Palaeogeography, Palaeoclimatology, Palaeoecology 393 (2014) 122–134

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Ungulate carrying capacity in Pleistocene Mediterranean ecosystems: Evidence from the Atapuerca sites

J. Rodríguez [a,*], H.-A. Blain [b,c], A. Mateos [a], J.A. Martín-González [a,d,1], G. Cuenca-Bescós [e], G. Rodríguez-Gómez [a]

[a] Centro Nacional de Investigación sobre la Evolución Humana (CENIEH), Paseo Sierra de Atapuerca s/n, 09002 Burgos, Spain
[b] IPHES, Institut Català de Paleoecologia Humana i Evolució Social, c/Escorxador s/n, 43003 Tarragona, Spain
[c] Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain
[d] Departamento de Matemáticas y Computación, Universidad de Burgos, Burgos, Spain
[e] Grupo Aragosaurus-IUCA, Paleontología, Ciencias de la Tierra, Universidad de Zaragoza, Pedro Cerbuna 12, 50009 Zaragoza, Spain

ARTICLE INFO

Article history:
Received 13 August 2013
Received in revised form 6 November 2013
Accepted 11 November 2013
Available online 22 November 2013

Keywords:
Atapuerca
Early-Middle Pleistocene
Resource availability
Large herbivores
Ungulates

ABSTRACT

Large herbivore carrying capacity, that is, the maximum biomass of large herbivorous mammals that an ecosystem is able to sustain for the long term, is a key factor in ecosystems trophic dynamics. The carrying capacity of Pleistocene ecosystems conditioned the survival opportunities and colonization capabilities of hominin populations in Europe. In this study, we use the amphibian and squamate record of two Early and Middle Pleistocene sites from Sierra de Atapuerca (Spain) to obtain estimates of past temperature and rainfall values. A function derived from the analysis of a wide set of recent mammalian communities is used to infer the large herbivore carrying capacity of the Atapuerca ecosystems during the Pleistocene from those climatic variables. This function provides reliable estimates of large herbivore carrying capacity in open environments but not in forest communities. The results presented in this study indicate that carrying capacity was higher at Atapuerca during most of the sequence than in the present. Our data also suggest that in most Mediterranean ecosystems, large herbivore biomass is currently below the carrying capacity of the environment due to the relatively low diversity of the large herbivore guild in most recent communities. Although the carrying capacity was high at Atapuerca in the periods the area was occupied by humans, it was also high in other periods for which no evidence of human presence has been recorded. Thus, the relationship between human occupation of the territory and carrying capacity does not appear to be simple.

1. Introduction

Carrying capacity is a theoretical concept that represents the maximum amount of biomass an ecosystem may support for the long term. In a mammalian community, the biomass of secondary consumers (carnivores) depends on the biomass of their prey, namely, the herbivores, and this biomass, in turn, depends on primary production (McNaughton et al., 1989; Oesterheld et al., 1992). Consequently, the carrying capacity at all trophic levels is ultimately controlled by primary production. Primary production is determined by a number of factors, including soil fertility and plant community composition, but the main determinants are temperature, water and solar radiation (Nemani et al., 2003). Thus, before the development of complex computational models fed with satellite data, such as the one presented in Sabbe and Veroustraete (2009), Net Primary Productivity was reliably estimated using simple climate variables, such as mean annual temperature (MAT) and annual rainfall (P) (Rosenzweigh, 1968; Lieth, 1973). Because the climate of the Earth, in particular temperature and humidity, experienced intense oscillations during the Pleistocene (Williams et al., 1988; Joannin et al., 2007), parallel fluctuations in ecosystems carrying capacity through time may be expected.

The European ecosystems in general, and the Mediterranean ones in particular, supported much more rich and diverse large herbivore guilds during the Pleistocene than in the present (Rodríguez, 2004; Kahlke et al., 2011). Meloro and Clauss (2012) estimated large herbivore biomass in Italian Pleistocene palaeocommunities based on the relationship between population density and body mass in mammals and found values between 1000 and 10,000 kg/km^2. These values are in general above the large herbivore biomass observed today in national parks such as Doñana, and Sierra de Cazorla in Spain (Escos and Alados, 1988; Fernandez Llario, 1996; Anonymous, 2005a) or Casentini and Castelporziano in Italy (Focardi et al., 2002; Mattioli et al., 2011).

Estimating the carrying capacity of Pleistocene ecosystems is a relevant topic from a strictly palaeoecological viewpoint, as carrying capacity played a key role in determining the trophic dynamics of past food webs. In many respects, the Pleistocene mammalian palaeocommunities of Europe lack recent analogues (Rodríguez, 2001, 2004, 2006). This lack

---

[*] Corresponding author at: CENIEH, Paseo Sierra de Atapuerca s/n 09002 Burgos, Spain. Tel.: +34 947040800; fax: +34 947040810.
E-mail address: jesus.rodriguez@cenieh.es (J. Rodríguez).
[1] Temporarily assigned to CENIEH.

0031-0182/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.palaeo.2013.11.011

of structural or compositional analogues also raises interesting questions about the functioning of those palaeocommunities. For example, Rodríguez et al. (2012) demonstrated that the Early Pleistocene food webs of southern Europe supported a very rich carnivore guild in comparison with their recent counterparts, although these secondary consumers relied on a relatively small number of prey species. High predator/prey ratios among Early Pleistocene European fauna have also been reported in other studies (Palombo and Mussi, 2006; Raia et al., 2007; Croitor and Brugal, 2010), leading to suggestions that it is possible that carnivores occurred in Early Pleistocene European communities at low population densities (Rodríguez et al., 2012; Rodríguez-Gómez et al., in press). However, to estimate the sustainable carnivore population density, or secondary consumer biomass, in a palaeocommunity, an estimation of prey biomass is necessary. Meloro and Clauss (2012) analysed the prey biomass–predator biomass ratio in recent mammal communities and Italian Plio-Pleistocene fossil communities and found similar values. Nevertheless, their biomass estimations were based on population densities estimated from average body mass and thus, they represent average values of biomass in several communities from a large area, the Italian Peninsula, along wide time intervals. Although this approach provides a general picture of the relationship between prey biomass and predator biomass in the past, analyses at the local scale are required to obtain a deeper knowledge of this relationship.

The carrying capacity of Pleistocene ecosystems, and its variation in time and space, is also highly relevant to evaluate the role played by resource availability, a key constraint for hominin populations, in the human settlement of Europe. Animal food is a key resource for most recent hunter–gatherer populations from temperate and cold regions (Cordain et al., 2000), and it is generally accepted that Palaeolithic hunter–gatherers relied heavily on ungulates and other large herbivores as food resources (Binford, 1981, 1985; Marean, 1989; Moigne and Barsky, 1999; Gaudzinski and Roebroeks, 2000; Roebroeks, 2001; Speth, 2010). The number of herbivore species is often taken as a proxy for prey abundance when analysing the environmental constraints to human settlement in the past (Gamble, 1995; Palombo et al., 2006; Rodríguez et al., 2012). However, prey abundance depends not only on the number of species but also on the number of individuals of each species the territory is able to sustain. Thus, estimating the carrying capacity of large herbivores in Pleistocene ecosystems is essential for evaluating resource availability and its influence on the distribution of hominin populations in time and space.

Amphibian and squamate remains have been proven to be reliable indicators of past climatic conditions (Blain et al., 2009, 2012, 2013a, b). Here, we use the amphibian and squamate record from two sites from the Sierra de Atapuerca complex (Gran Dolina and Sima del Elefante) to estimate ungulate carrying capacity and its variation through time. Recent data regarding herbivore biomass, MAT and P in several ecosystems are used to obtain a function that allows the prediction of ungulate carrying capacity from these climate variables. MAT and P values for the Pleistocene are estimated from the amphibian and squamate fossil record, and subsequently employed to estimate past carrying capacity using the function obtained in the previous step.

2. Material

2.1. Recent data

Data on ungulate biomass and climate were obtained from the literature for a set of 95 recent localities (Table 1, Fig. 1). In many cases, the original source does not report ungulate biomasses but rather the population densities of the ungulate species present in the area. In these cases, the biomass of each species was estimated by multiplying its population density by the average body weight of the species. Ungulate biomass was obtained by adding the biomasses of all the species present in the locality. Only natural areas were included in the database, mostly national parks and other protected areas. However, in many parks, traditional pastoralism is allowed inside the protected areas. In these cases, cattle consume a significant amount of primary production and contribute significantly to the total ungulate biomass. Consequently, wild ungulate biomass (B_w) and livestock biomass (B_L) were recorded separately for each locality, and the total ungulate biomass was calculated as $B_T = B_{w+} \cdot B_L$. The dataset was divided into two subsets, one of them including localities with both livestock and wild ungulates (17 cases) and a second one including localities where no livestock occurs (78 cases). These 95 recent localities were classified as “Forest” or “Open” ecosystems taking into account the information provided by the original sources and land cover data obtained from the Global Land Cover Characteristics Database created by the USGS EROS Data Center and provided with the Idrisi 16.05 Taiga software (ClarkLabs©). The “Forest” category includes temperate and tropical evergreen and deciduous forests and dense woodlands, whereas savannahs, open woodlands, grasslands and drylands were included in the “Open” category. Climate data were obtained from the United Nations Environmental Programme GRID dataset (Deichmann and Eklundh, 1991). Annual rainfall in mm/yr (P) was computed as the sum of monthly rainfall throughout the year, and mean annual temperature in °C was obtained as the mean of the average temperature for each month. Maps of P and MAT were computed using Idrisi 16.05 Taiga.

2.2. The Atapuerca record

The Sierra de Atapuerca (Atapuerca Hill), is situated in northern Spain 15 km east of Burgos. It is a highly karstified hill that includes several caves and karstic openings that yield several archaeological and paleontological sites of Pleistocene and Holocene age. The Atapuerca area known as Trinchera del Ferrocarril, or Railway Trench, includes several Pleistocene cave infillings, described in detail in Rodríguez et al. (2011), Ortega et al. (2013) and references therein. One of these sites is Sima del Elefante (TE), a 19 m-thick cave infill that has been divided into 16 stratigraphic units, named TE7 to TE21 from bottom to top (Rosas et al., 2006). The ten lowermost stratigraphic units (TE7 to TE16) are dated as Early Pleistocene on the basis of their faunal content, reversed polarity and radioactive decay of cosmogenic ^{26}Al and ^{10}Be dating (Parés et al., 2006; Carbonell et al., 2008; Cuenca-Bescós et al., 2013), whereas units TE17 to TE21 date to the Middle and Late Pleistocene (López-García et al., 2011; Rodríguez et al., 2011). The normal magnetic polarity short interval detected at the base of TE17 might correspond to the Jaramillo Subchron, or even to the Cobb Mountain (Cuenca-Bescós et al., 2013). A hominin mandible fragment and a phalanx were found in 2008 and 2009, respectively, in the TE9 unit associated to a number of stone tools (Carbonell et al., 2008; Bermúdez de Castro et al., 2010). Furthermore, several lithic instruments were recovered from units TE9, TE11, TE12, TE13 and TE14, suggesting a continuous hominin presence during the late Early Pleistocene (Ollé et al., 2013).

Gran Dolina (TD) is another cave infill located inside the Railway Trench, some 200 m away from the Sima del Elefante site. The 18 m-thick stratigraphic sequence of TD has been divided into 11 stratigraphic units named TD1 to TD11 from bottom to top by Gil and Hoyos (1987) and reviewed in Parés and Pérez-González (1999). A polarity reversal, interpreted as the Matuyama–Brunhes boundary, detected at the top of TD7 unit (Parés and Pérez-González, 1999), separates the lower stratigraphic units of Early Pleistocene age from the Middle Pleistocene upper units (TD8–TD11). Several dates obtained by luminescence and combined electronic spin resonance and uranium series (ESR/U–Th) techniques confirm this interpretation (Falguères et al., 1999, 2001; Berger et al., 2008; Moreno, 2011; Duval et al., 2012). In addition, a normal magnetic polarity short interval has been detected inside the TD7 unit by Parés et al. (2013) and interpreted as the Kamitsakura and Santa Rosa short chrons. According to this interpretation, the lower units of Gran Dolina (TD1 to TD6) are older than 0.94 Ma. The Gran

Table 1

Recent localities from where data on ungulate biomass were obtained. B_T total ungulate biomass in kg/km^2, obtained as the sum of wild ungulate biomass (B_w) plus livestock biomass (B_L). The ecosystems have been classified as Forest or Open (grasslands, savannahs, dryland, etc.) according to the dominant vegetation. Land cover data (Land Use) were obtained from the *Global Land Cover Characteristics Database*. Rainfall in mm/yr (P) and mean annual temperature in °C (MAT) were obtained from the United Nations Environmental Programme GRID dataset (Deichmann and Eklundh, 1991).

