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Carrying capacity, carnivoran richness and hominin survival in Europe

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ABSTRACT

Carrying capacity, the maximum biomass that an ecosystem can sustain over the long term, strongly influences several ecological processes and it is also one of the main determinants of biodiversity. Here, we estimate the carrying capacity (CC) of the late Early and early Middle Pleistocene ecosystems of Europe, using equations describing the relationship between CC and climatic variables observed in the present, as well as maps of inferred paleotemperature and paleoprecipitation. Maps of paleoclimate values were interpolated from the composite benthic stable oxygen isotope ratios and a transfer function was used to estimate ungulate carrying capacity (CC_U) from the interpolated mean annual temperature and annual precipitation values. Carnivoran carrying capacity was subsequently estimated from ungulate carrying capacity and the effect of CC on the carnivoran faunas was analyzed in 12 paleocommunities from Southern Europe. Our results show that carnivoran species richness is strongly related to ungulate carrying capacity in recent ecosystems, but the late Early Pleistocene paleocommunities from Southern Europe included much richer carnivore guilds than would be expected for a recent community with a similar ungulate carrying capacity. Thus, those late Early Pleistocene ecosystems supported a high number of carnivoran species, but the carnivoran biomass they could support was relatively low. Consequently, carnivorans occurred at low densities in Southern Europe compared to the recent African savanna ecosystems, but likely also compared to coeval East African ecosystems. Consequently, the first *Homo* populations that arrived in Europe at the end of the late Early Pleistocene found mammal communities consisting of a low number of prey species, which accounted for a moderate herbivore biomass, as well as a diverse but not very abundant carnivore guild. This relatively low carnivoran density implies that the hominin-carnivore encounter rate was lower in the European ecosystems than in the coeval East African environments, suggesting that an opportunistic omnivorous hominin would have benefited from a reduced interference from the carnivore guild.

1. Introduction

Although the precise time of the arrival of the first *Homo* populations into Europe is still a matter of dispute, strong evidence supports the presence of humans on the continent at the end of the late Early Pleistocene (Arzarello et al., 2007; Carbonell et al., 2008; Duval et al., 2012; Toro-Moyano et al., 2013). However, scholars are divided between those supporting an arrival in Europe before 1.2 Ma (e.g. Arzarello and Peretto, 2010; Dennell et al., 2010; Agustí et al., 2015) and those who refute the evidence of human presence before 1.0 Ma (Muttoni et al., 2010, 2015). Regardless, whether the environment facilitated or otherwise influenced the settlement and dispersal of *Homo* into Europe is at the center of the debate (O'Regan, 2008; Carrión et al., 2011; Palombo, 2013; Rolland, 2013), and the main factors that may have played a role in that event are the climate, vegetation structure, resource availability and interactions with carnivorans (Agustí and Antón, 2002; Agustí et al., 2009; Made and Mateos, 2010; Palombo, 2010; Kahlke et al., 2011; Leroy et al., 2011; Made, 2011; Rodríguez et al., 2012, 2016; Muttoni et al., 2014; Carotenuto et al., 2016; Belmaker, 2017; Madurell-Malapeira et al., 2017). Resource availability is strongly influenced by primary production, but the ability of a hominin population to obtain edible resources depends also on other factors, like interspecific competition and commensal interactions. Hominin interactions with carnivores might have been very complex, and may have included predation, competition and commensalism (Moleón et al., 2014). Regarding commensalism, it has been proposed that the carcasses abandoned by saber-toothed cats, especially by *Megantereon whitei*, contained large amounts of edible resources that might have been exploited by hominins

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(Martínez-Navarro and Palmqvist, 1995; Palmqvist et al., 1996). Intraguild competition has also been claimed to be an important factor for hominin survival. For example, in the scenario described above, hominins would have had to confront the giant hyaena (*Pachycrocuta brevirrostris*), a superb competitor for carrion (Turner et al., 2008). Thus, analyzing primary production, resource availability and carnivoran paleoecology in Europe during the late Early Pleistocene and the beginning of the Middle Pleistocene is highly relevant to the hot debate over the effect of the environment on the dispersal of *Homo* out of Africa and, more specifically, the early settlement of Europe (Palombo, 2013; Rodríguez et al., 2016).

Primary production is basic to determining resource availability in any ecosystem. Primary production ultimately determines the maximum biomass of primary and secondary consumers that an ecosystem may sustain over the long term (McNaughton et al., 1989; Oesterheld et al., 1992), i.e., the carrying capacity (CC; Sayre, 2008), and it also largely influences species diversity (Hawkins and Porter, 2003; Worm and Duffy, 2003; Šímová and Storch, 2017). Primary production is influenced by a number of factors, such as soil fertility, geomorphology, or the composition of the biological community, but it is mainly determined by climate (Lieth, 1973). Thus, primary production and CC show a marked geographical variation that is linked to variations in radiation, water availability and temperature (Lieth, 1973; Nemani et al., 2003). Since global climate underwent wide and cyclic changes during the Pleistocene, we may assume that primary production and CC varied spatially and temporally in response to these climate changes in a predictable way.

Rodríguez et al. (2014) showed that the ungulate carrying capacity (CC_U) of Pleistocene ecosystems can be calculated from historical temperature and precipitation estimates. Their CC_U estimates for the Atapuerca ecosystems (northern Spain) during the Pleistocene are larger than those for recent Mediterranean ecosystems. These differences are consistent with the high herbivore diversity of the European ecosystems during the Pleistocene compared with the present (Rodríguez, 2004; Kahlke et al., 2011). The high CC_U estimated by Rodríguez et al. (2014) for the Atapuerca ecosystems is also consistent with the estimates of herbivore biomass for other Southern European Pleistocene ecosystems (Meloro and Clauss, 2012; Palombo, 2017), but the differences between the Pleistocene and recent European ecosystems are not limited to the large herbivore guild (Rodríguez, 2004, 2006). Not surprisingly, the carnivore guild was also richer in the Pleistocene than in the present, especially at the end of the Early Pleistocene, when it exhibited its highest diversity, greatly increasing the predator/prey ratio (Palombo and Mussi, 2006; Raia et al., 2007; Croitor and Brugal, 2010). Indeed, species richness of the carnivore guild of the late Villafranchian and Epivillafranchian Mediterranean communities was similar to that of the guilds of the richer recent African communities. However, those rich Late Pleistocene carnivore guilds relied on a much fewer number of prey species than their recent African counterparts (Rodríguez et al., 2012). Undoubtedly, these specific characteristics of the Late Pleistocene mammalian communities affected the functioning of the food webs, and it has been proposed that carnivorans occurred in Europe at noticeably low population densities during the late Villafranchian and Epivillafranchian (Rodríguez et al., 2012). However, carnivoran richness and the predator/prey ratio decreased markedly at the beginning of the Middle Pleistocene as part of a deep reorganization of the mammalian communities, and the ecosystems in general, that occurred in connection with a drastic change in the climate system of the Earth (Suc and Popescu, 2005; Bertini et al., 2010; Croitor and Brugal, 2010; Kahlke et al., 2011; Leroy et al., 2011; Palombo, 2014, 2017). That change, known as the Mid-Pleistocene Revolution (MPR; Maslin and Ridgwell, 2005), was characterized by an increased frequency and amplitude of the glacial-interglacial oscillations and a shortening of the melting periods relative to the anaglacial phases (Head and Gibbard, 2005).

Our aim here is to estimate the carrying capacities of the European ecosystems at the end of the Early Pleistocene and the beginning of the Middle Pleistocene, evaluate their effect on the carnivore guild and, eventually, discuss how those changes might have affected the survival opportunities of the first European *Homo* populations. Our unit of analysis is the paleocommunity, which is defined as the inventory of species living in a biogeographically distinct area during a relatively static time period, i.e., a period without significant species turnover (Raia et al., 2006, 2007). The effect of the changes in CC on the diversity of the carnivore guild is analyzed by comparing the relationship between CC_U and carnivoran richness in recent faunas to that of European paleocommunities. Furthermore, we test the hypothesis that carnivoran population density was low in Europe during the end of the Early Pleistocene by estimating carnivoran carrying capacity (CC_C) in the paleocommunities. Finally, the consequences of the variations in CC for the human settlement of Europe at the end of the Early Pleistocene are discussed in detail.

2. Material and methods

2.1. Pleistocene carnivore faunas

Data on European Local Faunas (LFAs) were obtained from published sources and are available in Rodríguez (2017). European LFAs containing carnivorans and dated to the interval from 1.6 Ma to 0.5 Ma were selected from Rodríguez (2017); since our study focuses on large predators, mustelids and other species weighing less than 10 kg were excluded from the lists. The lists were reviewed and the taxonomy was homogenized by aiming to obtain a list of species, as short as possible, for each paleocommunity. Thus, we adopted a restrictive attitude in our review of the taxonomy, since our aim is to show that these paleocommunities were richer in carnivoran species than the recent faunas. Generally speaking, if species A is considered to be the ancestor of species B, we establish that species A and B cannot be present in the same paleocommunity. This may be incorrect, from a biostratigraphic point of view, if species A evolved into species B during one of the three time intervals that define the paleocommunities. However, accepting that A and B occurred at the same time would artificially inflate the species richness of that paleocommunity. Moreover, when different competing hypotheses existed among the specialists concerning the number of species that should be distinguished in a genus, we followed the hypothesis that was more conservative in terms of the number of species.

All occurrences of canids in the lineage *Canis etruscus*–*Canis mosbachensis* older than Jaramillo were considered as *C. etruscus*, and all occurrences of Jaramillo age or younger were considered *C. mosbachensis* (Croitor and Brugal, 2010; Brugal and Boudadi-Maligne, 2011). An alternative view is to consider a single species (*C. mosbachensis*; Bartolini Lucenti et al., 2017). However, this would not affect our results, because the number of species in each paleocommunity would be the same. *Canis apollonensis* is here included in *C. etruscus* after Brugal and Boudadi-Maligne (2011). Two chronospecies were considered to be in the genus *Lycaon*, following Martínez-Navarro and Rook (2003) and Madurell-Malapeira et al. (2013): *Lycaon falconeri* in assemblages older than the Olduvai subchron, and *Lycaon lycaonoides* in younger assemblages. Although several species have been referred to the genus *Homotherium* in Eurasia, as discussed by Sardella and Iurino (2012) and Serangeli et al. (2015), here we consider a single European species, *Homotherium latidens*, following Antón et al. (2014).

