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How Did Past Environmental Change Affect Carnivore Diversity and Home-Range-Size in Spain?

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1. Introduction

An important aspect of evolutionary biology is to know the faunal diversity changes through time. There is a general agreement that the knowledge of evolutionary patterns through time from an ecological perspective provides information that is not available from ecological studies on extant faunas (Vrba, 1985, 1995a; Behrensmeyer et al., 1992; Jablonski, 2005). Iberian Cenozoic basins provide an exceptional record of fossil mammals and continental environments, giving a great opportunity to evaluate the ecological and evolutionary responses of mammalian communities to climatic changes through the last millions years (Azanza et al., 1999, 2000; Hernández Fernández et al., 2007; Van Dam et al., 2006). This knowledge is essential for linking the dynamics of biotic change from ecological to evolutionary time scales and for understanding the processes that transform ecosystems over geologic times (Badgley et al., 2008).

Previous works have proposed different explanations for biodiversity changes through time, emphasizing the influence of both physic and biotic factors (e.g., Van Valen, 1973; Janis, 1989; Stucky, 1990; Vrba, 1995a, 1995b, 2000; Prothero, 1999, 2004; Alroy, 2000; Alroy et al., 2000; Barnosky, 2001, 2005; Vrba & DeGusta, 2004). The response of mammals throughout the late Cenozoic has been often reflected by migrations or variation of their area of distribution, related to the vegetation cover and latitudinal displacement of biomes. Patterns of change in the home range size (HR, the size of the minimum area that can sustain the individual's energetic requirements) through time can provide important insights into the ecological and evolutionary responses of mammalian communities to new environmental conditions. In a lesser degree, mammals can also respond evolving into new species. These events could modify the structure of mammalian communities, triggering new internal

dynamics. In this sense, different authors such as Kolfshoten (1995) and Koenigswald (2002, 2003) have postulated an alternation of “temperate faunas” and “cold faunas” in interglacial and glacial periods, respectively, in Central Europe; Spassov (2003) for Eastern Europe; and Vrba (1995a), Turner (1990, 1999), Behrensmeyer et al. (1997), McKee (2001) and Werdelin & Lewis (2005) have discussed the African faunal turnovers.

Among biotic factors that may alter the biodiversity, intra- and interspecific competition and niche occupancy seem to be related to the pre-existing community structure, while prey/predator interactions may differ from area to area (Abrams, 2000; Chesson, 2000). It seems reasonable to assume that several factors contributed in different ways to modify mammalian guilds. In the case of carnivores, the dynamics might depend more on prey-predator relationships and to the availability of prey than on climatic factors (Carbone & Gittleman, 2002). Consequently, one could assume that the diversity of carnivores would be less related to climatic-environmental conditions than that of herbivores.

A previous paper (Palombo et al., 2009) has tried to evaluate the progressive changes in the composition of carnivore guilds in north-western Mediterranean area as a direct response to climatic changes. As in other Mediterranean areas, Iberian Peninsula was influenced by the Plio-Pleistocene climatic oscillations that provoked migrations of taxa from East and Central Europe, as well as from Africa, across the Levantine corridor (Alberdi et al., 1997; Azanza et al., 1997, 2000, 2004; Palombo & Valli, 2005; Palombo, 2004, 2007a, 2007b). The present chapter summarizes an updated study on the relationships of biodiversity and HR size variation with climatic changes for the Spanish Plio-Pleistocene Carnivora.

2. Material and methods

Most data for the present study are based on the selected and taxonomically updated faunal lists of large predatory mammals that have been compiled from previous analyses on the Plio-Pleistocene mammals of the North-Western Mediterranean region (Alberdi et al., 1997; Azanza et al., 1999, 2000; Palombo et al., 2009), herein restricted to the Spanish area (Figure 1). The considered biochronological scale has followed discrete time intervals following the mammal ages broadly accepted for western Europe, the European Mammal Neogene System, or MN “zones” (Mein, 1975, 1990; Agustí et al., 2001; van Dam, 2001), which mainly concern Miocene-Pliocene times. In turn, four MmQ “zones” have been differentiated for the Spanish Early-Middle Pleistocene mammalian faunas (i.e., Agustí et al., 1987). From this general scheme, we have adapted thirteen biochronological units (BU; Figure 2), established by multivariate procedures (Azanza et al., 1999, 2004) and defined as “lapses of time during which faunas have certain taxonomic homogeneity, the discontinuity between them corresponding to faunal reconfigurations associated with major changes in environmental conditions”. Some localities count with absolute dating that allow estimating the duration of each unit (Palombo, 2007a; Palombo et al., 2009).