Code	Locality	Country	Long.	Lat.	P	MAT	B_T	B_L	B_w	Land Use	Vegetation	Reference
1	Umfolosi Game Reserve	South Africa	31.80	−28.29	720	19.7	8016	0	8016	Cropland/grassland mosaic	Open	Mentis (1970)
2	Kalakadu-Mundanthurai Tiger Reserve	India	77.33	8.75	1743	24.4	2614	0	2614	Evergreen broadleaf forests	Forest	Ramesh et al. (2012)
3	Taman Negara National Park	Malaysia	102.40	4.55	2862	23.3	5814	0	5814	Evergreen broadleaf forest	Forest	Kawanishi and Sunquist (2004)
4	Akagera National Park	Rwanda	30.53	−1.58	950	20.7	10895	0	10895	Cropland/woodland mosaic	Open	Montfort (1972)
5	Katavi National Park	Tanzania	31.04	−6.82	945	23.4	23,000	0	23,000	Cropland/woodland mosaic	Open	Caro (1999)
6	Sengwa Wildlife Research Area	Rhodesia	28.14	−18.10	680	22.7	4315	0	4315	Cropland/woodland mosaic	Open	Coe et al. (1976)
7	Doñana NP	Spain	−6.46	37.06	540	18.1	1630	1300	330	Cropland/woodland mosaic	Open	Fernandez Llario (1996) Anonymous (2005a)
8	Aggteleki National Park	Hungary	20.61	48.52	853	5.4	190	0	190	Deciduous broadleaf forest	Forest	Lanszki et al. (2012)
9	Casentini national Park	Italy	11.82	43.8	1290	9.0	740	0	740	Deciduous broadleaf forest	Forest	Mattioli et al. (2011)
10	Sierras de Cazorla y Segura	Spain	−2.68	38.18	1000	12.1	965	0	965	Deciduous broadleaf forest	Forest	Escos and Alados (1988)
11	Rabi Koumaga	Gabon	9.78	−2.00	1770	27.5	795	0	795	Deciduous broadleaf forest	Forest	Prins and Reitsman (1989)
12	Pench National Park	India	79.27	21.75	1401	26.0	6013	0	6013	Deciduous broadleaf forest	Forest	Biswas and Sankar (2002)
13	Selous	Tanzania	37.20	−8.65	1171	26.7	8975	0	8975	Deciduous broadleaf forest	Forest	East (1984)
14	Masai Mara	Kenya	35.07	−1.44	1612	19.2	14,676	0	14,676	Savanna	Open	Bhola et al. (2012)
15	Manyara National Park	Tanzania	35.78	−3.47	1131	18.4	15,288	0	15,288	Savanna	Open	Prins and Douglas-Hamilton (1990)
16	Petit Loango	Gabon	9.59	−2.24	1362	26.8	3113	0	3113	Deciduous broadlead forest	Forest	Morgan (2007)
17	Bialowieza Primeval Forest	Poland	23.86	52.68	608	6.7	1051	293	758	Deciduous broadleaf forest	Forest	Jedrzejewska et al. (1997)
18	Virungas	Rwanda	29.48	−1.48	1595	16.3	3100	0	3100	Tropical montane forest	Forest	Plumptre and Harris (1995)
19	Bunyoro North	Uganda	31.30	1.57	1109	24.5	13,261	0	13,261	Dryland cropland and pasture	Open	Laws (1970); Coe et al. (1976)
20	Gir Wildlife Sanctuary West	India	70.64	21.2	732	24.1	6380	4018	2362	Dryland cropland and pasture	Open	Khan et al. (1996)
21	Ruaha National Park	Tanzania	34.57	−7.58	822	22.6	5209	0	5209	Dryland cropland and pasture	Open	Barnes and Douglas-Hamilton (1982)
22	Rungwa and Kizigo Game Reserves	Tanzania	34.10	−6.97	837	21.7	2558	0	2558	Dryland cropland and pasture	Open	Barnes and Douglas-Hamilton (1982)
23	Rwindi plain Albert National Park	Zaire	29.29	−0.78	1373	19.2	17,448	0	17,448	Dryland cropland and pasture	Open	Coe et al. (1976)
24	Nairobi National Park	Kenya	36.85	−1.37	681	17.3	5534	159	5375	Dryland cropland and pasture	Open	Foster and Coe (1968)
25	Serengeti	Tanzania	34.45	−2.76	1107	21.1	11,595	0	11,595	Dryland cropland and pasture	Open	Robinson and Bennett (2004)
26	Kruger National Park, Northern section	South Africa	31.27	−23.31	499	22.8	984	0	984	Dryland cropland and pasture	Open	Coe et al. (1976)
27	Kruger National Park, Southern section	South Africa	30.65	−23.93	570	22.6	3783	0	3783	Dryland cropland and pasture	Open	Coe et al. (1976)
28	Bharatpur Wildlife Sanctuary	India	77.52	27.16	706	25.7	1550	0	1550	Dryland cropland and pasture	Open	Eisenberg and Seidensticker (1976)
29	Marahoué	Ivory coast	−5.90	7.07	1333	27.1	1478	0	1478	Dryland cropland and pasture	Open	Hoppe-Dominik (1989); Bodendorfer et al. (2006)
30	Gal Oya National Park	Sri Lanka	81.47	7.22	2107	25.4	886	0	886	Evergreen broadleaf forest	Forest	Eisenberg and Seidensticker (1976)
31	Wilpattu National Park	Sri Lanka	80.00	8.43	1319	26.3	766	0	766	Evergreen broadleaf forest	Forest	Eisenberg and Seidensticker (1976)
32	Biligiri Rangaswamy Temple Wildlife Sanctuary	India	77.13	11.94	1430	24.1	6423	0	6423	Evergreen broadleaf forest	Forest	Kumara et al. (2012)
33	Huai Kha Khaeng Wildlife Sanctuary	Thailand	99.29	15.46	2694	24.4	1451	0	1451	Evergreen broadleaf forest	Forest	Srikosamatara (1993)
34	Roraima (Brazilian Amazon)	Brazil	−61.71	3.41	1879	28.6	2396	0	2396	Evergreen broadleaf forest	Forest	Mendes Pontes (2004)
35	Royal Chitawan National Park	Nepal	84.62	27.43	1416	25.1	29,866	28,076	1790	Evergreen broadleaf forest	Forest	Eisenberg and Seidensticker (1976)
36	Kanha National Park	India	80.62	22.29	1454	23.2	6386	4678	1708	Evergreen broadleaf forest	Forest	Eisenberg and Seidensticker (1976)
37	Pendjari National Park	Benin	11.22	1.54	2102	22.7	1118	0	1118	Evergreen broadleaf forest	Forest	Sinsin et al. (2002)
38	El Mirador-Rio Azul National Park	Guatemala	−89.62	17.40	1907	25.0	518	0	518	Evergreen broadleaf forest	Forest	Novack et al. (2005)
39	Uauaçu Lake	Brazil	−62.42	−4.22	2452	26.6	144	0	144	Evergreen broadleaf forest	Forest	Haugaasen and Peres (2005)
40	Guatopo	Venezuela	−66.47	10.12	1460	25.5	270	0	270	Evergreen broadleaf forest	Forest	Eisenberg et al. (1979)
41	Nagarahole	India	76.15	12.02	1200	24.8	15,094	350	14,744	Evergreen broadleaf forest	Forest	Karanth and Nichols (1998); Varma (2007)
42	Acurizal Ranch	Brazil	−57.62	−17.82	1221	25.2	4034	3750	284	Evergreen broadleaf forest	Forest	Schaller (1983)
43	Hato Piñeiro	Venezuela	−68.13	8.83	1431	27.0	8222	7988	234	Evergreen broadleaf forest	Forest	Polisar et al. (2003)
44	Itaya Basin	Perú	−73.67	−4.29	2579	26.6	110	0	110	Evergreen broadleaf forest	Forest	Aquino et al. (2007)
45	Tauhayu (Tamshiyacu-Tahuayo Comunal Reserve)	Perú	−73.08	−4.35	2698	26.4	267	0	267	Evergreen broadleaf forest	Forest	Bodmer et al. (1994)

46	Yavari Miri (Tamshiyacu-Tahuayo Comunal Reserve)	Perú	−72.64	−4.88	2703	26.1	219	0	219	Evergreen broadleaf forest	Forest	Bodmer et al. (1994)
47	Manu National Park, NE area	Peru	−71.45	−11.91	1530	24.8	800	0	800	Evergreen broadleaf forest	Forest	Endo et al. (2010)
48	Cocha Cashu Biological Station	Peru	−71.41	−11.89	1530	23.6	475	0	475	Evergreen broadleaf forest	Forest	Janson and Emmons (1990)
49	Lopé	Gabon	11.46	−0.30	978	28.2	2781	0	2781	Evergreen broadleaf forest	Forest	White (1994); Morgan (2007)
50	Jigme Singye Wangchuck National Park	Bhutan	90.41	27.24	2139	9.6	994	615	379	Evergreen needleleaf forest	Forest	Wang (2010)
51	Forsmark	Sweden	18.10	60.36	564	5.2	410	0	410	Evergreen needleleaf forest	Forest	Truvé and Cederlund (2005)
52	Hållnäs	Sweden	17.89	60.53	566	4.4	341	0	341	Evergreen needleleaf forest	Forest	Truvé and Cederlund (2005)
53	Blankaholm	Sweden	16.41	57.59	532	5.1	282	0	282	Evergreen needleleaf forest	Forest	Truvé and Cederlund (2005)
54	Simpevarp	Sweden	16.59	57.41	555	5.8	329	0	329	Evergreen needleleaf forest	Forest	Truvé and Cederlund (2005)
55	Tarangire national Park	Tanzania	36.03	−4.04	744	20.6	1005	0	1005	Grassland	Open	Lamprey (1964)
56	Kaputei Plains	Kenya	36.91	−1.74	1266	19.9	21,335	12,200	9135	Grassland	Open	Owaga (1980)
57	Simanjiro Plains	Tanzania	36.50	−4.00	714	21.2	9512	4858	4654	Grassland	Open	Kahurananga (1981)
58	Henderson's ranch	Rhodesia	29.42	−22.04	317	23.2	2869	0	2869	Grassland	Open	Coe et al. (1976)
59	Willem Pretorius Nature Reserve	South Africa	27.25	−28.3	543	15.7	3344	0	3344	Grassland	Open	Coe et al. (1976)
60	Okavango Delta	Botswana	23.00	−19.50	437	22.2	1079	0	1079	Herbaceous wetland	Open	Astle and Graham (1976)
61	Kaziranga National Park	India	93.38	26.65	1747	23.4	2858	0	2858	Mixed forest	Forest	Eisenberg and Seidensticker (1976)
62	Jaldapara Wildlife Sanctuary	India	89.31	26.7	3019	24.7	984	0	984	Mixed forest	Forest	Eisenberg and Seidensticker (1976)
63	Chamela Biological Station	Mexico	−105.00	19.50	1021	25.1	853	0	853	Mixed forest	Forest	Mandujano (2007)
64	Karnali-Bardia Wildlife reserve	Nepal	81.26	28.50	1284	26.0	2981	0	2981	Mixed forest	Forest	Dinerstein (1979, 1980)
65	Barro colorado	Panama	−79.08	9.15	2087	24.8	542	0	542	Mixed forest	Forest	Robinson and Bennett (2004)
66	Denali National Park	USA	−151.00	63.34	148	−17.9	60	0	60	Mixed forest	Forest	Meier (2012)
67	Castelporziano Preserve	Italy	12.40	41.00	658	16.0	2032	0	2032	Mixed shrubland/grassland	Open	Focardi et al. (2002)
68	Cerro Cortado	Bolivia	−62.35	−19.48	671	22.8	343	0	343	Savanna	Open	Robinson and Bennett (2004)
69	Lake Mburu National Park	Uganda	30.95	−0.60	926	20.8	18,402	9738	8664	Savanna	Open	Rannestad et al. (2006)
70	Arli National Park	Burkina Faso	1.41	11.57	1007	28.2	2000	0	2000	Savanna	Open	Milligan et al. (1982); Payne and Andau (1991)
71	Lake Nakuru National Park	Kenya	36.09	−0.41	817	14.9	6688	0	6688	Savanna	Open	Kutilek (1974); Coe et al. (1976)
72	Chobe NationalPark	Botswana	24.08	41.00	520	22.4	3000	0	3000	Savanna	Open	Viljoen (1993)
73	Amboseli Game Reserve	Kenya	37.15	−2.39	350	21.1	7804	3483	4321	Savanna	Open	Western (1973) Coe et al. (1976)
74	Borgu National Park (Kainji Lake)	Nigeria	4.12	10.07	1118	27.2	1200	0	1200	Savanna	Open	Milligan et al. (1982)
75	Benoue National Park	Cameroun	13.85	8.24	1347	26.5	1325	0	1325	Savanna	Open	Stark (1986)
76	Bouba Njida National Park	Cameroon	14.60	8.63	1199	27.6	2700	0	2700	Savanna	Open	Van Lavieren and Esser (1979)
77	Lloldaiga Hills	Kenya	37.12	0.15	691	17.1	8020	6512	1508	Savanna	Open	Mizutani (1999)
78	Hwange National Park	Zimbabwe	26.50	−19.00	536	20.9	7211	0	7211	Savanna	Open	Valeix et al. (2007)
79	Gir Wildlife Sanctuary East	India	70.77	21.07	732	24.1	10717	8815	1902	Savanna	Open	Khan et al. (1996)
80	Ranthambhore Tiger Reserve	India	76.50	26.00	854	25.6	6089	0	6089	Savanna	Open	Bagchi et al. (2004)
81	Ngorongoro Crater	Tanzania	35.57	−3.17	1027	18.9	10,982	495	10,487	Savanna	Open	Runyoro et al. (1995)
82	Lochinvar ranch	Zambia	27.22	−15.88	749	21.0	7568	0	7568	Savanna	Open	Coe et al. (1976)
83	Samburu–Isiolo	Kenya	39.28	−3.79	519	25.3	2018	0	2018	Savanna	Open	Coe et al. (1976)
84	Luangwa Valley	Zambia	31.65	−12.68	1001	24.2	8555	0	8555	Savanna	Open	East (1984)
85	Saint Floris National Park	Central African Republic	21.25	9.07	1192	26.7	4032	0	4032	Savanna	Open	Milligan et al. (1982)
86	Udjung Kulong	Indonesia	105.33	−6.75	2765	26.6	494	0	494	Evergreen broadlead forest	Forest	Eisenberg and Seidensticker (1976)
87	Kuiseb River area Namib Desert	Namibia	15.20	−23.60	93	13.4	131	0	131	Shrubland	Open	Tilson and Henschel (1980)
88	Sibiloi National Park	Kenya	36.41	3.97	238	29.1	405	0	405	Shrubland	Open	East (1984)
89	Kibale National Park	Uganda	30.40	0.47	1181	21.6	2600	0	2600	Shrubland	Open	Wanyama et al. (2010)
90	Rwenzori National Park	Uganda	29.91	−0.09	1376	23.2	18,300	0	18,300	Shrubland	Open	Field and Laws (1970)
91	Lake Rudolf (East)	Kenya	36.59	3.33	350	26.5	405	0	405	Shrubland	Open	Coe et al. (1976)
92	Tsavo National Park (East) N. of Voi River	Kenya	38.85	3.25	528	25.5	4033	0	4033	Shrubland	Open	Coe et al. (1976)
93	Tsavo National Park (East) S. of Voi River	Kenya	38.87	−3.50	528	23.8	4388	0	4388	Shrubland	Open	Coe et al. (1976)
94	Mkomasi Game Reserve	Tanzania	38.28	−4.16	641	24.1	1731	0	1731	Shrubland	Open	Coe et al. (1976)
95	Katka-Kochitkali	Bangladesh	89.76	21.89	1940	25.8	3128	0	3128	Wodded wetland	Forest	Reza et al. (2002)