Concerning the European lynxes, it is generally considered that a single species, *Lynx issiodorensis*, occurred in the Villafranchian, and that the lineage of the Iberian lynxes, *Lynx spelaeus–Lynx pardinus*, evolved in Western Europe during the Epivillafranchian and the Galerian, with the Eurasian lynx (*Lynx lynx*) arriving in the Late Pleistocene (Croitor and Brugal, 2010). However, in a recent review of the evolution of the Iberian lynx lineage, Boscaini et al. (2016) presented convincing evidence for considering *Lynx spelaeus* a junior subjective synonym of *L. pardinus*, a species evolved in the middle Villafranchian from Iberian populations of *Lynx issiodorensis*. The first appearance of *L. pardinus* is recorded 1.6–1.7 Ma at Avenc Marcel (Boscaini et al., 2015). Here, following the restrictive criteria explained above, all lynxes older than Jaramillo are considered *L. issiodorensis–L. pardinus*, while younger occurrences are assumed to represent *L. pardinus*. Two species of *Megantereon* are distinguished in the European Pleistocene, the Pliocene species *Megantereon cultridens* being replaced by the African immigrant *M. whitei* around 1.8 Ma (Martínez-Navarro and Palmqvist, 1996; Palmqvist et al., 2007; Sardella et al., 2008; Madurell-Malapeira et al., 2014). Puma-like fossils have been assigned to *Puma pardoides* (Madurell-Malapeira et al., 2010a). The medium-sized hyaenid present in some Middle Pleistocene European localities is usually referred to as *Hyaena prisca* (e.g., Croitor and Brugal, 2010), although Arribas and Garrido (2008) considered that *H. prisca* is a junior synonym of *Hyaena brunnea* (currently in *Parahyaena*), which, according to Arribas and Garrido (2008) was present in the middle Villafranchian of Fonelas but would later disappear from the European record until the Middle Pleistocene, when it reappears in sites such as Ponte Galeria, Lunel Viel or L'Escale. Here, we adopt the name *H. brunnea* for the Fonelas hyaenid and *H. prisca* for the middle Pleistocene European taxon. García and Arsuaga (2001) described the bear species *Ursus dolinensis* on the basis of fossils from Atapuerca Gran Dolina, but there is an open debate about the phylogenetic position of this taxon and the fossil populations that should be included (Rabeder et al., 2009; Wagner, 2010). In contrast, other authors include all the late early Preistocene ursids in *Ursus deningeri* (see Madurell-Malapeira et al., 2010b, 2014). Here we consider the late Villafranchian and Galerian fossils as *U. deningeri* and the late Villafranchian fossils as *Ursus etruscus*.

The dataset (Rodríguez, 2017) contains 88 European faunas dated to the 1.6 Ma to 0.5 Ma interval, with at least one carnivoran species weighting more than 10 kg recorded, but only 71 out of those 88 LFAs are located in Southern Europe (see Supplementary Online Material (SOM) Table S1). Since ungulate carrying capacity can be estimated for only the three Mediterranean peninsulas and western Europe (see below), only those 71 LFAs were included in the analyses and treated as 'samples' of a number of paleocommunities. The paleocommunities were defined based on three time intervals (1.6 Ma to 1.07 Ma; <1.07 Ma to 0.78 Ma; and <0.78 Ma to 0.5 Ma) and four regions: the Iberian Peninsula (A1), Occitanie-Provence (A2), Apennine Peninsula (A3), and Balkan Peninsula (A4; Fig. 1A). These periods roughly correspond to the late Villafranchian, Epivillafranchian or early Galerian, and the middle Galerian, sensu Palombo (2014), respectively, and thus represent periods of relative faunal stability in the carnivoran faunas (Croitor and Brugal, 2010). Moreover, the intervals are delimited by magnetostratigraphic boundaries (the beginning of the Jaramillo subchron at 1.07 Ma and the end of the Matuyama chron at 0.78 Ma; Ogg, 2012), which makes assigning the LFAs to one of the intervals easier and more reliable. Thus, by combining the time periods and regions, 12 different paleocommunities may be distinguished (Table 1 and SOM Table S2). Since the distribution of LFAs inside those regions is not homogeneous, especially inside the three southern peninsulas, the areas where no LFAs are available have been excluded from the analyses of CC_U; therefore, the size of the sampled areas does not coincide with the size of the peninsulas (Table 1 and Fig. 1A).

Species accumulation curves are commonly used in ecology to estimate the completeness of a faunistic inventory based on several discrete samples and to compare the species richness of inventories consisting of a different numbers of samples. The basic assumption is that as the number of samples increases, the number of new species added to the list approaches an asymptote (Soberón and Llorente, 1993; Colwell and Coddington, 1994). In our case, the species accumulation curves may be defined as a plot of species richness as a function of the number of LFAs in a paleocommunity. The species richness of a given number of samples (LFAs) may be estimated from the species accumulation curve by extrapolation by fitting an asymptotic model to the observed data, and the Michaelis-Menten equation has been one of the preferred models (Colwell and Coddington, 1994). However, in a comprehensive study of the problems of rarefaction and extrapolation of species richness from sample sets, Colwell et al. (2012) provided a straightforward analytical solution based on the Bernoulli product model for sample-based incidence data. With this solution, the interpolation (rarefaction) curve and the extrapolation curve meet at the observed richness yielding a single curve. Thus, this method was applied to the reference samples composed by the LFAs of every paleocommunity to obtain an estimate of the expected species richness for each regional fauna with a sample size of 50 LFAs. This sample size (50 LFAs) was selected because it is much larger than the number of LFAs in any of the 12 paleocommunities and because the curve approaches the asymptote in all cases at this sample size. Eventually, paleocommunities with an observed richness (S_{obs}) lower than 70% of the richness expected for a sample of 50 LFAs (S_{50}) were considered to be severely incomplete and were removed from the subsequent analyses. For the remaining paleocommunities, both S_{obs} and S_{50} were used as two different estimates of carnivoran species richness. Rarefaction analyses were carried out with the software EstimateS version 9.1.0 (Colwell, 2013).

2.2. Recent carnivoran faunas

The species richness of the recent faunas was obtained from inventories provided by the Biological Inventories of the World Protected Areas Database (ICE, 2017) following a procedure similar to the one used to obtain the species richness of the paleocommunities. Protected areas with 'essentially complete,' 'complete' and 'mainly complete' inventories were plotted on a world map divided into cells of 5 × 5°, and the cells with five or more localities were selected. The list of selected protected areas is shown in SOM Table S3. A total of nine recent faunas (RFs) were obtained (Table 2 and Fig. 1B), but Asia is not represented in the sample because there are not cells with five or more protected areas in that region. Species composition of these nine recent faunas is shown in SOM Table S4. The grid size of 5 × 5° was selected to sample areas that are similar in size to the areas represented by the paleocommunities, a cell of that size encloses an area of 308,000 km^2 at the equator and 235,000 km^2 at mid-latitude (35ºN to 40ºN).

Similarly to the criteria for the fossil faunas, mustelids, viverrids, herpestids, procyonids and other carnivorans smaller than 10 kg were removed from the lists, as were species labeled as extinct. In contrast, introduced and invasive species were maintained in the lists. The logic under this procedure is that we want to know the actual number of carnivoran species which each area may support, independently of the identity of those species. The number of large carnivoran species in the nine recent faunas ranges from 1 to 11 and, as might be expected, the maximum richness is observed in

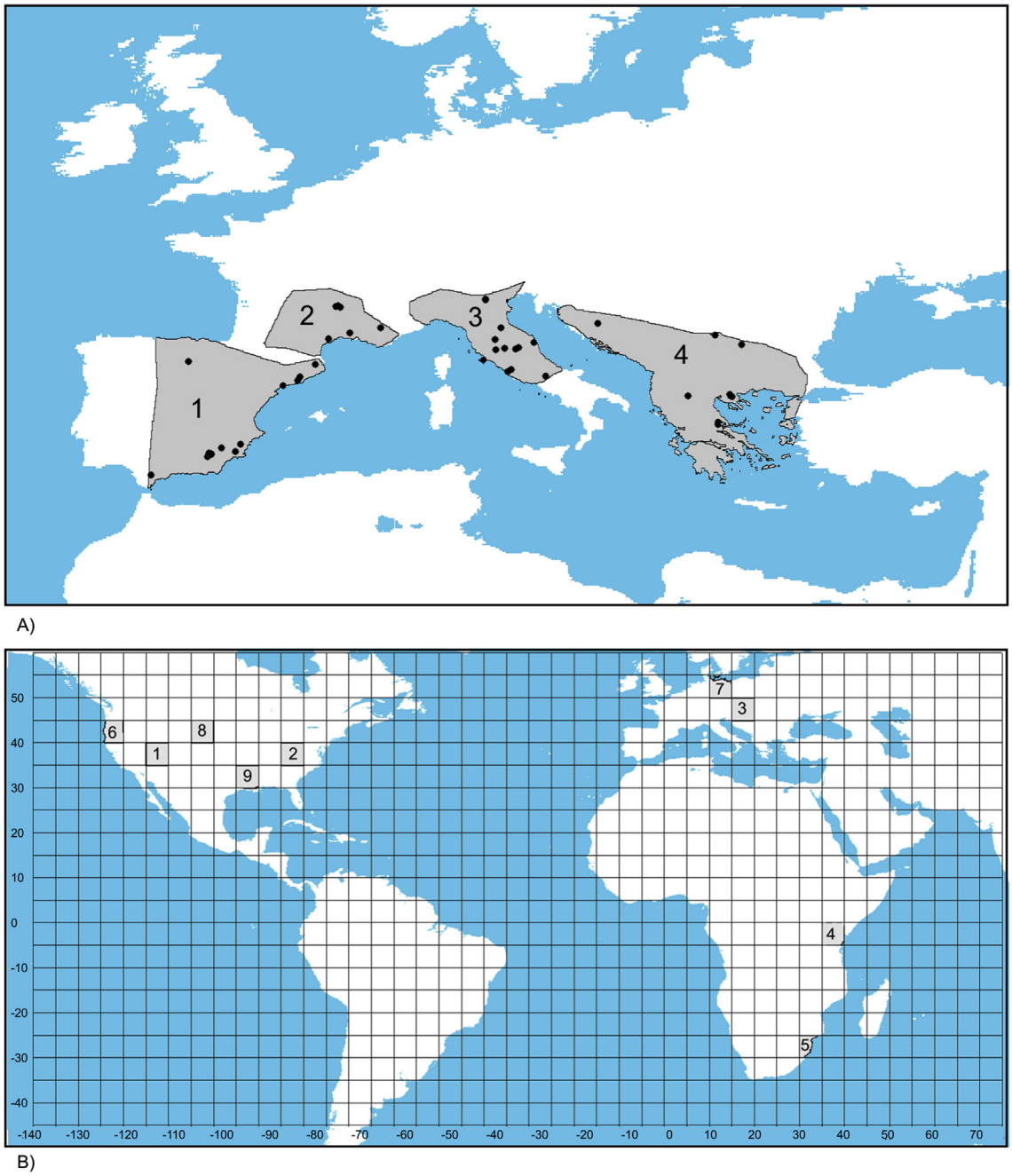

Figure 1. A) Distribution of the set of 71 LFAs used in the analyses. The codes for the areas are the same as in Table 1: 1 = A1, Iberian Peninsula; 2 = A2, Occitanie-Provence; 3 = A3, Apennine Peninsula; 4 = A4, Balkan Peninsula. B) Location of the nine recent faunas used for comparison. The codes are the same as in Table 2.

