



# 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.

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## 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 brevirostris*), 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 anaglacials 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).

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