Dolina TD6 unit includes the subunit TD6-2, also known as "Aurora stratum" (Bermúdez de Castro et al., 2008), which yielded a remarkable collection of human remains attributed to *Homo antecessor* associated to numerous stone tools and abundant faunal remains (Carbonell et al., 1995, 2005).

The palaeomagnetic reversal identified at TD7 in Gran Dolina and TE17 in Sima del Elefante allows the correlation of the two sequences (Fig. 2). Moreover, the faunal composition indicates that the early Pleistocene stratigraphic units of Gran Dolina are younger than the lower units of Sima del Elefante (TE7–TE16) (Cuenca-Bescós et al., 2013). Units TE8–TE14 are included in the local bioestratigraphic unit FU1, whereas TD3–4 corresponds to FU2, and TD5 and TD6 belong to FU3 (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2010). A detailed discussion of the correlation between the two stratigraphic sequences may be found in Rodríguez et al. (2011).

The small-vertebrate fossil remains used for this study consist of disarticulated bone fragments collected by water screening each year since 1992 during the field excavations in the two sites in Atapuerca. The sediment was water screened using superimposed 0.5, 5 and 10 mm mesh screens and bagged by square, layer and excavation sublevels. In subsequent years, the microfossils were processed, sorted and classed into large categories at the Palaeontology Section of the Earth Sciences Department of the University of Zaragoza (Spain). The systematic description and interpretation of the fossil amphibians and reptiles from Atapuerca have been performed as part of a PhD thesis (Blain, 2005) and published in various publications (Blain, 2005; Blain et al., 2008; Blain, 2009; Blain et al., 2010, 2011; Cuenca-Bescós et al., 2011; Rodríguez et al., 2011; Blain et al., 2012, 2013a).

3. Methods

3.1. Temperature and rainfall estimates

Palaeoclimatic interpretations are based on the presence of herpetile species from each level. The mutual climatic range (MCR) method has been used to quantify palaeotemperature and palaeoprecipitation whereby we simply identify the geographic region (divided into 10 × 10 km Universal Transverse Mercator (UTM) squares) where all the species present in a given locality and stratigraphical level currently live (Blain et al., 2009). Careful attention is paid to ensure that the current distribution corresponds to the potential ecological/climatic distribution and is not strongly affected by other limiting or perturbing parameters such as urban development, landscape anthropization, predation, competition with other species and other such factors. An analysis of the MCR in each level is based on the distribution atlases of the Iberian herpetofauna (Godinho et al., 1999; Pleguezuelos et al., 2004) divided into 10 × 10 km squares in the UTM coordinate system. Mean annual temperature (MAT) and annual rainfall (P) have been estimated for each 10 × 10 km UTM square, using climatic maps of the Iberian Peninsula (Ninyerola et al., 2005).

3.2. Carrying capacity

The term carrying capacity is widely used in ecology and other disciplines. Its origin dates back to the 19th century to designate a fixed quantity of *X* that some encompassing *Y* should carry in abstraction from time or history (Sayre, 2008). In ecology carrying capacity is the maximum number of individuals the environment is able to sustain in the long term. It is assumed here that carrying capacity (CC) is determined by primary production (Coe et al., 1976; Pettorelli et al., 2009), which, in turn, is determined by climate (mainly temperature and rainfall) and soil fertility (Rosenzweigh, 1968; Fritz and Duncan, 1994). Our aim was to obtain a function to estimate carrying capacity from MAT and P. Given that carrying capacity is defined as the maximum number of animals that an area can support in approximate equilibrium (McCullough, 1992), we must expect observed biomass to oscillate below CC in most natural communities. Several factors such as competition, predation pressure, poaching, epidemics and climatic oscillations, among others, may cause wild ungulate populations to be below carrying capacity. In contrast, free-ranging cattle are protected from most of those adverse factors by the care provided to them by pastoralists. The best proxy for CC in natural communities is the maximum observed biomass for a given value of MAT and P. As cattle make the most of primary production, the observed ungulate biomass is expected to approach CC in ecosystems with livestock. MAT and P are treated here as two independent limiting factors, in a similar manner as was performed by Lieth (1973) in the Miami model to estimate primary production. Linear least square regression was used to model the relationships of B_T with P and MAT in localities with livestock. Eventually, these models were validated against the sample of 78 recent localities with no livestock. The carrying capacity is then estimated as the minimum of two values: the maximum biomass sustainable under a given value of MAT and the maximum biomass sustainable under a given value of P. Statistical analyses were conducted with the Statistica 11 package (Statsoft©).

4. Results

4.1. Estimating CC

Forest and open ecosystems differ in the ungulate biomass they sustain for a given value of P or MAT, as was previously observed by other authors (Mandujano and Naranjo, 2010). Generally speaking, ungulate biomass is higher in open environments than in forest communities (Fig. 3) because of the different distribution of primary production amongst plant organs and tissues in these ecosystems, which results in different food availability for the large mammal herbivores. Linear functions were fitted to predict the Total Biomass (B_T) from rainfall in open and forest communities separately, including all localities with livestock (Table 1). The relationship is non-significant for forest communities but significant for open environments ($B_T = -3993.3164 + 18.3117 * P$; $p = 0.0062$ $r = 0.79$). This equation accurately predicts maximum ungulate biomass in natural communities without livestock (Fig. 3B). A linear regression line was also fitted to estimate B_T from MAT in localities with livestock (Fig. 3C). However, in this case, only the five extreme cases (maximum B_T for a given value of MAT) from either forest or open environments were included. The equation is significant and the correlation very high ($B_T = 1634\ \mathrm{MAT} - 12502$; $r = 0.98$; $p = 0.003$; $N = 5$). Note that this equation is only valid for localities with MAT above 8 °C. Below this temperature, the equation predicts negative values, likely because this temperature represents a threshold below which only relatively small ungulate populations are sustainable.

According to these results, the annual rainfall limits large herbivore biomass as described by the following equation:

$$\mathrm{maxB(P)} = 18.3\ \mathrm{P} - 3993 \tag{1}$$

where maxB(P) is maximum ungulate biomass as limited by rainfall.

Similarly, the mean annual temperature limits maximum sustainable biomass as

$$\mathrm{maxB(T)} = 1634\ \mathrm{MAT} - 12502 \tag{2}$$

where maxB(T) is maximum ungulate biomass as limited by mean annual temperature.

Thus, the ungulate carrying capacity in any given locality may be estimated as the minimum of the values predicted by Eqs. (1) and (2).

$$\mathrm{CC} = \mathrm{Min(\,maxB(P),\ max(BT)} \tag{3}$$

Fig. 4 shows the predicted CC from Eq. (3) against the observed ungulate biomass in the set of 78 recent localities with no livestock.

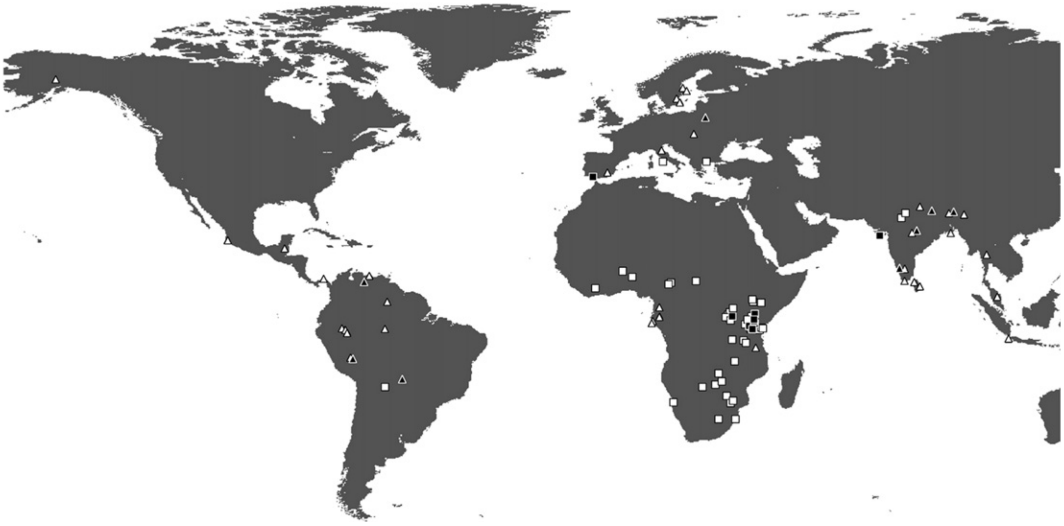

Fig. 1. Map showing the location of the 95 recent localities sampled to obtain ungulate biomass data. Black triangles: forest communities with livestock; white triangles: forest communities without livestock; black squares: open communities with livestock; white squares: open communities without livestock.