Table 1
Number of local faunas, with carnivoran species richness (S_{obs}) in parentheses, of the 12 Southern European paleocommunities included in the analyses.

	A1 Iberian Peninsula	A2 Occitanie-Provence	A3 Apennine Peninsula	A4 Balkan Peninsula
Area size (km^2)	342,800	118,800	141,600	380,000
0.5–0.78 Ma	3 (5)	2 (4)	4 (6)	1 (1)
<0.78–1.07 Ma	16 (10)	5 (9)	3 (5)	3 (5)
<1.07–1.6 Ma	14 (9)	3 (8)	8 (11)	9 (10)

the two African regions selected. Although, there is a slight variation in size between areas, carnivoran richness is not correlated with area size (Spearman's rho = 0.45, $p = 0.22$, $n = 9$), nor to the number of inventories, nor protected areas (Spearman's rho = −0.45, $p = 0.23$, $n = 9$). For purposes of comparison, the rarefaction analysis was also applied to the sample of recent faunas. In six out of the nine faunas the number of species expected for a sample of 50 inventories was the same as the observed richness, and in all cases the difference was less than one species (see SOM Table S5). This confirms the validity of our approach to obtain the faunal inventory of a region based on a set of exhaustive lists of species from a limited number of localities.

2.3. Ungulate carrying capacity

Ungulate carrying capacity (CC_U) was estimated using the function provided by Rodríguez et al. (2014):

Table 2
Number of localities, with carnivoran species richness in parentheses, of the nine recent faunas used in the analyses (see Fig. 1B).

	RF 1	RF 2	RF 3	RF 4	RF 5	RF 6	RF 7	RF 8	RF 9
Area (km^2)	244,687	244,687	208,317	299,675	132,718	377,741	189,224	228,732	261,531
n (S_{obs})	13 (6)	9 (5)	6 (3)	5 (11)	5 (9)	11 (7)	8 (1)	6 (8)	5 (8)

$$CC_U = \mathrm{Min}(18.3\,P - 3993; 1,634\,MAT - 12,502). \quad (1)$$

where P is annual rainfall in mm, and MAT is the mean annual temperature in °C. CC_U represents the maximum ungulate biomass that an area may support in approximate equilibrium with the climate (Rodríguez et al., 2014). It is important to note that CC_U is essentially different from the expected herbivore biomass estimated by Binford (2001). Binford's (2001) expected herbivore biomass is an estimation of the average standing crop for a locality under a given set of environmental conditions, which include soil properties, latitude and several water-balance characteristics. Thus, expected herbivore biomass is intended to predict the ungulate biomass that may be found at a given locality, although the actual biomass observed in that locality may be either above or below the estimated value. In contrast, CC_U estimates the maximum ungulate biomass, which may be observed in a locality under a given combination of P and MAT. Our method considers that annual rainfall and mean annual temperature are factors limiting ungulate biomass, but not predictors of ungulate biomass (Rodríguez et al., 2014). Our approach assumes that the actual ungulate biomass is usually below CC_U, only in some cases approaches CC_U and in many cases it is far below CC_U, because other factors not included in equation (1), like soil characteristics, seasonality or species composition, also limit ungulate biomass (see discussion in Rodríguez et al., 2014). Although entirely different from a computational point of view, CC_U is conceptually similar in some aspects to the ungulate biomass index introduced by Discamps (2014). The ungulate biomass index is computed from the relative abundance (number of identified specimens) of horses and large bovids in a fossil assemblage. Values of the ungulate biomass index close to 1 are considered to indicate a grassland environment, where ungulate biomass is known to be high (>3 t/km^2), whereas when that index is close to 0 it is indicative of a forest environment with a low ungulate biomass (<1 t/km^2). Thus, CC_U is similar to the ungulate biomass index because neither of them represents an estimate of ungulate biomass, but a limit (upper or lower) to the ungulate biomass we may expect to find. However, the ungulate biomass index is based on the composition of a fossil assemblage, used as a proxy for the type of vegetation or biome (grasslands vs. forests) not on climate variables like CC_U.

As discussed in Rodríguez et al. (2014), equation (1) provides rather good estimates of CC_U for open habitats, but in forest habitats the CC_U value obtained with this equation greatly exceeds the ungulate biomass observed in recent ecosystems. The overestimation of CC_U in forest communities is mainly explained because in closed environments, unlike in open habitats, ungulates are not the main secondary consumers, since most of the primary production is consumed by animals like small mammals, birds or invertebrates (Bodmer, 1989). Open habitats were likely dominant across Southern Europe during the middle Villafranchian and they were also widespread during the Epivillafranchian and the Early Galerian (Kahlke et al., 2011). However, coniferous and broadleaf forests were also present along the Early and Middle Pleistocene, and they were probably more abundant during the interglacials (Leroy et al., 2011). As a result, our methodology will overestimate CC_U in those cells of the map were the dominant vegetation cover was a forest, and consequently the maximum and average CC_U in each region (see below) will also be overestimated. The effect of the overestimation of CC_U on our results and interpretations is commented on the Discussion section.

Several paleotemperature and paleoprecipitation maps for the last glacial and last interglacial stages have been developed by climate modelers in recent decades (COHMAP, 1988; Ganopolski et al., 1998; Barron and Pollard, 2002; Hijmans et al., 2005; Jost et al., 2005; Strandberg et al., 2011), but no maps are available for the Middle and Early Pleistocene. Lawing and Polly (2011) developed an interpolation approach to obtain a paleoclimate map for any time interval in the Pleistocene. This consists of estimating the mean annual temperature and annual precipitation by proportional interpolation between two end-member climate datasets and scaling the interpolation by the composite benthic stable oxygen isotope ratios. Lawing and Polly (2011) used a climate map for the present and a paleoclimate model for the last glacial maximum (LGM) as end members and used the data on oxygen isotope values provided by Ruddiman et al. (1989) to scale the interpolation. The reliability of this approach was tested by comparing the interpolated maps for 6 kyr and 120 kyr with maps produced by three different general circulation models (Lawing and Polly, 2011). We use the same approach to obtain our paleoclimate maps here, but a model for the LGM and another one for the last interglacial (LIG) are used as end members and the oxygen isotope values from Ruddiman et al. (1989) are used to scale the interpolation. Based on the available paleoclimate maps, the LGM and LIG are the two Pleistocene time intervals with more extreme oxygen isotope values; therefore they qualify for selection as end members. This procedure has two implicit assumptions: 1) The relationship between the variation in δO^{18} values and the changes in the target climatic variable is linear for every pixel on the map and 2) The relationship between the δO^{18} values and the values of the target climatic variable is constant through time. The paleoclimate database produced by Hijmans et al. (2005) was downloaded in GIS format from http://www.worldclim.org/. The maps of total annual precipitation and mean annual temperature for the last interglacial are based on the climate simulation by Bette et al. (2006) and provided at a resolution of 30 arc-seconds. The total annual precipitation and mean annual temperature maps for the LGM are based on the CCSM4 simulation by the National Center for Atmospheric Research and are provided at a resolution of 2.5 min. All maps were scaled to a resolution of 2.5 min.

We performed a validation test using the LGM and the LIG stages as end-member climates to obtain the interpolated mean annual temperature (MAT) and total annual precipitation (P) maps for the present (see SOM S1 and SOM Fig. S1). Those interpolated maps were contrasted against current climate data obtained from the WorldClim v1 data set (Hijmans et al., 2005) available at http://www.worldclim.org/. The difference between the interpolated MAT and the observed MAT for the present was less than 5 °C across Europe, however the difference was less than 2 °C for Western and Southern Europe (SOM Fig. S1). Concerning P, the differences were relatively small (<100 mm/yr) for most of Europe and close to 0 in Southern Europe (SOM Fig. S1).

The three time intervals considered in this study include several climatic oscillations, which produced a wide variation in $\delta^{18}O$ values within each period. To summarize the differences between periods, while keeping the amount of information to be analyzed manageable, the paleoclimate maps were computed using the mean $\delta^{18}O$

Table 3
Oxygen isotope values obtained from Ruddiman et al. (1989) for the three periods under consideration. The mean $\delta^{18}O$ was used as to compute the scaling factor (K_t) that was applied to interpolate the maps.

Interval	$\delta^{18}O$ mean	$\delta^{18}O$ Max	$\delta^{18}O$ Min	K_t
0.5–0.78	3.63	5.20	2.49	0.70
<0.78–1.07	3.35	4.64	2.42	0.85
<1.07–1.6	3.43	4.51	2.34	0.80

value for each time interval (Table 3). This is intended to represent the 'average' conditions throughout the period, and it is mathematically equivalent to obtaining a map for each isotope value inside the interval and computing the mean value of the target climatic variable across the period. We are aware of the drawbacks that this oversimplification of climate variability involves. One of its major effects is that it may fail to reveal differences between periods which differ in the amplitude of the climatic oscillations. It is well known, indeed, that the amplitude of the climatic oscillations was higher in the Galerian than in the Villafranchian and Epivillafranchian (Head and Gibbard, 2005). Using an average paleoclimate map for each period also makes it impossible to discuss the different environmental scenarios represented by the glacial and the interglacial stages during each period. Generally speaking, it can be said that CC_U was higher in the interglacial stages than the mean value for the period reported here, while during the glacial stages CC_U would be markedly lower than the mean. However, variations in the composition of the fauna during each period are also not considered in our approach, since the composition of the paleocommunity is assumed to be constant along each time interval. All the above notwithstanding, and given the coarse temporal resolution of the paleocommunities, using the average climate for each period equates the temporal resolution of the paleoclimate maps to the temporal resolution of the paleocommunities.

