

Evaluating the impact of *Homo*-carnivore competition in European human settlements during the early to middle Pleistocene

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Abstract

Fossil remains and the technological complexes recorded in archaeological sites suggest that the human presence in Europe late in the early and middle Pleistocene was discontinuous. Moreover, competition for meat with other secondary consumers could have delayed the human dispersal through Europe. However, evaluation of the extent competition intensity among secondary consumers suggests this influenced the discontinuity of the human settlement of Europe between 1.1 and 0.2 Ma. Using a mathematical model, we estimate the amount of biomass available in a community for secondary consumers. The amount of available biomass is subsequently distributed among the guild of secondary consumers according to their requirements and prey preferences. Indexes that quantify the competition intensity among secondary consumers to compare the conditions in different paleoecosystems show that the competition intensity late in the early Pleistocene, early in the middle Pleistocene, and late in the middle Pleistocene does not support the view that an increase in competition intensity constrained the expansion of human populations early in the middle Pleistocene. Somewhat paradoxically, the lowest competition intensity is estimated to have occurred early in the middle Pleistocene, most likely because of an increase in the number of large herbivore species and a decrease in the number of secondary consumers. The early Pleistocene paleoecosystems supported higher competition intensity than the middle Pleistocene ecosystems, likely because of the different configuration in the food webs of these two periods (the early and middle Pleistocene).

Keywords: Competition intensity; Human presence; Europe; early and middle Pleistocene

INTRODUCTION

Assuming that large mammals were a relevant resource for humans during the early Pleistocene (e.g., Binford, 1981, 1985; Marean, 1989; Gaudzinski and Roebroeks, 2000; Roebroeks, 2001; McNabb, 2007; Speth, 2010), the ability of hominins to obtain meat was conditioned by prey abundance, their ecological characteristics, and the intensity of competition with other carnivorous mammals for this trophic resource. The percentage of animal resource in the diet of recent hunter-gatherer populations is variable (Cordain et al., 2000), representing between 30 and 60% of their nutritional intake (Jenike, 2001; Leonard et al., 2007). Binford (2001) showed that in recent hunter-gatherer populations hunting represents between 11 and 89% (mean 38%) of their food

resources; gathering, between 0.01 and 88% (mean 45%); and fishing, between 0 and the 70% (mean 18%). Animal food, large game in particular, is generally considered a key resource for the Paleolithic hunter-gatherer populations (Bunn and Ezzo, 1993; Mann, 2000; Bunn and Pickering, 2010; Domínguez-Rodrigo et al., 2014), although this does not imply that the different Pleistocene *Homo* species were strictly carnivorous. On the contrary, species in the genus *Homo* were omnivorous, and they likely included a significant amount of plant food in their diets, as highlighted by Hardy et al. (2017) and Prado-Nóvoa et al. (2017). The availability of resources and the competition with carnivores have been repeatedly proposed as key limiting factors for the early European human populations (e.g., Turner, 1992; Martínez-Navarro and Palmqvist, 1996; Arribas and Palmqvist, 1999; Palombo, 2007, 2010, 2013; Madurell-Malapeira et al., 2010b; Manzi et al., 2011; Rodríguez et al., 2012). Turner (1992) and Palombo (2010) proposed that competition with scavengers and/or predators could have

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delayed human expansion throughout Europe during the early Pleistocene because of the assumed limited technological capabilities of those first European humans. Palombo (2014) suggested that the changes in the structure of the mammal paleocommunities, together with an enlarged prey spectrum, played an important role in the success of human settlements at that time. Conversely, Meloro and Kovarovic (2013) suggested that human arrival modified the structure of the mammal paleocommunities. Some scholars propose that the early Pleistocene human populations were strongly dependent on the scavenging of ungulate carcasses (Turner, 1992; Martínez-Navarro and Palmqvist, 1996; Arribas and Palmqvist, 1999; Espigares et al., 2013). Saber-toothed felids likely yielded a high amount of carrion in the latter part of the early Pleistocene paleoecosystems, given their dental characteristics and killing capabilities (Marean, 1989; Turner, 1992; Martínez-Navarro and Palmqvist, 1995; Palmqvist et al., 1996, 2005, 2007, 2011; Arribas and Palmqvist, 1999). The giant hyena (*Pachycrocuta brevirostris*) was likely a powerful competitor for *Homo* in the search for carrion, and pack-hunting wild dogs and large felids, among others, were strong hunting competitors (Antón et al., 2005; Madurell-Malapeira et al., 2010b; Palombo, 2010).

Climatic conditions changed in the course of the early to middle Pleistocene transition (Schneider and Root, 1998; Shackleton, 1995; Maslin and Ridgwell, 2005) during the so-called mid-Pleistocene Revolution (MPR) (Maslin and Ridgwell, 2005). The MPR promoted the renewal of the mammalian faunal complex, with the appearance of new carnivores in Europe and a progressive increase of the herbivore richness (e.g., Turner, 1992; Azanza et al., 2004; Rodríguez et al., 2004; Cuenca-Bescós et al., 2005; Meloro et al., 2007; Palombo, 2007; Raia et al., 2007; Meloro, 2011b). Thus, it may be speculated that *Homo* had better access to carcasses after the MPR than in the former period, and that human weapons and tool kits became more effective, facilitating its dispersal across Europe (Palombo, 2010; Rodríguez et al., 2012). Nevertheless, the debate around the dispersal of human populations in Europe during the middle Pleistocene is still open. Several authors provide arguments in favor of an African or Near East source of hominins and technological modes, suggesting that *Homo antecessor* populations were replaced by a new, more technologically advanced African hominin species (the Acheulean [Mode 2] technology) (Lordkipanidze et al., 2007; Santonja and Pérez-González, 2010; Jiménez-Arenas et al., 2011; Pérez-Claros et al., 2015). Carbonell et al. (1999) suggest the replacement of human populations was slow, initially with two technological modes (Mode 1 and Mode 2) coexisting in Europe. Carbonell et al. (2010) argue that the Acheulean spread throughout Eurasia because of the demographic growth in both the Near East and Africa. However, the origin of the European Acheulean is much debated because of a lack of data on the (a) arrival of new traditions, (b) technological changes because of contact with new hominin groups, and (c) local origin of this technological mode (Mode 2 or Acheulean) (e.g., see Moncel et al., 2016c; Mosquera et al.,

2016). Whatever the causes and processes, the human expansion was evident around 0.6–0.5 Ma, when the number of archaeological sites increased significantly and the northern latitudes began to be frequently inhabited (e.g., Thieme, 1997; Mania and Vlcek, 1999; Roberts and Parfitt, 2000), showing the different paleoanthropological and cultural features that define the European middle Pleistocene (Doronichev and Golovanova, 2010; Jiménez-Arenas et al., 2011; Ollé et al., 2013). However, although the Acheulean culture was undoubtedly established in Europe around 0.6–0.5 Ma, a number of older lithic assemblages, dating back to the end of the early Pleistocene, exhibit early Acheulean or later Mode 1 features (Scott and Gibert, 2009; Barsky and de Lumley, 2010; Santonja and Pérez-González, 2010; Barsky et al., 2013; Mosquera et al., 2013, 2016; Walker et al., 2013; Vallverdú et al., 2014; Moncel et al., 2016a, 2016b), although the age of some of them is debatable (Jiménez-Arenas et al., 2011).

Several researchers and studies defend a depopulation or discontinuity in the human occupation of Europe during the early to middle Pleistocene transition (Moncel, 2010; Santonja and Pérez-González, 2010; Jiménez-Arenas et al., 2011; Moncel et al., 2013; Mosquera et al., 2013, 2016; Vallverdú et al., 2014). Environmental factors, such as the extinction of saber-toothed cats, have been frequently suggested as possible causes of the discontinuity in human occupation or the disappearance of Mode 1 technology in Europe (Martínez-Navarro and Palmqvist, 1995, 1996; Arribas and Palmqvist, 1999; Jiménez-Arenas et al., 2011; Palmqvist et al., 2011). The existence of several human migration waves into Europe during the early Pleistocene has also been proposed (O'Regan, 2008; Agustí et al., 2009; Carbonell et al., 2010; Made and Mateos, 2010; Muttoni et al., 2010; Muttoni et al., 2015; Palombo, 2010, 2013; O'Regan et al., 2011; Bermúdez de Castro et al., 2013, 2016; Mosquera et al., 2013, 2016; Carotenuto et al., 2016).

According to the hypothesis that human presence in Europe was conditioned by competition with carnivores (Martínez-Navarro, 1992; Arribas and Palmqvist, 1999; Palombo, 2007, 2010; Rodríguez et al., 2012), the discontinuity in human occupation during the early to the middle Pleistocene transition could be explained by high competition intensity among the secondary consumers, including humans, in this period. Competition might make access to meat more difficult for humans, making their presence in the paleocommunities less stable. Predator/prey ratios have been traditionally used in paleontology to measure the intensity of competition in paleocommunities (Stiner, 1992; Palombo and Mussi, 2006; Raia et al., 2007; Palmqvist et al., 2008; Croitor and Brugal, 2010; Feranec et al., 2010; Palombo, 2010; Meloro and Clauss, 2012; Rodríguez et al., 2012). This ratio is a measure of the efficiency of a guild of secondary consumers to consume prey biomass; lower values of the predator/prey ratio indicate that the guild of secondary consumers of a community is less efficient at using prey resources than the guild in another community with higher values, because in the former case the community requires more biomass of primary consumers to obtain the same number or biomass of secondary consumers (Rodríguez-Gómez et al., 2016a).

In some studies, the predator/prey ratios are based on species numbers, whereas in others the ratios are based on biomass and density estimations. Several studies showed a similar pattern of variation in the predator/prey ratios in the European paleocommunities from the latter part of the early Pleistocene (late Villafranchian) to the latter part of the middle Pleistocene (late Galerian) (Meloro et al., 2007; Raia et al., 2007; Croitor and Brugal, 2010; Palombo, 2010): an abrupt decrease in the predator/prey ratio (based on number of species) from the late Villafranchian (1.2 Ma) to the early Galerian (0.9 Ma), a slight increase in the middle Galerian (0.6 Ma), and, finally, a slight decrease in the late Galerian (0.45 Ma) to a value that was maintained approximately constant during the Aurelian (0.3 Ma). This pattern could be interpreted as a reduction of the efficiency of the predator guilds from the late Villafranchian to the Galerian with a slight increase in the middle Galerian; therefore, more resources were necessary to maintain the same number or biomass of secondary consumers in the Galerian than in the Epivillafranchian. The efficiency of a guild of secondary consumers is not directly related to competition intensity inside the community, because the efficiency depends on different aspects like the diet and prey preferences of the secondary consumer species, the composition of the secondary and primary consumers guilds, or the mortality rate of subadults of the primary consumer species. Thus, predator/prey ratios are not enough to measure the competition intensity inside the guild of secondary consumers. Hence, it is necessary to use others indexes to test the hypothesis that the discontinuity in the human occupation of Europe was because of a high competition for meat among the secondary consumers at that time (Rodríguez-Gómez et al., 2016a).

Rodríguez-Gómez et al. (2013) developed a quantitative model to estimate the availability of resources for secondary consumers and to study predator/prey relationships, which was inspired by previous studies (Bermúdez de Castro et al., 1995; Fariña, 1996; Palmqvist et al., 2003; Vizcaíno et al., 2004, 2010). That model was applied, at a local scale, to study the large mammal paleocommunity from the TD6 level of the Gran Dolina site (Sierra de Atapuerca, Spain). In Atapuerca, human settlements are documented between 1.2 and 0.9 Ma and between 0.5 and 0.25 Ma, but there is no evidence of human presence for the period between 0.9 and 0.5 Ma (Mosquera et al., 2013). The same methodology was used to compare the competition intensity among secondary consumers at Atapuerca in two time periods, represented by two fossil assemblages from the Gran Dolina site. Those assemblages were TD6, dated to 900 ka and with human presence, and TD8, dated to ~600 ka and without human presence. This methodology was used to evaluate competition intensity as a possible explanation for the discontinuity of human presence at a local scale (Rodríguez-Gómez et al., 2014b). Competition intensity was higher at TD8 than at TD6, and Rodríguez-Gómez et al. (2014b) concluded that this could be a factor relevant to determine human occupation opportunities. An extension of that study was carried out by Rodríguez-Gómez et al. (2017) showing that TD6 exhibited exceptionally low competition intensity, suggesting that the

TD6 paleocommunity likely included a large felid species that was not recorded in the fossil assemblage. However, the hypothesis that the lack of human presence in the TD8 assemblage might be related to high competition intensity inside the secondary consumer guild was not rejected. Moreover, this methodology was also applied to the study of the large mammal assemblages from two Orce sites (Spain), Barranco León D and Fuente Nueva 3, which preserve the oldest evidence of human presence in western Europe (Toro-Moyano et al., 2013). The analyses showed higher values of competition intensity in Orce than those recorded in the analyzed levels from the Gran Dolina and Galería sites of Atapuerca (Rodríguez-Gómez et al., 2016b). In spite of this, intraguild competition did not impede human settlement of Orce at 1.4 Ma. Using this methodology in the site of Venta Micena (Orce), a recent study (Rodríguez-Gómez et al. 2017) suggests that the human settlement in Orce was probably not a matter of ecological opportunity. Competition intensity in those studies was estimated via several indexes based on the estimated and expected densities of the occurring species and accounting for the ecological characteristics of the potential prey and prey preferences of the carnivores. These indexes have been shown to represent competition intensity in recent and past communities better than simple predator/prey ratios (Rodríguez-Gómez et al., 2016a).

Our aim is to extend the analyses carried out by Rodríguez-Gómez et al. (2014b, 2017) to a continental scale to test whether variations in competition intensity and availability of trophic resources acted as limiting factors for the human occupation of Europe. For this, we use the competition indexes described by Rodríguez-Gómez et al. (2016a). Our analysis focuses on three time intervals of the equivalent duration: the oldest interval is roughly defined by the beginning of the Jaramillo subchron and the Matuyama-Brunhes boundary (1.1–0.8 Ma) and represents the period when populations with Oldowan technologies were well established in southern Europe (Carbonell et al., 2008; Toro-Moyano et al., 2013); the second interval (0.8–0.5 Ma) coincides with an apparent decrease in human presence in Europe; and the third interval (0.5–0.2 Ma) coincides with an expansion and increased intensity of human occupation at the continental scale. We compare the competition intensity in the European ecological communities among these three periods using several indexes of intraguild competition to test whether the apparent depopulation of Europe from 0.8 to 0.5 Ma may be related to an increased difficulty in access to trophic resources.

MATERIALS

We selected local faunas as units of analysis because we consider them to be the best analogues of the biological communities. The term “paleocommunity” is often applied in paleoecology to the fossil fauna of a given age found in a large geographic area (e.g., the Italian peninsula, England, or central Europe) at a given period (Raia et al., 2005, 2007, 2009; Meloro et al., 2007; Meloro, 2011a; Meloro and Clauss, 2012).

Although it is not our intention here to discuss whether that use of the term “paleocommunity” is appropriate, what is clear is that those paleocommunities are not adequate units of analysis to evaluate competition inside a guild. For competition to exist, the potential competitors should coincide in time and space, and a paleocommunity may include species living, for whatever reason, in different environments or in different areas inside the region. Thus, information on European local faunal assemblages (LFAs) (longitude 10°00.00'W to 45°00.00'E and latitude 30°00.00'N to 55°00.00'N") dated from the latter part of the early Pleistocene to the latter part of the middle Pleistocene (1.1–0.2 Ma) was compiled from published sources. Initially, LFAs with mammal species weighing more than 10 kg were selected, and those with no reliable dating were rejected, yielding a total of 98 LFAs from 71 localities. Because complete or nearly complete faunas are required for this analysis, the LFAs were filtered according to the number of prey and predator species in the assemblage. Only those LFAs with both a number of prey and a number of carnivore species above the median for the 98 faunal assemblages (>8 primary consumer species, >4 secondary consumer species, and at least 12 species by LFA) were selected (Supplementary Tables 1 and 2). This criterion was met by 36 LFAs distributed in three groups, which correspond to the following three time intervals: interval 1, from 1.1 to 0.8 Ma; interval 2, from 0.8 to 0.5 Ma; and interval 3, from 0.5 to 0.2 Ma. Thus, we have 9 faunal assemblages in the first group, 7 in the second group, and 20 in the third group (Table 1, Fig. 1).

We reviewed all faunal lists and applied uniform taxonomic criteria (see Rodríguez et al., 2012 and references therein) to obtain a taxonomically consistent database. Our analysis was restricted to mammal species of more than 10 kg because they constitute the portion of the food web that allegedly included hominins (Binford, 1981, 1985; Marean, 1989; Díez et al., 1999; Gaudzinski and Roebroeks, 2000; Roebroeks, 2001; Speth, 2010; Saladié et al., 2011; Lozano et al., 2016). Primary consumer species included in this study belong to the families Bovidae, Castoridae, Cercopithecidae, Cervidae, Elephantidae, Equidae, Hippopotamidae, Hystricidae, Rhinocerotidae, and Suidae. The secondary consumers belong to the families Canidae, Felidae, Hominidae, Hyaenidae, and Ursidae. The family Mustelidae and the genus *Vulpes* were excluded because their diet is mainly based on small mammals (Seebeck, 1978; Carbone et al., 1999).