4.2. CC in the Pleistocene Atapuerca

The carrying capacity of the Atapuerca ecosystems was high during the Pleistocene in comparison to the present (Fig. 5 and Table 2). Only the estimated CC for TE14 level, dated to approximately 1.1 Ma is similar to the CC estimated for the present. For the remaining levels, the CC varies between 5766 kg/km^2 and 8021 kg/km^2 (Table 2). Excluding TE14, the general pattern at Atapuerca is a high CC, with low variation, throughout a time sequence almost 1 Ma long. This observation is in agreement with the long-term environmental stability

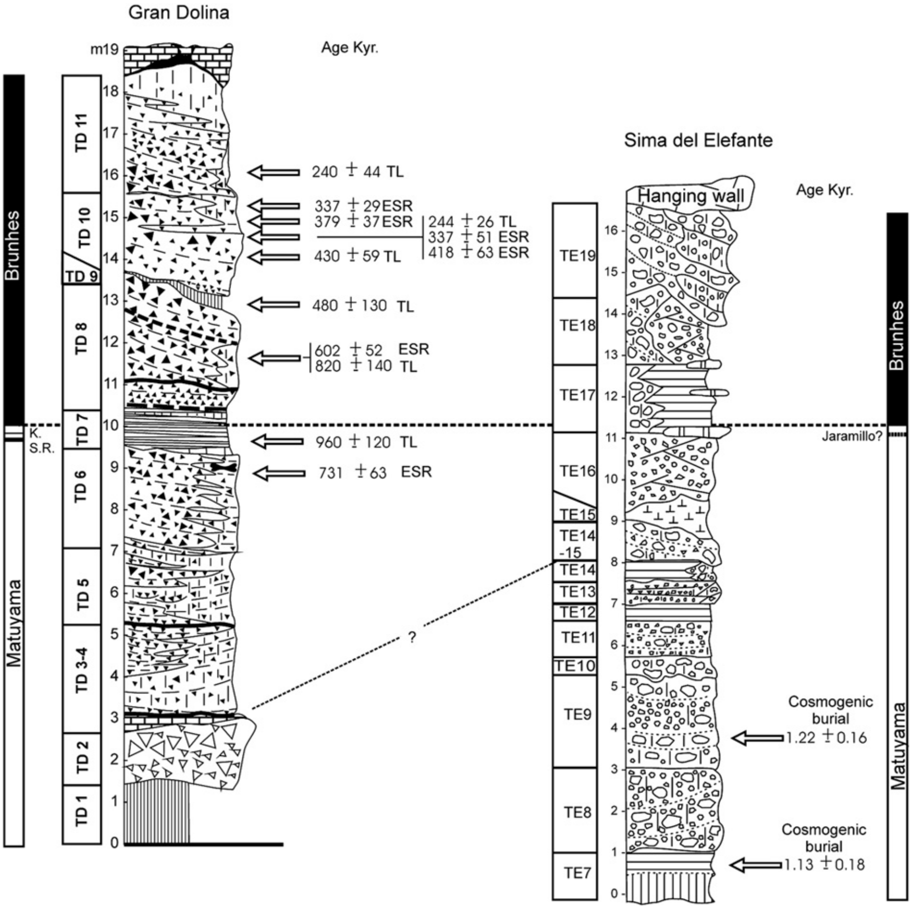

Fig. 2. Dates, magnetostratigraphy and correlation of the stratigraphic sections of Sima del Elefante and Gran Dolina. TL ages from Berger et al. (2008), ESR ages from Falguères et al. (2001) and cosmogenic burial ages from Carbonell et al. (2008). K. and S.R. refer to the Kamitsakura and Santa Rosa short chrons, respectively. Palaeomagnetic data from Carbonell et al. (2008) and Parés et al. (2013). Stratigraphic columns from Carbonell et al. (2008), and Parés and Pérez-González (1995).

at Atapuerca already noted by Rodríguez (2004) and Rodríguez et al. (2011).

The results reported in Table 2 also suggest that carrying capacity was limited at Atapuerca by temperature, not by precipitation, because maximum CC as limited by P is always higher than maximum CC limited by MAT. Because CC ultimately depends on primary production, it may be concluded that primary production was limited by available energy and not by humidity.

CC is not related to ungulate species richness of the fossil assemblages (Spearman's rho = 0.05, p = 0.83). This may be partly explained by the fact that the number of species is largely affected by several factors such as the number of fossils in the assemblage, the size of the excavation area, and selection by the accumulation agents. The excavation area and the number of fossils widely vary in the set of assemblages analysed here and differences in the accumulation agents also exist. Thus, though some assemblages, such as TD8, or TD6-2, TD10-1 and TD10-2, may be considered a good representation of the large herbivore guild living in the past, other assemblages such as TE10, TE11 or TD7 are very poor in species and likely do not provide a reliable picture of the past living community. The average carrying capacity per species is obtained dividing CC by the number of species in the assemblage, and it is also reported in Table 2. The average CC is reported for reference only, and it cannot be taken as a reliable estimate, mainly for two reasons. First, population density varies in nature by one or two orders of magnitude in a single species. Second, the number of large herbivore species is extremely low in some fossil assemblages, e.g., TE11 or TE10, which cannot be taken as adequate samples of the past living community.

5. Discussion

5.1. Reliability of the functions to estimate CC

Generally speaking, the total ungulate biomass is closer to estimated carrying capacity in open than in forest recent communities (Fig. 4B). Moreover, the ungulate biomass is far below the CC in tropical rainforests, where the estimated CC is highest. These results are not surprising, as it is well known that tropical rainforests are characterized by low large herbivore richness in comparison with grasslands and savannahs (Fritz and Loison, 2006). This phenomenon is likely explained by two factors. First, a large amount of primary production is seized in all types of forests in the form of non-edible plant tissues composed of cellulose and lignin (Duvigneaud, 1971). Second, but not less important, most primary production occurs in tropical forest in the canopy, far away the reach of terrestrial ungulates, and it is consumed by primates, small mammals and other vertebrates and a huge amount of invertebrate species (Bodmer, 1989). Thus, in tropical forests most of the biomass of secondary consumers is not in the form of ungulates. In

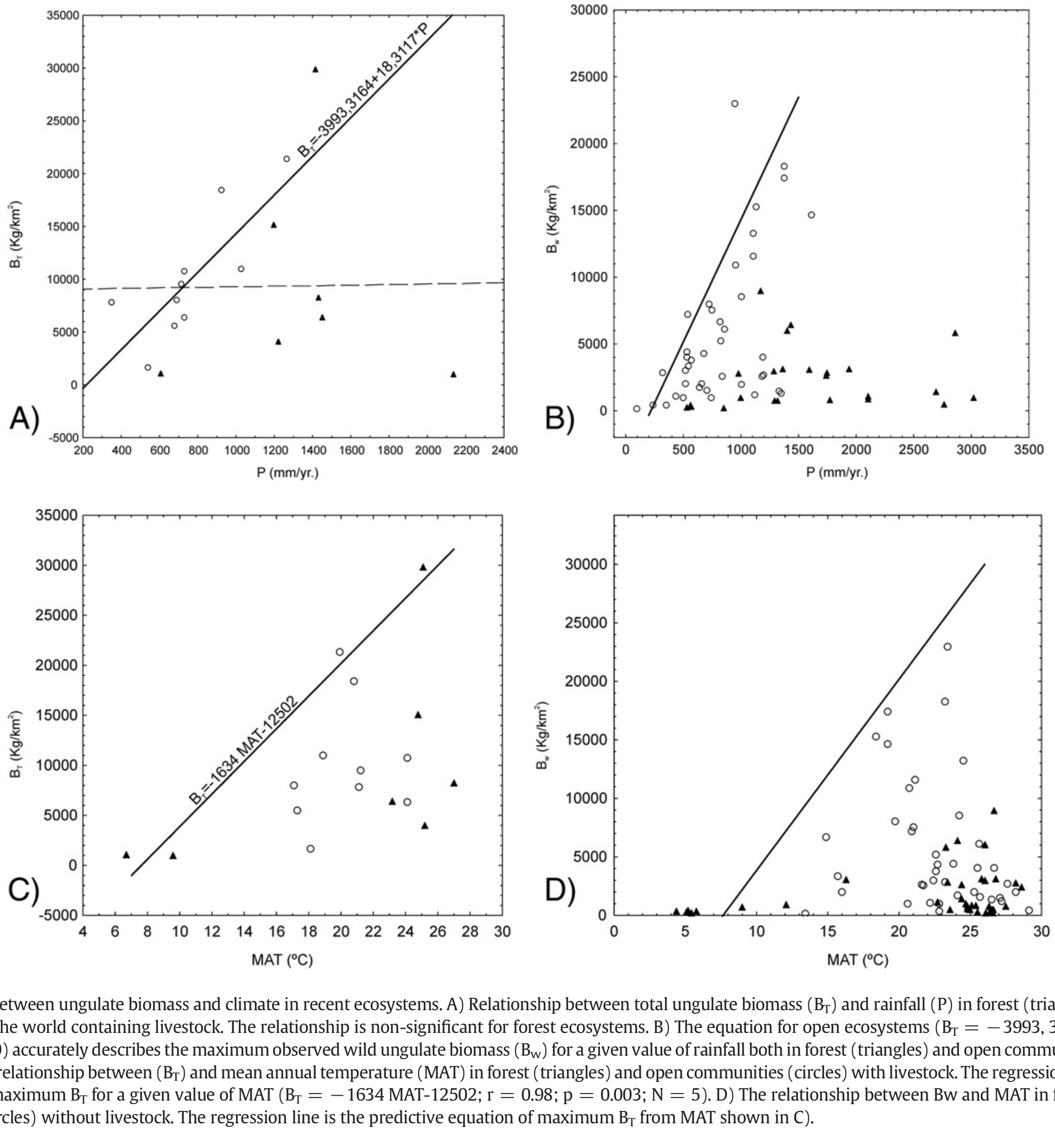

Fig. 3. Relationship between ungulate biomass and climate in recent ecosystems. A) Relationship between total ungulate biomass (B_T) and rainfall (P) in forest (triangles) and open ecosystems (circles) of the world containing livestock. The relationship is non-significant for forest ecosystems. B) The equation for open ecosystems ($B_T = -3993, 3164 + 18, 3117 * P$; $p = 0.0062$ $r = 0.79$) accurately describes the maximum observed wild ungulate biomass (B_w) for a given value of rainfall both in forest (triangles) and open communities (circles) without livestock. C) The relationship between (B_T) and mean annual temperature (MAT) in forest (triangles) and open communities (circles) with livestock. The regression line has been fitted to the 5 cases with maximum B_T for a given value of MAT ($B_T = -1634$ MAT-12502; $r = 0.98$; $p = 0.003$; $N = 5$). D) The relationship between Bw and MAT in forest (triangles) and open ecosystems (circles) without livestock. The regression line is the predictive equation of maximum B_T from MAT shown in C).

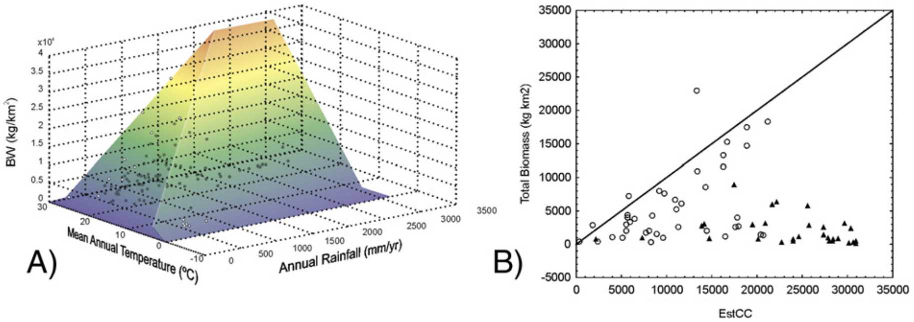

Fig. 4. The equations relating maximum ungulate biomass with rainfall (P) and mean annual temperature (MAT) may be represented in a set of three-dimensional axes as a surface. This surface is defined by two planes that cut each other. The minimum value of the z-coordinate of these two planes defines a surface that represents the carrying capacity of any combination of P and MAT (A). The observed ungulate biomass (Bw) in localities without livestock plot below the surface (black points) except in very few cases (white circles). Ungulate carrying capacity estimated in this way accurately marks the upper limit of observed wild ungulate biomass in a set of 78 recent localities with no livestock, especially in open environments (B).

contrast, ungulates seize a large amount of primary production in open environments, and they represent a large proportion of the biomass of primary consumers in those ecosystems.

Eq. (3) is thus appropriate to estimate ungulate CC in open environments only, which are characterized by a high ungulate richness. Open landscapes were spread over Europe throughout the Pleistocene and especially dominated the Mediterranean Peninsulas during the glacial and glacial–interglacial transitions (Suc and Popescu, 2005; Kahlke et al., 2011; Leroy et al., 2011). Though increased temperatures and precipitations during the interglacials favored temperate tree species and promoted the expansion of forests (Suc and Popescu, 2005), climate is not the single factor determining vegetation structure. Large herbivores play a key role currently as ecosystem engineers, largely affecting vegetation composition and structure (Danell et al., 2006; Levick et al., 2009). The European large herbivore guild was relatively rich during the Pleistocene, even in the interglacials, and was likely a key factor in creating open vegetation (Svenning, 2002). Not surprisingly, although pollen-based reconstructions often emphasize the expansion of forests during the interglacials, most environmental reconstructions based on fossil mammals suggest landscapes dominated by open woodlands and savannahs or mosaic landscapes (e.g., Kahlke et al., 2011).

