern communities.

Palaeoclimatic analysis of fossil mammal communities: It is generally assumed that past macroclimatic factors and landscape features may be recognized by the study of fossil mammal assemblages (van de Weerd and Daams, 1978; Artemiou, 1984; Andrews, 1995; Hernández Fernández, 2001; Nieto and Rodríguez, 2003). Several methods have been developed in order to describe the structure of mammalian communities, which can be defined as the whole set of occupied niches in a given community (Andrews, 1996; Nieto and Rodríguez, 2003). Community methods try to describe this structure using one or various variables defining the different niches and to use this data to compare fossil assemblages with recent communities in order to infer palaeoenvironmental features. Underlying these methods is the concept of community convergence, that is, communities developing under similar environmental conditions have similar community structures (Cody and Mooney, 1978; Crowder, 1980; Samuels and Drake, 1997).

Andrews et al. (1979) applied to palaeoecology the analysis of ecological diversity developed by Fleming (1973). This methodology uses the distribution of all the terrestrial mammal species (i.e. excluding bats) in taxonomical groups and ecological categories of body size, locomotor adaptation and feeding habits. Recent mammalian communities are used to establish patterns of community structure for different habitats, which are

compared with the patterns obtained from the fossil assemblages under study. Comparisons range from visual inspection of frequency histograms (Andrews et al., 1979) to multi-variate statistics (Andrews, 1992, 1996; Kay and Madden, 1997; Reed, 1998). The different categories have been subsequently reviewed and modified on several occasions (Guérin, 1984; Owen-Smith, 1988; de Bonis et al., 1992a; Alcalá, 1994; Kay and Madden, 1997; Fernández-Jalvo et al. 1998; Rodríguez, 2001; Mendoza et al., 2004; Rodríguez et al., 2004). The categories used in this work are shown in Table 2.

Cenograms are graphs of ranked body weight for the mammalian taxa composing a community, excluding bats and carnivores. They were developed by Valverde (1964, 1967) as an adequate system for mammal community description, and adapted by Legendre (1986) to palaeoenvironmental studies. In spite of its popularity (e.g. Gingerich, 1989; Pérez and Soria, 1990; Alcalá, 1994; Gunnell, 1994; Montuire and Desclaux, 1997; Croft, 2001; Galobart and Agusti, 2003; Storer, 2003), this methodology has been recently criticized because the relationships between cenogram's structure and climate, proposed originally by Legendre (1986, 1989), are not statistically significant (Rodríguez, 1999). Nevertheless, while Rodríguez (1999) centred his test in the study of the quantitative

Table 2
List of the variables used in the ecological diversity analysis

<i>Taxonomic categories</i>	
R	% Rodentia species
I	% Insectivora species
P	% Primates species
A	% Artiodactyla species
C	% Carnivora species
O	% species in other orders
<i>Trophic categories</i>	
I	% insectivorous species
F	% frugivorous and granivorous species
HB	% browser (brachyodont) species
HH	% grazer (hypsodont) species
C	% carnivorous species
O	% omnivorous species
<i>Locomotion categories</i>	
A	% arboreal species
S	% scansorial species
Aq	% aquatic species
F	% fossorial species
LGM	% large ground mammals
SGM	% small ground mammals
<i>Body size categories</i>	
A	% species 0.0–100.0 g
B	% species 100.1–1000.0 g
C	% species 1,000.1–10,000.0 g
D	% species 10,000.1–45,000.0 g
E	% species 45,000.1–90,000.0 g
F	% species 90,000.1–180,000.0 g
G	% species 180,000.1–360,000.0 g
H	% species > 360,000.0 g

relationships between the different analysed variables, a qualitative statistical approach in order to infer biomes has never been undertaken with this methodology. Besides, in our opinion the general structure of the cenogram may yield unique information about the body size structure of the non-carnivorous mammal community and, therefore, its use should not be omitted, although some problems arise when applying to fossil assemblages.

Typically, cenograms are considered as composed of two line segments separated by a gap of variable amplitude (Fig. 1). The first segment is determined by the species that weight less than 500 g. The second segment is delineated by the medium and large species (500–1,000,000 g). A breakpoint around 205 kg has been typically used in previous analyses of cenograms. Nevertheless, this division is arbitrary and has no functional basis. Therefore, here we shift the breakpoint to 1000 kg, which has a major ecological significance (Owen-Smith, 1988). A third-line segment, defined by the megaherbivores (> 1,000,000 g), is not considered in the analysis because it is not present in all the faunas. The magnitude of the gap between small and medium species has been regarded as associated to the openness of the environment. This relationship, however, has been rejected by Rodríguez's (1999) analyses. Further, there are frequently larger gaps than the one delimited by the largest small species and the smallest medium species. Therefore, in addition to the usual variables, we have analysed several new variables to describe the cenogram (Table 3).