To perform our analyses, it was necessary to estimate several physiological and life history parameters for every primary consumer species, such as adult body mass, body mass at birth, litter size, breeding interval, age at reproductive maturity, growth rate, and life span. Only adult body mass was required for secondary consumers. We obtained the values of these physiological variables for recent species from the PanTHERIA database (Jones et al., 2009). Values for the adult body mass of fossil species were obtained from the literature (Weers, 1994; Alberdi et al., 1995; Koufos et al., 1997; Rodríguez, 1997; Made, 1998; Nowak, 1999; Collinge, 2001; Crégut-Bonnoure and Spassov, 2002; Athanassiou, 2003; Palmqvist et al., 2003;

Brugal and Fosse, 2004; Prado et al., 2004; Antón et al., 2005; Breda and Marchetti, 2005; Crégut-Bonnoure and Tsoukala, 2005; Kahlke and Gaudzinski, 2005; Crégut-Bonnoure and Dimitrijevic, 2006; Croitor and Brugal, 2007; Meloro et al., 2007; Fostowicz-Frelik, 2008; Carotenuto, 2009; Jones et al., 2009; Lister and Stuart, 2010; Madurell-Malapeira et al., 2010a; Jiménez-Arenas et al., 2014; Made et al., 2014; Arsuaga et al., 2015). For species with living representatives and without body mass values, we took the values of the living populations. Sometimes, taxa were identified in the original source to the genus, subfamily, or family level only. In these cases, we computed the mean adult body weight of the species present in Europe in that time interval in the corresponding taxonomic group (genus, subfamily, or family). For instance, the adult body mass of a taxon identified in an LFA as “*Equus* indet.” was estimated as the mean body weight of the species in the genus *Equus* occurring in that period. In the case of *Homotherium* sp., the mean body mass of *Homotherium latidens* and *Homotherium crenatidens* was used (Brugal and Fosse, 2004; Antón et al., 2005), although likely they may be considered a single species (Antón et al., 2014). A least squares regression equation was computed for each primary consumer family or subfamily to estimate each physiological variable from the mean body weight (Supplementary Table 3). The equation was computed only when data for at least four species in the family were available. Only those regression equations in which body mass explained more than 80% of the variance in the dependent variable were used. If body mass explained less than 40% of the variance, we took the median for the family or subfamily. If it explained between 40 and 80%, we estimated the value of the physiological variable as the median for the species in the family or subfamily with a body weight similar to that of the species studied.

METHODS

The model

We investigated the distribution of meat resources (i.e., primary consumer biomass) among secondary consumers in the Pleistocene using a mathematical model that estimates the amount of primary consumer biomass available for the secondary consumers in a community (total available biomass, or TAB) and the requirements of secondary consumers (total demanded biomass, or TDB) (Rodríguez-Gómez et al., 2014a). These concepts were already dealt with and discussed by Prevosti and Vizcaíno (2006) for paleocommunities from South America. A summary description of the model components is provided subsequently; for a detailed formal description of this model, see Rodríguez-Gómez et al. (2013). The model was written and executed in Matlab R2009b.

TAB

Our model was developed on the assumption that all of the variations in population size and composition may be taken

Table 1. The early and middle Pleistocene faunal assemblages used in this study were distributed in three time intervals (see text) and assigned locality codes (LCs). The number of macromammal species of primary consumers (N1) and secondary consumers (N2) are indicated for each assemblage. HE indicates that the assemblage includes evidence of human presence.

LC	Locality	Layer	Longitude	Latitude	N1	N2	HE	References
1.1–0.8 Ma, interval 1								
1	Atapuerca-Dolina (Spain)	TD3-TD4	3.31.18°W	42°21.08'N	8	6	Yes	Rodríguez et al. (2011)
2	Atapuerca-Dolina (Spain)	TD6 1-2	3.31.18°W	42°21.08'N	10	5	Yes	Rodríguez et al. (2011)
3	Grotte du Vallonnet (France)	III	7°28.18'E	43°45.85'N	11	8	Yes	de Lumley et al. (1988)
4	Imola (Greece)	N/A	23°25.80'E	40°37.20'N	8	7	No	Palombo et al. (2006)
5	Kozarnika (Bulgaria)	12	22°40.80'E	43°37.80'N	16	9	Yes	Guadelli et al. (2005), Sirakov et al. (2010)
6	Kozarnika (Bulgaria)	13	22°40.80'E	43°37.80'N	14	9	Yes	Guadelli et al. (2005), Sirakov et al. (2010)
7	Untermassfeld (Germany)	N/A	10°25.20'E	50°33.00'N	14	10	No	Koenigswald and Heinrich (1999)
8	Vallparadís (Spain)	Lower unit	2°1.20'E	41°33.60'N	10	6	No	García et al. (2011), Madurell-Malapeira et al. (2014)
9	Vallparadís (Spain)	Middle unit	2°1.20'E	41°33.60'N	10	8	Yes	Madurell-Malapeira et al. (2014)
0.8–0.5 Ma, interval 2								
10	Atapuerca-Dolina (Spain)	TD8	3.31.18°W	42°21.08'N	10	6	No	Rodríguez et al. (2011)
11	Isernia La Pineta (Italy)	N/A	14°13.20'E	41°36.00'N	11	4	Yes	Palombo et al. (2000–2002)
12	Mauer (Germany)	N/A	8°49.2'E	49°19.80'N	12	9	Yes	Koenigswald and Heinrich (1999)
13	Pakefield/Kessingland (United Kingdom)	Rootlet bed	1°43.20'E	52°25.80'N	15	4	Yes	Mosquera et al. (2013), Stuart and Lister (2001)
14	Slivia (Italy)	N/A	13°39.60'E	45°45.60'N	16	5	No	Montuire and Marcolini (2002), Palombo et al. (2000–2002)
15	Sussenborn (Germany)	Hauptfauna	11°21.00'E	50°58.88'N	17	6	No	Koenigswald and Heinrich (1999)
16	Voigtstedt (Germany)	Lehmzone	11°19.20'E	51°24.00'N	13	4	No	Koenigswald and Heinrich (1999)
0.5–0.2 Ma, interval 3								
17	Atapuerca-Dolina (Spain)	TD10-1	3.31.18°W	42°21.08'N	8	5	Yes	Rodríguez et al. (2011)
18	Atapuerca-Galería (Spain)	GIIa	3.31.18°W	42°21.08'N	8	5	Yes	Rodríguez et al. (2011)
19	Atapuerca-Galería (Spain)	GIIb	3.31.18°W	42°21.08'N	9	4	Yes	Rodríguez et al. (2011)
20	Atapuerca-Galería (Spain)	GIII	3.31.18°W	42°21.08'N	9	4	Yes	Rodríguez et al. (2011)
21	Biache-Saint-Vaast (France)	Dépôts fluviatiles	2°57.60'E	50°18.60'N	11	5	Yes	Palombo et al. (2003–2004)
22	Bilzingsleben II (Germany)	II	11°4.20'E	51°16.80'N	11	4	Yes	Koenigswald and Heinrich (1999), Mania and Vlcek (1999)
23	Cueva del Congosto (Spain)	A1	3°1.20'W	41°00.00'N	11	6	Yes	Arribas and Jordá (1999)
24	Fontana Acetosa (Italy)	N/A	13°9.00'E	41°44.40'N	9	5	No	Palombo et al. (2000–2002)
25	Grotta Lina (Italy)	N/A	15°45.00'E	40°00.00'N	8	6	No	Barbera et al. (1995)
26	Grotte des Cèdres (France)	N/A	5°43.80'E	43°18.60'N	9	5	No	Palombo et al. (2003–2004)
27	Grotte du Lazaret (France)	CII inf	7°15.00'E	43°42.00'N	12	6	Yes	Valensi (2009)
28	Heppenloch (Germany)	N/A	9°31.20'E	48°31.80'N	11	5	No	Koenigswald and Heinrich (1999)
29	Hundsheim (Austria)	N/A	16°55.80'E	48°7.80'N	8	8	No	Koenigswald and Heinrich (1999)
30	Orgnac 3 (France)	6	4°32.40'E	44°16.80'N	9	5	No	Moncel et al. (2005)
31	Payre (France)	F	4°43.80'E	44.43.80'N	13	7	No	Daujeard and Moncel (2010)
32	Quisana-Certosa (Italy)	N/A	14°15.00'E	40°33.00'N	9	4	No	Barbato and Giozzi (1995)
33	Schöningen (Germany)	12 B	11°1.80'E	52°10.80'N	10	4	Yes	Serangeli et al. (2015)
34	Swanscombe (United Kingdom)	Lower loam	0°19.20'E	51.25.20'N	13	4	Yes	Ashton et al. (1994)
35	Tourville-la-Rivière (France)	D1	1°6.60'E	49°19.20'N	8	4	No	Auguste (2009)
36	Wannenköpfe (Germany)	Wa1-Wa3	7°22.20'E	50°22.20'N	8	4	Yes	Koenigswald and Heinrich (1999)

as oscillations around a mean value that is constant through time (i.e., population fluctuations are randomly distributed above and below the value of this mean), an assumption that is widely accepted in population dynamics studies (Owen-Smith, 2010). We represented the average long-term condition of every population using a Leslie matrix (Leslie, 1945, 1948). Leslie matrices are used in population dynamics to represent a population structure at different times and to

describe its oscillations. We conditioned Leslie matrices to obtain the average structure of a population that was stable (i.e., population size should be constant from year to year) and stationary (i.e., the age structure should be constant from year to year over time).

The input data of the model are species-specific physical and physiological variables, including adult body mass, body mass at birth, litter size, breeding interval, age at reproductive

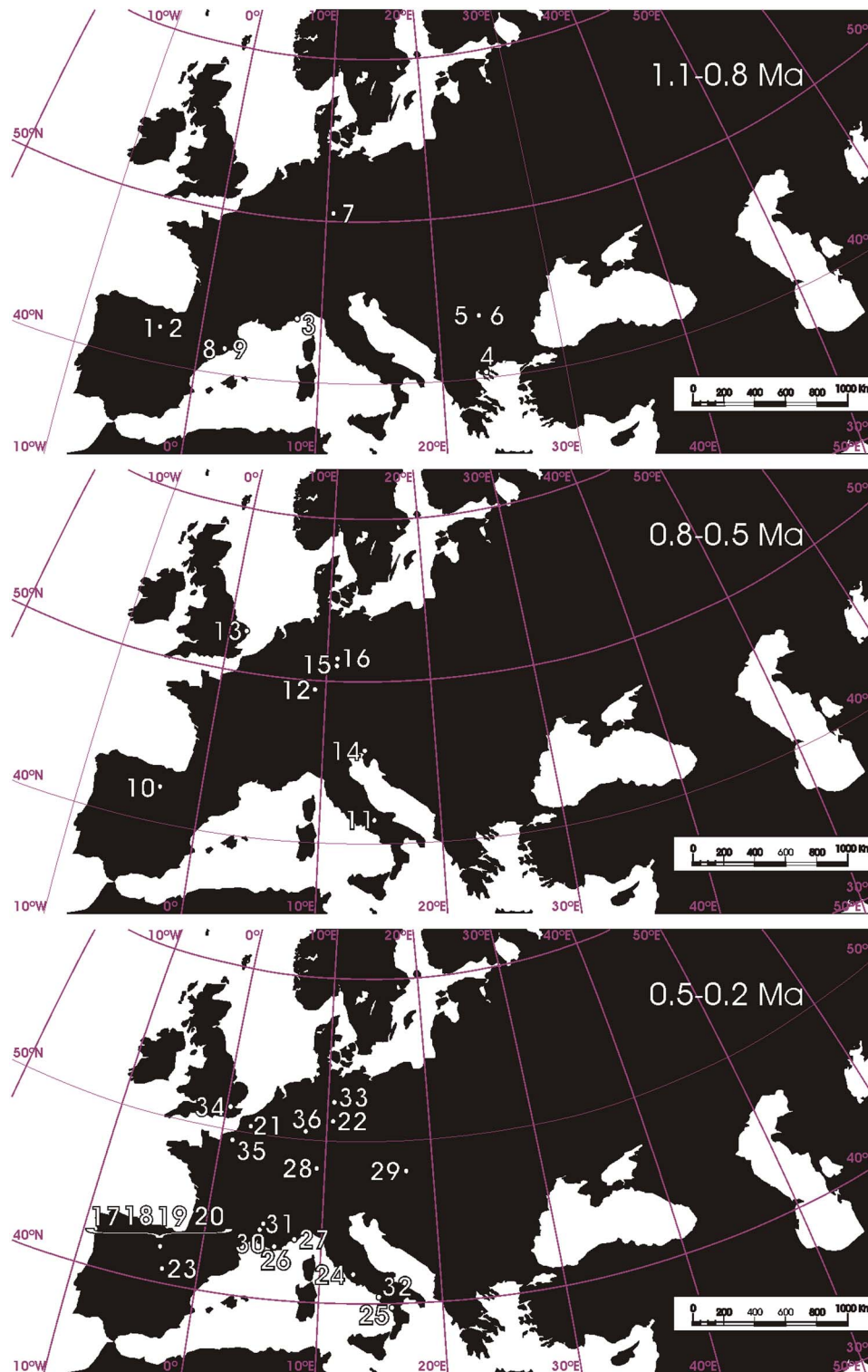


Figure 1. (color online) Geographic distribution of local faunas included in the analyses for the 1.1 to 0.2 Ma time intervals. There are 9 local faunas in interval 1 (1.1–0.8 Ma, top); 7 in interval 2 (0.8–0.5 Ma, middle); and 20 in interval 3 (0.5–0.2 Ma, bottom).

maturity, growth rate, and life span. The population profiles obtained from this model for every primary consumer population provide estimates of the average sustainable biomass output by age classes, which were eventually translated into body-size intervals. Biomass output by age interval was

obtained from the annual mortality rates obtained from the Leslie matrix. Each potentially dead individual of a primary consumer species was assigned to one of six size categories according to its average body mass at the age of death: 10–45, 45–90, 90–180, 180–360, 360–1000, or >1000 kg

(see Rodríguez et al., 2012). The biomass made available for secondary consumers by each single primary consumer population was obtained as the sum of the biomass of all dead individuals. Sustainable primary consumer biomass output was obtained as the sum of the biomass outputs in each size category from each primary consumer population.

Combining the mortality profiles obtained from the Leslie matrix with the mean body size per age class and the estimated population density of the species, the sustainable biomass output (total biomass output, or TBO) can be computed. A size-specific “wastage factor” (modified from Viljoen, 1993) is included in the model to account for the fact that a carcass includes a variable amount of nonedible tissues (e.g., horns, bones, and hide), which are included in the TBO provided by the model. Thus, this percentage of nonedible biomass is subtracted from the TBO to obtain the final amount of biomass available to secondary consumers, or total biomass or TAB, which is also distributed by body mass classes. See Rodríguez-Gómez et al. (2013) for the computational details.

The model yields several population profiles for each species, corresponding to different mortality rates. We selected extreme values with maximum and minimum pressure on subadults (or maximum and minimum mortality rates) that produce minimum and maximum TAB levels, respectively (TAB-m and TAB-M, respectively).

The model solutions are not dependent on population size: thus, we needed to estimate the population density of each primary consumer species. We used the equation provided by Damuth (1981) for European mixed temperate forest ecosystems for all primary consumer species included in this study:

$$\log(D) = -0.79 * \log(m) + 4.33, r^2 = 0.94, \quad (\text{Eq. 1})$$

where D is the population density (individuals/km²), and m is the body mass (g). We used Damuth’s (1981) equation instead of Silva and Downing’s (1995) equation because the former shows better goodness-of-fit values (Jones et al., 2009) than the latter, according to a chi-square test.

TDB

Carnivore-demanded resources should be estimated as a first step in evaluating resource distribution among secondary consumers. The secondary consumer intake rate was estimated using the equation reported by Farlow (1976):

$$\log I = (0.69686 \pm 0.01276) \log(m) + 0.27747, r^2 = 0.97, \quad (\text{Eq. 2})$$

where I is the intake rate (km/day), and m is the body mass (g). We used the maximum value for the slope (0.70962) to estimate the maximum demanded biomass for secondary consumer species. Some adjustments were made for some secondary consumers according to their inferred dietary preferences based on Rodríguez et al. (2012) and

Rodríguez-Gómez et al. (2012) (and references cited therein) (Table 2). We estimated that large-mammal flesh represented 20% of the energetic requirements of *Canis arnensis*, *Canis etruscus*, and *Canis mosbachensis*; 10% for *Lynx pardinus* and *Lynx* sp.; 80% for *Lynx issidorensis*; 98% for *Chasmaporthetes lunensis*, *Crocota crocota*, *Crocota* sp., and *Pachycrocota brevirostris* (because 2% of the total requirements could be obtained from bone marrow); 45% for *Homo antecessor*, *Homo heidelbergensis*, and *Homo* sp. because 45% is the average animal resource consumption of recent hunter-gatherer populations (Jenike, 2001; Leonard et al., 2007); 75% for *Hyaena* sp.; 10% for *Ursus arctos*, *Ursus deningeri*, *Ursus dolinensis*, *Ursus etruscus*, *Ursus* sp., and *Ursus thibetanus*; and 1% for *Ursus spelaeus*. For other secondary consumers, we assumed that flesh represented 100% of their energetic requirements (Fig. 2A).