Concerning the Sierra de Atapuerca ecosystems, and taking into consideration the combined evidence provided by pollen, micromammals, herpetofauna and large mammals, the Pleistocene landscapes were dominated by open woodlands, steppes and meadows (see Rodríguez et al., 2011 for a synthesis). In summary, Eq. (3) may be taken as a reliable predictor of CC in the ungulate dominated Pleistocene landscapes of Sierra de Atapuerca.

5.2. CC in the Pleistocene

The carrying capacity inferred for the Pleistocene ecosystems of Atapuerca is higher than the estimated value for the present except for two cases, TE14 and TE19, although, as noted above, the estimate for TE19 should be taken with caution. Moreover, most of the estimated carrying capacities are in the range of 5750 kg/km^2 to 8000 kg/km^2 (Table 2), far beyond the ungulate biomass observed in the present in natural areas from Spain and Italy (Table 1). Differences in climate and vegetation between the recent Mediterranean ecosystems included in Table 1 and the Pleistocene ecosystems may partially explain these differences. Nevertheless, it has been observed in recent African savannahs that large herbivore biomass is positively correlated with species richness. Biomass is significantly higher, up to ten times, in richer communities at low and intermediate levels of primary productivity (Fritz and Duncan, 1994), most likely due to a better resource use by functionally diverse communities. Recent large herbivore diversity is relatively low in Europe, and this may help to explain the low biomass observed, in comparison to the predicted values, in the two open environment Mediterranean communities included in the sample: Doñana and Castelporziano (Table 1). Only three large herbivores are present in those communities, namely *Sus scrofa*, *Dama dama* and *Cervus elaphus* in Doñana (Fernandez Llario, 1996; Anonymous, 2005b) and *S. scrofa*, *Capreolus capreolus* and *D. dama* in Castelporciano (Imperio et al., 2012), although in Doñana National Park, the large herbivore community also includes a number of domestic horses and cattle. It may be speculated that these low diversity large herbivore guilds are not able to use primary production with maximum efficiency and approach carrying capacity. In contrast, the Pleistocene palaeocommunities display a higher species richness and functional diversity (Rodríguez, 2001, 2004; Palombo and Mussi, 2006), and their populations were likely more prone to approach carrying capacity.

It is tempting to link the lower CC of the recent European ecosystems with the extinction of the megafauna that occurred at the end of the Pleistocene through the insufficiency of recent primary production to sustain a rich and diverse large herbivore guild. However, estimated carrying capacity for Sierra de Atapuerca today is close to 5000 kg/km^2, which is very similar to the large herbivore biomass observed in Ruaha National Park (Barnes and Douglas-Hamilton, 1982). The Ruaha National Park large herbivore guild, with a biomass of 5200 kg/km^2 is composed of 11 species, including elephant and rhino populations. Thus, the existence of an impoverished large herbivore guild in the present cannot be explained by the inability of the Holocene Mediterranean ecosystems to sustain a richer and more diverse mammalian community. Moreover, European large herbivore guilds were also more diverse during the last glacial period than in the present (Vereshchagin and Baryshnikov, 1992; García and Arsuaga, 2003; Kahlke, in press), whereas a lower CC may be expected for the last glacial than for the present. The functions used here to estimate CC lack resolution for localities with MAT below 8 °C, a value likely higher than the MAT for most of Europe during OIS3 and OIS2 isotopic stages (Barron et al., 2003; Leroy and Arpe, 2007). However, based on the data shown in Fig. 3D, it may be speculated that the CC was likely below 1000 kg/km^2 throughout the continent. Silva and Downing (1994) provide allometric equations to estimate the minimum viable population size from body weight in mammals. The minimum viable population size for the species of a typical Last Glacial herbivore guild may be estimated using Silva and Downing's equations. The faunal assemblage from Labeko Koba layer IX, located in Arrasate, northern Spain (Altuna and Mariezkurrena, 2000) and dated to approximately 40,000 yr BP (Soto Barreiro, 2003) may be taken as representative of a typical mammalian community of OIS3. It includes *Bos*/*Bison* sp., *Rupicapra rupicapra*, *Capreolus capreolus*, *Cervus elaphus*, *Megaloceros giganteus*, *Rangifer tarandus*, *Sus scrofa*, *Equus ferus*, *Coelodonta antiquitatis*, and *Mammuthus primigenius.* Based on the minimum viable population sizes estimated from body mass, the minimum large herbivore biomass of this typical and diverse OIS3 community may be estimated as some 600 kg/km^2, which is not in conflict with the output of the model presented here.

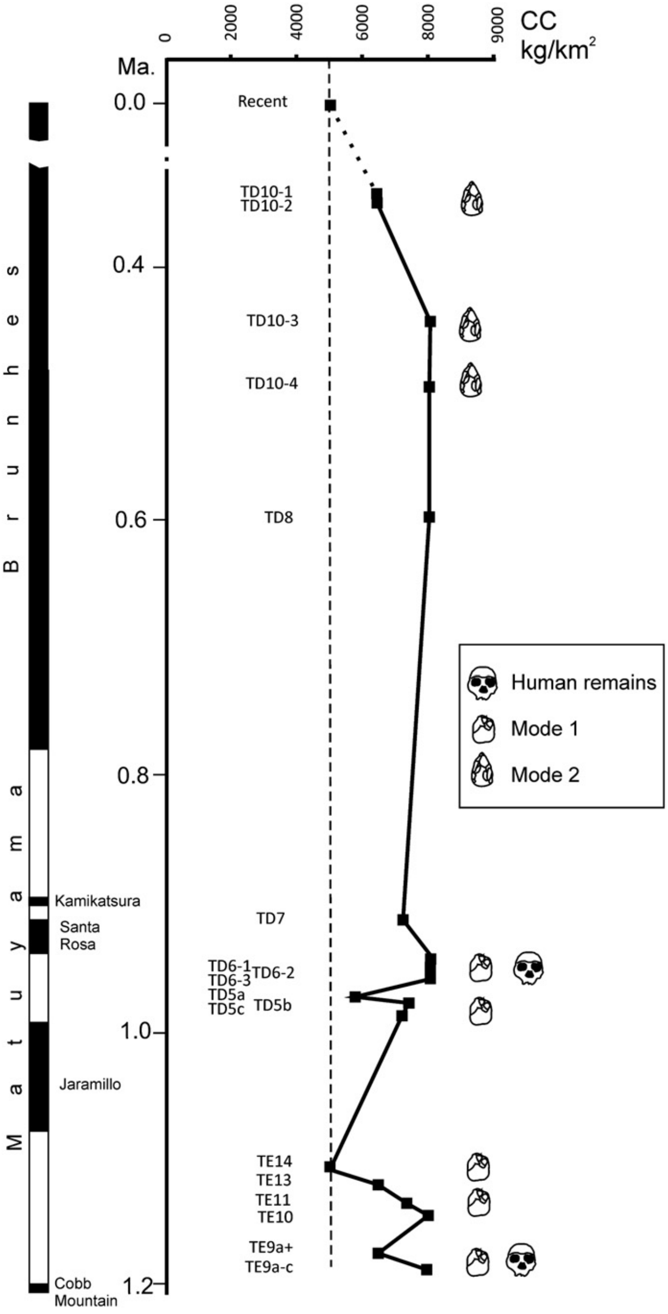

Fig. 5. Changes in carrying capacity (kg/km^2) through time at Atapuerca. The dashed line shows the estimated CC for the present for reference, as based on the observed MAT and P values.

5.3. Carrying capacity and human occupation

Human presence/absence appears not to be correlated with fluctuations in ungulate carrying capacity at Atapuerca as a general pattern (Fig. 5). The oldest human presence at Atapuerca dates back to 1.2 Ma, as evidenced by the lithic tools and human remains recovered from the TE9 unit of Sima del Elefante (Carbonell et al., 2010), and it corresponds to a period of high CC. However, the lowest value of CC along the entire Atapuerca sequence is recorded at TE14, although evidence of human presence in the form of flint lithic objects has been recovered from this unit (Ollé et al., 2013). Thus, apparently, the Atapuerca area was inhabited by humans throughout the pre-Jaramillo period despite variations in ungulate carrying capacity (Fig. 5). Ungulate CC was high again 800 Kyr ago, when *Homo antecessor* produced the TD6 assemblage, and it remained high up to, at least, 400 Kyr ago. Based on the TD sequence, Atapuerca was not inhabited by humans from the end of the early Pleistocene up to 500 Kyr ago. This time interval is recorded at Gran Dolina in the sediments of the units TD7 to TD9, all of them with no evidence of human presence (Rodríguez et al., 2011). Nevertheless, a date of 600 Kyr has been proposed on the basis of high-resolution U-series dates for the nearby site Sima de los Huesos (Bischoff et al., 2007). If such an old date for the SH human population were confirmed, it would be roughly synchronous to the TD8 assemblage. Alternatively, if the lack of evidence from Gran Dolina corresponds to an actual depopulation of Atapuerca in the 800–500 Kyr interval, it occurred when carrying capacity was high. It should be acknowledged, however, that CC represents only one criterion in the evaluation of the available resources for a human population. The second criterion is the carnivore guild and the competition between secondary consumers to access resources (Rodríguez-Gómez et al., 2013). Thus, a high ungulate CC does not necessary imply a high resource availability, as a rich carnivore guild with a high intraguild competition may make it difficult for some secondary consumers to obtain resources and, eventually, one or more species may be expelled from the community through competitive exclusion. To evaluate whether competitive exclusion played a role in the apparent retraction of the human populations at the beginning of the Middle Pleistocene, not only at Atapuerca but in Europe as a whole (Doronichev, 2010; Palombo, 2010; Dennell et al., 2011; Jiménez-Arenas et al., 2011; Mosquera et al., 2013), a good characterization of the carnivore guild of this period and the human competitive abilities are necessary. This aim is beyond the scope of the present paper, but the estimated carrying capacities presented here may be taken as a basis for future studies.

Another factor that may influence the complex relationship between carrying capacity and resource availability is related to the optimal foraging theory (Pianka, 1978). Carrying capacity represents only a crude approach to resource availability, as it represents the total amount of biomass obtained adding the biomasses of all the primary consumer populations in the area. However, not all the primary consumer species are equally suitable as food resources, and it is likely that a large amount of the biomass existing in their environment was not suitable for hominins, just because they were not able to exploit those resources with efficiency.

6. Conclusions

Ungulate carrying capacity in open environments may be estimated from the data on mean annual temperature and annual rainfall. Using this relationship, the carrying capacity of Pleistocene ecosystems may be reliably estimated from inferred values of those climatic variables in the past. The Atapuerca record indicates that the carrying capacity in this Mediterranean locality was higher throughout most of the Pleistocene than in the present. These relatively high values of CC during the Pleistocene are in accordance with the rich and diverse large herbivore guilds typical of most of the European Pleistocene mammalian communities. Although the Atapuerca archaeological record suggests the existence of discontinuities in the human occupation of this territory, variations in human occupation cannot be easily related to oscillations in ecosystems carrying capacity. Nevertheless, further research is needed to integrate the ungulate carrying capacity of past ecosystems, the competition among secondary consumers and the procurement strategies and competing capacity of early Palaeolithic populations in a model suitable to evaluate the ability of each of these three factors to explain variations in the colonization success of ancient hominin populations.

Role of funding source

The funding source had no involvement neither in study design, nor in the collection, analysis and interpretation of data.

Table 2
Mean annual temperature (MAT) in °C and annual rainfall (P) in mm/yr at Atapuerca were estimated from amphibian and reptile assemblages and subsequently used to estimate maximum sustainable ungulate biomass as limited by temperature and rainfall (maxBwT and maxBwP) in kg/km^2. The carrying capacity (CC) in kg/km^2 is obtained as the minimum of maxBwT and maxBwP. The CC is divided by the number of ungulate species in the fossil assemblage to obtain the average carrying capacity per individual species (Bsp) in kg/km^2.