Those interpolated MAT and P maps were used to obtain a map of CC_U for each of the three time periods, that represent the average CC_U in the Late Villafranchian, the Epivillafranchian and the Galerian, respectively. A map of CC_U in the present (Fig. 3) was also obtained by using equation (1) and the climate data provided by Hijmans et al. (2005). Mean and maximum CC_U values were computed for each region and time interval, excluding the cells with missing CC_U data. Mean and maximum CC_U were obtained using the 'extract' tool in the 'database query' module of Idrisi v.16.02 (Clark Labs, 2009). The 'extract' tool produces basic statistics of all cells in the analyzed image map for each identifier in a feature definition image. We used the CC_U maps as analyzed images and a map with the areas shown in Figure 1 as the feature definition image. In this way, the mean and maximum CC_U values of all the cells included inside each area are obtained. All GIS analyses were carried out in Idrisi v. 16.02.

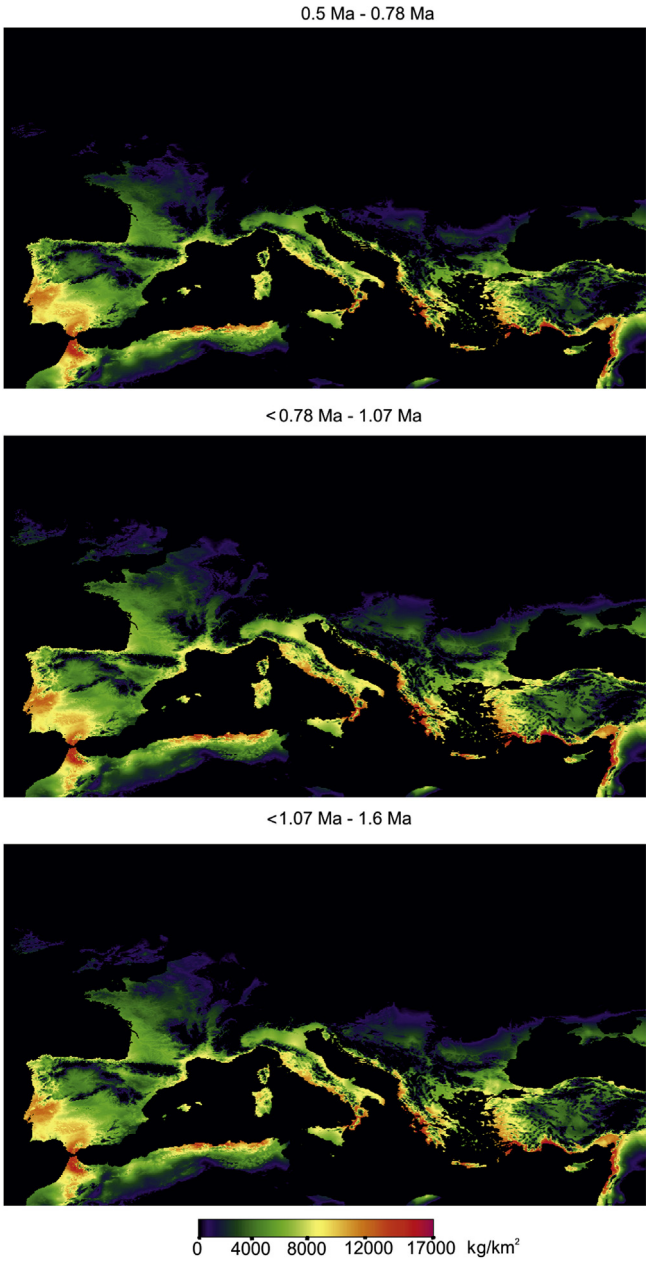

Figure 2. Estimated maximum ungulate carrying capacity (CC_U) in Southern Europe during the period of 1.6 Ma to 0.5 Ma, based on interpolated paleoclimate maps. The black areas correspond to pixels with no data (see text).

2.4. Carnivoran carrying capacity

Hatton et al. (2015) found a predator-prey power law for the scaling of biomass along a productivity gradient; data from both aquatic and terrestrial ecosystems and across several taxonomic groups fit the law with an exponent close to 0.75 for the relationship between predator biomass and prey biomass. In particular, for carnivores >20 kg and ungulates in the 5–500 kg interval in African savannas, the equation is:

$$B_c = 0.094 B_u^{0.73}; R^2 = 0.92 \quad (2)$$

where B_c is the biomass of carnivorans and B_u is the biomass of ungulates, both in kg/km^2. The data provided by Hatton et al. (2015) have been used to recalculate equation (2), in order to be able to compute the 95% confidence interval for the estimates. The recalculated equation is used here to estimate carnivoran carrying capacity (CC_C) in the Pleistocene paleocommunities from CC_U as:

$$\log_{10} CC_C = 0.73 \pm 0.03 \log_{10} CC_U - 1.029 \pm 0.111; R^2 = 0.92 \quad (3)$$

Eventually, the maximum population densities of the Pleistocene carnivorans are estimated by distributing CC_C among all the carnivoran species in the paleocommunity as:

$$CC_C = \sum_{i=1}^{n} D_i W_i \quad (4)$$

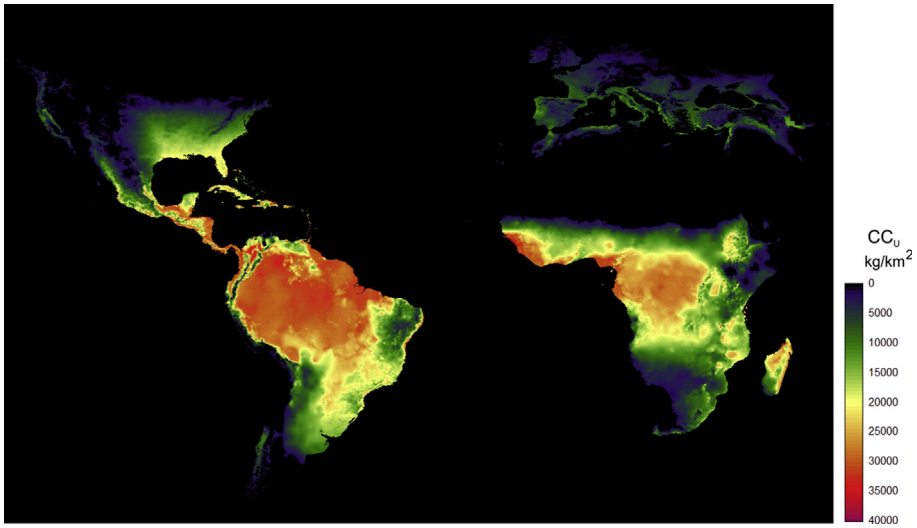

Figure 3. Maximum ungulate carrying capacity (CC_U) in the present estimated from mean annual temperature (MAT) and annual precipitation (P) values using equation (1). The black areas correspond to pixels with no data (see text).

where D_i is the population density of the ith species in individuals/km^2; W_i is the body mass of the ith carnivoran species in kg; and n is the number of species in the paleocommunity. The body masses for the carnivorans were obtained from Rodríguez-Gómez et al. (2017a).

It is well known that population density strongly depends on body size in mammals. Damuth (1987) showed that the population density of mammals, including secondary consumers, scaled to body mass as:

$$D = aW^b \quad (5)$$

where $b = -0.75$ and a is a constant (but see also Silva and Downing, 1995; Silva et al., 2001). If we accept the existence of an allometric relationship between carnivoran density and body mass, and that equation (5) adequately describes that relationship, we may substitute the value of D in equation (4):

$$CC_C = \sum_{i=1}^{n} a\, W_i^{-0.75} W_i \;\rightarrow a = \frac{CC_C}{\sum_{i=1}^{n} W_i^{0.25}} \quad (6)$$

The parameter a is assumed to be specific of each paleocommunity. Substituting the value of a in equation (5) the population density of every carnivoran in the paleocommunity may be estimated as:

$$D_i = \frac{CC_C}{\sum_{i=1}^{n} W_i^{0.25}} W_i^{0.75} \quad (7)$$

where D_i is the population density of the ith species and W_i is its body mass in kg. In this way, the carnivoran carrying capacity estimated with equation (2) is non-linearly distributed among all the species in the paleocommunity as a function of their body masses. The upper and lower values of the 95% confidence interval for CC_C are used to obtained a maximum and a minimum value of a for each paleocommunity. Those two values of a are subsequently used to obtain a maximum and a minimum D_i for the ith species in each paleocommunity. In the end, we report an average and an interval for the estimated density of each carnivoran in each paleocommunity, derived from the 95% confidence interval for the predicted CC_C. That population density (D_i) is not intended to be an estimation of the actual population density of the species i in the paleocommunity. Instead, those values are simply used as an index to compare different communities according to the maximum population densities of carnivorans that the environment could support given a particular community composition.

2.5. Statistical analyses

The correlation between carnivoran richness and CC_U was tested using both Pearson's r correlation coefficient and Spearman's rank correlation tests. The Spearman's non-parametric test has less statistical power than Pearson's r, but it does not assume a linear relationship between the variables (Siegel and Castellan, 1988). Statistical tests were run in Statistica v 13.0 (Dell Inc., 2015).

3. Results

The results of the rarefaction analyses of the set of 12 paleocommunities are shown in Table 4. The paleocommunities of the <0.78–1.07 Ma time interval from the Balkan and Apennine

Table 4
Results of the rarefaction analyses of the 12 paleocommunities.[a] In two cases, the rarefaction analysis could not be performed because the number of samples (LFAs) was less than three.