The annual energetic requirements of a carnivore population per square kilometer are obtained by multiplying the individual annual intake by the population density. The equation provided by Damuth (1993) for African flesh eaters was used to estimate the typical secondary consumer density because it included species more similar to those present in European Pleistocene fauna:

$$\log(D) = -0.64 * \log(m) + 2.23, r^2 = 0.36, \quad (\text{Eq. 3})$$

where D is the population density (individuals/km²), and m is the body mass (g). As for the primary consumer, we used Damuth’s (1993) equation instead of Silva and Downing’s (1995) equation for the same reasons.

As in the case of TAB, TDB was distributed over the same six body-size categories based on the inferred prey-size preferences of each predator and based on the behavior of their living relatives (Table 2) (Rodríguez et al., 2012). The preference of a predator for a body-size category is represented by the percentage of predation (PD) that this size category was presumed to represent in its diet. If a predator was presumed to be unable to kill prey in a given size category and to not consume carrion, a PD of 0 was assigned to the predator in that size category (Fig. 2B and C).

Distribution of TAB between secondary consumers

The distribution of TAB among secondary consumers is based on the proportional predation pressure (PPP_{ij}) of each species in each body-size category (Fig. 2D). PPP_{ij} represents the relative amount of biomass demanded by the j th secondary consumer species from the i th primary consumer body-size category and is calculated as the proportion of the total amount of biomass demanded from a prey body-size category by all carnivores that corresponds to the requirements of a single carnivore species. PPP_{ij} incorporates intraguild competition in the model (Fig. 2D). A detailed formal description of resource distribution computation is available in Rodríguez-Gómez et al. (2013). For a numerical example, we refer the reader to Supplementary Table 4.

Table 2. The guild of secondary consumers present in the set of European assemblages included in this study (1.1–0.2 Ma) with their body mass in kilograms and their energetic requirements in kilocalories per square kilometer per year. The requirements of secondary consumers were corrected according to their diet by multiplying the total requirements of each species by a correction factor. The last six columns represent the preference, expressed in percentage, of each species of secondary consumer for the primary consumers in different body-size categories (see text).

Order	Family	Genus	Species	Body mass (kg)	Requirements (kcal/km ² /yr)	Correction factor	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Carnivora	Canidae	<i>Canis</i>	<i>arnensis</i>	16	46,077	0.20	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Canidae	<i>Canis</i>	<i>etruscus</i>	21	46,958	0.20	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Canidae	<i>Canis</i>	<i>lupus</i>	43	246,599	1.00	11.76	17.65	29.41	35.29	5.88	0.00
Carnivora	Canidae	<i>Canis</i>	<i>mosbachensis</i>	23	47,184	0.20	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Canidae	<i>Cuon</i>	<i>alpinus</i>	18	231,827	1.00	37.50	31.25	25.00	6.25	0.00	0.00
Carnivora	Canidae	<i>Cuon</i>	<i>priscus</i>	16	229,876	1.00	37.50	31.25	25.00	6.25	0.00	0.00
Carnivora	Canidae	<i>Cuon</i>	sp.	15	229,703	1.00	37.50	31.25	25.00	6.25	0.00	0.00
Carnivora	Canidae	<i>Lycan</i>	<i>lycaonoides</i>	36	243,766	1.00	12.50	37.50	25.00	25.00	0.00	0.00
Carnivora	Felidae	<i>Acinonyx</i>	<i>pardinensis</i>	80	257,701	1.00	27.27	54.55	18.18	0.00	0.00	0.00
Carnivora	Felidae	<i>Homotherium</i>	<i>crenatidens</i>	150	269,229	1.00	0.00	10.53	21.05	26.32	31.58	10.53
Carnivora	Felidae	<i>Homotherium</i>	<i>latidens</i>	187	273,394	1.00	0.00	10.53	21.05	26.32	31.58	10.53
Carnivora	Felidae	<i>Homotherium</i>	sp.	169	271,418	1.00	0.00	10.53	21.05	26.32	31.58	10.53
Carnivora	Felidae	<i>Lynx</i>	<i>issiodorensis</i>	22	188,440	0.80	60.00	40.00	0.00	0.00	0.00	0.00
Carnivora	Felidae	<i>Lynx</i>	<i>pardinus</i>	14	22,825	0.10	75.00	25.00	0.00	0.00	0.00	0.00
Carnivora	Felidae	<i>Lynx</i>	sp.	18	23,228	0.10	75.00	25.00	0.00	0.00	0.00	0.00
Carnivora	Felidae	<i>Megantereon</i>	<i>cultridens</i>	63	253,450	1.00	6.25	18.75	25.00	31.25	18.75	0.00
Carnivora	Felidae	<i>Megantereon</i>	sp.	59	252,296	1.00	6.25	18.75	25.00	31.25	18.75	0.00
Carnivora	Felidae	<i>Megantereon</i>	<i>whitei</i>	56	251,256	1.00	6.25	18.75	25.00	31.25	18.75	0.00
Carnivora	Felidae	<i>Panthera</i>	<i>gombaszogensis</i>	105	262,626	1.00	11.11	11.11	33.33	22.22	22.22	0.00
Carnivora	Felidae	<i>Panthera</i>	<i>leo</i>	170	271,586	1.00	14.29	28.57	23.81	19.05	9.52	4.76
Carnivora	Felidae	<i>Panthera</i>	<i>pardus</i>	63	253,310	1.00	54.55	27.27	18.18	0.00	0.00	0.00
Carnivora	Felidae	<i>Panthera</i>	sp.	170	271,586	1.00	14.29	28.57	23.81	19.05	9.52	4.76
Carnivora	Felidae	<i>Puma</i>	<i>pardoides</i>	38	244,685	1.00	37.50	31.25	25.00	6.00	0.00	0.00
Carnivora	Hyaenidae	<i>Chasmaporthetes</i>	<i>lunensis</i>	76	251,647	0.98	16.67	33.33	27.78	22.22	0.00	0.00
Carnivora	Hyaenidae	<i>Crocuta</i>	<i>crocuta</i>	65	248,922	0.98	15.00	30.00	25.00	15.00	10.00	5.00
Carnivora	Hyaenidae	<i>Crocuta</i>	sp.	64	248,654	0.98	15.00	30.00	25.00	15.00	10.00	5.00
Carnivora	Hyaenidae	<i>Hyaena</i>	sp.	44	185,396	0.75	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Hyaenidae	Hyaenidae	Indet.	44	185,396	0.75	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Hyaenidae	<i>Pachycrocuta</i>	<i>brevirostris</i>	73	250,822	0.98	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Hyaenidae	<i>Pliocrocuta</i>	<i>perrieri</i>	50	249,405	1.00	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Ursidae	<i>Ursus</i>	<i>arctos</i>	260	27,974	0.10	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Ursidae	<i>Ursus</i>	<i>deningeri</i>	475	29,173	0.10	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Ursidae	<i>Ursus</i>	<i>dolinensis</i>	300	28,254	0.10	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Ursidae	<i>Ursus</i>	<i>etruscus</i>	230	27,736	0.10	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Ursidae	<i>Ursus</i>	sp.	203	27,496	0.10	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Ursidae	<i>Ursus</i>	<i>spelaeus</i>	600	2965	0.01	16.67	16.67	16.67	16.67	16.67	16.67
Carnivora	Ursidae	<i>Ursus</i>	<i>thibetanus</i>	128	26,620	0.10	16.67	16.67	16.67	16.67	16.67	16.67
Primate	Hominidae	<i>Homo</i>	<i>antecessor</i>	54	112,806	0.45	23.81	28.57	19.05	14.29	9.52	4.76
Primate	Hominidae	<i>Homo</i>	<i>heidelbergensis</i>	69	114,789	0.45	23.81	28.57	19.05	14.29	9.52	4.76
Primate	Hominidae	<i>Homo</i>	sp.	54	112,806	0.45	23.81	28.57	19.05	14.29	9.52	4.76

Analytic methods

Predator/prey ratios have been traditionally used in paleontology to measure the intensity of competition in the fossil faunas of the past (Palombo and Mussi, 2006; Raia et al., 2007; Palmqvist et al., 2008; Croitor and Brugal, 2010; Feranec et al., 2010; Palombo, 2010; Meloro and Clauss, 2012; Rodríguez et al., 2012; Stiner, 1992; but see Volmer and Hertler, 2016). Rodríguez-Gómez et al. (2016a) discussed the utilization of predator/prey ratio versus estimated/expected density indexes to measure competition intensity among

secondary consumers and concluded that the indexes based on estimated/expected densities were more accurate than predator/prey indexes. Therefore, we used estimated/expected density indexes (the global competition index [GCI] and the global competition index biomass [GCIb]) to compare the competition intensity in the different faunal assemblages selected in our analysis (see Rodríguez-Gómez et al., 2014b, 2017).

The GCI is obtained from the following:

$$GCI = 1 - \left(\frac{\sum_{j=1}^n Ds_j}{\sum_{j=1}^n Dx_j} \right), \quad (\text{Eq. 4})$$

where Dx_j is the expected density for secondary consumer species j obtained from the allometric equation in Damuth (1993). Dsj is the estimated density for the secondary

consumer species j obtained from the model. The GCI index shows to what degree the secondary consumers satisfy their requirements according to their population densities in a given environment. GCIs with TAB-m and TAB-M are denoted as GCI-m and GCI-M, respectively.

The GCIB is computed as follows:

$$GCIB = 1 - \left(\frac{\sum_{j=1}^n Dsj \times W_j}{\sum_{j=1}^n Dx_j \times W_j} \right), \quad (\text{Eq. 5})$$

where W_j is the body mass of the j th species. The GCIB relates the estimated and expected biomasses of the secondary consumer species and provides information about the type of secondary consumers in different paleoecosystems according to body size. We obtained one GCIB for TAB-m and another for TAB-M (GCIB-m and GCIB-M, respectively). For computational examples of both indexes, please refer to Supplementary Tables 5 and 6.

These indexes provide information on the degree of fulfillment of the secondary consumers' requirements and, thus, the degree of competition intensity in the ecosystem compared to an ideal condition in which all species would reach optimal densities and maximum population biomass. For both the GCI and GCIB, higher competition among secondary consumers is represented by values close to 1, whereas values close to 0 indicate reduced competition where all species would reach densities near to their maximum population density (see White et al., 2007). Thus, these indexes provide information about the competition intensity in the ecosystem with regard to an ideal condition in which all species reach optimal densities, because the Dx_j values are taken as references to evaluate the Dsj values.

To compare competition intensity in different time intervals, we used the nonparametric Mann-Whitney U -test to detect differences in the median value of these two indexes.

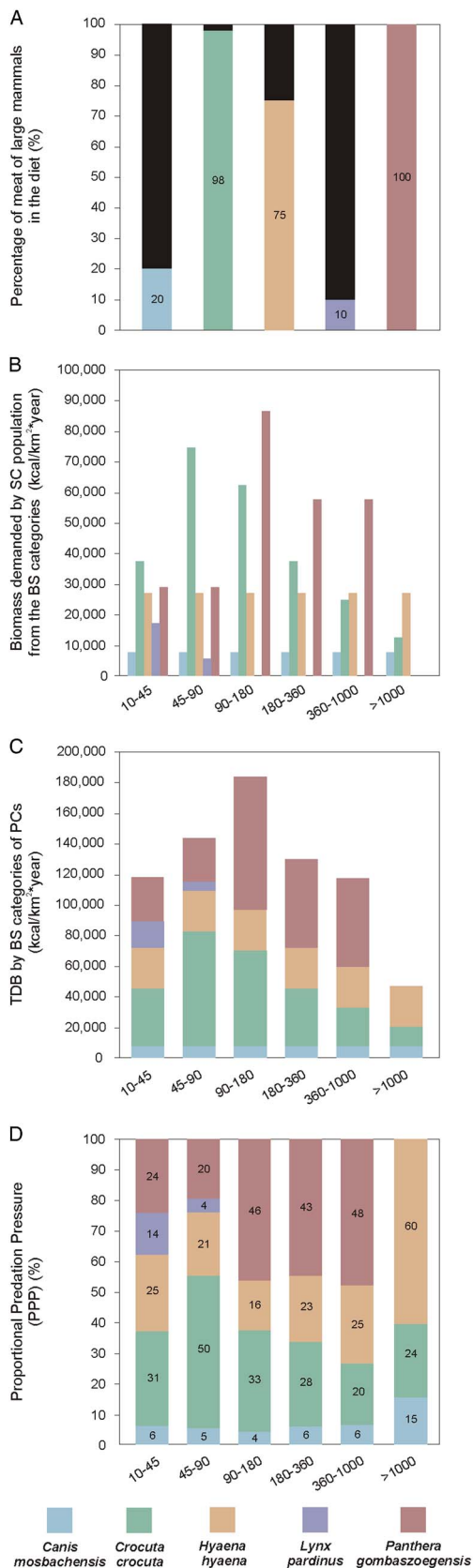


Figure 2. Graphic representation of the computation steps to obtain the total biomass demanded (TDB) and the proportional predation pressure (PPP) used to distribute the total available biomass among secondary consumers (SCs). (A) Percentage of meat of large mammals (>10 kg) in the diet of the different species in the guild of SCs of a hypothetical assemblage. Color bars and the numbers inside them indicate the percentage of the diet consisting of meat of large mammals. Black bars indicate the part of the diet represented by other food resources (e.g., mammals weighing <10 kg, birds, reptiles, amphibians, or plant resources). (B) Biomass demanded by each SC population from the primary consumer (PC) species (kcal/km²/yr) in different body-size (BS) categories. The total requirements of each population are distributed among the six categories according to the prey preference profile or percentage of predation of the SC (see text and Table 2). These total requirements would be met in an optimal condition with maximum densities. (C) TDB by BS categories of PCs (kcal/km²/yr). Each bar represents the sum of the biomasses demanded by all the SCs from each BS category of PCs, according to panel B. (D) PPP (%) for each BS category of PCs according to the estimations obtained in panel C. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Similarly, the Mann-Whitney *U*-test was also used to test for differences in TAB and the TDB between time intervals.

RESULTS

We obtain minimum and maximum TAB for each LFA in the three intervals of this study, the predator requirements in optimal conditions or expected requirements (TDB), and the distribution of TAB among secondary consumers (Table 3). According to our results, on average the TAB was higher in the LFAs from the interval 0.8–0.5 Ma (interval 2) than it was before or after this period, considering TAB-m or

TAB-M (Fig. 3A and B, Table 4). However, these differences are statistically significant only when comparing intervals 2 and 3 (0.5–0.2 Ma) (Table 5).

A gradual tendency toward a reduction in the requirements of secondary consumers (TDB) from the interval 1.1–0.8 Ma (1,379,501 kcal/km²/yr) to the intervals 0.8–0.5 Ma (862,091 kcal/km²/yr) and 0.5–0.2 Ma (650,748 kcal/km²/yr) is apparent (Table 4, Fig. 3C), although the differences are statistically significant only between intervals 1 and 3 (Table 5). This might be explained by a decrease in the number of secondary consumers and/or by a change in the guild of secondary consumers because of the appearance of

Table 3. A number of different parameters are estimated by the model for from each faunal assemblage. TAB-m, minimum total available biomass; TAB-M, maximum total available biomass; TDB, total demanded biomass; GCI-m, global competition index with minimum TAB; GCI-M, global competition index with maximum TAB; GCIB-m, biomass global competition index for minimum TAB; GCIB-M, biomass global competition index for maximum TAB. Units for TAB-m, TAB-M, and TDB are kcal/km²/yr. GCI-m, GCI-M, GCIB-m, and GCIB-M are parameters without units because their values are parts per unit.