	MAT (s.d.)	P (s.d.)	maxBwT (95% conf. int.)	maxBwP (95% conf. int.)	CC	N	Bsp
Recent	10.70 (—)	762 (—)	4982	9952	4982	–	–
TE19	10.30 (0.80)	667 (153)	4328 (1714–6943)	8213 (2613–13813)	4328	6	721
TD10-1	11.60 (1.83)	876 (153)	6452 (472–12433)	12038 (6438–17638)	6452	7	922
TD10-2	11.60 (1.83)	876 (153)	6452 (472–12433)	12038 (6438–17638)	6452	7	922
TD10-3	12.56 (1.18)	981 (46)	8021 (4165–11877)	13959 (12276–15643)	8021	5	1604
TD10-4	12.56 (1.18)	981 (46)	8021 (4165–11877)	13959 (12276–15643)	8021	–	–
TD8	12.56 (1.18)	981 (46)	8021 (4165–11877)	13959 (12276–15643)	8021	9	891
TD7?	12.07 (1.08)	907 (169)	7220 (3691–10750)	12605 (6420–18791)	7220	4	1805
TD6-1	12.56 (1.18)	981 (46)	8021 (4165–11877)	13959 (12276–15643)	8021	3	2674
TD6-2	12.56 (1.18)	981 (46)	8021 (4165–11877)	13959 (12276–15643)	8021	7	1146
TD6-3	12.56 (1.18)	981 (46)	8021 (4165–11877)	13959 (12276–15643)	8021	7	1146
TD5a	11.18 (1.92)	955 (116)	5766 (0–12041)	13484 (9238–17729)	5766	5	1153
TD5b	12.18 (0.96)	977 (117)	7400 (4263–10537)	13886 (9604–18168)	7400	5	1480
TD5c	12.15 (1.25)	938 (160)	7351 (3266–11436)	13172 (7316–19028)	7351	5	1470
TE14	10.70 (1.50)	883 (76)	4982 (80–9884)	12166 (9384–14948)	4982	5	996
TE13	11.60 (1.90)	864 (133)	6452 (243–12662)	11818 (6950–16686)	6452	–	–
TE11	12.10 (2.40)	687 (191)	7269 (0–15113)	8579 (1589–15570)	7269	1	7269
TE10	12.50 (1.30)	897 (111)	7923 (3675–12171)	12422 (8360–16485)	7923	2	3962
TE9a+	11.60 (1.90)	864 (133)	6452 (243–12662)	11818 (6950–16686)	6452	5	1290
TE9a	12.50 (1.30)	897 (111)	7923 (3675–12171)	12422 (8360–16485)	7923	5	1585
TE9b	12.50 (1.30)	897 (111)	7923 (3675–12171)	12422 (8360–16485)	7923	5	1585
TE9c	12.50 (1.30)	897 (111)	7923 (3675–12171)	12422 (8360–16485)	7923	5	1585

Acknowledgments

We are very grateful to the participants in the fieldwork and all the members of the Atapuerca Research Team. The excavation campaigns and the sorting of material were supported by the Junta de Castilla y León, the Fundación Atapuerca, the INAEM, MICINN projects CGL2006-13532-C03-02, CGL2009-12703-C03-01/02/03 and the University of Zaragoza. Dr. G. S. Boardman and another anonymous reviewer provided useful comments on the manuscript. This research was funded by the MINECO projects, CGL2012-38434-C03-02, CGL2012-38358 and SGR2009-324. G. Rodríguez-Gómez is the beneficiary of a predoctoral FPI Grant from the Spanish MICINN. An anonymous editor from Elsevier's Language services improved the English of the original manuscript.

References

Altuna, J., Mariezkurrena, K., 2000. Macromamíferos del yacimiento de Labeko Koba (Arrasate, pais Vasco). Munibe (Antropol.-Arkeol.) 52, 107–181.
Anonymous, 2005a. Censo de ungulados silvestres (Ciervos y Gamos) 2004. Area de Conservación.Parque Nacional de Doñana 1–8.
Anonymous, 2005b. Memoria de Actividades y Resultados del año 2005. Parque Nacional de Doñana 77.
Aquino, R., Terrones, C., Terrones, W., 2007. Assessing impact of hunting mammals in Alto Itaya river basin, Peruvian Amazon. Rev. Peru. Biol. 14, 181–186.
Astle, W.L., Graham, A.D., 1976. Ecological investigations of the UNDP in the Okavango Delta. Okavango Delta Symposium, Gaborne, pp. 81–91.
Bagchi, S., Goyal, S.P., Sankar, K., 2004. Herbivore density and biomass in a semi-arid tropical dry deciduous forest of western India. J. Trop. Ecol. 20, 475–478.
Barnes, I., Douglas-Hamilton, I., 1982. The numbers and distribution patterns of large mammals in the Ruaha-Rungwa Area of Southern Tanzania. J. Appl. Ecol. 19, 411–425.
Barron, E., Andel, T.H.v, Pollard, D., 2003. Glacial environments II: Reconstructing the climate of Europe in the LAst Glaciation. In: Andel, T.H.v, Davis, W. (Eds.), Neanderthals and Modern Humans in the European Landscape During the Last Glaciation. McDonald Institute for Archaeological Research, Cambridge, pp. 57–78.
Berger, G.W., Pérez-González, A., Carbonell, E., Arsuaga, J.L., Bermúdez de Castro, J.-M., Ku, T.-L., 2008. Luminescence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain. J. Hum. Evol. 55, 300–311.
Bermúdez de Castro, J.M., Pérez-González, A., Martinón-Torres, M., Gómez-Robles, A., Rosell, J., Prado, L., Sarmiento, S., Carbonell, E., 2008. A new early Pleistocene hominin mandible from Atapuerca-TD6, Spain. J. Hum. Evol. 55, 729–735.
Bermúdez de Castro, J.M., Martinón-Torres, M., Robles, A.G., Prado, L., Carbonell, E., 2010. New human evidence of the Early Pleistocene settlement of Europe, from Sima del Elefante site (Sierra de Atapuerca, Burgos, Spain). Quat. Int. 223–224, 431–433 (Oldest Human Expansions in Eurasia: Favouring and Limiting Factors).
Bhola, N., Ogutu, J.O., Piepho, H.P., Said, M.Y., Reid, R.S., Hobbs, N.T., Olff, H., 2012. Comparative changes in density and demography of large herbivores in the Masai Mara Reserve and its surrounding human-dominated pastoral ranches in Kenya. Biodivers. Conserv. 21, 1509–1530.
Binford, L.R., 1981. Bones. Ancient Men and Modern Myths. Academic Press, Orlando.
Binford, L.R., 1985. Human ancestors: changing views of their behavior. J. Anthropol. Archaeol. 4, 292–327.
Bischoff, J.L., Williams, R.W., Rosenbauer, R.J., Aramburu, A., Arsuaga, J.L., García, N., Cuenca-Bescós, G., 2007. High-resolution U-series dates from the Sima de los Huesos hominids yields: implications for the evolution of the early Neanderthal lineage. J. Archaeol. Sci. 34, 763–770.
Biswas, S., Sankar, K., 2002. Prey abundance and food habit of tigers (*Panthera tigris tigris*) in Pench National Park, Madhya Pradesh, India. J. Zool. 256, 411–420.
Blain, H.A., 2005. Contribution de la Paléoherpétofaune (Amphibia et Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne. Muséum National d'Histoire Naturelle, Paris.
Blain, H.A., 2009. Contribution de la Paléoherpétofaune (Amphibia et Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne. Treballs del Museu de Geología de Barcelona, 16 39–170.
Blain, H.A., Bailon, S., Cuenca-Bescós, G., 2008. The Early–Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 177–192.
Blain, H.A., Bailon, S., Cuenca-Bescós, G., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009. Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain. J. Hum. Evol. 56, 55–65.
Blain, H.A., Bailon, S., Cuenca-Bescós, G., Bennàsar, M., Rofes, J., López-García, J.M., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010. Climate and environment of the earliest West European hominins inferred from the amphibian and squamate reptile assemblages: Sima del Elefante Lower Red Unit, Atapuerca, Spain. Quat. Sci. Rev. 29, 3034–3044.
Blain, H.-A., López-García, J.M., Cuenca, G., 2011. A very diverse amphibian and reptile assemblage from the late Middle Pleistocene of the Sierra de Atapuerca (Sima del Elefante, Burgos, Northwestern Spain). Geobios 157–172.
Blain, H.-A., Cuenca-Bescós, G., Lozano-Fernández, I., López-García, J.M., Ollé, A., Rosell, J., Rodríguez, J., 2012. Investigating the Mid-Brunhes Event in the Spanish terrestrial sequence. Geology 40, 1051–1054.
Blain, H.-A., Cuenca-Bescós, G., Burjachs, F., López-GarcÍA, J.M., Lozano-Fernández, I., Rosell, J., 2013a. Early Pleistocene palaeoenvironments at the time of the Homo antecessor settlement in the Gran Dolina cave (Atapuerca, Spain). J. Quat. Sci. 28, 311–319.
Blain, H.A., Gleed-Owen, C.P., López-García, J.M., Carrión, J.S., Jennings, R., Finlayson, G., Finlayson, C., Giles Pacheco, F., 2013b. Climatic conditions for the last Neanderthals: herpetofaunal record of Gorham's Cave, Gibraltar. J. Hum. Evol. 64, 289–299.
Bodendorfer, T., Hoppe-Dominik, B., Fischer, F., Eduard Linsenmair, K., 2006. Prey of the leopard (*Panthera pardus*) and the lion (*Panthera leo*) in the Comoé and Marahoué National Parks, Côte d'Ivoire, West Africa. Mammalia 70, 231–246.
Bodmer, R.E., 1989. Ungulate biomass in relation to feeding strategy wthin Amazonian forests. Oecologia 81, 547–550.
Bodmer, R.E., Fang, T.G., Moya, I.L., Gill, R., 1994. Managing wildlife to conserve amazonian forests: population biology and economic considerations of game hunting. Biol. Conserv. 67, 29–35.

Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L., Díez, J.C., Rosas, A., Cuenca-Bescós, G., Sala, R., Mosquera, M., Rodríguez, X.P., 1995. Lower Pleistocene hominids and artifacts from Atapuerca TD6 (Spain). Science 269, 826–830.

Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L., Allue, E., Bastir, M., Benito, A., Cáceres, I., Canals, T., Díez, J.C., van der Made, J., Mosquera, M., Ollé, A., Pérez-González, A., Rodríguez, J., Rodríguez, X.P., Rosas, A., Rosell, J., Sala, R., Vallverdú, J., Vergés, J.M., 2005. An Early Pleistocene hominin mandible from Atapuerca-TD6, Spain. Proc. Natl. Acad. Sci. U. S. A. 102, 5674–5678.

Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Olle, A., Mosquera, M., Huguet, R., van der Made, J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D.E., Martinón-Torres, M., Rodríguez, X.P., Stock, G.M., Vergès, J.M., Allué, E., Burjachs, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodríguez, J., Rosell, J., Arsuaga, J.L., 2008. The first hominin of Europe. Nature 452, 465–470.

Carbonell, E., Cáceres, I., Lozano, M., Saladié, P., Rosell, J., Lorenzo, C., Vallverdú, J., Huguet, R., Canals, A., Bermúdez de Castro, J.M., 2010. Cultural cannibalism as a Paleoeconomic System in the European Lower Pleistocene. Curr. Anthropol. 51, 539–549.

Caro, T.M., 1999. Abundance and distribution of mammals in Katavi National Park, Tanzania. Afr. J. Ecol. 37, 305–313.

Coe, M.J., Cumming, D.H., Phillipson, J., 1976. Biomass and production of large african herbivores in relation to rainfall and primary production. Oecologia 22, 341–354.

Cordain, L., Miller, J.B., Eaton, S.B., Mann, N., Holt, S.H.A., Speth, J.D., 2000. Plant–animal subsistence ratios and macronutrient energy estimations in worldwide hunter–gatherer diets. Am. J. Clin. Nutr. 71, 682–692.

Croitor, R., Brugal, J.-P., 2010. Ecological and evolutionary dynamics of the carnivore community in Europe during the last 3 million years. Quat. Int. 212, 98–108.

Cuenca-Bescós, G., García, N., 2007. Biostratigraphic succession of th e Early and Middle Pleistocene mammal faunas of the Atapuelca cave sites (Burgos, Spain). Cour. Forschungstinst. Senckenb. 259, 99–110.

Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., De Marfá, R.J., Galindo-Pellicena, M.A., Bennásar-Serra, M.L., Melero-Rubio, M., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010. Biochronology of Spanish Quaternary small vertebrate faunas. Quat. Int. 212, 109–119.

Cuenca-Bescós, G., Melero-Rubio, M., Rofes, J., Martínez, I., Arsuaga, J.L., Blain, H.A., López-García, J.M., Carbonell, E., Bermudez de Castro, J.M., 2011. The Early–Middle Pleistocene environmental and climatic change and the human expansion in Western Europe: a case study with small vertebrates (Gran Dolina, Atapuerca, Spain). J. Hum. Evol. 60, 481–491.

Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., Rabal-Garcés, R., Sauqué, V., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. The small mammals of Sima del Elefante (Atapuerca, Spain) and the first entrance of Homo in Western Europe. Quat. Int. 295, 28–35.