In order to make the analysis, some consistent and reasonably accurate mean of estimating body mass from fossils is required. The only adequate method available at present seems to be estimation using allometric equations relating weight with dental surface mainly (Creighton, 1980; Legendre, 1989). Although there are some acknowledged problems using teeth as a basis for body mass estimation (Gould, 1975; Smith, 1984, 1993; Damuth, 1990), in general species are more easily identified by their teeth than they are by post-cranial elements, and teeth are often the only parts of the animal that are preserved in sufficient numbers to be useful.

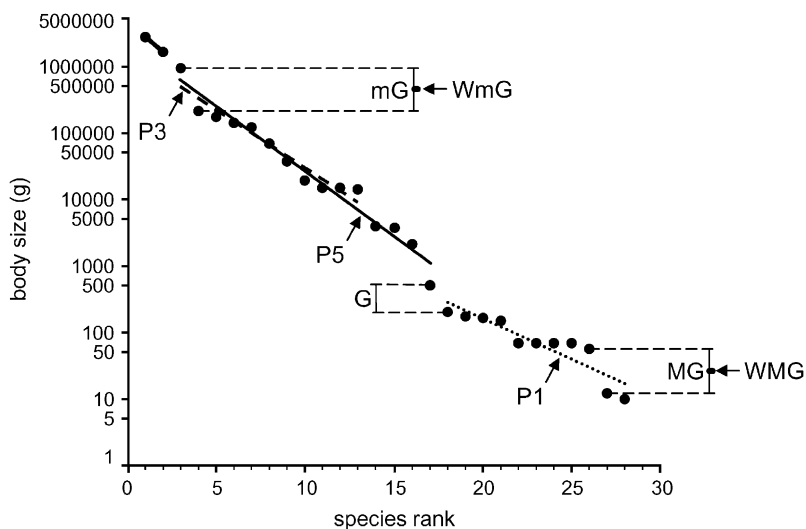


Fig. 1. Cenogram of a modern mammal fauna (Patna, India). The variables used in the analysis of cenograms are shown (see Table 3).

Table 3

List of the variables used in the cenogram analysis

P1 ^{a,b}	Slope of the line segment determined by species <500.0 g (small mammals)
P3 ^{a,b}	Slope of the line segment determined by species 8,000.0–1,000,000.0 g (large mammals)
P5 ^{a,b}	Slope of the line segment determined by species 500.0–1,000,000.0 g (medium-large mammals)
P5–P1 ^a	Difference in slope between the line segments determined by medium-large and small mammals
P5–P3	Difference in slope between the line segments determined by large and medium-large mammals
G ^a	Magnitude of the gap between small and medium-large mammals (in logarithmic units)
mG	Magnitude of the major gap between two consecutive species within the medium-large mammals (in logarithmic units)
MG	Magnitude of the major gap between two consecutive species within the whole fauna of small and medium-large mammals (in logarithmic units)
WmG	Mean weight (in logarithmic units) of the two species defining mG
WMG	Mean weight (in logarithmic units) of the two species defining MG

^aModified after Rodríguez (1999).^bThe slope has been calculated using the ln (body size in g) as independent variable and the rank as dependent variable.

Carnivores' body masses were estimated from the lower carnassial crown area using equations developed by Legendre and Roth (1988). In the very few cases where the area of the lower carnassial was unknown, the body mass was estimated using the length of M_1 , following the regression equation developed by Van Valkenburgh (1990). For Perissodactyla (excepting Equidae) and Artiodactyla species, body masses were calculated using Janis' (1990) equations. Only when there were no dental data available we used post-cranial measurements and Scott's (1990) equations to estimate body mass. Following Alberdi et al. (1995), we used appendicular elements in order to infer body mass of Equidae species. Body mass of rodents and insectivores was calculated using the allometric relationship between the surface of the first lower molar and weight (Legendre, 1989). The body masses of Lagomorpha and Proboscideans were taken from Alcalá (1994), Palmqvist et al. (1996), and Rodríguez (1997).