The comparison of carnivoran guilds implies some difficulties related to the usual lesser representation of this group with respect to other mammals, for instance herbivore ungulates, with the subsequent underestimation of their taxonomic diversity. In any case, the whole sample of a site is always a partial reflect of the actual diversity of the community that once lived there. Trying to avoid this bias, we consider faunal complexes gathering several local faunal assemblages, and assume that these complexes allow checking the main faunal turnovers through time (Palombo et al., 2009).

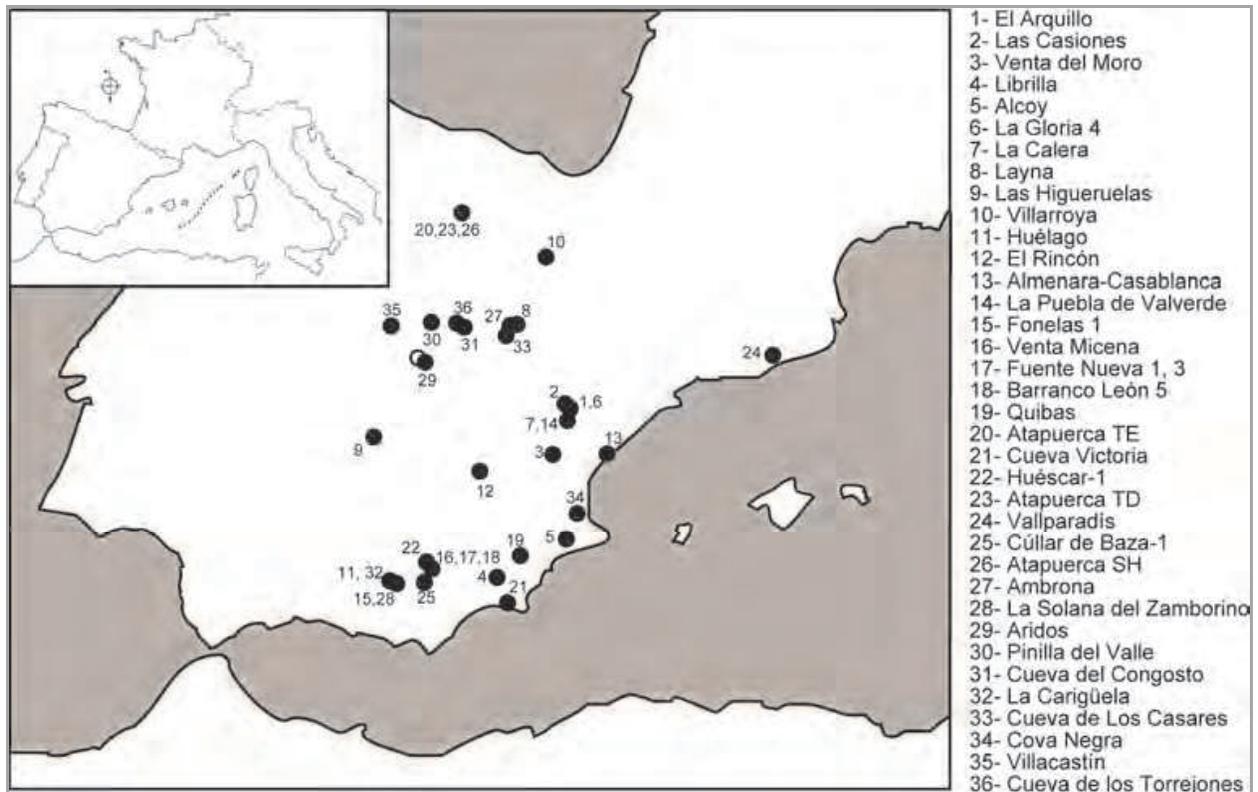


Fig. 1. Geographical distribution of the selected localities from Spain.