Area	Interval	S_{obs}	S_{50}	S_{50}/S_{obs}%
A1 Iberia	0.5–0.78 Ma	5	5.44	92%
	<0.78–1.07 Ma	10	10	100%
	<1.07–1.6 Ma	9	9.53	91%
A2 Occitanie-Provence	0.5–0.78 Ma	4	insufficient data	
	<0.78–1.07 Ma	9	12.6	71%
	<1.07–1.6 Ma	8	10.78	74%
A3 Apennine	0.5–0.78 Ma	6	15.36	39%
	<0.78–1.07 Ma	5	10.33	48%
	<1.07–1.6 Ma	11	14.5	76%
A4 Balkan	0.5–0.78 Ma	1	insufficient data	
	<0.78–1.07 Ma	5	11.67	43%
	<1.07–1.6 Ma	10	13.55	74%

[a] Abbreviations: S_{obs} = number of carnivoran species observed in the LFAs of the paleocommunity; S_{50} = expected number of species for a sample of 50 LFAs based on the analytical approach in Colwell et al. (2012). The ratio S_{50}/S_{obs}% is used as an index of the completeness of the carnivoran fauna of the paleocommunities.

peninsulas and the paleocommunity of the 0.5–0.78 Ma from the Apennine Peninsula show S_{50}/S_{obs} ratio values below 50%; therefore they seem to be severely undersampled. Moreover, the paleocommunities of the 0.5–0.78 Ma interval from the Balkan Peninsula and the Occitanie-Provence include less than three LFAs: therefore they could not be included in the rarefaction analysis. The remaining seven paleocommunities exhibit S_{50}/S_{obs} ratio values above 70% and may be considered reasonably complete. These seven paleocommunities include the late Villafranchian faunas from the three areas, and the Epivillafranchian faunas from the two more western areas (Occitanie-Provence and Iberia). Among the Galerian paleocommunities, only the one from Iberia seems to be reasonably complete. Interestingly, Iberia is the only area for which the paleocommunities of the three intervals were reasonably sampled: these paleocommunities show the highest $S_{50}/S_{obs,}$ ratio values, which range from 91% to 100% (Table 4).

The maps of estimated ungulate carrying capacity during the three time intervals are shown in Figure 2. In the maps, CC_U was computed for every pixel with interpolated MAT values above 8 °C, since equation (1) cannot be extrapolated below this value (Rodríguez et al., 2014); therefore the maps of estimated CC_U contain data for only Southern and Western Europe. For both the present and the Pleistocene, mean and maximum CC_U values were computed for each region excluding the cells with missing CC_U data. Estimated CC_U values in the areas occupied by the recent faunas and the paleocommunities are shown in Table 5, mean CC_U ranges from 1569 kg/km^2 to 16,378 kg/km^2 for the recent faunas and from 4678 kg/km^2 to 6302 kg/km^2 for the paleocommunities. Maximum CC_U ranges from 2694 kg/km^2 to 22,890 kg/km^2 in recent faunas and from 10,222 kg/km^2 to 16,224 kg/km^2 for the paleocommunities. Using a non-parametric test, carnivoran species richness is significantly correlated to both maximum CC_U and mean CC_U in recent faunas (Table 6), but according to a Pearson's r test only maximum CC_U is correlated to carnivoran richness (Table 6). The reason for this discrepancy is likely that Pearson's test assumes a linear relationship between the variables, while the relationship between richness and mean CC_U seems to be nonlinear (Fig. 4B). The correlation between carnivoran richness and mean CC_U is also significant when the paleocommunities and the recent faunas are analyzed together (Table 6) as well as when the subset of paleocommunities is considered, using either S_{obs} as the richness estimator. However, maximum CC_U is not correlated with carnivoran richness in the subset of paleocommunities (Table 6).

Table 5
Maximum and mean maximum ungulate carrying capacity (CC_U) values in the areas occupied by the recent faunas and the Pleistocene paleocommunities.[a]

Recent fauna/Paleocommunity	Max CC_U kg/km^2	Mean CC_U kg/km^2
RF1	5743	2164
RF2	13,642	7048
RF3	6779	3886
RF4	22,890	9282
RF5	18,589	11,127
RF6	14,949	4157
RF2	2694	1569
RF8	4982	1756
RF9	20,505	16,378
A1 0.5–0.78	13,875	4763
A1 <0.78–1.07	14,160	5101
A1 <1.07–1.6	14,280	4991
A2 <0.78–1.07	10,222	4943
A2 <1.07–1.6	10,135	4678
A3 <1.07–1.6	12,335	6302
A4 <1.07–1.6	16,224	5483

[a] The codes for the recent faunas are the same as in Figure 1 and Table 2 and the codes for the paleocommunities consist of the code for the area used in Table 1 and the time interval in Ma.

Table 6
Correlation between carnivoran richness and the maximum ungulate carrying capacity (CC_U) in recent faunas and Pleistocene paleocommunities. Two measures of CC_U are shown: the maximum CC_U in the area (Max CC_U), and the average CC_U across the area (Mean CC_U). Two estimates of species richness have been used for the paleocommunities: the observed richness in the sampled LFAs (S_{obs}) and the expected richness for a sample of 50 LFAs (S_{50}). The numbers indicate the values of Spearman's rho and Pearson's r statistics, and the asterisks mark significant correlations at the 95% (*) and the 99% (**) confidence levels.

	Spearman's rank correlation		Pearson's r	
	S_{obs}	S_{50}	S_{obs}	S_{50}
Whole sample $n = 16$				
Max CC_U	0.62*	0.47	0.68**	0.51*
Mean CC_U	0.65**	0.52*	0.44	0.30
Recent faunas $n = 9$				
Max CC_U	0.88**	–	0.88**	–
Mean CC_U	0.79*	–	0.66	–
Paleocommunities $n = 7$				
Max CC_U	0.33	−0.14	0.09	−0.13
Mean CC_U	0.94*	0.61	0.71	0.69

Comparing the patterns observed in the recent faunas and in the paleocommunities, it is apparent that the single paleocommunity from the 0.5–0.78 Ma time interval fits the pattern exhibited by the recent faunas (Fig. 4). In contrast, the Late Villafranchian and Epivillafranchian paleocommunities show higher carnivoran richness than the recent communities with similar values of CC_U, and the values for all paleocommunities are clearly above the regression line for recent faunas (Fig. 4). This trend is even more noticeable when S_{50} is used to estimate richness instead of S_{obs} (Fig. 4B,D).

Table 7 shows the average CC_C values estimated for the paleocommunities from the average CC_U for the interval. The CC_C values in the paleocommunities range from 45 to 50 kg/km^2, or from 25 to 95 kg/km^2 when the 95% confidence interval for the prediction is considered, which is similar to the observed carnivoran biomass in recent African ecosystems (Hatton et al., 2015). However, in the paleocommunities the carrying capacity was distributed among a large number of species. Thus, assuming that population density scales to body mass as explained in the Material and methods section, the population density for a carnivoran species in those paleocommunities would range from 0.035 to 0.548 individuals/km^2, or from 0.02 to 0.95 individuals/km^2 if the upper and lower limits of the intervals are considered (Table 7 and Fig. 5). Interestingly enough, the estimated population densities are, on average, higher in the single Galerian paleocommunity than in the late Villafranchian and Epivillafranchian paleocommunities.

4. Discussion

The rarefaction analysis showed that five out of the 12 initially considered paleocommunities are clearly undersampled and should thus be excluded from the analyses. Undoubtedly, this limits the conclusions that may be derived from this study, especially since only one of the four Galerian paleocommunities passed the test. We acknowledge that setting the value of the S_{50}/S_{obs} ratio at 70% as the criterion for considering a paleocommunity to be reasonably sampled is arbitrary, as there is not a strong criterion for this threshold; therefore this rule may be questioned. It may also be argued that, although the value of 70% excludes severely undersampled paleocommunities, it does not guarantee that the selected paleocommunities are reasonably complete. However, the three paleocommunities from the Iberian Peninsula, with S_{50}/S_{obs} ratios of 91%, 92% and 100% exhibit exactly the same relationship between carnivoran richness and CC_U as the other four paleocommunities with lower values of the S_{50}/S_{obs} ratio. This highly consistent