Comparison with modern faunas: In order to interpret palaeoenvironmental conditions, data from fossil localities were compared with data from modern Old World mammal faunas (Table 4). Three localities containing both faunal and climatic information were selected from each of the biomes that a priori might be inferred for the studied periods in the Iberian Peninsula (Nieto and Rodríguez, 2003). These biomes are tropical deciduous woodland (II), savanna (II/III), tropical desert (III) and temperate evergreen forest (V) for the Miocene localities (Alcalá, 1994; Hernández Fernández et al., 2003). The climates in the Iberian Peninsula between 1.8 and 0.5 ma might correspond to the biomes of tropical desert (III), sclerophyllous woodland (IV), nemoral forest (VI) and steppe (VII) (Azanza et al., 1999, 2000; Hernández Fernández and Peláez-Campomanes, 2003, 2005; Rodríguez et al., 2004; Hernández Fernández, 2005). Faunal lists for these 21 modern localities were taken from the references in Table 4. Body masses and ecological data for living taxa were taken from Smith et al. (2003) and Nowak (1991). For those few taxa for which no mass data were found, masses were estimated based on the average mass of other members of the genus. Finally, the ecological diversity and cenogram statistics presented in Tables 2 and 3 were calculated for each fauna.

Table 4
Geographic data for 21 modern Old World mammal faunas

N	Cl. ^a	Locality	Country	Latitude	Longitude	Altitude (m)	References
1	II	Moundou	Chad	8°37'N	16°04'E	420	Kingdon (1971), Kingdon (1974a), Kingdon (1974b), Kingdon (1977), Kingdon (1979), Kingdon (1982a), Kingdon (1982b), Nowak (1991), Dorst and Dandelot (1973)
2	II	Mtwara	Tanzania	10°16'S	40°16'E	113	Kingdon (1971), Kingdon (1974a), Kingdon (1974b), Kingdon (1977), Kingdon (1979), Kingdon (1982a); Kingdon (1982b)
3	II	Patna	India	25°37'N	85°10'E	53	Corbet and Hill (1992)
4	II/III	Zinder	Niger	13°48'N	8°59'E	510	Kingdon (1971), Kingdon (1974a), Kingdon (1974b), Kingdon (1977), Kingdon (1979), Kingdon (1982a); Kingdon (1982b)
5	II/III	Gaberone	Botswana	24°41'S	25°55'E	983	Skinner and Smithers (1990)
6	II/III	Jaipur	India	26°49'N	75°48'E	390	Corbet and Hill (1992)
7	III	Lüderitz Bay	Namibia	26°38'S	15°06'E	23	Skinner and Smithers (1990)
8	III	Assuan	Egypt	23°58' N	33° 40' E	194	Corbet (1978)
9	III	Mascate	Oman	23°37'N	58° 35' E	4	Corbet (1978)
10	IV	Sanlucar de Barrameda	Spain	36°47'N	6°21'W	30	Corbet (1978)
11	IV	Tunis	Tunisia	36°50'N	10°14'E	3	Corbet (1978)
12	IV	Aleppo	Syria	36°11'N	37°13'E	395	Corbet (1978)
13	V	East London	South Africa	33°02'S	27°50'E	127	Skinner and Smithers (1990)
14	V	Nanchang	China	28°40'N	115°58'E	49	Corbet and Hill (1992)
15	V	Kagoshima	Japan	31°34'N	130°33'E	4	Corbet (1978)
16	VI	Vlissingen	The Netherlands	51°27'N	3°36'E	12	Corbet (1978)
17	VI	Brest	Byelorussia	52°07'N	23°41'E	144	Corbet (1978)
18	VI	Dairen	China	38°54'N	121°38'E	96	Corbet (1978)
19	VII	Fort Schevchenko	Kazakhstan	44°33'N	50°17'E	23	Corbet (1978)
20	VII	Urumchi	China	43°47'N	87°37'E	912	Corbet (1978)
21	VII	Paotou	China	40°34'N	109°50'E	1044	Corbet (1978)

^aCl. Climate zone (see Table A).

In order to verify if the community structure described by means of ecological diversity and cenogram analyses can provide information on the biome in which the mammal faunas live, discriminant analyses were performed. Since these methodologies are very different, five separated analyses were performed using different sets of variables: (1) taxonomic, (2) trophic, (3) locomotion and (4) body size categories of the ecological diversity analysis, and (5) cenogram variables. The minimal tolerance level used was 0.001. These coupled analyses were repeated for each studied time period using different modern faunas for comparison. We used the modern faunas from biomes II, II/III, III and V in the analyses of the Aragonian and Turolian faunas. For the analyses of the Pleistocene faunas we used the modern faunas from biomes III, IV, VI and VII.

Subsequently, the validation of the models obtained after the analysis of the 21 modern mammal faunas was done using seven new modern faunas, different from the ones used to calculate the discriminant functions. Each of these new faunas comes from one of the studied biomes (Table 5).

Finally, the canonical discriminant functions computed for each model were applied, in the case of being satisfactory, to the data from fossil assemblages. This should allow us to infer the environmental conditions in which the Neogene–Quaternary Spanish mammalian faunas lived.