Danell, K., Duncan, P., Bergström, R., Pastor, J., 2006. Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Cambridge University Press, Cambridge.

Deichmann, U., Eklundh, L., 1991. Global Digital Data Sets for Land Degradation Studies: A GIS Approach. UNEP/GEMS and GRID, Nairobi, Kenya.

Dennell, R.W., Martinón-Torres, M., Bermúdez de Castro, J.M., 2011. Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. Quat. Sci. Rev. 30, 1511–1524.

Dinerstein, E., 1979. An ecological survey of the royal Karnali-Bardia Wildlife Reserve, Nepal. Part I: Vegetation, modifying factors, and successional relationships. Biol. Conserv. 15, 127–150.

Dinerstein, E., 1980. An ecological survey of the Royal Karnali-Bardia Wildlife Reserve, Nepal: Part III: Ungulate populations. Biol. Conserv. 18, 5–37.

Doronichev, V.G.L., 2010. Beyond the Acheulean: a review on the Lower Paleolithic occupation of Western Eurasia. Quat. Int. 1–18.

Duval, M., Falguères, C., Bahain, J.-J., 2012. Age of the oldest hominin settlements in Spain: contribution of the combined U-series/ESR dating method applied to fossil teeth. Quat. Geochronol. 10, 412–417.

Duvigneaud, P., 1971. Productivity of forest ecosystems. Proceedings of the Brussels symposium organized by Unesco and the International Biological Program, París.

East, R., 1984. Rainfall, soil nutrient status and biomass of large African savanna mammals. Afr. J. Ecol. 22, 245–270.

Eisenberg, J.F., Seidensticker, J., 1976. Ungulates in southern Asia: a consideration of biomass estimates for selected habitats. Biol. Conserv. 10, 293–308.

Eisenberg, J.F., O'connell, M.A., August, P.V., 1979. Density, productivity, and distribution of mammals in two Venezuelan habitats. In: Eisenberg, J.F. (Ed.), Vertebrate Ecology in the Northern Neotropics. Smithsonian Institution Press, Wasinhgton D. C., pp. 187–207.

Endo, W., Peres, C.A., Salas, E., Mori, S., Sanchez-Vega, J.-L., Shepard, G.H., Pacheco, V., Yu, D.W., 2010. Game vertebrate densities in hunted and nonhunted forest sites in Manu National Park, Peru. Biotropica 42, 251–261.

Escos, J., Alados, C.L., 1988. Estimating mountain ungulate density in Sierras de Cazorla y Segura. Mammalia 52, 425–428.

Falguères, C., Bahain, J.-J., Yokoyama, Y., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., Bischof, J.L., Dolo, J.M., 1999. Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. J. Hum. Evol. 37, 343–352.

Falguères, C., Bahain, J.-J., Yokoyama, Y., Bischoff, J.L., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., Dolo, J.M., 2001. Datations par RPE et U–Th des sites Pleistocenes d'Atapuerca: Sima de los Huesos, Trinchera Dolina et Trinchera Galería. Bilan géochronologique. L'Anthropologie 105, 71–81.

Fernandez Llario, P., 1996. Ecologia del jabali en Doñana: parametros reproductivos e impacto ambiental. Extremadura.

Field, C.R., Laws, R.M., 1970. The distribution of the larger herbivores in the Queen Elizabeth National Park, Uganda. J. Appl. Ecol. 7, 273–294.

Focardi, S., Isotti, R., Tinelli, A., 2002. Line transect estimates of ungulate populations in a Mediterranean forest. J. Wildl. Manag. 66, 48–58.

Foster, J.B., Coe, M.J., 1968. The biomass of game animals in Nairobi National Park, 1960–66. J. Zool. 155, 413–425.

Fritz, H., Duncan, P., 1994. On the carrying capacity for large ungulates of African savanna ecosystems. Proc. R. Soc. Lond. B 256, 77–82.

Fritz, H., Loison, A., 2006. Large herbivores across biomes. In: Danell, K., Duncan, P., Bergström, R., Pastor, J. (Eds.), Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Cambridge University Press, Cambrige, pp. 19–49.

Gamble, C., 1995. Large mammals, climate and resource richness in Upper Pleistocene Europe. Acta Zool. Cracov. 38, 155–175.

García, N., Arsuaga, J.L., 2003. Last Glaciation cold-adapted faunas in the Iberian Peninsula. Deinsea 9, 159–169.

Gaudzinski, S., Roebroeks, W., 2000. Adults only. Reindeer hunting at the Middle Paleolithic site Salzgitter Lebenstedt, Northern Germany. J. Hum. Evol. 38, 497–521.

Gil, E., Hoyos, M., 1987. Contexto estratigráfico. In: Aguirre, E., Carbonell, E., Bermúdez de Castro, J.M. (Eds.), El hombre fósil de Ibeas y el Pleistoceno de la Sierra de Atapuerca. Junta de Castilla y León. Consejería de Cultura y Bienestar Social, Valladolid, pp. 45–47.

Godinho, R., Teixeira, J., Rebelo, R., Segurado, P., Loureiro, A., Álvares, F., Gomes, N., Cardoso, P., Camilo-Alves, C., Brito, J.C., 1999. Atlas of the continental Portuguese herpetofauna: an assemblage of published and new data. Rev. Esp. Herpetol. 13, 61–82.

Haugaasen, T., Peres, C.A., 2005. Mammal assemblage structure in Amazonian flooded and unflooded forests. J. Trop. Ecol. 21, 133–145.

Hoppe-Dominik, B., 1989. Premier recensement des grands mammifères dans le Parc National de la Marahoué en Côte d'Ivoire. Rev. Zool. Afr. 103, 21–27.

Imperio, S., Focardi, S., Santini, G., Provenzale, A., 2012. Population dynamics in a guild of four Mediterranean ungulates: density-dependence, environmental effects and interspecific interactions. Oikos 121, 1613–1626.

Janson, C.H., Emmons, L.H., 1990. Ecological structure of the non flying mammal community at Cocha Casu Biological station, Manu National Park, Perú. In: Gentry, A.H. (Ed.), Four Neotropical Rainorests. Yale University Press, New Haven, pp. 314–338.

Jedrzejewska, B., Jedrzejewski, W., Bunevich, A.N., Miłkowski, L., Krasiński, Z.A., 1997. Factors shaping population densities and increase rates of ungulates in Bialowieza Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. Acta Theriol. 42, 399–451.

Jiménez-Arenas, J.M., Santonja, M., Botella, M., Palmqvist, P., 2011. The oldest handaxes in Europe: fact or artefact? J. Archaeol. Sci. 38, 3340–3349.

Joannin, S., Quillevere, F., Suc, J.-P., Lecuyer, C., Martineau, F., 2007. Early Pleistocene climate changes in the central Mediterranean region as inferred from integrated pollen and planktonic foraminiferal stable isotope analyses. Quat. Res. 67, 264–274.

Kahlke, R.-D., 2013. The origin of Eurasian Mammoth Faunas (Mammuthus–Coelodonta Faunal Complex). Quat. Sci. Rev. http://dx.doi.org/10.1016/j.quascirev.2013.01.012 (in press).

Kahlke, R.-D., García, N., Kostopoulos, D.S., Lacombat, F., Lister, A.M., Mazza, P., Spassov, N., Titov, V.V., 2011. Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. Quat. Sci. Rev. 11–12, 1368–1395.

Kahurananga, J., 1981. Population estimates, densities and biomass of large herbivores in Simanjiro Plains, Northern Tanzania. Afr. J. Ecol. 19, 225–238.

Karanth, K.U., Nichols, J.D., 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79, 2852–2862.

Kawanishi, K., Sunquist, M.E., 2004. Conservation status of tigers in a primary rainforest of Peninsular Malaysia. Biol. Conserv. 120, 329–344.

Khan, J.A., Chellam, R., Rodgers, W.A., Johnsingh, A.J.T., 1996. Ungulate densities and biomass in the tropical dry deciduous forests of Gir, Gujarat, India. J. Trop. Ecol. 12, 149–162.

Kumara, H.N., Rathnakumar, S., Sasi, R., Singh, M., 2012. Conservation status of wild mammals in Biligiri Rangaswamy Temple Wildlife Sanctuary, the Western Ghats, India. Curr. Sci. 103, 933–940.

Kutilek, M.J., 1974. The density and biomass of large mammals in Lake Nakuru National Park. Afr. J. Ecol. 12, 201–212.

Lamprey, H.F., 1964. Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the masai steppe in Tanganyika. Afr. J. Ecol. 2, 1–46.

Lanszki, J., Márkus, M., Újváry, D., Szabó, A., Szemethy, L., 2012. Diet of wolves *Canis lupus* returning to Hungary. Acta Theriol. 57, 189–193.

Laws, R.M., 1970. Elephants and habitats in Nort Bunyoro, Uganda. Afr. J. Ecol. 8, 163–180.

Leroy, S.A.G., Arpe, K., 2007. Glacial refugia for summer-green trees in Europe and southwest Asia as proposed by ECHAM3 time-slice atmospheric model simulations. J. Biogeogr. 34, 2115–2128.

Leroy, S.A.G., Arpe, K., Mikolajewicz, U., 2011. Vegetation context and climatic limits of the Early Pleistocene hominin dispersal in Europe. Quat. Sci. Rev. 30, 1448–1463.

Levick, S.R., Asner, G.P., Kennedy-Bowdoin, T., Knapp, D.E., 2009. The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. Biol. Conserv. 142, 1693–1700.

Lieth, H.F.H., 1973. Primary production: terrestrial ecosystems. Hum. Ecol. 1, 303–332.

López-García, J., Blain, H.A., De Marfá, R., García, A., Martinell, J., Bennásar, M.L., Cuenca-Bescós, G., 2011. Small-mammals from the Middle Pleistocene layers of the Sima del Elefante (Sierra de Atapuerca, Burgos, northwestern Spain). Geol. Acta 9, 29–43.

Mandujano, S., 2007. Carrying capacity and potential production of ungulates for human use in a Mexican tropical dry forest. Biotropica 39, 519–524.

Mandujano, S., Naranjo, E.J., 2010. Ungulate biomass across a rainfall gradient: a comparison of data from neotropical and palaeotropical forests and local analyses in Mexico. J. Trop. Ecol. 26, 13–23.

Marean, C.W., 1989. Sabertooth cats and their relevance for early hominid diet and evolution. J. Hum. Evol. 18, 559–582.

Mattioli, L., Capitani, C., Gazzola, A., Scandura, M., Apollonio, M., 2011. Prey selection and dietary response by wolves in a high-density multi-species ungulate community. Eur. J. Wildl. Res. 57, 909–922.

McCullough, D.R., 1992. Concepts of large herbivore population dynamics. In: McCullough, D.R., a.R.H.B. (Eds.), Wildlife 2001: Populations. Elsevier, London, pp. 967–984.

McNaughton, S.J., Oesterheld, M., Frank, D.A., Williams, K.J., 1989. Ecosystems level patterns of primary productuvity and herbivory in terrestrial habitats. Nature 341, 142–144.

Meier, T., 2012. Large Mammals…How many are there? Center for Science, Resources, and Learning Denali National Park and Preserve.

Meloro, C., Clauss, M., 2012. Predator–prey biomass fluctuations in the Plio-Pleistocene. Palaios 27, 90–96.

Mendes Pontes, A.R., 2004. Ecology of a community of mammals in a seasonally dry forest in Roraima, Brazilian Amazon. Mamm. Biol. 69, 319–336.

Mentis, M.T., 1970. Estimates of natural biomasses of large herbivores in the Unfolosi Game Reserve Area. Mammalia 84, 363–393.

Milligan, K., Ajayi, S.S., Hall, J.B., 1982. Density and biomass of the large herbivore community in Kainji Lake National Park, Nigeria. Afr. J. Ecol. 20, 1–12.

Mizutani, F., 1999. Biomass density of wild and domestic herbivores and carrying capacity on a working ranch in Laikipia District. Afr. J. Ecol. 37, 226–240.

Moigne, A.M., Barsky, R., 1999. Large mammal assemblages from Lower Palaeolithic sites in France: La Caune de l'Arago, Terra Amata, Orgnac 3 and Cagny l'Epinette. In: Gaudzinski, S., Turner, E. (Eds.), The Role of Early Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages. Habelt, Bonn, pp. 219–235.

Montfort, A., 1972. Densities, biomasses and structures des populations d'Oungulés sauvages au Parc de L'Akagera (Rwanda). Terre et Vie 20, 210–256.

Moreno, D., 2011. Datation par esr de quartz optiquement blanchis (esr-ob) de la région de Atapuerca (Burgos, Espagne). application au site préhistorique de Gran Dolina (contexte karstique) et aux systèmes fluviatiles quaternaires de l'Arlanzón et l'Arlanza. Universitat Rovira i Virgili, Tarragona.