Van Valkenburgh (1985, 1988, 1989) confined large terrestrial carnivore guilds to predators weighting 7 kg or more (jackal size and larger), proposing this size threshold because of the evidence in extant species for strong competitive interactions among carnivores larger than 7 kg, being weaker among smaller carnivores; in addition, the representation of large carnivores in the fossil record is better. On the other hand, because larger predators achieve a higher net gain rate by concentrating on large prey, Carbone et al. (2007) predicted the threshold of 14.5 kg, where predators switch from small to large prey. We follow this criterion, and restrict our study to species of the three families that include top terrestrial predators: Canidae, Felidae and Hyaenidae. Ursidae are excluded due to their omnivorous feeding behaviour that rarely includes meat.

For each species, we compiled data of its presence in fossil sites, body-size, diet and preferred habitat. We used a taxon-free characterization by means of two ecological criteria of classification. According to the feeding behavior, species were classified in two trophic categories: (1) Carnivore (C): hypercarnivores with a diet that consists of 70% or more flesh meat, bone-eaters, bone-crushers and scavenging bone-crackers; and (2) Carnivore-Omnivore (OM): including flesh-eaters (with less than 10% flesh in their diet), taxa feeding on invertebrates, and occasionally on fruit. Concerning the preferred habitat, three major ecological categories were considered: (1) Forest dwellers (FH): taxa inhabiting forest, closed woodland, bushland, Mediterranean “macchia”, open woodland, and miscellaneous woodland; (2) Ubiquitous (MXH): including more flexible taxa, inhabitants of shrubland or woodland, as well as open landscape, or at the edge of both; and (3) Open landscape dwellers (OH): including taxa inhabiting grassland, steppe or savanna (Figure 2).