Additionally, two principal component analyses (PCA) were performed including, respectively, all the Pleistocene and temperate modern faunas, and all the Miocene and tropical modern faunas. In order to obtain an ordination of the mammalian faunas as a function of their ecological structure, all the descriptor variables of the ecological diversity and cenograms were included jointly in these analyses. We calculated the correlations between each PCA factor and the values for annual precipitation (mm) and drought length (number of months in which precipitation is less than twice the temperature; Walter, 1970) in each modern locality with the purpose of detect which of these PCA factors is

Table 5
Geographic data for 7 modern Old World mammal faunas used in the validation of the models

N	Cl. ^a	Locality	Country	Latitude	Longitude	Altitude (m)	References
22	II	Ho Chi Minh	Vietnam	10°47'N	106°42'E	11	Corbet and Hill (1992)
23	II/III	Voi	Kenya	3°24'S	38°34'E	560	Kingdon (1971), Kingdon (1974a), Kingdon (1974b), Kingdon (1977), Kingdon (1979), Kingdon (1982a), Kingdon (1982b)
24	III	Smara	W Sahara	26°44'N	11°26'W	140	Corbet (1978)
25	IV	Esfahan	Iran	32°37'N	51°40'E	1598	Corbet (1978)
26	V	Foochow	China	26°05'N	119°18'E	88	Corbet and Hill (1992)
27	VI	Tsingtao	China	36°04'N	120°19'E	77	Corbet (1978)
28	VII	Genichesk	Ukraine	46°10'N	34°49'E	15	Corbet (1978)

^aCl. Climate zone (see Table A).

Table 6
Discriminant analysis results for the tropical modern mammal faunas and the Miocene Iberian faunas

Climate zone	Locality	Ecological diversity				Cenograms
		T	Tr	L	BS	
<i>Modern faunas (models)</i>		91.7%	83.3%	83.3%	100%	100%
II	Moundou	II	II	II	II	II
II	Mtwara	II	II	II	II	II
II	Patna	II	II	II/III	II	II
II/III	Zinder	II/III	III	II/III	II/III	II/III
II/III	Gaberone	II/III	II	II/III	II/III	II/III
II/III	Jaipur	II/III	II/III	II/III	II/III	II/III
III	Lüderitz Bay	III	III	II/III	III	III
III	Assuan	III	III	III	III	III
III	Mascate	III	III	III	III	III
V	East London	II/III	V	V	V	V
V	Nanchang	V	V	V	V	V
V	Kagoshima	V	V	V	V	V
<i>Modern faunas (validation)</i>		75.0%	50.0%	75.0%	100%	100%
II	Ho Chi Minh	II	II	V	II	II
II/III	Voi	II	V	II/III	II/III	II/III
III	Smara	III	II	III	III	III
V	Foochow	V	V	V	V	V
<i>Aragonian faunas</i>						
	Paracuellos 3	II/III	V	III	II	III
	Paracuellos 5	II/III	V	III	II	II
	Puente de Vallecas + Arroyo del Olivar	II/III	V	III	II	III
	Paseo de las Acacias	II	II	II/III	II	II
	Estacion Imperial	II/III	II	III	II	II
<i>Turolian faunas</i>						
	Venta del Moro	II/III	V	II	II	III
	El Arquillo	II/III	V	II	II	V
	Cerro de la Garita	III	V	II	II	V
	Los Mansuetos	III	II/III	II	II	III
	Puente Minero	II/III	V	II	II	III
	Crevillente 2	III	V	II/III	II	III

The observed and the predicted climate zones (see Table 1), based on the ecological diversity or the cenogram variables, are shown for each locality. The percentage of correctly classified localities is shown for both the models and the validation analyses (T, taxonomic categories; Tr, trophic categories; L, locomotion categories; BS, body size categories). See Appendix 3 for more detail.

significantly related to aridity. Finally, the scores of the fossil assemblages in the “aridity PCA factors” were used to order them in the aridity gradient.

4. Results

The ecological diversity and cenogram statistics calculated for both sets of modern Old World mammal faunas (21 + 7) are available, along with the same statistics calculated for

the 16 Neogene–Quaternary fossil localities, as supplementary material (Appendices 1 and 2), which is available at the National Museum of Natural Sciences of Madrid web site (<http://www.mncn.csic.es/>).

4.1. The discriminant models

Tables 6 and 7 show a summary of the results of the ten different models developed by means of discriminant analysis, respectively, for tropical and temperate faunas. More detailed results are provided in Appendices 3 and 4 (available at <http://www.mncn.csic.es/>).