Faunal assemblages	TAB-m	TAB-M	TDB	GCI-m	GCI-M	GCIB-m	GCIB-M
1.1–0.8 Ma, interval 1							
1 Atapuerca Dolina, TD3-TD4	416,452	524,072	723,021	0.33	0.22	0.39	0.24
2 Atapuerca Dolina, TD6 1-2	535,743	651,271	459,636	0.00	0.00	0.00	0.00
3 Grotte du Vallonnet, III	551,110	699,625	1,400,625	0.60	0.49	0.59	0.45
4 Imola, N/A	412,097	536,058	1,057,475	0.62	0.50	0.60	0.45
5 Kozarnika, 12	835,441	1,079,195	1,835,212	0.54	0.44	0.55	0.41
6 Kozarnika, 13	752,045	989,510	1,657,696	0.54	0.43	0.56	0.40
7 Untermassfeld, N/A	741,078	887,369	2,046,157	0.59	0.52	0.63	0.54
8 Vallparadís, lower unit	454,177	578,301	1,010,640	0.54	0.43	0.51	0.35
9 Vallparadís, middle unit	454,177	578,301	1,379,501	0.67	0.58	0.64	0.51
0.8–0.5 Ma, interval 2							
10 Atapuerca, TD8	493,342	602,598	794,853	0.29	0.22	0.35	0.22
11 Isernia La Pineta, N/A	542,574	686,155	459,641	0.00	0.00	0.00	0.00
12 Mauer, N/A	622,694	758,038	1,451,923	0.56	0.47	0.57	0.46
13 Pakefield/Kessingland, rootlet bed	762,345	947,447	879,913	0.13	0.00	0.13	0.00
14 Slivia, N/A	681,179	845,450	862,091	0.18	0.02	0.20	0.02
15 Sussenborn, Hauptfauna	905,515	1,129,825	1,110,145	0.15	0.00	0.17	0.01
16 Voigtstedt, Lehmzone	696,436	845,518	603,060	0.00	0.00	0.00	0.00
0.5–0.2 Ma, interval 3							
17 Atapuerca Dolina, TD10-1	386,343	490,233	681,715	0.31	0.26	0.37	0.25
18 Atapuerca Galería, GIIa	395,132	512,006	885,642	0.54	0.49	0.54	0.42
19 Atapuerca Galería, GIIb	435,372	564,398	639,043	0.36	0.30	0.30	0.13
20 Atapuerca Galería, GIII	435,372	564,398	641,026	0.36	0.31	0.30	0.13
21 Biache-Saint-Vaast, Dépôts fluviatiles	536,810	655,479	688,137	0.21	0.05	0.16	0.02
22 Bilzingsleben, II	548,516	649,705	660,470	0.16	0.04	0.14	0.02
23 Cueva del Congosto, A1	618,647	746,859	889,210	0.22	0.11	0.29	0.15
24 Fontana Acetosa, N/A	407,110	531,561	623,888	0.32	0.12	0.32	0.13
25 Grotta Lina, N/A	406,180	498,056	1,051,356	0.60	0.51	0.54	0.44
26 Grotta des Cèdres, N/A	525,420	658,243	575,744	0.10	0.00	0.10	0.00
27 Grotte du Lazaret, CII inf	519,318	672,370	666,479	0.25	0.18	0.11	0.08
28 Heppenloch, N/A	552,874	668,337	780,950	0.28	0.17	0.22	0.07
29 Hundsheim, N/A	398,860	495,495	1,524,687	0.73	0.67	0.73	0.64
30 Orgnac 3, 6	466,830	571,794	575,493	0.11	0.01	0.16	0.00
31 Payre, F	642,923	790,646	1,052,429	0.33	0.25	0.30	0.15
32 Quisana-Certosa, N/A	391,607	492,431	552,381	0.17	0.14	0.15	0.12
33 Schöningen, 12 B	595,795	713,051	413,977	0.00	0.00	0.00	0.00
34 Swanscombe, lower loam	635,340	771,019	633,956	0.01	0.40	0.00	0.15
35 Tourville-la-Rivière, D1	426,395	525,626	526,460	0.18	0.00	0.16	0.00
36 Wannenköpfe, Wa1-Wa3	341,204	439,489	633,956	0.45	0.30	0.39	0.24

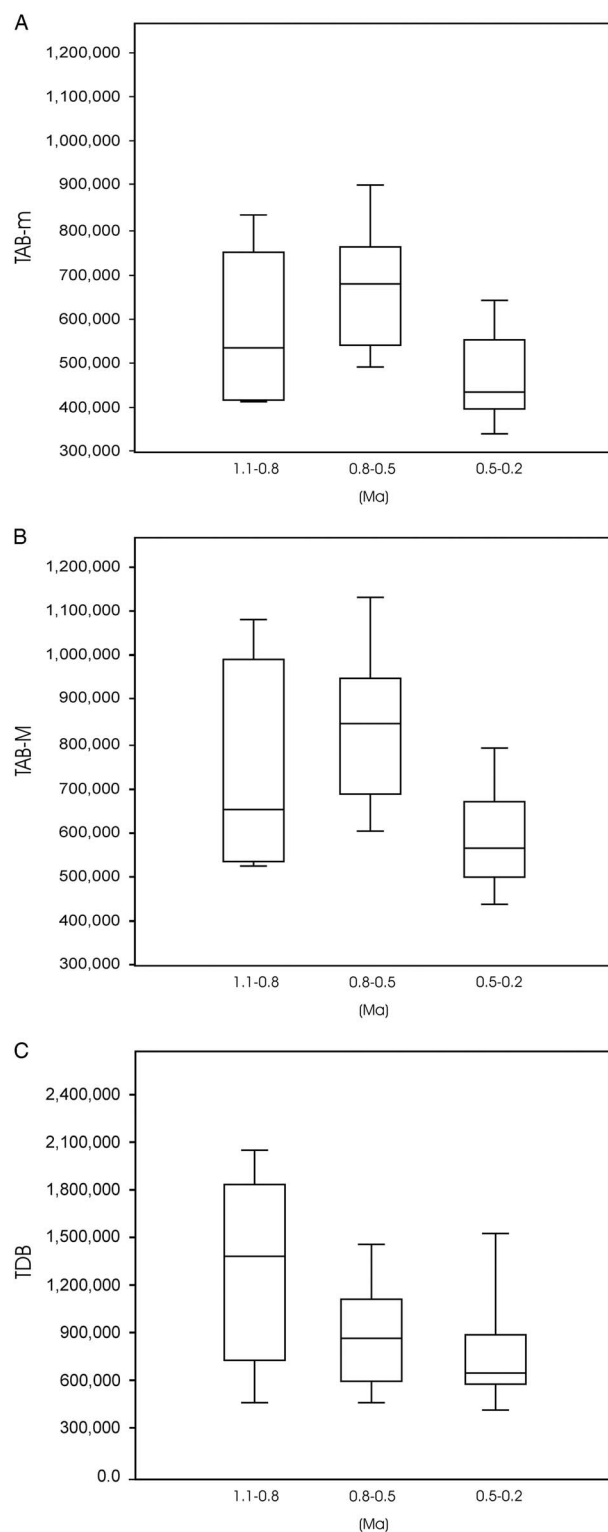


Figure 3. Boxplot representation of total available biomass (TAB) and total demanded biomass (TDB) for the three intervals of this study (i.e., 1.1–0.8 Ma [interval 1], 0.8–0.5 Ma [interval 2], and 0.5–0.2 Ma [interval 3]) in kcal/km²/yr. (A) Minimum TAB (TAB-m). (B) Maximum TAB (TAB-M). (C) TDB.

species with lower meat requirements. The three intervals show a similar absolute minimum value of TDB of ~400,000 kcal/km²/yr (Fig. 3C). This is likely an artifact of

Table 4. Median values of different parameters (see Table 3) in the three time intervals considered in this study (i.e., 1.1–0.8, 0.8–0.5, and 0.5–0.2 Ma), with all faunal assemblages (Total), for faunal assemblages with human presence (with *Homo*), and for faunal assemblages without human presence (without *Homo*). Units for TAB-m, TAB-M, and TDB are kcal/km²/yr. GCI-m, GCI-M, GCIB-m, and GCIB-M are parameters without units because their values are parts per unit.

Scenario	Parameter	1	2	3
Total	TAB-m	535,743	681,179	451,104
Total	TAB-M	651,271	845,450	568,096
Total	TDB	1,379,501	862,091	650,748
Total	GCI-m	0.54	0.15	0.26
Total	GCI-M	0.44	0.00	0.18
Total	GCIB-m	0.56	0.17	0.26
Total	GCIB-M	0.41	0.01	0.13
With <i>Homo</i>	TAB-m	543,427	622,694	519,318
With <i>Homo</i>	TAB-M	675,448	758,038	649,705
With <i>Homo</i>	TDB	1,390,063	879,913	660,470
With <i>Homo</i>	GCI-m	0.54	0.13	0.25
With <i>Homo</i>	GCI-M	0.43	0.00	0.26
With <i>Homo</i>	GCIB-m	0.56	0.13	0.29
With <i>Homo</i>	GCIB-M	0.40	0.00	0.13
Without <i>Homo</i>	TAB-m	454,177	688,807	426,395
Without <i>Homo</i>	TAB-M	578,301	845,484	531,561
Without <i>Homo</i>	TDB	1,057,475	828,472	623,888
Without <i>Homo</i>	GCI-m	0.59	0.16	0.28
Without <i>Homo</i>	GCI-M	0.50	0.01	0.14
Without <i>Homo</i>	GCIB-m	0.60	0.19	0.22
Without <i>Homo</i>	GCIB-M	0.45	0.01	0.12

our method because we selected sites with a minimum number of secondary consumer species. This tendency is not observed for the maximum values of TDB; the value of maximum TDB is lower in interval 2 than in the first and third intervals.

Concerning the competition indexes, GCI was significantly higher during 1.1–0.8 Ma than in the two younger intervals (Table 4 and 5), both with TAB-m (Fig. 4A) and with TAB-M (Fig. 4B), in accordance with the results from previous studies (Meloro et al., 2007; Raia et al., 2007; Croitor and Brugal, 2010; Palombo, 2010). Differences in GCI between the second and third intervals are not significant (Table 5). Similarly, GCIB was not significantly different comparing the second and third time intervals, but it was significantly higher in the LFAs for 1.1–0.8 Ma (Fig. 4C and D, Table 5). Thus, competition intensity for meat resources between the secondary consumer species was higher in the latter part of the early Pleistocene than in the middle Pleistocene, but it was similar during 0.8–0.5 Ma and 0.5–0.2 Ma. The three intervals include some LFAs with an absolute minimum value of competition intensity (0.0). Intervals 1 and 3 show LFAs with absolute maximum values higher than the second interval. In summary, the same pattern in GCI and GCIB along the three time intervals is observed for TAB-m and for TAB-M, although, as it may be expected, with less competition when resources are more abundant (TAB-M).

Table 5. Exact P values from Mann-Whitney U -test comparing a number of parameters (see Table 3) among the three time intervals of this study (1.1–0.8, 0.8–0.5, and 0.5–0.2 Ma). The time intervals are compared two by two with this statistical test (i.e., column “1 and 2” compares the values of the parameters between the first and the second time intervals. The P values in bold show significant differences: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.005$.

Exact P	Parameter	1 and 2	1 and 3	2 and 3
Total	TAB-m	19 ($P = 0.2008$)	58 ($P = 0.1364$)	17 ($P = 0.0020$)***
Total	TAB-M	20 ($P = 0.2407$)	56 ($P = 0.1127$)	15 ($P = 0.0012$)***
Total	TDB	18 ($P = 0.1738$)	31 ($P = 0.0041$)***	51 ($P = 0.3085$)
Total	GCI-m	10 ($P = 0.0218$)*	39 ($P = 0.0144$)*	44.5 ($P = 0.1657$)
Total	GCI-M	9.5 ($P = 0.0166$)*	43 ($P = 0.0253$)*	38 ($P = 0.07673$)
Total	GCIB-m	10 ($P = 0.0226$)*	31.5 ($P = 0.0043$)***	58 ($P = 0.5231$)
Total	GCIB-M	11.5 ($P = 0.0321$)*	35.5 ($P = 0.0084$)**	49 ($P = 0.2583$)
With <i>Homo</i>	TAB-m	6 ($P = 0.5476$)	22 ($P = 0.2896$)	5 ($P = 0.0852$)
With <i>Homo</i>	TAB-M	7 ($P = 0.7143$)	22 ($P = 0.2896$)	4 ($P = 0.0604$)
With <i>Homo</i>	TDB	7 ($P = 0.7143$)	12 ($P = 0.0347$)*	12 ($P = 0.5330$)
With <i>Homo</i>	GCI-m	5.5 ($P = 0.4286$)	15.5 ($P = 0.0817$)	13.5 ($P = 0.6813$)
With <i>Homo</i>	GCI-M	5 ($P = 0.3810$)	19 ($P = 0.1712$)	11 ($P = 0.4341$)
With <i>Homo</i>	GCIB-m	5.5 ($P = 0.4167$)	11.5 ($P = 0.0289$)*	15 ($P = 0.8681$)
With <i>Homo</i>	GCIB-M	6 ($P = 0.5238$)	15 ($P = 0.0735$)	12 ($P = 0.5275$)
Without <i>Homo</i>	TAB-m	3 ($P = 0.4000$)	9 ($P = 0.4818$)	3 ($P = 0.0196$)*
Without <i>Homo</i>	TAB-M	3 ($P = 0.4000$)	7 ($P = 0.2818$)	3 ($P = 0.0196$)*
Without <i>Homo</i>	TDB	2 ($P = 0.2286$)	4 ($P = 0.1000$)	12 ($P = 0.4140$)
Without <i>Homo</i>	GCI-m	0 ($P = 0.0571$)	5 ($P = 0.1455$)	10.5 ($P = 0.2741$)
Without <i>Homo</i>	GCI-M	0 ($P = 0.0571$)	5 ($P = 0.1364$)	11 ($P = 0.3091$)
Without <i>Homo</i>	GCIB-m	0 ($P = 0.0571$)	4 ($P = 0.0909$)	15 ($P = 0.6825$)
Without <i>Homo</i>	GCIB-M	0 ($P = 0.0571$)	4 ($P = 0.0955$)	14.5 ($P = 0.6336$)

Considering the 36 LFAs selected for our study, *Homo* was present in 67% of them during 1.1–0.8 Ma, in 43% during 0.8–0.5 Ma, and in 55% during 0.5–0.2 Ma. The presence of *Homo* in a site does not imply that the assemblage includes hominin fossils; human presence may also be inferred from other evidence such as the existence of lithic tools (see Rodríguez et al., 2015). We explore the relationship between the presence of *Homo* in an LFA and the values of the competition indexes GCI and GCIB in the three time intervals in Figures 5 and 6. Both the GCI and GCIB indexes show a wide variation in the three intervals when all sites are considered, although the variation is smaller in the second interval. There are not significant differences in GCI or GCIB among the three intervals considering only the faunal assemblages with human presence. It is apparent, however, that the presence of *Homo* is not recorded in the LFA with the highest GCI value (Hundsheim, N/A = 0.73; Fig. 5). Indexes for LFAs with human presence were similar in the three intervals. There are significant differences in GCI and GCIB between the first and second intervals considering LFAs without *Homo* with TAB-m and TAB-M, but there are not differences between the second and the third intervals.

DISCUSSION

Our results do not support the hypothesis that competition among secondary consumers was higher between 0.8 and 0.5 Ma (interval 2) than in the previous (1.1–0.8 Ma) and later (0.5–0.2 Ma) intervals. On the one hand, the TAB

(TAB-m and TAB-M) was higher in interval 2 than in the other two intervals, and thus, there was more biomass available to secondary consumers. In contrast, we found no significant differences in the trophic requirements of secondary consumers (TDB), which appeared to decrease through time, being highest during 1.1–0.8 Ma. Herbivores are well known to have increased in size during this period, and a significant number of primary consumer species were free, or almost free, of predators (Meloro et al., 2007; Raia et al., 2007; Croitor and Brugal, 2010; Meloro and Clauss, 2012; Rodríguez et al., 2012). On the other hand, the competition intensity was at its highest during the first interval and at its lowest in the second interval. The variability in the intensity of competition inside an interval could be a reflection of the diversity of paleocommunity structures, and it is moderately higher in the first than in the other two intervals. The second interval shows the lowest diversity of LFAs, suggesting that it was more homogeneous from an ecological point of view. The competition intensity in the guild of secondary consumers during the latter part of the early Pleistocene and the middle Pleistocene seems to be characteristic of each period. Therefore, each time interval could have its own properties from the point of view of competition and ecological interactions. The pattern of change in TAB is similar to the pattern observed in the predator/prey ratio in previous studies, which rose in the middle Galerian (Meloro et al., 2007; Raia et al., 2007; Croitor and Brugal, 2010; Palombo, 2010) (see “Introduction”). Thus, the increased efficiency of the secondary consumer guild during the middle Galerian