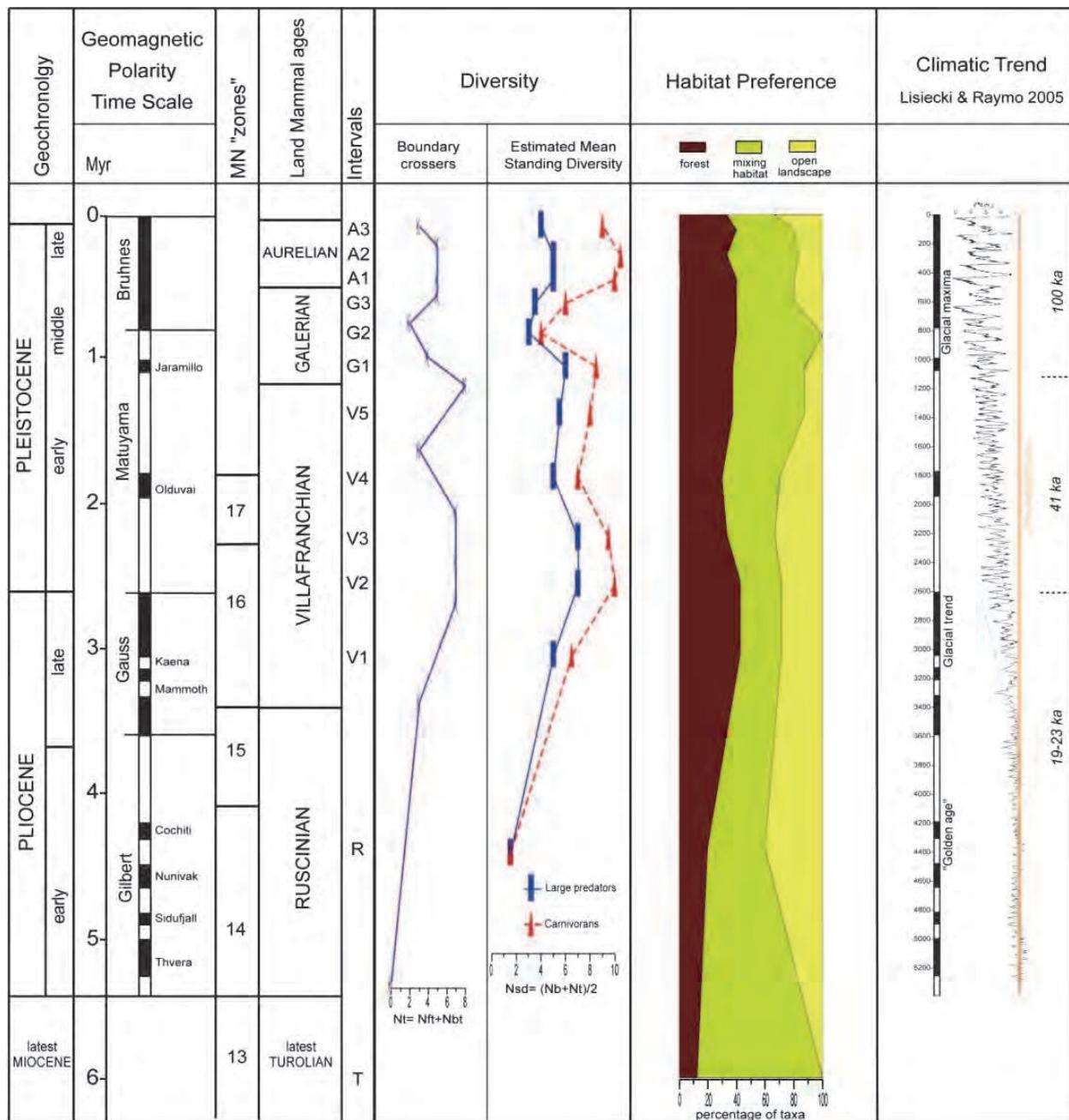


Fig. 2. Biochronological framework. Carnivoran standing diversity, habitat preferences over the Plio-Pleistocene and climatic trend.

The HR-size of fossil species was estimated using the regression for each family, habitat preference and trophic categories. The relationship between HR-size and body size (or body weight, BW) has been stated by McNab (1963) using the allometric equation $HR = a BW^b$. This author considered two categories: hunters and croppers, the former having a greater allometric coefficient (a), a fact he attributed to the relatively low density of their preferred food items. Posterior studies, such as that by Gittleman & Harvey (1982), have established that carnivorous species had larger HR-size than herbivorous species of similar body mass, and that the distribution of food resources is more homogeneous for herbivores than for carnivores. However, other studies (Kelt & Van Vuren, 1999) defend that scaling relations of

HR-size are not statistically different between carnivorous and herbivorous or omnivorous species. Among terrestrial mammals, carnivore guilds have the broadest range of HR-sizes. Some of the variation in the HR-size of Carnivora can be explained by diet.

Paleobiodiversity refers to the richness of species, measured as the total number of taxa in a time interval. To avoid over estimation of taxa, we use the “Estimated mean standing Diversity” (N_{sd}), following the methodology developed by Foote (2000). The N_{sd} has been calculated for each time interval using both the initial data base and the data base resulting from the taxon-free characterization (following Palombo et al., 2009).

The quality of the fossil data is crucial for validating results and conclusions, because the fluctuating frequencies of coexisting species may reflect actual changes in diversity or may depend simply on sampling bias. Incomplete preservation is usually estimates by the proportion of range-through taxa (or Lazarus taxa) supposing that their existence is mainly a consequence of deficient sampling. Sampling adequacy was explored using the completeness indices ($CI = [(N_{tot} - N_{rt}) / N_{tot}] \times 100$ and $CI_{bda} = (N_{bda} / N_{bi}) \times 100$) proposed by Maas et al. (1995).