Each model consists of three canonical discriminant functions, which have been calculated using the 12 tropical or temperate modern mammal faunas. Each function is highly correlated with one or two of the studied variables, allowing the separation of localities belonging to different climate zones.

The best performing models are those based on cenogram variables and on the ecological diversity variables related to body size, for both tropical and temperate faunas.

Table 7

Discriminant analysis results for the temperate modern mammal faunas and the Pleistocene Iberian faunas

Climate zone	Locality	Ecological diversity				Cenograms
		T	Tr	L	BS	
<i>Modern faunas (models)</i>		83.3%	91.7%	100%	100%	100%
III	Lüderitz Bay	III	III	III	III	III
III	Assuan	III	III	III	III	III
III	Mascate	VII	III	III	III	III
IV	Sanlúcar de Barrameda	IV	IV	IV	IV	IV
IV	Tunis	IV	IV	IV	IV	IV
IV	Aleppo	VII	VII	IV	IV	IV
VI	Vlissingen	VI	VI	VI	VI	VI
VI	Brest	VI	VI	VI	VI	VI
VI	Dairen	VI	VI	VI	VI	VI
VII	Fort Schevchenko	VII	VII	VII	VII	VII
VII	Urumchi	VII	VII	VII	VII	VII
VII	Paotou	VII	VII	VII	VII	VII
<i>Modern faunas (validation)</i>		50.0 %	25.0 %	50.0 %	100 %	75.0 %
III	Smara	III	III	III	III	III
IV	Esfahan	III	III	VII	IV	VII
VI	Tsingtao	VI	IV	III	VI	VI
VII	Genichesk	VI	VI	VII	VII	VII
<i>Pleistocene faunas</i>						
	Cúllar de Baza 1	III	VII	VII	III	III
	Atapuerca TD6	IV	VI	VII	III	VII
	Atapuerca TD4	III	VII	VII	III	VII
	Huéscar 1	III	VII	III	III	III
	Venta Micena	III	VII	VI	III	IV

The observed and the predicted climate zones (see Table 1), based on the ecological diversity or the cenogram variables, are shown for each locality. The percentage of correctly classified localities is shown for both the models and the validation analyses (T, taxonomic categories; Tr, trophic categories; L, locomotion categories; BS, body size categories). See Appendix 4 for more detail.

Additionally, the models based in taxonomic diversity and locomotion diversity were quite accurate for tropical and temperate faunas respectively. Since their performance in either the original discriminant analyses or the validation analyses was relatively poor, the rest of the models are considered not accurate.

4.2. The principal component analyses

The PCA results are summarized in Appendices 5 and 6 (available at <http://www.mncn.csic.es/>). Ten and eighth significant components have been retained in the tropical data set and the temperate data set, respectively, because their eigenvalues are larger than 1. These components account for about 90% of the variance in the original data for both groups of faunas. The first component separates fossil assemblages and modern faunas in both data sets (Fig. 2). Therefore, these PCA factors 1 seem to absorb the differences in the structure of the mammalian communities between fossil and modern faunas. This result indicates that the fossil assemblages show a somehow different structure from the modern localities and this could be the result of the fossilization process. However, it is not clear that different taphonomical conditions influence the results in a different way, since all assemblages are ordered similarly in the first PCA factor respect to modern communities. In our opinion, the influence on the resulting structure of the general loss of information due to fossilization is probably stronger than the differences in the taphonomical processes at work. The latter probably have stronger influence in the relative abundances of fossil taxa, which are not involved in any of the used methodologies.

The correlations between the PCA factors of each data set and the values of annual precipitation (P) and drought length (D) of the modern communities are shown in Table 8. In the tropical faunas, P and D are significantly correlated with both PCA factor 1 and 4. D is also significantly correlated with PCA factor 8. Since PCA factor 1 is related to the difference in ecological structure between fossil and modern assemblages, here we consider