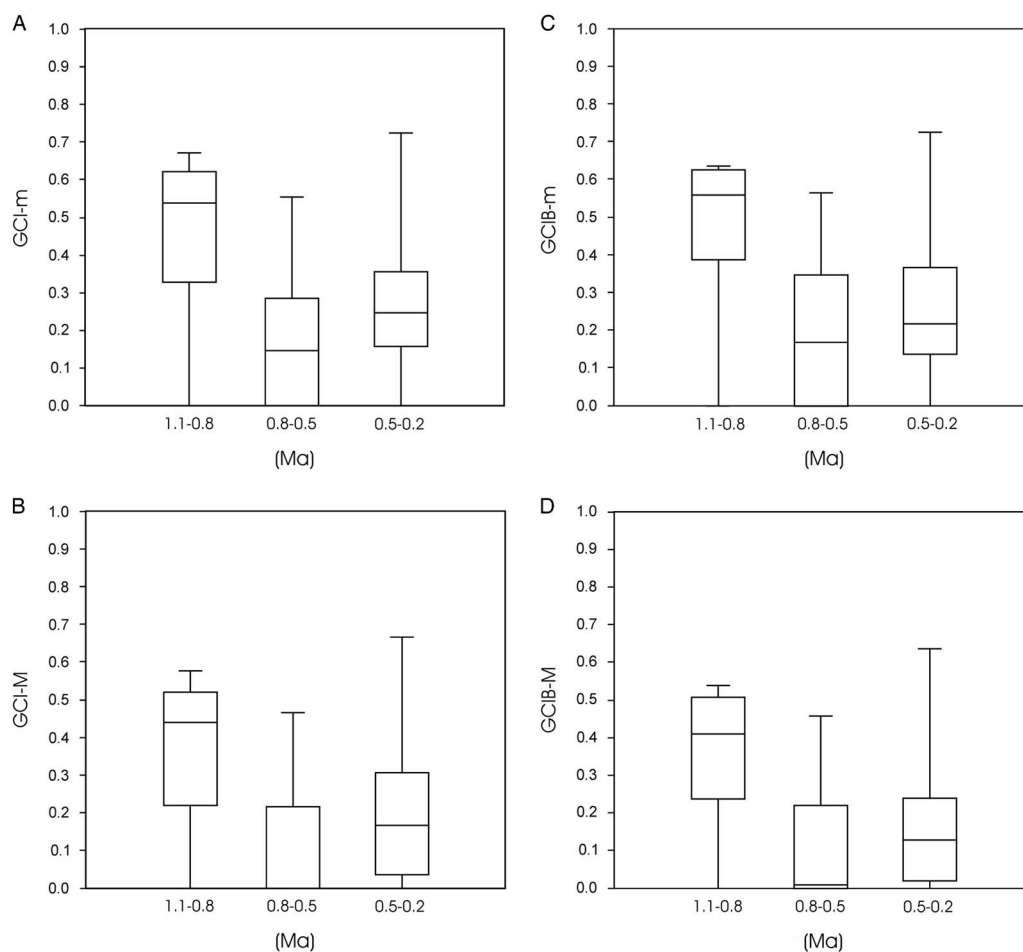


Figure 4. Boxplot representation of global competition index (GCI) and global competition index biomass (GCIB) values for the three intervals of this study (i.e., 1.1–0.8 Ma [interval 1], 0.8–0.5 Ma [interval 2], and 0.5–0.2 Ma [interval 3]), in two scenarios: with minimum and maximum total available biomass (TAB) in all assemblages. GCI and GCIB take the value of 0 when there is no competition among secondary consumers because all species reach their requirements. When GCI and GCIB are 1, competition among the secondary consumers species is maximum. (A) GCI-m (GCI with minimum TAB). (B) GCI-M (GCI with maximum TAB). (C) GCIB-m (GCIB with minimum TAB). (D) GCIB-M (GCIB with maximum TAB).

could be related to an increase in the available biomass (TAB) for this guild. Note that the pattern observed for the predator/prey ratios is not directly comparable with the changes in the GCI and GCIB indexes because of their different conceptualization and nature (Rodríguez-Gómez et al., 2016a).

Considering the three periods together, *Homo* was present only in LFAs in which the secondary consumers satisfied at least one-third of their requirements (GCI and GCIB are <0.67). Moreover, this threshold (GCI = 0.67) is obtained in the middle unit from the Vallparadís site (Spain), but human presence in this LFA is controversial (Martínez et al., 2010; Garcia et al., 2013; but see Madurell-Malapeira et al., 2012). If the middle unit from Vallparadís is not considered, the threshold value for human presence would be GCI = 0.62, as in Imola (Greece). However, *Homo* was present in some LFAs during the three time intervals, and our results suggest that there were not significant differences in competition intensity among LFAs with human presence from different time intervals, nor between faunas from the same period with

and without hominins (analyses not shown). Therefore, human populations occurred in places under similar conditions during the three periods.

On the other hand, differences in the competition indexes (GCI and GCIB) between sites without human presence from the first versus the second interval were nonsignificant, considering either the TAB-m or the TAB-M, although in the first interval competition intensity was very high and in the second interval it was lower (Table 4, Figs. 5 and 6). Our results show that competition tends to be higher in assemblages from the first interval than in the assemblages from the two younger periods (Figs. 5 and 6). According to these results, *Homo* was present in ecosystems with a wide range of competition intensity values during the three intervals, but it was not present in conditions of extreme competition intensity. Nevertheless, those extreme conditions have been detected only in two sites, one from the first interval (the latter part of the early Pleistocene Vallparadís middle unit from Spain) and the other from the third interval (the latter part of the middle Pleistocene Hundsheim site from

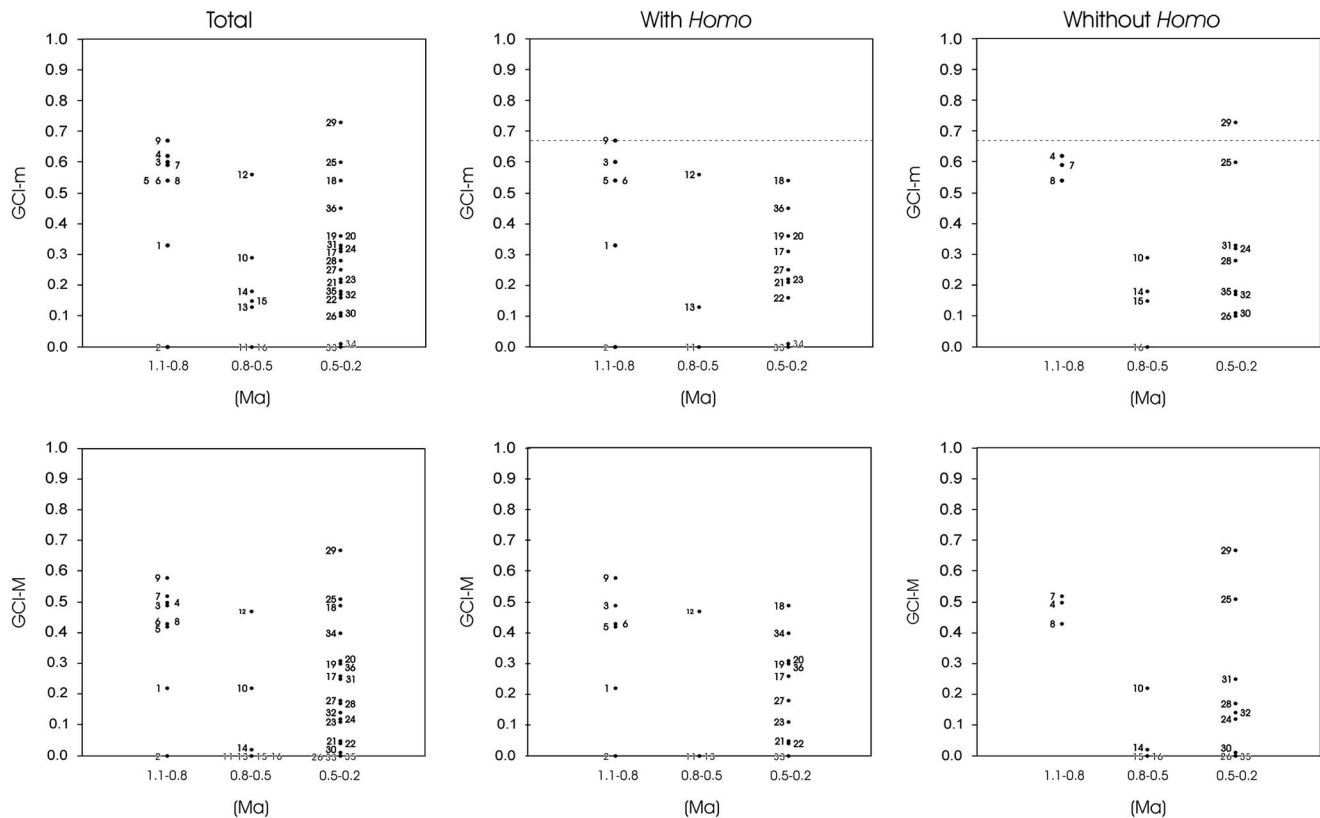


Figure 5. Graphic distribution of global competition index (GCI) values in each local faunal assemblage for the three intervals of this study (i.e., 1.1–0.8 Ma [interval 1], 0.8–0.5 Ma [interval 2], and 0.5–0.2 Ma [interval 3]), in two scenarios: with minimum (GCI-m; top) and maximum (GCI-M; bottom) total available biomass in all assemblages. The first column (Total) contains all assemblages, the second column (with *Homo*) includes assemblages with evidence of the presence of *Homo*, and the third column (without *Homo*) includes assemblage lacking this evidence. GCI is equal to 0 when competition intensity is minimum and 1 when it is maximum. Locality codes used are as shown in Table 1.

Germany; Table 3). Thus, *Homo* was able to successfully compete with other secondary consumers in most conditions, exhibiting a similar and remarkable adaptation capacity during the three periods studied. However, humans were not in communities where competition was extremely high. Moreover, the latter part of the middle Pleistocene Hundsheim site was excavated at the beginning of the twentieth century, and it no longer exists (Frank and Rabeder, 1998). The probability that this assemblage was affected by a time-averaging phenomenon cannot be ruled out. Hundsheim is a faunal assemblage rich in biodiversity with different kinds of secondary consumer (omnivores, scavengers, and hypercarnivorous like canids, felids, hyenids, and ursids). In our sample, Hundsheim appears as an outlier for its time interval regarding competition intensity. If Hundsheim were removed from the sample, there would not be any middle Pleistocene site with competition intensity comparable to the latter part of the early Pleistocene sites, and this would suggest opposite tendencies for the early and middle Pleistocene LFAs.

In light of the results presented here, the discontinuity in the human occupation of Europe observed by Mosquera et al. (2013) on the basis of the scarcity of evidence of occupation and the apparent gap between the Mode 1 and Mode 2 technocomplexes in Europe cannot be explained by high

competition inside the paleocommunities from 0.8 to 0.5 Ma. In the previous section, we commented on the relative frequency of human presence in the LFAs selected for this study. Wider analyses with the whole sample of 98 LFAs initially compiled, which includes LFAs that did not meet the selection criteria (see “Methods”), provide a more complete view. Thirty out of the 98 LFAs belong to the first interval, 12 to the second interval, and 56 to the third interval. Evidence of human presence is recorded in this sample in 43% of the LFAs from the first interval, 25% of the LFAs from the second interval, and 34% of the LFAs from the third interval. Taking these data into consideration, the lowest relative frequency of human presence corresponds to interval 2, being 18% and 9% lower than intervals 1 and 2, respectively. These figures show a reduction in the number of sites and in human presence in the early Middle Pleistocene.

If a reduction in human abundance during the middle Galerian is taken for granted, a priori, both the local extinction and/or the demographic decrease of humans might be caused by adverse conditions. From a paleoecological point of view focused on macromammals and resource availability, two scenarios might explain human local extinction and/or demographic decrease by adverse conditions, where climatic changes are considered intrinsically. In the first one, the

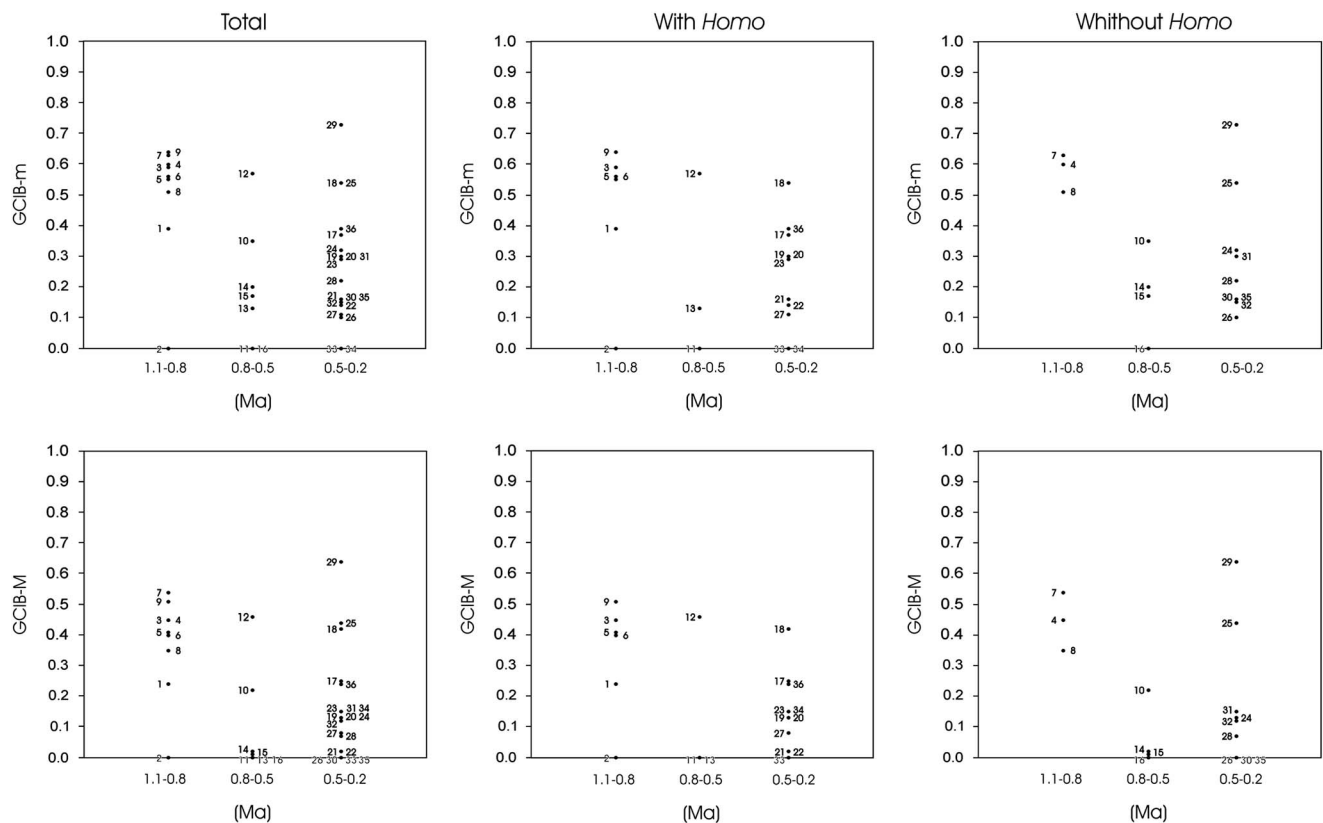


Figure 6. Graphic distribution of the global competition index biomass (GCIB) values in each local faunal assemblage for the three intervals of this study (i.e., 1.1–0.8 Ma [interval 1], 0.8–0.5 Ma [interval 2], and 0.5–0.2 Ma [interval 3]), in two scenarios: with minimum (GCIB-m; top) and maximum (GCIB-M; bottom) total available biomass in all assemblages. The first column (Total) contains all assemblages, the second column (with *Homo*) includes assemblages with evidence of the presence of *Homo*, and the third column (without *Homo*) includes assemblages lacking this evidence. GCIB is equal to 0 when competition intensity is minimum and 1 when it is maximum. Locality codes used are as shown in Table 1.

competition among secondary consumers reached a high level during 0.8–0.5 Ma across Europe. The human populations were unable to address this competition, and they became extinct. However, according to the results presented here, competition intensity was lower during the middle Pleistocene than in the latter part of the early Pleistocene, except for Hundsheim, and this hypothesis is not supported. In an alternative scenario, changes in the configuration of paleocommunities might displace human populations from many faunal assemblages, although they were able to survive in areas where the structure of the mammalian communities allowed them to successfully compete for resources.

With respect to changes in community configuration or food web structure, the limit between the first and second intervals at 0.8 Ma roughly coincides with the Matuyama-Brunhes boundary and the MPR (Maslin and Ridgwell, 2005). Carrion et al. (2011) suggest a cyclic replacement of forested landscapes with open landscapes between 0.9 and 0.4 Ma coincident with the changes in climatic periodicity from 41 ka to 100 ka cycles. A faunal turnover also occurred in Europe at this time with the appearance of new carnivores and increased herbivore richness that modified the structure of mammalian communities (Turner, 1992; Palombo, 2007, 2010, 2013, 2014; Rodríguez et al., 2012). However, Meloro (2011a) suggests a

similar exploitation of the ungulates by the guild of secondary consumers throughout the entire Plio-Pleistocene in Italy based on the relative stability of the disparity in the shape of the mandibular corpus. Palombo (2013, 2016) concludes that during this transition, each mammal species varied its distribution and abundance according to its own environmental tolerances and ecological flexibility because the factors that triggered its dispersal varied from one species to another. Palombo (2013, 2016) suggests that climate change and environmental instability facilitated the settlement of the European ecosystems by new species with wider ecological niches, such as humans. According to the results presented here, the mid-Pleistocene turnover produced conditions more favorable to *Homo*, from the point of view of meat resources, with lower competition intensity and better access to carcasses than in the former period. Surprisingly, these improved environmental conditions did not coincide with an increased presence of *Homo*. Human populations only increased and expanded much later, at ~0.5 Ma. It is also conceivable that other aspects of the human-fauna interactions not included in our analyses limited the viability of human population in this period.