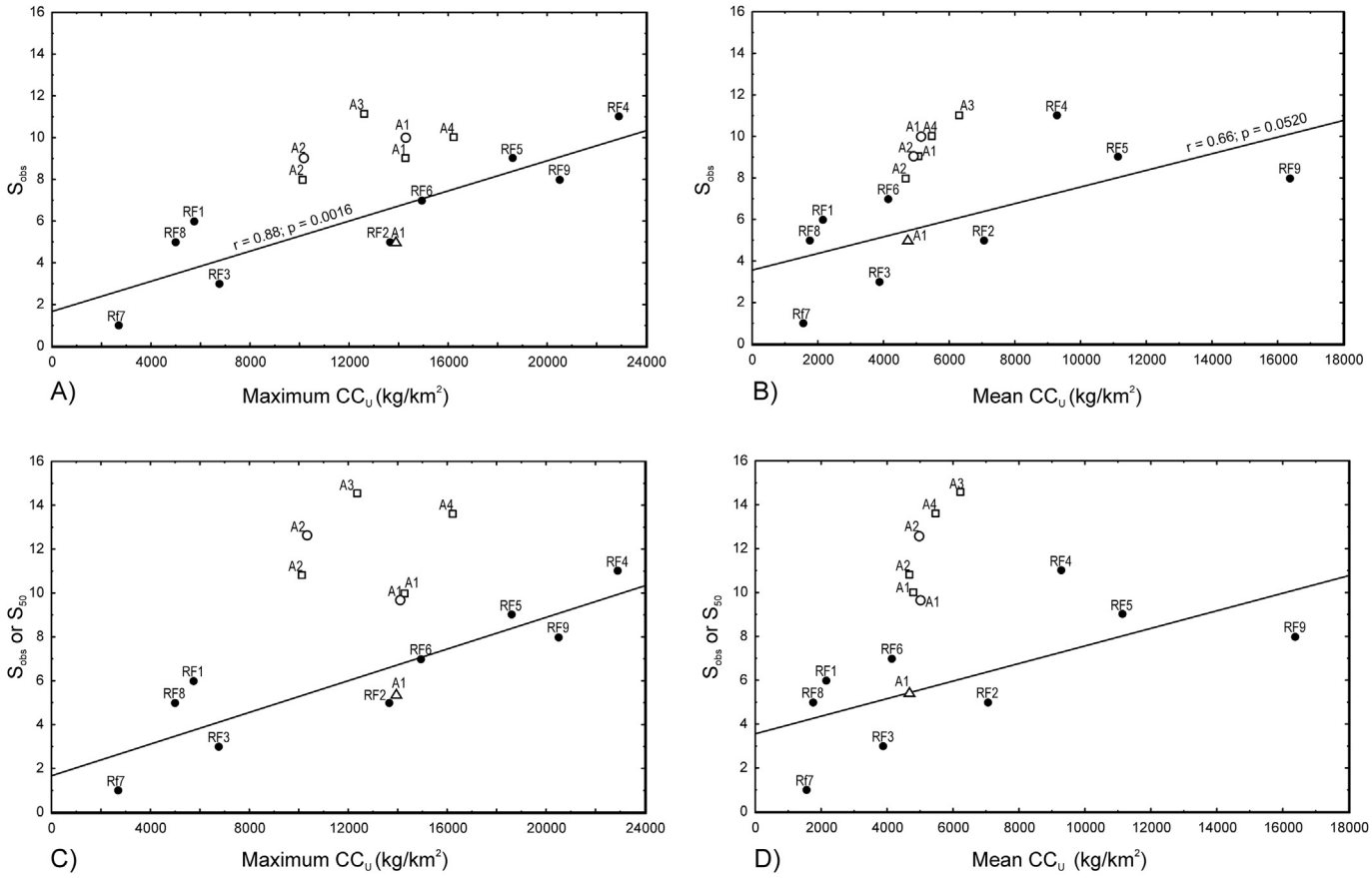

Figure 4. Relationship between carnivoran richness and maximum ungulate carrying capacity (CC_U) in recent faunas and Pleistocene paleocommunities. Two measures of CC_U are shown: the maximum CC_U in the area (A and C), and the average CC_U across the area (B and D). Two estimates of species richness have been used for the paleocommunities: the observed richness in the sampled LFAs (A and B) and the expected richness for a sample of 50 LFAs (S_{50}; C and D). Note that the y-axis represents S_{50} for the LFAs and the observed richness (S_{obs}) for the recent faunas in C and D. The regression line for the recent faunas is shown in the four graphics, and the Pearson's correlation coefficient and significance level are shown in A) and B). The codes for the recent faunas (black dots) are the same as in Table 2. For the paleocommunities, the labels indicate the region according to the codes in Table 1, and the time interval is indicated by the symbols as follows: open squares = <1.07–1.6 Ma; open circles = <0.78–1.07 Ma; open triangles = 0.5–0.78 Ma.

pattern suggests that our estimates of species richness in the four paleocommunities with S_{50}/S_{obs} between 70% and 80% are fairly good.

Ungulate carrying capacity shows a marked latitudinal gradient in the present (Fig. 3), with the highest values toward the equator. In the present, the maximum CC_U value in Mediterranean Europe ranges from 11,000 to 17,000 kg/km^2, while the average CC_U in this area is between approximately 4600 and 7700 kg/km^2. In comparison, the estimated maximum CC_U for the paleocommunities ranges from 10,135 to 16,224 kg/km^2, and the average CC_U ranges from 4678 to 6302 kg/km^2 (Table 5). Thus, the Pleistocene values are not very different from those observed in the present. Estimates of the theoretical herbivore biomass (or on-crop biomass) in the Apennine Peninsula and in Western Europe during the Pleistocene have been published (Meloro and Clauss, 2012; Palombo, 2017). The theoretical herbivore biomass is estimated from the average body mass of the herbivore species in a paleocommunity through allometric equations. However, a direct comparison with the values obtained by is not possible, because those authors only estimated the biomass of the herbivore species weighing less than 450 kg or less than 1000 kg, and the exact values of the estimates are not reported. Interestingly, the on-crop biomass estimated by Palombo (2017) for France and for the Italian and Iberian Peninsulas during the late Villafranchian and the Epivillafranchian is approximately 5000–6000 kg/km^2, which is somewhat higher than the average CC_U estimated here (Table 5). However, the on-crop biomass estimated for the first part of the Middle Pleistocene is markedly higher, especially for the Apennine Peninsula and France (6000–10,000 kg/km^2 in Palombo, 2017), and Meloro and Clauss (2012:Fig. 3) also suggests values around or above 10,000 kg/km^2 for total herbivore biomass in the Galerian. This apparent disagreement between the estimates of herbivore biomass obtained in this study and those reported by other authors is easy to explain, since CC_U and theoretical herbivore biomass are not equivalent. Theoretical herbivore biomass is obtained by multiplying the species body mass (in kg) by the estimated number of individuals per km^2 (population density) and summing across all species. In Meloro and Clauss (2012) and Palombo (2017), population density is estimated from body mass using allometric equations, and when estimated in this way it is generally assumed to represent the average density of a mammal species of a given body size across different environments. However, population density shows large intraspecific variation, usually of one or two orders of magnitude. As an example, population densities reported for hartebeest (*Alcelaphus buselaphus*) are 0.3 individuals/km^2 in Niokolo Koba National Park, Senegal (Galat et al., 2009), 0.9 individuals/km^2 in Saint Floris National Park, Central African Republic (Milligan et al., 1982), 3.18 individuals/km^2 in Bouba Njida National Park, Cameroon (Van Lavieren and Esser, 1979), and 7.36 individuals/km^2 in Nairobi National Park, Kenya (Foster and Coe,

Table 7
Expected maximum population densities (D) of the carnivoran species in the Early and Middle Pleistocene paleocommunities. Expected maximum population density has been estimated distributing the estimated carnivoran carrying capacity among all the species in the paleocommunity, assuming that population density scales to body mass according to the equation $D = aW^{-0.75}$. See text for details on the computation of the coefficient a for each paleocommunity. The numbers in parentheses represent the 95% confidence interval for CC_C, a, and *D*. CC_C has been computed according to the equation $CC_C = 0.094\ CC_U^{0.73}$, $R^2 = 0.92$ (Hatton et al., 2015). The body masses of the carnivoran species in each paleocommunity were obtained from Rodríguez-Gómez et al. (2017b).[a]

		Iberia			Occitanie-Provence		Apennine	Balkan
		0.5–0.78 Ma	<0.78–1.07 Ma	<1.07–1.6 Ma	<0.78–1.07 Ma	<1.07–1.6 Ma	<1.07–1.6 Ma	<1.07–1.6 Ma
CC_U (kg/km^2)		4763	5101	4991	4943	4678	5483	6302
CC_C (kg/km^2)		45.5 (25.8, 76.8)	47.8 (27.1 80.8)	47.1 (26.7 79.5)	46.7 (26.5, 79)	44.9 (25.4, 75.8)	50.4 (28.5, 85.2)	55.8 (31.5, 94.4)
a		3.612 (2.045, 6.098)	1.446 (0.937 2.796)	1.568 (1.030 3.074)	1.759 (0.997 2.974)	1.891 (1.071, 3.192)	1.643 (0.930, 2.777)	2.021 (1.141, 3.418)
Dc (individuals/km^2)								
Canidae	*Canis arnensis*	–	–	–	–	–	0.201 (0.116, 0.347)	0.247 (0.143, 0.427)
	Canis etruscus	–	–	0.181 (0.105, 0.313)	–	0.188 (0.109, 0.325)	0.164 (0.095, 0.283)	0.201 (0.116, 0.348)
	Canis mosbachensis	0.548 (0.317, 0.946)	0.251 (0.145, 0.434)	,	0.267 (0.155, 0.461)	–	–	–
	Lycaon lycaonoides	–	0.11 (0.064, 0.190)	0.121 (0.070, 0.209)	0.117 (0.068, 0.202)	–	0.109 (0.063, 0.189)	0.134 (0.078, 0.233)
Felidae	*Acinonyx pardinensis*	–	–	–	0.064 (0.037, 0.111)	0.069 (0.040, 0.119)	0.06 (0.035, 0.104)	,
	Homotherium latidens	–	0.032 (0.019, 0.055)	0.035 (0.020, 0.061)	0.034 (0.020, 0.059)	0.037 (0.021, 0.063)	0.032 (0.018, 0.055)	0.039 (0.023, 0.068)
	Lynx issiodorensis–Lynx pardinus	–	–	0.175 (0.101, 0.303)	–	0.182 (0.105, 0.314)	0.158 (0.092, 0.273)	0.194 (0.112, 0.336)
	Lynx pardinus	0.488 (0.283, 0.843)	0.224 (0.129, 0.386)	–	0.238 (0.138, 0.411)	–	–	–
	Megantereon whitei	–	0.079 (0.046, 0.137)	0.087 (0.050, 0.150)	–	0.09 (0.052, 0.156)	0.078 (0.045, 0.136)	—,
	Panthera gombaszoegensis	0.108 (0.062, 0.186)	0.049 (0.029, 0.085)	0.054 (0.031, 0.094)	0.053 (0.030, 0.091)	0.056 (0.033, 0.097)	0.049 (0.028, 0.085)	0.06 (0.035, 0.104)
	Panthera leo	–	–	–	—,	–	–	–
	Panthera pardus	–	–	–	0.077 (0.045, 0.133)	–	–	–
	Puma pardoides	–	0.106 (0.061, 0.183)	–	–	–	0.105 (0.061, 0.181)	0.129 (0.075, 0.223)
Hyaenidae	*Crocuta crocuta*	0.139 (0.080, 0.239)	0.064 (0.037, 0.110)	–	–	–	–	–
	Hyaena prisca	0.188 (0.109, 0.324)	–	–	–	–	–	–
	Pachycrocuta brevirostris	–	0.065 (0.038, 0.112)	0.071 (0.041, 0.123)	0.069 (0.040, 0.119)	0.074 (0.043, 0.128)	0.064 (0.037, 0.111)	0.079 (0.046, 0.137)
	Pliocrocuta perrieri	–	–	0.095 (0.055, 0.163)	–	–	–	0.105 (0.061, 0.182)
Ursidae	*Ursus deningeri*	–	0.016 (0.009, 0.027)	–	0.017 (0.010, 0.029)	–	–	–
	Ursus etruscus	–	–	0.03 (0.017, 0.052)	–	0.031 (0.018, 0.054)	0.027 (0.016, 0.047)	0.033 (0.019, 0.058)

[a] Abbreviatons: CC_U = ungulate carrying capacity; CC_C = carnivoran carrying capacity.

1968). Similarly, reported population densities for the red deer (*Cervus elaphus*) are 0.03 individuals/km^2 in Simpevarp, Sweden (Truvé and Cederlund, 2005), 3.2 individuals/km^2 in Casentini National Park, Italy (Mattioli et al., 2011), and 7.3 individuals/km^2 in the Sierra de Cazorla, Spain (Escos and Alados, 1988). Moreover, many ecologists consider that the estimates obtained using this method represent maximum population densities rather than average population densities (White et al., 2007 and references therein); therefore, computed in this way, the theoretical herbivore biomass likely overestimates actual biomass, since all the species present in the paleocommunity are assumed to occur at the average, or maximum, population density for their body size. However, this is not the case in natural communities where some species occur at densities above the overall average density and other species are less abundant than average, and total herbivore density is limited by CC_U. In summary, theoretical herbivore biomass may be a useful index for comparing the composition of different paleocommunities, but it does not provide an estimate of the actual herbivore biomass. However, CC_U is also not an estimate of actual herbivore biomass, but an estimate of the maximum ungulate biomass that the environment might sustain over the long term. We may expect actual herbivore biomass to be below, or markedly below, CC_U in many cases as is indeed observed in recent communities (Rodríguez et al., 2014). Although actual ungulate biomass is strongly conditioned by ecosystem primary productivity, which in turn depends on climate (McNaughton et al., 1989), ungulate biomass is also influenced by other factors, such as species richness (Fritz and Duncan, 1994) or the composition of the predatory guild (Ripple and Beschta, 2012).