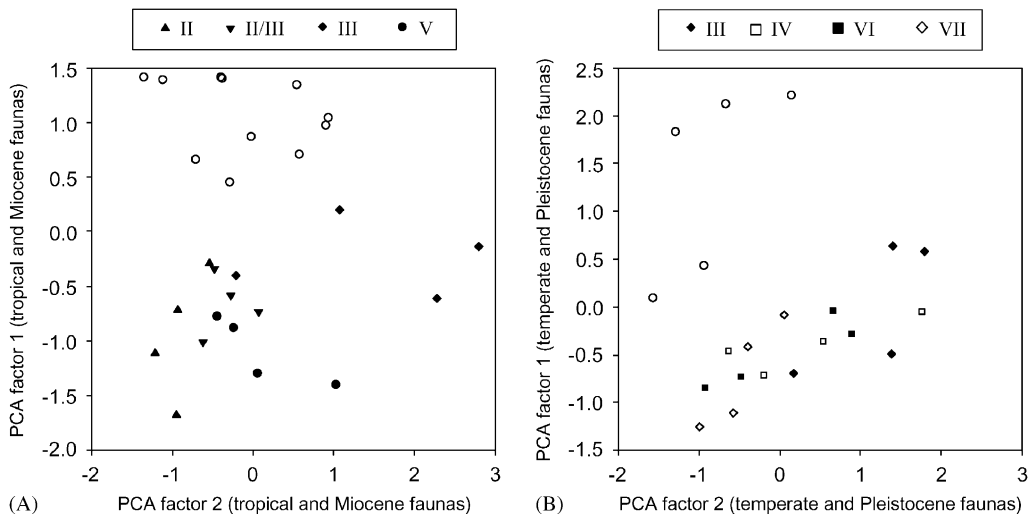


Fig. 2. Scatterplot of the two first PCA factors for both the tropical (A) and the temperate (B) data sets. Fossil assemblages are represented by white circles. The rest of the symbols represent the modern faunas (see Table 1).

Table 8

Coefficients and their significance for the correlations between the PCA factors, annual precipitation (P) and drought length (D) for the analyses of both tropical and temperate faunas

	Tropical faunas				Temperate faunas			
	P		D		P		D	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
PCA factor 1	−0.755	0.001	0.680	0.004	−0.240	0.370	0.306	0.248
PCA factor 2	−0.401	0.124	0.431	0.096	−0.303	0.254	0.443	0.085
PCA factor 3	0.041	0.881	−0.169	0.531	0.689	0.003	−0.538	0.031
PCA factor 4	0.682	0.004	−0.542	0.030	0.016	0.952	0.049	0.858
PCA factor 5	0.311	0.241	−0.312	0.240	−0.004	0.989	−0.085	0.753
PCA factor 6	−0.033	0.904	−0.031	0.909	−0.203	0.452	0.239	0.372
PCA factor 7	−0.272	0.308	0.353	0.180	−0.125	0.645	0.206	0.444
PCA factor 8	0.392	0.133	−0.535	0.033	−0.057	0.835	−0.171	0.526
PCA factor 9	0.408	0.116	−0.132	0.625				
PCA factor 10	−0.313	0.238	0.423	0.103				

Significant correlations are in bold.

PCA factor 4 as the aridity factor and we used its scores for each fossil assemblage in order to place them in the aridity gradient (Fig. 3A). In the temperate data set, PCA factor 3 is the only component significantly correlated with *P* and *D* (Fig. 3B). Therefore, this is considered as the aridity factor.

Nevertheless, the correlations of both aridity factors with *P* or *D* are very low. The associated regressions only explain about 50% of the variability in these factors (Fig. 3). Therefore, other variables are implied in the variability of the PCA factors. To avoid that variations in these other unknown variables concerning fossil assemblages affect the correct understanding of the aridity factors, we will interpret only the relative ordination of fossil sites from similar time periods, as suggested by de Bonis et al. (1992b). As a standard time framework for the Miocene we use the MN system. In the Pleistocene assemblage, only Atapuerca TD4 and Atapuerca TD 6 are close in time (Hernández Fernández et al., 2004).

4.3. The Neogene–Quaternary faunas

4.3.1. Aragonian faunas

The different discriminant models offer different results regarding the biomes of these fossil sites (Table 6). Whereas the body size diversity classifies all the assemblages as tropical deciduous forests, the taxonomic diversity assigns all of them to the savanna biome, excepting Paseo de las Acacias, which is classified as a tropical forest. The model based on cenograms classifies most of these assemblages as tropical deciduous forest, but Paracuellos 3 and Puente de Vallecas are allocated as deserts.

Within the aridity gradient Paseo de las Acacias and Estación Imperial occupy the most humid extreme, whereas the other fossil assemblage of the MN 5, Puente de Vallecas, is drier. The fossil assemblages from the MN 6 are in a similar position within this gradient, although Paracuellos 3 is somewhat more humid than Paracuellos 5 (Fig. 3). These results