A high biodiversity, with many complex ecological interactions, induces speciation, reduces extinction rates, and

may facilitate the support of biodiversity in an ecosystem (Bascompte et al., 2006; Ricklefs, 2010). The number of secondary consumer species was higher in the latter part of the early Pleistocene than in the middle Pleistocene, and perhaps this higher biodiversity induced specialization, made paleocommunities more stable, and allowed paleocommunities to support higher levels of competition intensity. In contrast, the faunal turnover associated with the MPR induced the breakup of the existing relationships and perhaps made it more difficult for secondary consumers to enter and survive inside a Galerian paleocommunity. Moreover, the Galerian secondary consumers were more generalist than the Epivillafranchian species (Croitor and Brugal, 2010), making their niches more prone to overlap and promoting territorial competition and spatial exclusion, as has been observed for recent cheetahs and wild dogs (Laurenson et al., 1995; Mills and Gorman, 1997). In any case, human populations overcame these difficulties between 0.5 and 0.2 Ma when they increased in numbers. Niche overlap may be analyzed by looking at the species that co-occur with *Homo* in the LFAs. Only six species did not show co-occurrences with *Homo* at any LFAs, but if analyzed at the genus scale, *Homo* coincided with all genera (see Supplementary Table 2) in at least one LFA. For this reason, we assume that the human niche did not overlap completely with the niche of any other genus. The flexibility and diversity of the omnivorous human diet and the lack of exclusion with other secondary consumers hampers a better understanding of the role played by humans in these paleoecosystems.

There are not enough middle Pleistocene LFAs with high competition intensity to discuss in detail the relevance of the improvements in lithic technology in this period (Jiménez-Arenas et al., 2011; Mosquera et al., 2013). However, our results show that, considering ecological competition intensity, the Acheulean technology spread in Europe when environmental conditions were more favorable for secondary consumers (reduced competition). Moreover, human subsistence strategies were successful with both Oldowan and Acheulean technologies (Blasco et al., 2013; Huguet et al., 2013), but the latter coincided with the demographic increase and the range expansion (Roebroeks, 2001). Perhaps these technological improvements allowed humans to attain a higher performance with the same resources. Kahlke et al. (2011) suggest that improvements in hunting, gathering, food-processing techniques, and other cognitive capacities supplied opportunities for subsistence and dispersal during latter part of the early to early middle Pleistocene interglacials. They suggest that technological innovation occurred along with unfavorable conditions, high seasonality, and low levels of habitat variability because in stable environmental conditions hominins could rely on traditional subsistence strategies rather than develop technological innovations, as Moncel (2010) also defends. Our results show more favorable conditions for secondary consumers during 0.8–0.5 Ma than 1.1–0.8 Ma. The earliest European Mode 2 appears in Barranc de la Boella (Spain) at approximately 1.0 Ma (Vallverdú et al., 2014), but Mode 1 remained in Europe at

least until around 0.61 Ma at Isernia La Pineta (Italy) (Coltorti et al., 2005; Peretto, 2006; Mosquera et al., 2013). Under the premise that hostile environments promote technological innovation, and assuming that the European Acheulean could be a local innovation, it would be expected to appear during a period of high intraguild competition. Interestingly, intraguild competition was high during the latter part of the early Pleistocene, when the late Mode 1 or early Mode 2 industries appeared (Scott and Gibert, 2009; Barsky and de Lumley, 2010; Santonja and Pérez-González, 2010; Barsky et al., 2013; Moncel et al., 2013; Mosquera et al., 2013; Walker et al., 2013; Vallverdú et al., 2014). If the human occupation of Europe was continuous from 1.0 to 0.5 Ma, these pre-Mode 2 technologies would be progressively developed into a full Mode 2 from 0.8 to 0.5 Ma, a period of moderate intraguild competition. The lithic complex from Barranc de la Boella might be a good candidate to represent an initial stage in the progressive development of the European Mode 2, although Mosquera et al. (2016) suggest that it was actually a dead line, based on the apparent archaeological gap that occurred in Europe between 0.9 and 0.6 Ma. According to that interpretation, those first stages of the European Acheulean would be unsuccessful in providing significant survival advantages to those populations, and only the appearance of the full Acheulean around 0.5 Ma would represent a real step forward. Otherwise, if the Acheulean evolved locally during the Middle Pleistocene, it was not triggered by harsh environmental conditions, at least with reference to intraguild competition. Finally, if the Acheulean arrived in Europe from overseas, as claimed by several scholars (e.g., Carbonell et al., 1999, 2010; Santonja and Pérez-González, 2010; Jiménez-Arenas et al., 2011), its appearance had nothing to do with the variations in intraguild competition. As an example, Carbonell et al. (2010) defend that the expansion of the Acheulean across Europe was because of a demographic increase in the Near East and Africa. To date, current knowledge of the European bifacial technology does not clarify the arguments in favor of a phenomenon from an African origin or in favor of a local substratum (Moncel et al., 2016b). The debate is still open. In any case, it is beyond the scope of this article to support any of the three possible scenarios; our intention here is only to provide an environmental background to them.

The results in the present study are in disagreement with those presented in Rodríguez-Gómez et al. (2014b). Applying the same methodology, it was shown that at the local scale, the depopulation of the Sierra de Atapuerca area by ~0.6 Ma coincided with a relatively high intraguild competition (Rodríguez-Gómez et al., 2014b). Studies at a local scale may provide information about the evolution of faunal assemblages in the long term, but analyses at the continental scale focus on average paleocommunities. An average is a simplification, so there is a loss of information when it is applied to obtain a global perspective. From the continental point of view, competition does not appear to be a relevant factor to limit human presence in the early middle Pleistocene. Combined analyses are desirable to help track the changes in intraguild competition both at the continental and local scales, although unfortunately,

there are few local sequences like Atapuerca that are long enough to apply this approach.

This study addresses the constraints imposed by the communities of large mammals to the human presence in the European Pleistocene from a paleoecological point of view. We aimed to describe with precision the role of humans in the paleocommunities of the studied period. However, to understand human behavior during the MPR, it is not enough to know the limitations imposed on them by the availability of trophic resources. To obtain a more accurate view of the human niche in this period, it will be necessary to improve our knowledge of the interactions between species and/or food web structure in the paleocommunities.

CONCLUSION

Measurement of the intensity of intraguild competition as a limiting factor in human expansion across Europe tests whether the apparently scarce human presence at the beginning of the middle Pleistocene could be attributable to this factor. Our results show that competition intensity was higher in the latter part of the early Pleistocene LFAs than in the middle Pleistocene LFAs. This decrease in the intensity of competition inside the guild of secondary consumers parallels a decrease in human presence across Europe; the more abundant evidence of human presence is observed in our sample for the latter part of the early Pleistocene, and it is particularly scarce for the early part of the middle Pleistocene. Surprisingly, this decrease in human presence coincided, at the European scale, with a period of more favorable conditions from the point of view of competition for meat resources. Thus, it could be concluded that competition with carnivores was not the main cause of the apparent crisis suffered by human populations at the beginning of the middle Pleistocene, although the ecological interactions and the intensity of competition show a marked variation from the latter part of the early Pleistocene to the latter part of the middle Pleistocene. Humans were not present where competition intensities were the highest but showed a great adaptation capacity, being present in paleoecosystems with widely different levels of intraguild competition intensities. Remarkably, the niche of *Homo* in the early Pleistocene paleoecosystems did not completely overlap with that of any other genus, because the complete exclusion between *Homo* and another genus of secondary consumer was not observed. The analyses presented here, focused at a continental scale, suggest different conclusions than the analyses carried out at a local scale. Thus, future research should combine both scales of analyses to obtain a more comprehensive view of what seems to be a complex pattern. Moreover, a better knowledge of the role of *Homo* in the Pleistocene ecosystems could be obtained by delving into the structure of the paleocommunities and the relationships among the species included in them.

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Supplementary material

To view supplementary material for this article, please visit <https://doi.org/10.1017/qua.2017.20>

REFERENCES

- Agustí, J., Blain, H.-A., Cuenca-Bescós, G., Bailon, S., 2009. Climate forcing of first hominid dispersal in western Europe. *Journal of Human Evolution* 57, 815–821.
- Alberdi, M.T., Prado, J.L., Ortiz-Jaureguizar, E., 1995. Patterns of body size changes in fossil and living Equini (Perissodactyla). *Biological Journal of the Linnean Society* 54, 349–370.
- Antón, M., Galobart, A., Turner, A., 2005. Co-existence of scimitar-toothed cats, lions and hominins in the European Pleistocene. Implications of the post-cranial anatomy of *Homotherium latidens* (Owen) for comparative palaeoecology. *Quaternary Science Reviews* 24, 1287–1301.
- Antón, M., Salesa, M.J., Galobart, A., Tseng, Z.J., 2014. The Plio-Pleistocene scimitar-toothed felid genus *Homotherium* Fabrini, 1890 (Machairodontinae, Homotherini): diversity, palaeogeography and taxonomic implications. *Quaternary Science Reviews* 96, 259–268.
- Arribas, A., Jordá, J.F., 1999. Los mamíferos del Cuaternario kárstico de Guadalajara (Castilla - La Mancha, España). In: Aguirre, E., Rábano, I. (Eds.), *La Huella del Pasado. Fósiles de Castilla-La Mancha. Patrimonio Histórico. Arqueología Castilla-La Mancha*. Junta de Comunidades, Toledo, Spain, pp. 327–353.
- Arribas, A., Palmqvist, P., 1999. On the ecological connection between sabre-tooths and hominids: faunal dispersal events in the Lower Pleistocene and a review of the evidence for the first human arrival in Europe. *Journal of Archaeological Science* 26, 571–585.
- Arsuaga, J.L., Carretero, J.-M., Lorenzo, C., Gómez-Olivencia, A., Pablos, A., Rodríguez, L., García-González, R., et al., 2015. Postcranial morphology of the middle Pleistocene humans from Sima de los Huesos, Spain. *Proceedings of the National Academy of Sciences of the United States of America* 12, 11524–11529.
- Ashton, N., McNabb, J., Irving, B., Lewis, S., Parfitt, S., 1994. Contemporaneity of Clactonian and Acheulian flint industries at Barnham, Suffolk. *Antiquity* 68, 585–589.

- Athanassiou, A., 2003. *Gazellospira toriticornis* (Aymard, 1854) from the Late Pliocene locality of Sésklo (Thessaly, Greece). *Quaternaire Hors-Série 2*, 137–144.
- Auguste, P., 2009. Évolution des peuplements mammaliens en Europe de Nord-Ouest durant le Pleistocène moyen et Supérieur. Le cas de la France Septentrionale. *Quaternaire 20*, 527–550.
- Azanza, B., Palombo, M.R., Alberdi, M.T., 2004. Large mammal turnover pulses and palaeoclimate changes from the Miocene to the Late Pleistocene in Italy. *Rivista Italiana di Paleontologia e Stratigrafia 110*, 531–545.
- Barbato, L.C., Gliozzi, E., 1995. Biochronological and palaeogeographical implications of a well-balanced late Middle Pleistocene fauna from Quisisana-Certosa (Capri, Southern Italy). *Bollettino della Società Paleontologica Italiana 34*, 235–261.
- Barbera, C., Petronio, C., Biblia, E., Virgili, A., Candeloro, M., Zarlunga, F., 1995. Short report on Pleistocene fauna from Grotta Lina (Marina di Maratea, southern Italy): palaeoecological and geochronological implications. *Bollettino della Società Paleontologica Italiana 34*, 341–350.
- Barsky, D., de Lumley, H., 2010. Early European Mode 2 and the stone industry from the Caune de l'Arago's archeostratigraphical levels "P." *Quaternary International 223–224*, 71–86.
- Barsky, D., Garcia, J., Martínez, K., Sala, R., Zaidner, Y., Carbonell, E., Toro-Moyano, I., 2013. Flake modification in European Early and Early–Middle Pleistocene stone tool assemblages. *Quaternary International 316*, 140–154.
- Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science 312*, 431–433.
- Bermúdez de Castro, J.M., Díez Fernández-Lomana, J.C., Mosquera Martínez, M., Nicolás Checa, M.E., Pérez Pérez, A., Rodríguez Méndez, J., Sánchez Marco, A., 1995. El nicho ecológico de los homínidos del Pleistoceno Medio de Atapuerca. *Complutum 6*, 9–56.
- Bermúdez de Castro, J.M., Martínón-Torres, M., Blasco, R., Rosell, J., Carbonell, E., 2013. Continuity or discontinuity in the European Early Pleistocene human settlement: the Atapuerca evidence. *Quaternary Science Reviews 76*, 53–65.
- Bermúdez de Castro, J.M., Martínón-Torres, M., Rosell, J., Blasco, R., Arsuaga, J.L., Carbonell, E., 2016. Continuity versus discontinuity of the human settlement of Europe between the late Early Pleistocene and the early Middle Pleistocene. The mandibular evidence. *Quaternary Science Reviews 153*, 51–62.
- Binford, L.R., 1981. *Bones. Ancient Men and Modern Myths*. Academic Press, Orlando, FL.
- Binford, L.R., 1985. Human ancestors: changing views of their behavior. *Journal of Anthropological Archaeology 4*, 292–327.
- Binford, L.R., 2001. *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Ethnographic and Environmental Data Sets*. University of California Press, Berkeley.
- Blasco, R., Rosell, J., Fernández Peris, J., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). *Quaternary Science Reviews 70*, 124–144.
- Breda, M., Marchetti, M., 2005. Systematical and biochronological review of Plio-Pleistocene Alceini (Cervidae; Mammalia) from Eurasia. *Quaternary Science Reviews 24*, 775–805.
- Brugal, J.-P., Fosse, P., 2004. Carnivores et Hommes au Quaternaire en Europe de l'Ouest. *Revue de Paléobiologie, Genève 23*, 575–595.
- Bunn, H.T., Ezzo, J.A., 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. *Journal of Archaeological Science 20*, 365–398.
- Bunn, H.T., Pickering, T.R., 2010. Bovid mortality profiles in paleoecological context falsify hypotheses of endurance running-hunting and passive scavenging by early Pleistocene hominins. *Quaternary Research 74*, 395–404.
- Carbone, C., Mace, G.M., Roberts, S.C., Macdonald, D.W., 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature 402*, 286–288.
- Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., et al., 2008. The first hominin of Europe. *Nature 452*, 465–469.
- Carbonell, E., Mosquera, M., Rodríguez, X.P., Sala, R., Made, J.v.d., 1999. Out of Africa: the dispersal of the earliest technical systems reconsidered. *Journal of Anthropological Archaeology 18*, 119–136.
- Carbonell, E., Sala Ramos, R., Rodríguez, X.P., Mosquera, M., Ollé, A., Vergès, J.M., Martínez-Navarro, B., Bermúdez de Castro, J.M., 2010. Early hominid dispersals: a technological hypothesis for "out of Africa." *Quaternary International 223–224*, 36–44.
- Carotenuto, F., 2009. The Plio-Holocene Large Mammals of the Western Eurasia: Macroecological and Evolutionary Analyses of the Faunas. PhD dissertation, Università degli studi di Napoli Federico II, Naples, Italy.
- Carotenuto, F., Tsikaridze, N., Rook, L., Lordkipanidze, D., Longo, L., Condemi, S., Raia, P., 2016. Venturing out safely: the biogeography of *Homo erectus* dispersal out of Africa. *Journal of Human Evolution 95*, 1–12.
- Carrión, J.S., Rose, J., Stringer, C.B., 2011. Early human evolution in the western Palaearctic: ecological scenarios. *Quaternary Science Reviews 30*, 1281–1295.
- Collinge, S.E., 2001. *Body Size and Community Structure in British Pleistocene Mammals*. University of London, London.
- Coltorti, M., Feraud, G., Marzoli, A., Peretto, C., Ton-That, T., Voinchet, P., Bahain, J.-J., Minelli, A., Thun-Hohenstein, U., 2005. New ⁴⁰Ar/³⁹Ar, stratigraphic and palaeoclimatic data on the Isernia La Pineta Lower Palaeolithic site, Molise, Italy. *Quaternary International 131*, 11–22.
- Cordain, L., Miller, J.B., Eaton, S.B., Mann, N., Holt, S.H., Speth, J.D., 2000. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *American Journal of Clinical Nutrition 71*, 682–692.
- Crégut-Bonnoure, E., Dimitrijevic, V., 2006. *Megalovis balcanicus* sp. nov. and *Soergelia intermedia* sp. nov. (Mammalia, Bovidae, Caprinae), new Ovisovini from the Early Pleistocene of Europe. *Revue de Paléobiologie, Genève 25*, 723–773.
- Crégut-Bonnoure, E., Spassov, N., 2002. *Hemitragus orientalis* nov. sp. (Mammalia, Bovidae, Caprinae), un nouveau taxon d'Europe orientale. *Revue de Paléobiologie, Genève 21*, 553–573.
- Crégut-Bonnoure, E., Tsoukala, E., 2005. The Pleistocene bovids from the Petralona Cave (Macedonia, Greece): new interpretations and biogeographical implications. In: Crégut-Bonnoure, E. (Ed.), *Les ongulés holarctiques du Pliocène et du Pléistocène*. Maison de la géologie, Paris, pp. 161–178.