According to our results, the expected carnivoran carrying capacity (CC_C) in the Pleistocene paleocommunities is approximately 45–50 kg/km^2. In contrast, the carnivoran biomass observed in the richest recent African ecosystems is twice the estimated CC_C of the European paleocommunities (Hatton et al., 2015), although the carnivoran biomass in the paleocommunities was distributed among a similar number of species, or an even larger number if S_{50}

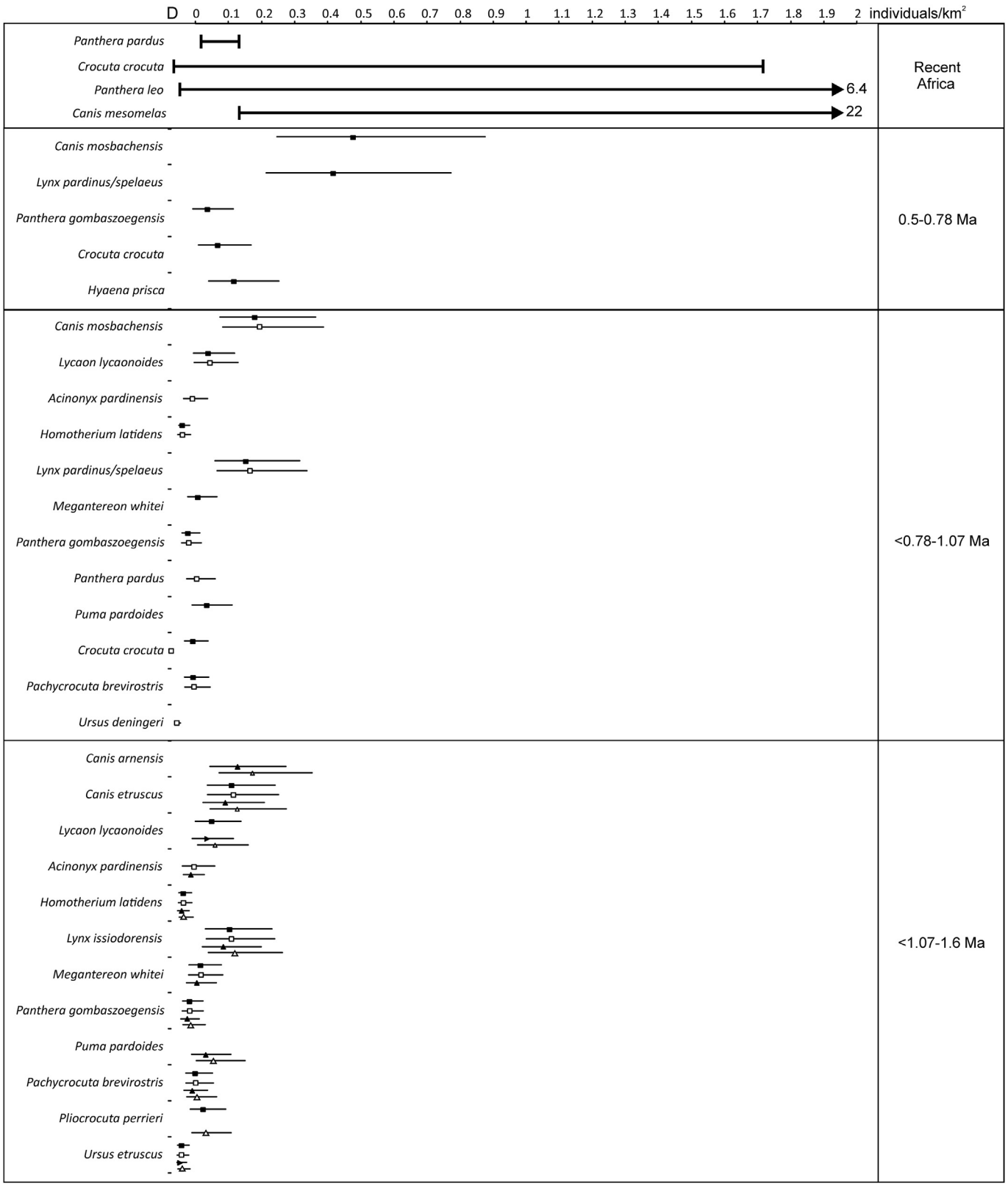

Figure 5. Expected maximum population densities (D) of the carnivoran species in the Early and Middle Pleistocene paleocommunities compared to the typical densities of some representative recent African carnivores (data in Table 7). The numbers at the right of the arrowhead in some recent species indicate the maximum observed population density. The horizontal bars for the fossil species represent the uncertainty in their estimated densities (see Table 7). Black squares: Iberian faunas; open squares: Occitanie-Provence faunas; black triangles: Apennine faunas; open triangles: Balkan faunas.

is considered, as in the recent African communities. Certainly, when the 95% confidence interval for the prediction is considered, the CC_C of the paleocommunities overlaps the range of carnivoran on crop biomasses observed in recent African ecosystems (see data in Hatton et al., 2015). However, it should be noticed that CC_C and on crop biomass are not equivalent, and that these values cannot be directly compared. CC_C is an estimate of the maximum sustainable carnivoran biomass as limited by MAT and P on a large area, while on crop biomass is a direct measure of carnivoran biomass in a concrete ecosystem. The CC_C of the recent African localities is markedly higher than the CC_C of the paleocommunities (SOM Fig. S2). Moreover, when interpreting this results it is important to realize that, as explained in the Material and methods section, our methods tend to overestimate CC_U, and consequently also CC_C, because equation (1) overestimates CC_U in forest habitats. Thus, even if forest was not the dominant vegetation in Mediterranean Europe during the Early Pleistocene, the actual CC_U of the middle Villafranchian, Epivillafranchian and early Galerian ecosystems was below the value estimated here. Consequently, the values of CC_C reported here should be considered as a maximum, and likely an overestimation of the actual CC_C in the Early Pleistocene.

Even accepting the likely overestimated values of CC_C reported here as valid, the Early Pleistocene European carnivorans had to occur on average at markedly lower population densities than their recent African counterparts. In the Early Pleistocene paleocommunities, the maximum population density of the small-bodied species would be below 1 individual/km^2, even considering the upper limit of the 95% confidence interval for the estimation of population density (Table 7 and Fig. 5). Moreover, only the smallest carnivoran species, *C. mosbachensis* and *L. pardinus*, could reach population densities above 0.5 individuals/km^2, and this only in the Galerian. During the Epivillafrachian and the late Villafranchian, even those small species would have occurred at relatively low population densities. In comparison, the similarly-sized black jackal (*Canis mesomelas*) occurs in recent African ecosystems at densities of 0.3–0.4 to 22 individuals/km^2 (Walton and Joly, 2003). Concerning the large-bodied species, the maximum estimated density for *H. latidens* in the Early Pleistocene is 0.06 individuals/km^2. In comparison, the similarly-sized African lion (*Panthera leo*) occurs in recent savannas at densities between 0.02 and 6.4 individuals/km^2 (Foster and Coe, 1968; Viljoen, 1993; Caro, 1999; Haas et al., 2005). Certainly the maximum densities estimated for *M. whitei* (around 0.16 individuals/km^2) are similar to the population densities of the recent African leopard (*Panthera pardus*), reported to be between 0.009 and 0.2 individuals/km^2 (Foster and Coe, 1968; Kutilek, 1974; Prins and Reitsman, 1989; Mizutani, 1999). However, *P. pardus* is a threatened species and its African populations are known to be in severe decline (Stein et al., 2016). Concerning hyaenas, reported densities for recent spotted hyaenas (*Crocuta crocuta*) range from 0.008 individuals/km^2 in the poor Kalahari environment to 1.8 individuals/km^2 in the rich Ngorongoro ecosystem (Trinkel et al., 2004), while the maximum densities estimated for *Pachycrocuta brevirostris* and Pleistocene *C. crocuta* are 0.1–0.2 individuals/km^2 (Table 7). In summary, maximum carnivoran density in the paleocommunities would be, at least, an order of magnitude lower than that in recent African ecosystems. Moreover, when comparing the estimated population densities reported in Table 7 with the densities reported in the literature for recent populations, it should be kept in mind that the actual population densities of those Pleistocene species would be likely lower. First, because the estimated densities are maximum theoretical densities that could only be reached if the on crop biomass of the carnivoran populations approached the carrying capacity of those ecosystems, estimated under the assumption that CC_U was only limited by MAT and P. However, CC_C is also dependent on other factors apart from temperature and precipitation, as discussed in the Material and methods section, and thus the actual values of CC_C should have been lower. Second, because the CC_C of the Pleistocene ecosystems has been estimated from CC_U and our methodology tends to overestimate CC_U (see Material and methods).

It may also be instructive to compare the European paleocommunities with the coeval paleocommunities in East Africa. The East African large carnivore guild in the 1.6–1.07 Ma period consisted of 11 species, including the last occurrences of *Homotherium* sp., *Acinonyx* sp. and *M. whitei* in that area, all at the Okote Mb. of the Koobi Fora Formation, dated to 1.64–1.38 Ma (Werdelin and Lewis, 2005). Thus, carnivoran richness was similar in Southern Europe and East Africa during the late Villafranchian, but it was higher in Europe during the Epivillafranchian. However, since CC_U and CC_C increase toward the equator, we may expect CC_C, as well as actual carnivoran biomass, to be much higher in East Africa than in Mediterranean Europe. Consequently, it may be assumed that carnivoran population density was also higher in the East African paleocommunity than in those of the late Early Pleistocene Mediterranean.