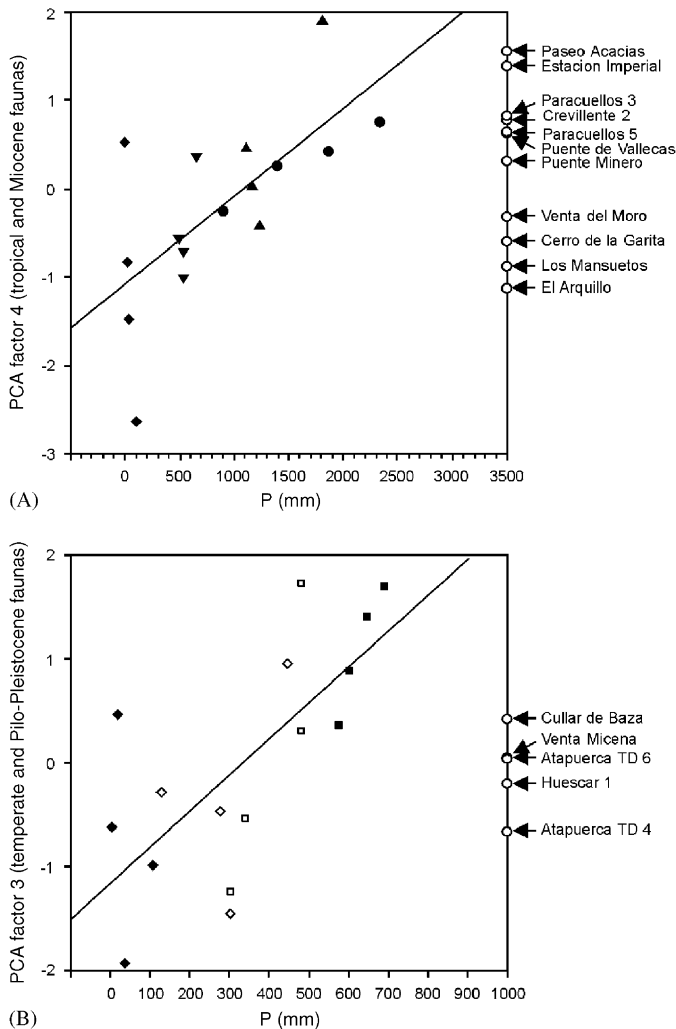


Fig. 3. Scatterplot of the aridity PCA factors and the precipitation gradient for both the tropical (A) and the temperate (B) data sets. The regression line for the modern faunas is shown. Symbols as in Fig 2.

are roughly coincident with those by Hernández Fernández et al. (2003), based on the taxonomic structure of the palaeocommunities of large herbivores from the Aragonian of Spain.

4.3.2. Turolian faunas

A similar problem has been raised in the Turolian mammalian assemblages; different models offer different biomic assignments (Table 6). The PCA results obtained for the early Turolian localities show that Crevillente 2 is more humid than Puente Minero (MN11). The relatively humid character of the lower part of the Crevillente stratigraphic sequence has been already pointed out by Martín Suárez et al. (2001), Mazo and Montoya (2003) and Montoya and Morales (2004), based on different mammalian groups.

Concerning the middle Turolian localities, Cerro de la Garita is similar to Los Mansuetos (MN12) but the latter is somewhat drier than the former. In the late Turolian localities the aridity gradient shows that the ecological structure of Venta del Moro is more humid than the one of El Arquillo (MN13). Sedimentological data support this interpretation because Venta del Moro belongs to a lacustrine sequence where several cycles of flooding and desiccation have been recorded (Mathisen and Morales, 1981; Marín et al., 2002). Furthermore, levels with important concentrations of leaves from caducifolious trees have been registered in this fossil site, which indicates the presence of significant woodlands, at least in riverine environments.

4.3.3. Pleistocene faunas

The biomic assignments of these fossil assemblages by the different discriminant models are shown in Table 7. In general, the ecological structure of these faunas is similar to that in modern steppe or desert faunas. The model based in body size diversity classifies all the fossil assemblages as deserts. The model based in cenogram variables classifies Venta Micena as sclerophyllous woodlands, the Atapuerca assemblages as steppes, and Cúllar de Baza 1 and Huéscar 1 as deserts. The model based in locomotion variables classifies Venta Micena as temperate forest, Huéscar 1 as desert and the Atapuerca assemblages and Cúllar de Baza 1 as steppes. According to the ordination in the aridity gradient, Atapuerca TD 4 is dryer than Atapuerca TD 6, which agrees with the interpretation of the rodent faunas made by López Antoñanzas and Cuenca Bescós (2002) and Hernández Fernández (2005) and with the vegetation recorded in palynological analysis (García Antón, 1995).

5. Discussion

A striking result of our analysis is that the Iberian fossil faunas differ in ecological structure from all recent faunas. Although the ecological structure of the modern mammalian faunas is clearly related to the environmental conditions, the application of models developed from them to fossil assemblages shows a poor performance of such models. Several explanations may account for it.