- Croitor, R., Brugal, J.-P., 2007. New insights concerning Early Pleistocene cervids and bovids in Europe: dispersal and correlation. In: Kahlke, R.-D., Maul, L.C., Mazza, P.P.A. (Eds.), *Late Neogene and Quaternary Biodiversity and Evolution: Regional Developments and Interregional Correlations*. Courier Forschungsinstitut Senckenberg, 259. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany, pp. 47–59.
- Croitor, R., Brugal, J.-P., 2010. Ecological and evolutionary dynamics of the carnivore community in Europe during the last 3 million years. *Quaternary International* 212, 98–108.
- Cuenca-Bescós, G., Rofes, J., García-Pimienta, J.C., 2005. Early Europeans and environmental change across the Early–Middle Pleistocene transition: small mammalian evidence from Trinchera Dolina cave, Atapuerca, Spain. In: Head, M.J., Gibbard, P.L. (Eds.), *Early–Middle Pleistocene Transitions: The Land–Ocean Evidence*. Geological Society, London, pp. 277–286.
- Damuth, J., 1981. Population density and body size in mammals. *Nature* 290, 699–700.
- Damuth, J., 1993. Cope's rule, the island rule and the scaling of mammalian population density. *Nature* 365, 748–750.
- Daujeard, C., Moncel, M.-H., 2010. On Neanderthal subsistence strategies and land use: a regional focus on the Rhone Valley area in southeastern France. *Journal of Anthropological Archaeology* 29, 368–391.
- de Lumley, H., Kahlke, H.-D., Moigne, A.-M., Moulle, P.-E., 1988. Les faunes de grands mammifères de la grotte du Vallonet, Roquebrune-Cap-Martin, Alpes-Maritimes. *L'Anthropologie* 92, 465–495.
- Díez, J.C., Fernández-Jalvo, Y., Rosell, J., Cáceres, I., 1999. Zooarchaeology and taphonomy of Aurora Stratum (Gran Dolina, Sierra de Atapuerca, Spain). *Journal of Human Evolution* 37, 623–652.
- Domínguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Baquedano, E., Uribealarea, D., Pérez-González, A., Gidna, A., et al., 2014. On meat eating and human evolution: a taphonomic analysis of BK4b (Upper Bed II, Olduvai Gorge, Tanzania), and its bearing on hominin megafaunal consumption. *Quaternary International* 322–323, 129–152.
- Doronichev, V., Golovanova, L., 2010. Beyond the Acheulean: a view on the Lower Paleolithic occupation of western Eurasia. *Quaternary International* 223–224, 327–344.
- Espigares, M.P., Martínez-Navarro, B., Palmqvist, P., Ros-Montoya, S., Toro, I., Agustí, J., Sala, R., 2013. *Homo* vs. *Pachyrocata*: earliest evidence of competition for an elephant carcass between scavengers at Fuente Nueva-3 (Orce, Spain). *Quaternary International* 295, 113–125.
- Fariña, R.A., 1996. Trophic relationships among Lujanian mammals. *Evolutionary Theory* 11, 125–134.
- Farlow, J.O., 1976. A consideration of the trophic dynamics of a Late Cretaceous large-dinosaur community (Oldman Formation). *Ecology* 57, 841–857.
- Feranec, R., García, N., Díez, J.C., Arsuaga, J.L., 2010. Understanding the ecology of mammalian carnivores and herbivores from Valdegoba cave (Burgos, northern Spain) through stable isotope analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 297, 263–272.
- Fostowicz-Frelik, Ł., 2008. First record of *Trogontherium cuvieri* (Mammalia, Rodentia) from the middle Pleistocene of Poland and review of the species. *Geodiversitas* 30, 765–778.
- Frank, C., Rabeder, G., 1998. Hundsheim. In: Döppes, D., Rabeder, G. (Eds.), *Pliozäne und pleistozäne Faunen Österreichs. Mitteilungen der Kommission für Quartärforschung*. Verlag der Österreichischen Akademie der Wissenschaften, Vienna, pp. 270–274.
- García, J., Landeck, G., Martínez, K., Carbonell, E., 2013. Hominin dispersals from the Jaramillo subchron in central and south-western Europe: Untermassfeld (Germany) and Vallparadís (Spain). *Quaternary International* 316, 73–93.
- García, J., Martínez, K., Carbonell, E., 2011. Continuity of the first human occupation in the Iberian Peninsula: closing the archaeological gap. *Comptes Rendus Palevol* 10, 279–284.
- Gaudzinski, S., Roebroeks, W., 2000. Adults only. Reindeer hunting at the Middle Palaeolithic site Salzgitter Lebenstedt, northern Germany. *Journal of Human Evolution* 38, 497–521.
- Guadelli, J.L., Sirakov, N., Ivanova, S.T., Sirakova, S.V., Anastassova, E., Courtaud, P., Dimitrova, I., et al., 2005. Une séquence du paléolithique inférieur au paléolithique récent dans les Balkans: la grotte Kozamika à Orechets (Nord-Ouest de la Bulgarie). In: Molines, N., Moncel, M.H., Monnier, J.L. (Eds.), *Les premiers peuplements en Europe*. British Archaeological Reports International Series, 1364. John and Erica Hedges, Oxford, UK, pp. 87–103.
- Hardy, K., Radini, A., Buckley, S., Blasco, R., Copeland, L., Burjachs, F., Girbal, J., Yll, R., Carbonell, E., Bermúdez de Castro, J.M., 2017. Diet and environment 1.2 million years ago revealed through analysis of dental calculus from Europe's oldest hominin at Sima del Elefante, Spain. *Science of Nature* 104, 2. <http://dx.doi.org/10.1007/s00114-016-1420-x>.
- Huguet, R., Saladié, P., Cáceres, I., Díez, C., Rosell, J., Bennàsar, M., Blasco, R., et al., 2013. Successful subsistence strategies of the first humans in south-western Europe. *Quaternary International* 295, 168–182.
- Jenike, M.R., 2001. Nutritional ecology: diet, physical activity and body size. In: Panter-Brick, C., Layton, R.H., Rowley-Conwy, P. (Eds.), *Hunter-Gatherers: An Interdisciplinary Perspective*. Cambridge University Press, Cambridge, pp. 205–238.
- Jiménez-Arenas, J.M., Pérez-Claros, J.A., Aledo, J.C., Palmqvist, P., 2014. On the relationships of postcanine tooth size with dietary quality and brain volume in primates: implications for hominin evolution. *BioMed Research International* 2014, 406507. <http://dx.doi.org/10.1155/2014/406507>.
- Jiménez-Arenas, J.M., Santonja, M., Botella, M., Palmqvist, P., 2011. The oldest handaxes in Europe: fact or artefact? *Journal of Archaeological Science* 38, 3340–3349.
- Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., et al., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90, 2648.
- Kahlke, R.-D., García, N., Kostopoulos, D.S., Lacombe, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Western Palaeartic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. *Quaternary Science Reviews* 30, 1368–1395.
- Kahlke, R.-D., Gaudzinski, S., 2005. The blessing of a great flood: differentiation of mortality patterns in the large mammal record of the Lower Pleistocene fluvial site of Untermassfeld (Germany) and its relevance for the interpretation of faunal assemblages from archaeological sites. *Journal of Archaeological Science* 32, 1202–1222.
- Koenigswald, W.V., Heinrich, W.-D., 1999. Mittelpleistozäne Säugetierfaunen Mitteleuropas - der Versuch einer biostratigraphischen Zuordnung. *Kaupia* 9, 53–112.
- Koufos, G.D., Kostopoulos, D.S., Sylvestrou, I.A., 1997. *Equus apolloniensis* n. sp. (Mammalia, Equidae) from the latest Villafranchian locality of Apollonia, Macedonia, Greece. *Paleontologica i evolució* 30–31, 49–76.

- Laurenson, M.K., Wielebnowski, N., Caro, T.M., 1995. Extrinsic factors and juvenile mortality in cheetahs. *Conservation Biology* 9, 1329–1331.
- Leonard, W.R., Robertson, M.L., Snodgrass, J.J., 2007. Energetic models of human nutritional evolution. In: Ungar, P.S. (Ed.), *Evolution of the Human Diet. The Known, the Unknown, and the Unknowable. Human Evolution Series*. Oxford University Press, Oxford, pp. 344–359.
- Leslie, P.H., 1945. On the use of matrices in certain population mathematics. *Biometrika* 33, 183–212.
- Leslie, P.H., 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 35, 213–245.
- Lister, A.M., Stuart, A.J., 2010. The West Runton mammoth (*Mammuthus trogontherii*) and its evolutionary significance. *Quaternary International* 228, 180–209.
- Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C.P.E., Rightmire, G.P., Pontzer, H., et al., 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449, 305–310.
- Lozano, S., Mateos, A., Rodríguez, J., 2016. Exploring paleo food-webs in the European Early and Middle Pleistocene: a network analysis. *Quaternary International* 413, 44–54.
- Made, J.v.d., 1998. A preliminary note on the cervids from Bilzingsleben. *Praehistoria Thuringica* 2, 108–122.
- Made, J.v.d., Mateos, A., 2010. Longstanding biogeographic patterns and the dispersal of early *Homo* out of Africa and into Europe. *Quaternary International* 223–224, 195–200.
- Made, J.v.d., Stefaniak, K., Marciszak, A., 2014. The Polish fossil record of the wolf *Canis* and the deer *Alces*, *Capreolus*, *Megaloceros*, *Dama* and *Cervus* in an evolutionary perspective. *Quaternary International* 326–327, 406–430.
- Madurell-Malapeira, J., Alba, D.M., Minwer-Barakat, R., Aurell-Garrido, J., Moyà-Solà, S., 2012. Early human dispersals into the Iberian Peninsula: a comment on Martínez et al. (2010) and Garcia et al. (2011). *Journal of Human Evolution* 62, 169–173.
- Madurell-Malapeira, J., Alba, D.M., Moyà-Solà, S., Aurell-Garrido, J., 2010a. The Iberian record of the puma-like cat *Puma pardoides* (Owen, 1846) (Carnivora, Felidae). *Comptes Rendus Palevol* 9, 55–62.
- Madurell-Malapeira, J., Minwer-Barakat, R., Alba, D.M., Garcés, M., Gómez, M., Aurell-Garrido, J., Ros-Montoya, S., Moyà-Solà, S., Berástegui, X., 2010b. The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe. *Quaternary Science Reviews* 29, 3972–3982.
- Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Alba, D.M., Aurell-Garrido, J., 2014. Villafranchian large mammals from the Iberian Peninsula: paleobiogeography, paleoecology and dispersal events. *Journal of Iberian Geology* 40, 167–178.
- Mania, D., Vlcek, E., 1999. The Bilzingsleben site: *Homo erectus*, his culture and his ecosphere. In: Ullrich, H. (Ed.), *Hominid Evolution: Lifestyles and Survival Strategies*. Archaea, Gelsenkirchen, Germany, pp. 293–314.
- Mann, N.J., 2000. Dietary red meat and human evolution. *European Journal of Nutrition* 39, 71–79.
- Manzi, G., Magri, D., Palombo, M.R., 2011. Early–Middle Pleistocene environmental changes and human evolution in the Italian peninsula. *Quaternary Science Reviews* 30, 1420–1438.
- Marean, C.W., 1989. Sabertooth cats and their relevance for early hominid diet and evolution. *Journal of Human Evolution* 18, 559–582.
- Martínez, K., Garcia, J., Carbonell, E., Agustí, J., Bahain, J.-J., Blain, H.-A., Burjachs, F., et al., 2010. A new Lower Pleistocene archeological site in Europe (Vallparadís, Barcelona, Spain). *Proceedings of the National Academy of Sciences of the United States of America* 107, 5762–5767.
- Martínez Navarro, B., 1992. Estudio cuantitativo y consideraciones paleoecológicas de la comunidad de mamíferos del yacimiento de Venta Micena (Orce, Granada). In: Gibber, J. (Ed.), *Presencia humana en el Pleistoceno inferior de Granada y Murcia*. Museo de Prehistoria José Gibert, Orce, Granada, Spain, pp. 155–188.
- Martínez-Navarro, B., Palmqvist, P., 1995. Presence of the African Machairodont *Megantereon whitei* (Broom, 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. *Journal of Archaeological Science* 22, 569–582.
- Martínez-Navarro, B., Palmqvist, P., 1996. Presence of the African saber-toothed felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) in Apollonia-1 (Mygdonia Basin, Macedonia, Greece). *Journal of Archaeological Science* 23, 869–872.
- Maslin, M.A., Ridgwell, P.L., 2005. Mid-Pleistocene revolution and the “eccentricity myth.” In: Head, M.J., Gibbard, E.L. (Eds.), *Early–Middle Pleistocene Transitions: The Land–Ocean Evidence*. Geological Society, London, pp. 19–34.
- McNabb, J., 2007. 1.9 MYR–300,000 years ago in Europe. In: Elias, S.A., (Ed.), *Encyclopedia of Quaternary Science*. Elsevier, Amsterdam, pp. 89–98.
- Meloro, C., 2011a. Locomotor adaptations in Plio-Pleistocene large carnivores from the Italian peninsula: palaeoecological implications. *Current Zoology* 57, 269–283.
- Meloro, C., 2011b. Morphological disparity in Plio-Pleistocene large carnivore guilds from Italian peninsula. *Acta Palaeontologica Polonica* 56, 33–44.
- Meloro, C., Clauss, M., 2012. Predator-prey biomass fluctuations in the Plio-Pleistocene. *Society for Sedimentary Geology* 27, 90–96.
- Meloro, C., Kovarovic, K., 2013. Spatial and ecometric analyses of the Plio-Pleistocene large mammal communities of the Italian peninsula. *Journal of Biogeography* 40, 1451–1462.
- Meloro, C., Raia, P., Barbera, C., 2007. Effect of predation on prey abundance and survival in Plio-Pleistocene mammalian communities. *Evolutionary Ecology Research* 9, 505–525.
- Mills, M.G.L., Gorman, M.L., 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conservation Biology* 11, 1397–1406.
- Moncel, M.-H., 2010. Oldest human expansions in Eurasia: favouring and limiting factors. *Quaternary International* 223–224, 1–9.
- Moncel, M.-H., Arzarello, M., Boëda, É., Bonilauri, S., Chevrier, B., Gaillard, C., Forestier, H., Yinghua, L., Sémah, F., Zeitoun, V., 2016a. The assemblages with bifacial tools in Eurasia (first part). What is going on in the West? Data on western and southern Europe and the Levant. *Comptes Rendus Palevol* (in press). <http://dx.doi.org/10.1016/j.crpv.2015.09.009>.
- Moncel, M.-H., Arzarello, M., Boëda, É., Bonilauri, S., Chevrier, B., Gaillard, C., Forestier, H., Yinghua, L., Sémah, F., Zeitoun, V., 2016b. Assemblages with bifacial tools in Eurasia (third part). Considerations on the bifacial phenomenon throughout Eurasia. *Comptes Rendus Palevol* (in press). <http://dx.doi.org/10.1016/j.crpv.2015.11.007>.
- Moncel, M.-H., Despriée, J., Voinchet, P., Courcimault, G., Hardy, B., Bahain, J.-J., Puaud, S., Gallet, X., Falguères, C., 2016c. The Acheulean workshop of la Noira (France, 700 ka) in the European technological context. *Quaternary International* 393, 112–136.