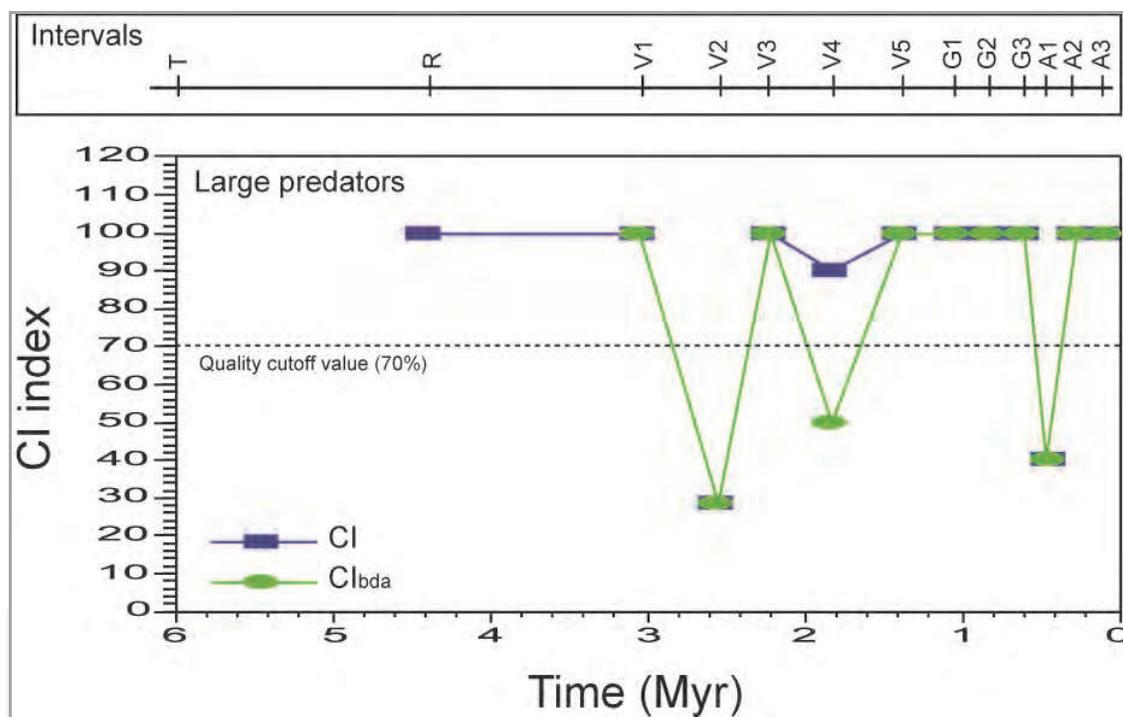


Fig. 3. Quality assessment of the carnivoran data from Spain.

The values of the completeness indices are affected by BU duration, because increasing the length of a time span means that it can potentially include a more extensive fossil record and also reduces the number of the Lazarus taxa. We use as cut-off threshold the value of 0.14 that results of dividing the minimum acceptable index value of 70% by the canonical span time (500 ka) suggested by Maas et al. (1995).

3. Results

Figure 3 shows the values of completeness indices for the data of large predators. The more conservative CI_{bda} index has a value below 70% in three BUs: V2, V4 and A1, whereas if the

more generous CI index is used, the quality of the record is only deficient in two (V2 and A1 BUs), indicating that data from these BUs should be treated circumspectly (Maas et al., 1995).

The diversity trends (N_t and N_{sd}) show three “increase plus decrease” pulses, with peaks at the Plio-Pleistocene boundary (V2 to V3 BUs), at the beginning of the Middle Pleistocene (G1 BU) and at the Middle-Late Pleistocene boundary (A1 to A2 BUs). This general pattern is also observed in Italy and France, but in non-synchronous pulses (Palombo et al., 2009). Despite these fluctuations, diversity increases during the Plio-Pleistocene, but large predators show a more moderate increase than other carnivores. The lowest diversity outstandingly corresponds to the Early Pliocene (R BU) that is, by far, the longest BU. This can be related to the most relevant extinction event in Iberian Peninsula, occurred at the Mio-Pliocene transition, when all the Turolian large predators became extinct. These trends roughly correlate with the general global climate signal (Lisiecki & Raymo, 2005, see Figure 2). The first peak is coincident with the onset of Northern Hemisphere Glaciations and the following decrease in diversity began when glacial-interglacial cycles of 41 Ka were clearly installed. The second peak coincides with the intensification of glacial cycles that change from 41 to 100 ka periodicity. The third maximum, during the Middle Pleistocene, correlates with a hot period (Holstein stage) between Mindel and Riss glaciations. The first and third peaks are herein considered to be more reliable, because the diversity of the second one (V2 and A1 Bus) could be under estimated (Palombo et al., 2009).