Morgan, B.J., 2007. Group size, density and biomass of large mammals in the Reserve de Faune du Petit Loango, Gabon. Afr. J. Ecol. 45, 508–518.

Mosquera, M., Ollé, A., Rodríguez, X.P., 2013. From Atapuerca to Europe: tracing the earliest peopling of Europe. Quat. Int. 295, 130–137.

Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B., Running, S.W., 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300, 1560–1563.

Ninyerola, M., Pons, X., JM.R., 2005. Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. [Data base on CD]. Barcelona U.A.d., Bellaterra.

Novack, A.J., Main, M.B., Sunquist, M.E., Labisky, R.F., 2005. Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. J. Zool. 267, 167–178.

Oesterheld, M., Sala, O.E., McNaughton, S.J., 1992. Effect of animal husbandry on herbivore-carrying capacity at a regional scale. Nature 356, 234–236.

Ollé, A., Mosquera, M., Rodríguez Xosé, P., de Lombera-Hermida, A., García-Antón, M.D., García-Medrano, P., Peña, L., Menéndez, L., Navazo, M., Terradillos, M., Bargalló, A., Márquez, B., Sala, R., Carbonell, E., 2013. The Early and Middle Pleistocene technological record from Sierra de Atapuerca (Burgos, Spain). Quat. Int. 295, 138–167.

Ortega, A.I., Benito-Calvo, A., Pérez-González, A., Martín-Merino, M.A., Pérez-Martínez, R., Parés, J.M., Aramburu, A., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. Evolution of multilevel caves in the Sierra de Atapuerca (Burgos, Spain) and its relation to human occupation. Geomorphology 196, 122–137.

Owaga, M.A., 1980. Primary productivity and herbage utilization by herbivores in Kaputei Plains, Kenya. Afr. J. Ecol. 18, 1–5.

Palombo, M.R., 2010. A scenario of human dispersal in the northwestern Mediterranean throughout the Early to Middle Pleistocene. Quat. Int. 223–224, 179–194.

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. Quat. Int. 149, 94–103.

Palombo, M.R., Valli, A.F.M., 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, pp. 329–347.

Parés, J.M., Pérez-González, A., 1995. Paleomagnetic age for hominid fossils at Atapuerca archaeological site. Nature 269, 830–832.

Parés, J.M., Pérez-González, A., 1999. Magnetochronology and stratigraphy at Gran Dolina section, Atapuerca (Burgos, Spain). J. Hum. Evol. 37, 325–342.

Parés, J.M., Pérez-González, A., Rosas, A., Benito, A., Bermúdez de Castro, J.M., Carbonell, E., Huguet, R., 2006. Matuyama-age lithic tools from the Sima del Elefante site, Atapuerca (northern Spain). J. Hum. Evol. 50, 163–169.

Parés, J.M., Arnold, L., Duval, M., Demuro, M., Pérez-González, A., Bermúdez de Castro, J.M., Carbonell, E., Arsuaga, J.L., 2013. Reassessing the age of Atapuerca-TD6 (Spain): new paleomagnetic results. J. Archaeol. Sci. 40, 4586–4595.

Payne, J., Andau, M., 1991. Large mammals in Sabah. In: Kiew, R. (Ed.), The state of nature conservation in Malaysia, pp. 177–183.

Pettorelli, N., Bro-Jorgensen, J., Durant, S.M., Blackburn, T., Carbone, C., 2009. Energy availability and density estimates in African ungulates. Am. Nat. 173, 698–704.

Pianka, E.R., 1978. Evolutionary Ecology. Harper and Row, New York.

Pleguezuelos, J.M., Márquez, M., Lizana, M., 2004. Atlas y libro rojo de los Anfibios y Reptiles de España. Direccion General de Conservacion de la Naturaleza. Asociacion Herpetologica Española, Madrid.

Plumptre, A.J., Harris, S., 1995. Estimating the biomass of large mammalian herbivores in a tropical montane forest: a method of faeca. J. Appl. Ecol. 32, 111–120.

Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M.E., Eisenberg, J.F., 2003. Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. Biol. Conserv. 109, 297–310.

Prins, H.H.T., Douglas-Hamilton, I., 1990. Stability in a multi-species assemblage of large herbivores in East Africa. Oecologia 83, 392–400.

Prins, H.H.T., Reitsman, J., 1989. Mammalian biomass in an African ecuatorial rain forest. J. Anim. Ecol. 58, 851–861.

Raia, P., Meloro, C., Barbera, C., 2007. Inconstancy in predator/prey ratios in Quaternary large mammal communities of Italy, with an appraisal of mechanisms. Quat. Res. 67, 255–263.

Ramesh, T., Sridharan, N., Sankar, K., Qureshi, Q., Selvan, K.M., Gokulakkannan, N., Francis, P., Narasimmarajan, K., Jhala, Y.V., Gopal, R., 2012. Status of large carnivores and their prey in tropical rainforests of South-Western Ghats, India. Trop. Ecol. 53, 137–148.

Rannestad, O.T., Danielsen, T., Moe, S.R., Stokke, S., 2006. Adjacent pastoral areas support higher densities of wild ungulates during the wet season than the Lake Mburo National Park in Uganda. J. Trop. Ecol. 22, 675–683.

Reza, A.H.M.A., Feeroz, M.M., Islam, M.A., 2002. Prey species density of bengal tiger in the Sundarbanks. J. Asiat. Soc. Bangladesh 28, 35–42.

Robinson, J.G., Bennett, E.L., 2004. Having your wildlife and eating it too: an analysis of hunting sustainability across tropical ecosystems. Anim. Conserv. 7, 397–408.

Rodríguez, J., 2001. Structure de la communauté de mammifères pléistocenes de Gran Dolina (Sierra de Atapuerca, Burgos, Espagne). L'Anthropologie 105, 131–157.

Rodríguez, J., 2004. Stability in Pleistocene Mediterranean mammalian communities. Palaeogeogr. Palaeoclimatol. Palaeoecol. 207, 1–22.

Rodríguez, J., 2006. Structural continuity and multiple alternative stable states in Middle Pleistocene European mammalian communities. Palaeogeogr. Palaeoclimatol. Palaeoecol. 239, 355–373.

Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., Van der Made, J., Pérez González, A., Blain, H.A., Expósito, I., López-García, J.M., García Antón, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez, X.P., Díez, C., Rofes, J., Sala, R., Saladié, P., Vallverdú, J., Bennasar, M.L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quat. Sci. Rev. 30, 1396–1412.

Rodríguez, J., Rodríguez-Gómez, G., Martín-González, J.A., Goikoetxea, I., Mateos, A., 2012. Predator–prey relationships and the role of Homo in Early Pleistocene food webs in Southern Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol. 365–366, 99–114.

Rodríguez-Gómez, G., Rodríguez, J., Martín-González, J.Á., Goikoetxea, I., Mateos, A., 2013. Modeling trophic resource availability for the first human settlers of Europe: the case of Atapuerca TD6. J. Hum. Evol. 64, 645–657.

Rodríguez-Gómez, G., Rodríguez, J., Mateos, A., Martín-González, J.A., Goikoetxea, I., 2013. Food web structure in the European Pleistocene. J. Taphonomy (in press).

Roebroeks, W., 2001. Hominid behaviour and the earliest occupation of Europe: an exploration. J. Hum. Evol. 41, 437–461.

Rosas, A., Huguet, R., Pérez-González, A., Carbonell, E., Bermúdez de Castro, J.M., Vallverdú, J., van der Made, J., Allué, E., García, N., Martínez-Pérez, R., Rodríguez, J., Sala, R., Saladié, P., Benito, A., Martínez-Maza, C., Bastir, M., Sánchez, A., Parés, J.M., 2006. The "sima del Elefante" cave site at Atapuerca (Spain). Estud. Geol. 62, 327–348.

Rosenzweigh, M., 1968. Net primary productivity of terrestrial communities: prediction from climatological data. Am. Nat. 102, 67–74.

Runyoro, V.A., Hofer, H., Chausin, E.B., Moehlman, P.D., 1995. Long-term trends in the herbivore populations of the Ngorongoro Crater, Tanzania. In: Sinclair, A.R.E., Arcese, P. (Eds.), Serengeti II. Chicago University Press, Chicago, pp. 146–468.

Sabbe, H., Veroustraete, F., 2009. Estimation of net primary and net ecosystem productivity of European terrestrial ecosystems by means of the C-Fix model and NOAA/AVHRR data. Int. J. Remote Sens. 30, 41–56.

Sayre, N.F., 2008. The genesis, history and limits of carrying capacity. Ann. Assoc. Am. Geogr. 98, 120–134.

Schaller, G.B., 1983. Mammals and their biomass on a Brazilian ranch. Arq. Zool. 31, 1–36.

Silva, M., Downing, J.A., 1994. Allometric scaling of minimal mammal densities. Conserv. Biol. 8, 732–743.

Sinsin, B., Tehou, A.C., Daouda, I., Saidou, A., 2002. Abundance and species richness of larger mammals in Pendjari National Park in Benin. Mammalia 66, 369–380.

Soto Barreiro, M.J., 2003. Cronología radiométrica, ecología y clima del Paleolítico Cantábrico. Monografías Museo Nacional y Centro de Investigación de Altamira 19.

Speth, J.D., 2010. The Paleoanthropology and Archaeology of Big-Game Hunting. Springer.

Srikosamatara, S., 1993. Density and biomass of large herbivores and other mammals in a dry tropical forest, Western Thailand. J. Trop. Ecol. 9, 33–43.

Stark, M.A., 1986. The numbers, seasonal distribution patterns, densities and biomass of the large herbivores, Benoue National Park, Cameroon. Mammalia 50, 341.

Suc, J.P., Popescu, S.-M., 2005. Pollen records and climatic cycles in the North Mediterranean region since 2.7 Ma. In: Head, M.J., Gibbard, P.L. (Eds.), Early–Middle Pleistocene Transitions: the Land–Ocean Evidence. Geological Society, Special Publications, London, pp. 147–158.

Svenning, J.-C., 2002. A review of natural vegetation openness in north-western Europe. Biol. Conserv. 104, 133–148.

Tilson, R., Henschel, J., 1980. Prey selection by spotted hyaena (*Crocuta crocuta*) in the Namib Desert. Madoqua 12, 41–49.

Truvé, J., Cederlund, G., 2005. Mammals in the Areas Adjacent to Forsmark and Oskarshamn. Svensk Kärnbränslehantering AB, Stockholm.

Valeix, M., Fritz, H., Dubois, S., Kanengoni, K., Alleaume, S., Saïd, S., 2007. Vegetation structure and ungulate abundance over a period of increasing elephant abundance in Hwange National Park, Zimbabwe. J. Trop. Ecol. 23, 87–93.

Van Lavieren, L.P., Esser, J.D., 1979. Numbers, distribution and habitat prefrence of large mammals in Bouba Ndjida National Park, Cameroon. Afr. J. Ecol. 17, 141–143.

Varma, S., 2007. Population Estimation of Mammals in Nagarahole National Park: Validation of the results from Large Mammal Census and Long-term Study from Rajiv Gandhi National Park (Nagarahole NP). Asian Elephant Research & Conservation Centre (A Division of Asian Nature Foundation), C/o Centre for Ecological Sciences, Indian Institute of Science, Bangalore.

Vereshchagin, N.K., Baryshnikov, G.F., 1992. The ecologycal structure of the "Mammoth Fauna" in Eurasia. Ann. Zool. Fenn. 28, 253–259.

Viljoen, P.C., 1993. The effects of changes in prey availability on lion predation in a large natural ecosystem in northern Botswana. Symp. Zool. Soc. Lond. 1993, 193–213.

Wang, S.W., 2010. Estimating population densities and biomass of ungulates in the temperate ecosystem of Bhutan. Oryx 44, 376–382.

Wanyama, F., Muhabwe, R., Plumptre, A.J., Chapman, C.A., Rothman, J.M., 2010. Censusing large mammals in Kibale National Park: evaluation of the intensity of sampling required to determine change. Afr. J. Ecol. 48, 953–961.

Western, D., 1973. The structure dynamics and changes of the Amboseli ecosystem. (Ph. D. Thesis) Nairobi University (S.l.).

White, L.J.T., 1994. Biomass of rain forest mammals in the Lopé Reserve, Gabon. J. Anim. Ecol. 63 (3), 499–512 (63, 499–512).

Williams, D.F., Thunell, R.C., Tappa, E., Rio, D., Raffi, I., 1988. Chronology of the Pleistocene isotope record 0–1.88 my BP. Palaeogeogr. Palaeoclimatol. Palaeoecol. 64, 221–240.