A possible source of error would be the ecological characterization of the extinct species. Nevertheless, the variables used to describe the ecological structure of the mammal faunas were broad enough to allow a correct categorization of most of the extinct species. On the other hand, since these variables were markedly vague and imprecise, the methodology used to describe and compare community structure might be inadequate to reflect differences between fossil assemblages. Nevertheless, the method has largely reflected ecological variability in recent communities, which indicates the general usefulness of our approach.

Additionally, the initial selection of biomes from which the recent faunas used for comparison were taken might be inadequate. Although in general the selection of modern analogue faunas could be problematical when studying fossil assemblages, we have incorporated the biomes that would occupy the extremes in the environmental gradients that may include the studied fossil sites. Therefore, our initial selection of biomes should cover all the potential biomes implied. Another potential limitation of this approach is the possible existence in the past of biomes unknown today. Nevertheless, Neogene–Quaternary biomes seem to have been substantially similar to modern ones (CLIMAP, 1976; PRISM, 1995; Ruddiman et al., 1997).

In addition to the potential taphonomical bias in the structure of the fossil assemblage, the PCA results could be interpreted as a lack of direct modern analogues, which is supported by other studies (de Bonis et al., 1992a,b; Rodríguez, 2001; Hernández Fernández et al., 2003; Rodríguez et al., 2004). This indicates that the ecological structure of mammalian faunas is not only dependent on environmental factors, but other aspects such as biogeography and history may be also important (Rodríguez et al., 2004; Hernández Fernández and Vrba, 2005a–c). The palaeobiogeographic conditions in south-western Europe were very different in Miocene and Plio-Pleistocene times to those nowadays. During the Miocene the Iberian climate was mainly tropical (Sanz de Siria Catalán, 1985; Gregor, 1990; Barrón et al., 1996; Barrón and de Santisteban, 1999) and thus the Iberian mammal faunas were ecologically very different from those in the temperate Europe and supposedly more related to tropical communities. Nevertheless, the faunal connections with tropical biogeographic realms were not constant during this period (Pickford and Morales, 1994). Additionally, the isolated position of the Iberian Peninsula at the western extreme of Europe, which is a peninsula itself, probably made these connections difficult even during the periods of faunal interchange. Thus, it could be argued that the Iberian Miocene mammal faunas were relatively impoverished in comparison to the tropical faunas in other areas, and their ecological structure might be affected by this fact. In contrast, during the last 2.5 million years the climate in the Iberian Peninsula has been temperate and its ecosystems have been closely related to those in continental Europe (Menéndez Amor and Florschütz, 1963; Julia and Suc, 1980; Roiron, 1983; Suc and Zagwijn, 1983; Diniz, 1984; Suc, 1984; Sanz de Siria Catalán, 1987; García Antón, 1995; Barrón et al., 1996). Nevertheless, the environmental conditions during the Pleistocene have been markedly influenced by the recurrent cycles of glacial–interglacial, which may also affect the comparability of Pleistocene and modern faunas. The latter belong always, by definition, to the current interglacial phase, while the Pleistocene faunas may belong to either an interglacial or a glacial phase.

On the other hand, our analysis has also shown that, despite the lack of direct analogues between fossil and modern faunas, PCA can absorb the differences in structure and some of the PCA components can be interpreted as environmental indicators. Although their explanatory power may not be very high, the restriction of environmental interpretation to delimited time periods allows obtaining significant information on the environmental conditions (aridity in the present case). Therefore, the inclusion of climatic data for the modern faunas is shown to be essential in order to interpret adequately the significance of the different PCA factors. In the same line of thinking, it is essential to include ecotonal faunas because, since they occupy areas with intermediate values in different environmental variables, they can provide a smoother gradient for these variables. More generally, it is convenient to increase the number of modern faunas that are included in predictive models, which will allow to reflect the diversity in ecological structures that each biome may present (e.g. our model for temperate faunas based on trophic diversity was able to classify correctly 92% of the faunas included in it, but most of the faunas included in the validation test were wrongly classified).

Finally, our results imply that the use of independent methodologies of palaeoecological analysis is essential when attempting to reconstruct palaeoenvironments. It also becomes clear that the development of new methods for the description of the ecological structure of mammalian communities is indispensable in order to achieve a greater knowledge of the Neogene–Quaternary palaeoenvironments. These new methods should be able to perform

adequately even when studying mammal communities with no analogues in the modern faunas. An example of such a methodology is the bioclimatic analysis (Hernández Fernández, 2001; Hernández Fernández and Peláez-Campomanes, 2003, 2005), which is based on climatic and mammalian distributional data. It has already applied to Spanish rodent faunas providing very satisfactory results even for periods as early as the lower Pliocene (Hernández Fernández, 2005), when the paleobiogeographic relationships of the Iberian Peninsula were closely similar to those during the Miocene.

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