The HR size quantifies the animal's inherent ability to move. Thus, dispersal distance and HR-size co-vary across mammal species when considered independently of body size (Bowman et al., 2002). Figure 4 documents the patterns of HR-size change through time. Reference lines represent the predicted threshold of 14.5 kg where predators switch from small to large prey (Carbone et al., 2007). In general, the HR-size for Canidae decreases during the Pliocene, independently of which estimation of HR-size is considered (family, habitat preference and trophic categories). The Canidae species are clearly separated by the predicted threshold of 14.5 kg. Those with carnivorous diet have a larger HR-size than the omnivorous species. Around 8 Ma ago, Beringia allowed the dispersal of Canidae throughout Eurasia. The first Eurasian record is *Canis cipio*, only present in the Iberian Peninsula during the Latest Miocene. From 7.2 to 5.3 Ma the genus *Eucyon* was represented by *E. monticinensis*. The genus probably dispersed again in Spain at the end of the Early Pliocene (Sotnikova & Rook, 2010).

Figure 4 shows that HR-size decreases in *Eucyon* during the Pliocene. The small HR-size diversified with the occurrence of the genus *Nyctereutes* and later with *Vulpes*. All these taxa are small predators and remain in the omnivore niche. The main change in HR-size structure among canids occurred at the Early Pleistocene when the glacial-interglacial cycles were well established. A new large HR-size appears for Canidae related to the switch on carnivore niche. These canids are coyote-like and wolf-like forms with hypercarnivore diets. The dispersal of hypercarnivore canids in Iberian Peninsula during the Early Pleistocene is evidenced by an increasing number of fossils not only of large wild dogs (*Lycaon falconeri* as cited in Martínez-Navarro & Rook, 2003) but also Villafranchian wolves (*Canis* ex gr. *C. etruscus*). This is the traditionally called “Wolf Event” due to the massive appearance of these canids in the fossil record (Azzaroli, 1983; Sardella & Palombo, 2007; Rook & Torre, 1996). Even the *C. accitanus* coyote-like dogs increased the HR-size of omnivore canids at this time. This event integrates a faunal renewal that occurred at approximately 2 Ma,

The Felidae HR-size structure is rather different from that of Canidae. There are four groups of HR-size clearly distinguished from Middle to Late Pleistocene (Figure 4). The smallest HR-sizes correspond to the latest Miocene and the latest Middle to Late Pleistocene. During the Late Pliocene, the intermediate HR-sizes overlap. This moment was characterized by the predominance of open and mixed habitats. In the present African landscape, most of the large predators are abundant in open savannas and savannas-woodlands, coincident with the highest ungulate densities. Rodriguez et al. (2004) showed an increase of size for the ungulates of that time, and without small-sized herbivores. This pattern remains a more close fit between prey and predator. New species appear during Lower Pleistocene and seem to begin a competitive displacement of the four groups of HR-size. After the "Wolf Event" (latest Early Pleistocene), the intermediate niche is segregated into two. This pattern suggests competitive size displacements as the main influence that might have caused HR-size changes.