Our results show that a significant relationship exists between carnivoran species richness and ungulate carrying capacity in recent ecosystems, with greater diversity in the more productive areas, as predicted by ecological theory (Hawkins and Porter, 2003; Šímová and Storch, 2017). However, the Early Pleistocene paleocommunities do not fit the relationship observed in the present, although the single Middle Pleistocene paleocommunity that passed the completeness test does; therefore, it is tempting to relate this difference to the profound rearrangement of the European ecosystems caused by the Mid-Pleistocene Revolution (MPR; Palombo, 2017). It may be speculated that, during the Early Pleistocene, the ecosystems of Southern Europe were able to sustain high carnivoran richness, but low population densities, with a relatively low carrying capacity due to the specific structure of those mammal communities (Rodríguez et al., 2012; Lozano et al., 2016). According to this hypothesis, the relationship between species richness and productivity at an equilibrium state in those paleocommunities would be different from that observed in the present communities. The existence of multiple alternative stable states in the ecological systems is supported by strong theoretical and empirical evidence (Grover and Lawton, 1994; Beisner et al., 2003; Shurin, 2004; Schröder et al., 2005; Rodríguez, 2006). According to this hypothesis, the ecosystem reconfiguration related to the MPR moved the European ecosystems to a different equilibrium state, resulting in the present relationship between species richness and productivity. We acknowledge that there is meager evidence to support this interpretation since only one Middle Pleistocene paleocommunity could be included in the analyses. However, this hypothesis may be tested in the future by analyzing the relationship between species richness and productivity during the Middle and Late Pleistocene.

Interaction with carnivorans has repeatedly been proposed as a key factor influencing hominin dispersal and survival (Turner, 1992; Peters and Blumenschine, 1995; Blumenschine and Peters, 1998; Domínguez-Rodrigo et al., 2010; Egeland, 2014; Rodríguez-Gómez et al., 2016). Did the composition of the carnivore guild and the low carnivoran population density in Southern Europe affect the dispersal and survival opportunities of *Homo* during the late Early Pleistocene? Lower population densities mean a lower encounter probability; therefore the European environment could have been less dangerous for hominins than the coeval African ecosystems. However, it is generally accepted that *Homo* was, at least in part, a scavenger (Binford, 1981; Blumenschine, 1987; Brantingham, 1998; Bunn, 2001; Moleón et al., 2014; Pobiner,

2015). Therefore, the relationship between hominins and carnivorans was not only competitive, but also commensal. Although different types of scavenging opportunities for early hominins have been previously hypothesized, this food behavior has typically been dichotomized as passive or non-confrontational (Binford, 1981) and as active or power scavenging (Bunn, 2001). Nevertheless, carnivorans directly contribute to the distribution of carcasses available for passive scavenging across the landscape. Therefore, a lower carnivoran density likely resulted in a reduced carrion density in European ecosystems relative to that of the East African ecosystems (Van Valkenburgh, 1988; Lewis, 1997). A lower carcass density was undoubtedly a disadvantage for a scavenger hominin, but the different composition of the European and East African guilds, with saber-toothed cats surviving in Europe long after the Jaramillo, together with a lower density of the carnivorans competing for carrion, might have partially counterbalanced that effect. It has been proposed that *M. whitei*, in particular, created a niche for scavengers in the European ecosystems due to its inability to consume the entire carcasses of their ungulate prey (Martínez-Navarro and Palmqvist, 1996; Palmqvist et al., 1996, 2007). Nevertheless, given also the relatively low ungulate biomass, competition for resources among secondary consumers would have been high in the late Villafranchian and Epivillafranchian ecosystems from Southern Europe. The existence of a high intraguild competition in the Early Pleistocene has also been suggested by other studies (Rodríguez et al., 2012; Rodríguez-Gómez et al., 2016, 2017b).

Based on the above, it is apparent that the effect of the relatively low CC_C of the European ecosystems on the survival opportunities of a hominin population largely depended on the food acquisition strategies of the hominins. The hot debate over hunting vs. scavenging has a long history in the study of human evolution, but it is far from being resolved (Blumenschine, 1987; O'Connell et al., 1988; Speth, 1989; Domínguez-Rodrigo, 2001, 2002 and references therein; Watts, 2008). The evidence from 'Ubeidiya (Belmaker, 2006, 2017) and Barranco León (Espigares et al., 2013) seems to support scavenging as the main procurement strategy for the first human settlers of Europe, but Huguet et al. (2017) interpreted the evidence of primary access to carcasses at Sima del Elefante level TE9c as indicative of active hunting—although early access to carcasses does not necessarily imply hunting. Moreover, several studies support the theory that hunting was a common strategy among the African Early Pleistocene hominin populations (Bunn and Pickering, 2010; Domínguez-Rodrigo et al., 2014). In any case, most scholars agree that meat and fat were key resources for the Early Pleistocene hominins (Turner, 1992; Leonard et al., 2007; Speth, 2010), as it is also for recent hunter gatherers (Cordain et al., 2000; Binford, 2001). Moreover, it has been proposed that animal resources were even more important for the European populations than they were for the Early Pleistocene African hominins since other food resources, like vegetables or invertebrates, are less abundant in temperate than in tropical or subtropical ecosystems. The dependence on meat and fat as edible resources would be even higher in winter (Martínez-Navarro, 2010), due to the scarcity of plant resources during this part of the year in temperate ecosystems.

Primary production, carrying capacity and carnivoran diversity affected the efficiency of hunting and scavenging as meat procurement strategies in the European Early Pleistocene ecosystems in different ways. According to our results, ungulate carrying capacity in Mediterranean Europe during the Early Pleistocene was similar to its present values, but it was markedly lower than in the recent African savanna biomes. Moreover, it may be assumed that, in the late Villafranchian and Epivillafranchian, CC_U was also higher in the African savannas than in Southern Europe. These differences are usually omitted from the debate on the ecological constraints of the hominin dispersal into Europe. For example, it has been proposed that hominins entered Europe through a corridor of open grasslands and reduced woody cover opened along the Danube-Po Gateway during glacial/interglacial transitions. That ecosystem is reported as a good analog of the African savannas, able to sustain a rich, large mammal fauna (Muttoni et al., 2014). Maybe hominins used that corridor, but from an ecological point of view that ecosystem had important differences from the coeval African savannas, and one of the most important differences was that the on-crop biomass of large herbivores was certainly lower than in the African savannas.

From an ecological perspective, hominins found in Europe a highly diverse carnivore guild and a lower ungulate biomass than in coeval African savannas. Thus, animal resources for a dedicated hunter were markedly lower in Europe than in coeval African savannas, while competition was higher. As a consequence, hominins, like any other secondary consumer, had to occur in Europe at lower population densities than in the African savannas, especially if they were dedicated hunters. Indeed, it has been proposed that hominins were a relatively frequent species in Europe during the late Early Pleistocene, although their population density was usually low (Rodríguez et al., 2015). Though, lower population densities imply a lower encounter rate between competitors, making direct confrontation less likely to occur. The relatively low ungulate biomass in the European ecosystems would also affect a dedicated scavenger. However, the effect of a low density of carcasses in the landscape might be partially compensated if those carcasses were still rich in edible resources. That would be the case if we accept that saber-toothed cats provided large carcasses still containing a great amount of food (fat, bone grease and lean meat), as proposed by some authors (Palmqvist et al., 1996), and if that trophic resource was not being used by other scavengers. However, the niche for a hyperscavenger was not empty, being already occupied by the giant hyena (Turner, 1992; Palmqvist et al., 2011). Competition between hominins and giant hyaenas was probably intense (Espigares et al., 2013), although these two species coexisted in Europe during a long period (Madurell-Malapeira et al., 2017). The prolonged coexistence of hominins and giant hyenas implies that their niches did not overlap completely and that neither of the two competitors overcame the other. Existence of both hyenas and hominins at low population densities, as suggested by our results, might be also a factor explaining the coexistence of both scavengers.

Nevertheless, hominins were likely neither dedicated hunters nor dedicated scavengers, but opportunistic omnivores. This interpretation is supported by the evidence that vegetables played a significant role in the diet of the early European populations (Hardy et al., 2016; Pérez-Pérez et al., 2017) as well as by the apparently contradictory evidence of scavenging and hunting activities provided by different fossil assemblages. Moreover, the Early Pleistocene European hominins did not show competitive exclusion with any member of the carnivore guild, suggesting that their niche did not completely overlap that of any other species (Rodríguez-Gómez et al., 2017b), and a similar situation was proposed by Brantingham (1998) for Olduvai and Koobi Fora, where hominins capitalized the niche spacing between top predators and confrontational scavengers. Indeed, opportunism might have been the more successful strategy for the survival of hominins in the Early Pleistocene European ecosystems. Interestingly, the analysis of the structure of Early Pleistocene paleofood webs including *Homo* species by Lozano et al. (2016) suggests that hominins were a relevant species in channeling the energy fluxes. If hominins were opportunistic omnivores, they would have benefited from a low encounter rate with predators, while taking advantage of the abundant edible resources found in the carcasses abandoned in the landscape by *Megantereon*, opportunistically hunting ungulates,

and complementing their diets with plant foods and other edible resources.

5. Conclusions

As predicted by ecological theory, carnivoran richness is correlated with ungulate carrying capacity in recent ecosystems and the single Middle Pleistocene paleocommunity analyzed here follows the same relationship. In contrast, the Southern European late Villafranchian and Epivillafranchian paleocommunities were markedly richer than expected for a recent fauna from a region with a similar CC_U, which suggests that the Early Pleistocene paleocommunities from Southern Europe included a large number of carnivoran species occurring at low population densities. This community structure implies a more even distribution of resources among the members of the carnivore guild, and the inability of any of the late Villafranchian and Epivillafranchian carnivore species to overcome their competitors. The coexistence of such a large number of species sharing a moderately abundant resource in those paleocommunities suggests a finer resource partitioning among the members of the carnivore guild, and narrow niches for the secondary consumers. In turn, this suggests that trophic web functioning and intraguild interactions in the late Early Pleistocene paleocommunities of Southern Europe were not the same as in recent African ecosystems. If this conclusion is correct, the distinctive characteristics of the European paleocommunities, with a moderate ungulate on-crop biomass and carnivorans occurring at low population densities, should be included in the models describing hominin survival strategies.

The characteristics of the late Villafranchian and Epivillafranchian paleocommunities of Southern Europe undoubtedly influenced the dispersal and survival opportunities of the first hominin populations arriving on the continent. *Homo* evolved in Africa in highly productive ecosystems that sustained a high ungulate biomass and a rich carnivore guild, and the first *Homo* populations arriving in Europe found an equally diverse carnivore guild that, in contrast, relied on a lower prey biomass to sustain its populations. In this ecological context, and in comparison with the coeval African ecosystems, an opportunistic hominin would benefit from a reduced encounter rate with its predators and competitors. Those hominins could have exploited the abundant, but low-density, resources in the carcasses left behind by saber-toothed cats, consumed plant resources, and hunted ungulates with less interference from carnivorans than in their African ecosystems of origin.

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