- Moncel, M.-H., Despriée, J., Voinchet, P., Tissoux, H., Moreno, D., Bahain, J.-J., Courcimault, G., Falguères, C., 2013. Early evidence of Acheulean settlement in northwestern Europe - La Noira Site, a 700 000 year-old occupation in the center of France. *PLoS ONE* 8, e75529. <https://doi.org/10.1371/journal.pone.0075529>.
- Moncel, M.-H., Moigne, A.-M., Combier, J., 2005. Pre-Neandertal behaviour during isotopic stage 9 and the beginning of stage 8. New data concerning fauna and lithics in the different occupation levels of Ornac 3 (Ardèche, south-east France): occupation types. *Journal of Archaeological Science* 32, 1283–1301.
- Montuire, S., Marcolini, F., 2002. Palaeoenvironmental significance of the mammalian faunas of Italy since the Pliocene. *Journal of Quaternary Science* 17, 87–96.
- Mosquera, M., Ollé, A., Rodríguez, X.P., 2013. From Atapuerca to Europe: tracing the earliest peopling of Europe. *Quaternary International* 295, 130–137.
- Mosquera, M., Ollé, A., Saladié, P., Cáceres, I., Huguet, R., Rosas, A., Villalaín, J., et al., 2016. The Early Acheulean technology of Barranc de la Boella (Catalonia, Spain). *Quaternary International* 393, 95–111.
- Muttoni, G., Kent, D.V., Scardia, G., Martin, R.A., 2015. Bottleneck at Jaramillo for human migration to Iberia and the rest of Europe? *Journal of Human Evolution* 80, 7–190.
- Muttoni, G., Scardia, G., Kent, D.V., 2010. Human migration into Europe during the late Early Pleistocene climate transition. *Palaeogeography, Palaeoclimatology, Palaeoecology* 296, 79–93.
- Nowak, R.M., 1999. *Walker's Mammals of the World*. Johns Hopkins University Press, Baltimore, MD.
- Ollé, A., Mosquera, M., Rodríguez, X.P., Lombera-Hermida, A., de García-Antón, M.D., García-Medrano, P., Peña, L., et al., 2013. The Early and Middle Pleistocene technological record from Sierra de Atapuerca (Burgos, Spain). *Quaternary International* 295, 138–167.
- O'Regan, H.J., 2008. The Iberian Peninsula – corridor or cul-de-sac? Mammalian faunal change and possible routes of dispersal in the last 2 million years. *Quaternary Science Reviews* 27, 2136–2144.
- O'Regan, H.J., Turner, A., Bishop, L.C., Lamb, A.L., 2011. Hominins without fellow travellers? First appearances and inferred dispersals of Afro-Eurasian large-mammals in the Plio-Pleistocene. *Quaternary Science Reviews* 30, 1343–1352.
- Owen-Smith, N., 2010. *Dynamics of Large Herbivore Populations in Changing Environments: Towards Appropriate Models*. Blackwell, Chichester, West Sussex, UK.
- Palmqvist, P., Gröcke, D.R., Arribas, A., Fariña, R.A., 2003. Paleoeological reconstruction of a lower Pleistocene large mammal community using biogeochemical ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{18}\text{O}$, Sr: Zn) and ecomorphological approaches. *Paleobiology* 29, 205–229.
- Palmqvist, P., Martínez-Navarro, B., Arribas, A., 1996. Prey selection by terrestrial carnivores in a Lower Pleistocene paleocommunity. *Paleobiology* 22, 514–534.
- Palmqvist, P., Martínez-Navarro, B., Pérez-Claros, J.A., Torregrosa, V., Figueirido, B., Jiménez-Arenas, J.M., Espigares, M.P., Ros-Montoya, S., De Renzi, M., 2011. The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking behavior of an extinct carnivore. *Quaternary International* 243, 61–79.
- Palmqvist, P., Martínez-Navarro, B., Toro, I., Espigares, M.P., Ros-Montoya, S., Torregrosa, V., Pérez-Claros, J.A., 2005. Réévaluation de la présence humaine au Pléistocène inférieur dans le Sud de l'Espagne [A re-evaluation of the evidence of human presence during Early Pleistocene times in southeastern Spain]. *L'Anthropologie* 109, 411–450.
- Palmqvist, P., Pérez-Claros, J.A., Janis, C.M., Gröcke, D.R., 2008. Tracing the ecophysiology of ungulates and predator–prey relationships in an early Pleistocene large mammal community. *Palaeogeography, Palaeoclimatology, Palaeoecology* 266, 95–111.
- Palmqvist, P., Torregrosa, V., Pérez-Claros, J.A., Martínez-Navarro, B., Turner, A., 2007. A re-evaluation of the diversity of *Megantereon* (Mammalia, Carnivora, Machairodontinae) and the problem of species identification in extinct carnivores. *Journal of Vertebrate Paleontology* 27, 160–175.
- Palombo, M.R., 2007. What is the boundary for the Quaternary period and Pleistocene epoch? The contribution of turnover patterns in large mammalian complexes from north-western Mediterranean to the debate. *Quaternaire* 18, 35–53.
- Palombo, M.R., 2010. A scenario of human dispersal in the northwestern Mediterranean throughout the Early to Middle Pleistocene. *Quaternary International* 223–224, 179–194.
- Palombo, M.R., 2013. What about causal mechanisms promoting early hominin dispersal in Eurasia? A research agenda for answering a hotly debated question. *Quaternary International* 295, 13–27.
- Palombo, M.R., 2014. Deconstructing mammal dispersals and faunal dynamics in SW Europe during the Quaternary. *Quaternary Science Reviews* 96, 50–71.
- Palombo, M.R., 2016. To what extent could functional diversity be a useful tool in inferring ecosystem responses to past climate changes? *Quaternary International* 413, 15–31.
- Palombo, M.R., Azanza, B., Alberdi, M.T., 2000–2002. Italian mammal biochronology from the latest Miocene to the Middle Pleistocene: a multivariate approach. *Geologica Romana* 36, 335–368.
- Palombo, M.R., Milli, S., Rosa, C., 2003–2004. Remarks on the biochronology of the late Middle Pleistocene mammalian faunal complexes of the Campagna Romana (Latium, Italy). *Geologica Romana* 37, 135–143.
- Palombo, M.R., Mussi, M., 2006. Large mammal guilds at the time of the first human colonization of Europe: the case of the Italian Pleistocene record. *Quaternary International* 149, 94–103.
- Palombo, M.R., Valli, A.M.F., Kostopoulos, D.S., Alberdi, M.T., Spassov, N., Vislobokova, I., 2006. Similarity relationships between the Pliocene to middle Pleistocene large mammal faunas of southern Europe from Spain to the Balkans and the north Pontic region. In: Kahlke, R.-D., Maul, L.C., Mazza, P.P.A. (Eds.), *Late Neogene and Quaternary Biodiversity and Evolution: Regional Developments and Interregional Correlations*. Courier Forschungsinstitut Senckenberg, 256. E. Schweizerbart-Gesellschaft Senckenberg, M. Stuttgart, Germany, pp. 392–347.
- Peretto, C., 2006. The first peopling of southern Europe: the Italian case. *Comptes Rendus Palevol* 5, 283–290.
- Pérez-Claros, J.A., Jiménez-Arenas, J.M., Palmqvist, P., 2015. Neurocranium versus face: a morphometric approach with classical anthropometric variables for characterizing patterns of cranial integration in extant hominoids and extinct hominins. *PLoS ONE* 10, e0131055. <https://doi.org/10.1371/journal.pone.0131055>.
- Prado, J.L., Alberdi, M.T., Azanza, B., Rodríguez, J., 2004. Patterns of body-size change in large mammals during the Late Cenozoic in the northwestern Mediterranean. *Paleontología: Miscelánea en homenaje a Emiliano Aguirre* 2, 467–479.

- Prado-Nóvoa, O., Mateos, A., Zorrilla-Revilla, G., Vidal-Cordasco, M., Rodríguez, J., 2017. Efficiency of gathering and its archaeological implications for an European Early Paleolithic population. *Journal of Anthropological Archaeology* 45, 131–141.
- Prevosti, F.J., Vizcaíno, S.F., 2006. Paleoecology of the large carnivore guild from the late Pleistocene of Argentina. *Acta Palaeontologica Polonica* 51, 407–422.
- Raia, P., Carotenuto, F., Meloro, C., Piras, P., Barbera, C., Kotsakis, T., 2009. More than three million years of community evolution. The temporal and geographical resolution of the Plio-Pleistocene western Eurasia mammal faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 276, 15–23.
- Raia, P., Meloro, C., Barbera, C., 2007. Inconstancy in predator/prey ratios in Quaternary large mammal communities of Italy, with an appraisal of mechanisms. *Quaternary Research* 67, 255–263.
- Raia, P., Piras, P., Kotsakis, T., 2005. Turnover pulse or Red Queen? Evidence from the large mammal communities during the Plio-Pleistocene of Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 221, 293–312.
- Ricklefs, R.E., 2010. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proceedings of the National Academy of Sciences of the United States of America* 107, 1265–1272.
- Roberts, M.B., Parfitt, S.A., 2000. Boxgrove: a Middle Pleistocene hominid site at Earham Quarry, Boxgrove, West Sussex. *Geoarchaeology* 15, 819–822.
- Rodríguez, J., 1997. Análisis de la estructura de las comunidades de mamíferos del Pleistoceno de la Sierra de Atapuerca. Revisión de metodologías. PhD dissertation, Universidad Autónoma de Madrid, Madrid.
- Rodríguez, J., Alberdi, M.T., Azanza, B., Prado, J.L., 2004. Body size structure in north-western Mediterranean Plio-Pleistocene mammalian faunas. *Global Ecology and Biogeography* 13, 163–176.
- Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., Made, J.v.d., Pérez González, A., Blain, H.-A., et al., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). *Quaternary Science Reviews* 30, 1396–1412.
- Rodríguez, J., Mateos, A., Martín-González, J.A., Rodríguez-Gómez, G., 2015. How rare was the human presence in Europe during the Early Pleistocene? *Quaternary International* 389, 119–130.
- Rodríguez, J., Rodríguez-Gómez, G., Martín-González, J.A., Goikoetxea, I., Mateo, A., 2012. Predator–prey relationships and the role of *Homo* in Early Pleistocene food webs in Southern Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 365–366, 99–114.
- Rodríguez-Gómez, G., Martín-González, J.A., Goikoetxea, I., Mateos, A., Rodríguez, J., 2014a. A new mathematical approach to model trophic dynamics of mammalian palaeocommunities. The case of Atapuerca-TD6. In: Pardo-Igúzquiza, E., Guardiola-Albert, C., Heredia, J., Moreno-Merino, L., Durán, J.J., Vargas-Guzmán, J.A. (Eds.), *Mathematics of Planet Earth: 15th Annual Conference of the International Association for Mathematical Geosciences. Lectures Notes in Earth System Sciences*. Springer, Madrid, pp. 739–745.
- Rodríguez-Gómez, G., Mateos, A., Martín-González, J.A., Blasco, R., Rosell, J., Rodríguez, J., 2014b. Discontinuity of human presence at Atapuerca during the early Middle Pleistocene: a matter of ecological competition? *PLoS ONE* 9, e101938. <https://doi.org/10.1371/journal.pone.0101938>.
- Rodríguez-Gómez, G., Mateos, A., Martín-González, J.A., Rodríguez, J., 2016a. Measuring intraguild competition from faunal assemblages to compare environmental conditions among paleocommunities. *Quaternary International* 413, 55–68.
- Rodríguez-Gómez, G., Palmqvist, P., Rodríguez, J., Mateos, A., Martín-González, J.A., Espigares, M.-P., Ros-Montoya, S., Martínez-Navarro, B., 2016b. On the ecological context of the earliest human settlements in Europe: resource availability and competition intensity in the carnivore guild of Barranco León-D and Fuente Nueva-3 (Orce, Baza Basin, SE Spain). *Quaternary Science Reviews* 143, 69–83.
- Rodríguez-Gómez, G., Palmqvist, P., Ros-Montoya, S., Espigares, M. P. and Martínez-Navarro, B. (2017). Resource availability and competition intensity in the carnivore guild of the Early Pleistocene site of Venta Micena (Orce, Baza Basin, SE Spain). *Quaternary Science Reviews* 164, 154–167.
- Rodríguez-Gómez, G., Rodríguez, J., Martín-González, J.A., Goikoetxea, I., Mateos, A., 2013. Modeling trophic resource availability for the first human settlers of Europe: the case of Atapuerca-TD6. *Journal of Human Evolution* 64, 645–657.
- Rodríguez-Gómez, G., Rodríguez, J., Martín-González, J.A., Mateos, A., 2017. Carnivores and humans during the Early and Middle Pleistocene at Sierra de Atapuerca. *Quaternary International* 433, 402–414.
- Rodríguez-Gómez, G., Rodríguez, J., Mateos, A., Martín-González, J.A., Goikoetxea, I., 2012. Food web structure in the European Pleistocene. *Journal of Taphonomy* 10, 165–184.
- Roebroeks, W., 2001. Hominid behaviour and the earliest occupation of Europe: an exploration. *Journal of Human Evolution* 41, 437–461.
- Saladié, P., Huguet, R., Díez, C., Rodríguez-Hidalgo, A., Cáceres, I., Vallverdú, J., Rosell, J., Bermúdez de Castro, J.M., Carbonell, E., 2011. Carcass transport decisions in *Homo antecessor* subsistence strategies. *Journal of Human Evolution* 61, 425–446.
- Santonja, M., Pérez-González, A., 2010. Mid-Pleistocene Acheulean industrial complex in the Iberian Peninsula. *Quaternary International* 223–224, 154–161.
- Schneider, S.H., Root, T.L., 1998. Impacts of climate changes on biological resources. In: Mac, M.J., Opler, P.A., Puckett Haecker, C.E., Doran, P.D. (Eds.), *Status and Trends of the Nations Biological Resources*. U.S. Department of the Interior, Reston, VA, pp. 89–116.
- Scott, G.R., Gibert, L., 2009. The oldest hand-axes in Europe. *Nature* 461, 82–85.
- Seebeck, J.H., 1978. Diet of the fox *Vulpes vulpes* in a western Victorian forest. *Austral Ecology* 3, 105–108.
- Serangeli, J., Böhner, U., Van Kolfschoten, T., Conard, N.J., 2015. Overview and new results from large-scale excavations in Schöningen. *Journal of Human Evolution* 89, 27–45.
- Shackleton, N.J., 1995. New data on the evolution of Pliocene climatic variability. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, CT, pp. 311–318.
- Silva, M., Downing, J.A., 1995. The allometric scaling of density and body mass: a nonlinear relationship for terrestrial mammals. *American Naturalist* 145, 704–727.
- Sirakov, N., Guadelli, J.-L., Ivanova, S., Sirakova, S., Boudadi-Maligne, M., Dimitrova, I., Fernandez, P., et al., 2010. An ancient continuous human presence in the Balkans and the beginnings of human settlement in western Eurasia: a Lower Pleistocene example of the Lower Palaeolithic levels in Kozarnika cave (north-western Bulgaria). *Quaternary International* 223–224, 94–106.

- Speth, J.D., 2010. *The Paleoanthropology and Archaeology of Big-Game Hunting*. Springer, New York.
- Stiner, M.C., 1992. Overlapping species “choice” by Italian Upper Pleistocene predators. *Current Anthropology* 33, 433–451.
- Stuart, A. J., Lister, A.M., 2001. The mammalian faunas of Pakefield/Kessingland and Corton, Suffolk, UK: evidence for a new temperate episode in the British early Middle Pleistocene. *Quaternary Science Reviews* 20, 1677–1692.
- Thieme, H., 1997. Lower Palaeolithic hunting spears from Schöningen, Germany. *Nature* 358, 807–810.
- Toro-Moyano, I., Martínez-Navarro, B., Agustí, J., Souday, C., Bermúdez de Castro, J.M., Martínón-Torres, M., Fajardo, B., et al., 2013. The oldest human fossil in Europe, from Orce (Spain). *Journal of Human Evolution* 65, 1–9.
- Turner, A., 1992. Large carnivores and earliest European hominids: changing determinants of resource availability during the Lower and Middle Pleistocene. *Journal of Human Evolution* 22, 109–126.
- Valensi, P., 2009. Évolution des peuplements de grands mammifères en Europe Méditerranéenne Occidentale durant le Pléistocène moyen et supérieur. Un exemple régional: Les Alpes du sud Françaises et italiennes. *Quaternaire* 20, 551–567.
- Vallverdú, J., Saladié, P., Rosas, A., Huguet, R., Cáceres, I., Mosquera, M., Garcia-Taberner, A., et al., 2014. Age and date for early arrival of the Acheulian in Europe (Barranc de la Boella, la Canonja, Spain). *PLoS ONE* 9, e103634. <https://doi.org/10.1371/journal.pone.0103634>.
- Viljoen, P.C., 1993. The effects of changes in prey availability on lion predation in a natural ecosystem in northern Botswana. *Symposia of the Zoological Society of London* 65, 193–213.
- Vizcaíno, S.F., Bargo, M.S., Kay, R.F., Fariña, R.A., Giacomo, M.D., Perry, J.M.G., Prevosti, F.J., Toledo, N., Cassini, G.H., Femicola, J.C., 2010. A baseline paleoecological study for the Santa Cruz Formation (late–early Miocene) at the Atlantic coast of Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 292, 507–519.
- Vizcaíno, S.F., Fariña, R.A., Zárate, M.A., Bargo, M.S., Schultz, P., 2004. Palaeoecological implications of the mid-Pliocene faunal turnover in the Pampean Region (Argentina). *Palaeogeography, Palaeoclimatology, Palaeoecology* 213, 101–113.
- Volmer, R., Hertler, C., 2016. The effect of competition on shared food resources in carnivore guilds. *Quaternary International* 413, 32–43.
- Walker, M.J., López-Martínez, M., Carrión-García, J.S., Rodríguez-Estrella, T., San-Nicolás del-Toro, M., Schwenninger, J.-L., López-Jiménez, A., et al., 2013. Cueva Negra del Estrecho del Río Quípar (Murcia, Spain): a late Early Pleistocene hominin site with an “Acheulo-Levalloiso-Mousteroid” Palaeolithic assemblage. *Quaternary International* 294, 135–159.
- Weers, D.J. van, 1994. The porcupine *Hystrix refossa* Gervais, 1852 from the Plio-Pleistocene of Europe, with notes on other fossil and extant species of the genus *Hystrix*. *Scripta Geologica* 106, 35–52.
- White, E.P., Ernest, S.K.M., Kerkhoff, A.J., Enquist, B., 2007. Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution* 22, 323–330.