The Hyaenidae pattern is similar to that of Canidae (Figure 4). The distribution of HR-size is conditioned by the diet, but this pattern was acquired previously and the presence of omnivorous species is occasional. The Hyaenidae were more diverse during the Late Miocene. Together with a precocious bone-eater hyaenidae, *Adcrocuta eximia*, two thalassictine forms were recorded. The "thalassictine group" is basically canid-like and establishes the general trend toward hypercarnivory (Werdelin & Solounias, 1991). All these taxa disappeared at the end of the Miocene and were replaced by a new hyaenid fauna. The canid-likehyaenids show a decrease in diversity that is strongly correlated with the arrival of Canidae into Eurasia during the Late Miocene-Early Pliocene. However, the only hunting hyaenid, *Chasmaportetes lunensis*, continues successfully during the Pliocene. Its disappearance in the Early Pleistocene seems to be related to the "Wolf Event". *C. lunensis* was the only cursorial, meat and bone eater hyaenid (Turner et al., 2008), adapted to open habitats. The Pliocene shows the full emergence of an organised guild of large carnivores in Europe. The appearance of *Pliocrocuta* at the R BU, followed by the gigantic *Pachycrocuta* at Late Pliocene-Early Pleistocene, shows that hyenas were able to obtain a consistent living from scavenging when necessary. In these taxa, the bone cracking component of the dentition is developed at the expense of the shearing component. Scavenging and hunting form part of a spectrum of behaviours. Living hyenas show a range of food-obtaining strategies that go through various aspects of their skeletal morphology (Werdelin & Solounias, 1991; Turner et al., 2008). The "Wolf Event" did not represent any important change despite the immigration of *Pachycrocuta brevirostris*, the largest true hyena ever recorded. Only one species of hyaenid was recorded from this event to latest Pleistocene, *Crocuta crocuta*.

4. Remarks

The analysis of Spanish Carnivora diversity trends shows that the hypothesis of a direct influence by climate change is partially supported by the data. There are two main moments of maximum diversity. The first one occurred during the late Pliocene, followed by a detached decrease during the Early Pleistocene. This lapse of time coincides with the progressive development of the Mediterranean double seasonality (related to the emergence of cold winters) that culminated with the start of the Pliocene glacial trend at 2.7-2.6 Ma (Suc et al., 1995; Suc & Popescu, 2005). The establishment of glacial cycles of 41 Ka is consistent with the diversity decrease during the Late Pliocene-Early Pleistocene. The second increase

happened in the middle Pleistocene and was followed by a minimum during the last Glacial. These diversity changes can be correlated with the general global climate signal (Shackleton, 1995); the beginning of this phase is roughly correlated with the shift of the 100 Ka glacial cycles at 1.0 Ma.

Among Plio–Pleistocene Carnivora, only a few are specialized species; many others were ubiquitous or generalist, occupying broad niches. This fact would favor that a high number of carnivoran taxa survives major environmental changes. Comparing diversity trends and shifts in the percentage of carnivorans in each of the habitat categories, it seems that trends in diversity are roughly correlated with the variations of the relative abundance of forest habitat through time. This rough correspondence should be explained as an ecological response, given that the forest-dwelling species were generally more dependent on environmental conditions and shifts of the vegetation cover. On the other hand, the relative increase of ubiquitous taxa during the Pleistocene could be related to the environmental fluctuations associated with the glacial cycles, because these taxa are expected to be more able to adapt to environmental changes. Indeed, forest carnivores seem to be much more sensitive to climate and humidity changes.

In sum, climatic changes altered the ecological equilibrium of palaeocommunities. The effect this had in shaping local patterns of carnivoran diversity was possibly significant. Even during the recent past, environmental conditions have differentially affected migration and dispersal of large mammals towards and across the Iberian Peninsula. Carnivora that progressively dispersed into this region did not occupy preexisting free niches, but new ones that became available as a consequence of the environmental change (Palombo et al., 2007a, 2009). Consequently, their organization of guilds seems to be more closely related to the time and mode of dispersal events of the Carnivora than to the major climatic changes.

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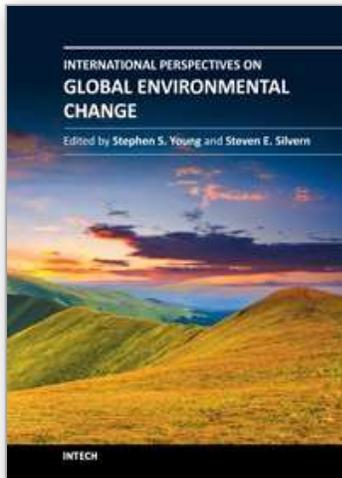
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