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From meat availability to hominin and carnivore biomass: A paleosynecological approach to reconstructing predator-prey biomass ratios in the Pleistocene

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ABSTRACT

Reconstructing the conditions and circumstances under which the human lineage evolved is of great interest to those disciplines related to human evolution, especially in fields such as archaeoecology and human paleoecology. A mathematical model was presented almost a decade ago aimed to reconstructing the human populations that the Pleistocene paleoecosystems could support. This model followed a paleosynecological perspective, being focused on: (i) estimating the availability of meat resources in the paleoecosystems, as these resources are vital for human survival; and (ii) measuring the level of competition for these resources among the members of the carnivore guild, including hominins. The model has been applied since then to several Pleistocene localities of Europe, with particular emphasis on the Orce and Sierra de Atapuerca sites. In this study, we use the model for estimating predator-prey biomass ratios and compare the model outputs with the values measured in present-day African ecosystems. The results obtained confirm that our paleosynecological approach provides estimates of predator-prey biomass ratios that are broadly similar to those measured in the extant ecosystems. However, our estimates tend to be slightly higher than expected, which is probably due to the weight of species that satisfy part of their nutritional requirements with resources other than the meat from large herbivores. This allows us to assume that our model performs relatively well, although it has room for methodological improvements.

1. Introduction

Knowing the characteristics of past ecosystems is of great interest, as it allows to gain deeper insights on how species evolved and which parameters may have constrained their evolution. Several approaches allow (i) reconstructing paleoenvironments; (ii) evaluating resource availability; (iii) deciphering trophic niches; and (iv) assessing the level of interspecific competition in the paleocommunities. Some of these approaches are based on inferences from physical parameters and climate predictions (e.g., Kay and Madden, 1997; Kay et al., 2012; Mendoza, 2002; Mendoza et al., 2002; Rodríguez et al., 2014; Rodríguez and Mateo, 2018; Vidal-Cordasco et al., 2022). Others evaluate the access to food resources through analyzing community structure and taphonomic biases based on actualistic studies: for example, those aimed

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to studying the evolution of our lineage (e.g., Blumenschine and Marean, 1993; Domínguez-Rodrigo and Organista, 2007; Faith et al., 2007; Egeland, 2008; Saladié et al., 2014; Lozano et al., 2016; Konidaris, 2022). In other cases, competition intensity in the access to environmental resources has been inferred from predator-prey relationships (e.g., Raia et al., 2007; Meloro and Clauss, 2012). Inspired by previous studies (e.g., Bermúdez de Castro et al., 1995; Fariña, 1996; Palmqvist et al., 2003; Vizcaíno et al., 2004, 2010), Rodríguez-Gómez et al. (2013, 2014a, 2015, 2016a) developed a paleosynecological model (called in this study PSEco) that estimates the production of meat resources available to the secondary consumers of a paleocommunity of large mammals. Compared to previous approaches, the main contribution of this model was the possibility of reconstructing prey mortality profiles for the species of primary consumers (Fig. 1). This, in turn, allows estimating how many individuals from different age intervals could die annually without destabilizing their populations, which provides estimates on the biomass by prey size classes that would be available yearly in the paleoecosystem. This is important because body mass is a crucial factor in the selection of prey by predators (Palmqvist et al., 1996; Carbone et al., 1999; Radloff and Toit, 2004; Ercoli et al., 2014). As a result, our approach allows to distinguish between the mortality of subadult and adult prey individuals, which is relevant for those predators that do not usually prey upon adult individuals of a given prey species (e.g., megaherbivores) but consume their juveniles. In addition to quantifying meat availability, PSEco distributes this resource according to the profiles of demand and consumption of the secondary consumers (i.e., predators and/or scavengers, including hominins if present; see Rodríguez-Gómez et al., 2013, 2016a). The final outputs of PSEco are the average densities of the species of secondary consumers that the paleoecosystem could support in the long term, as well as several standardized indices that measure competition intensity for meat among the members of the carnivore guild present in the paleoecosystem (Fig. 1) (Rodríguez-Gómez et al., 2013, 2014a, 2016b, 2017a, 2017b, 2017c).

The initial goal of PSEco was to infer the role of humans in the Early and Middle Pleistocene communities of large mammals. The model has provided interesting results on the first hominin settlements of Western Europe (Rodríguez-Gómez et al., 2013, 2014b, 2016b, 2017a, 2017b, 2017c; Domingo et al., 2017). This has allowed to: (i) reject that cannibalism at Gran Dolina level TD6 was the result of long-term resource scarcity (Rodríguez-Gómez et al., 2013); (ii) support that the absence of humans in the Sierra de Atapuerca ~600 ka ago could have resulted from a high level of competition among carnivores (Rodríguez-Gómez et al., 2014b); (iii) propose that the taphocoenosis of level TD6 is probably incomplete, as it should include at least one large felid (Rodríguez-Gómez et al., 2017a); (iv) suggest that the delay of ~400 ka in the human occupation of Southwestern Europe with respect to the Georgian site of Dmanisi was not due to increased competition for meat resources (Rodríguez-Gómez et al., 2016a, 2017b); (v) argue that competition for meat was not the cause of the apparent decline of humans in Europe during early Middle Pleistocene times (Rodríguez-Gómez et al., 2017c); or (vi) propose that human presence may have led to ecological instability in the paleocommunities of large mammals, such as the one recorded at Punta Lucero (Domingo et al., 2017). In addition, Rodríguez-Gómez et al. (2020) applied PSEco to the Miocene paleocommunity of the Santa Cruz Formation (Argentina), in which several researchers have previously argued that the predator guild was impoverished. The results obtained allowed to reject that this paleocommunity was depauperate in carnivores, although it showed a deficit of species that could consume megaherbivores (Rodríguez-Gómez et al., 2020). Furthermore, Wilson and Parker (2023) recently used this model to estimate the intensity of competition among secondary consumers at the Miocene site of La Venta (Colombia). They proposed that giant reptiles occupied macropredator niches due to low predation pressure from mammalian carnivores.

Many biological and population parameters (e.g., metabolism, production, consumption, density, birth rate, gestation length, postnatal growth duration, population turnover rates, etc.) scale to the 0.75 (i.e., ¾) power of species body mass, both with positive and negative sign (e.g., von Bertalanffy, 1957; Fenchel, 1974; Farlow, 1976; Case, 1978; Western, 1979, 1980; Damuth, 1981, 1987, 1991; Calder, 1982, 1984; Cyr and Pace, 1993; Peters, 1983; West et al., 2001; Ernest et al., 2003; Brown et al., 2004; Makarieva et al., 2004; Hou et al., 2008; Pawar et al., 2012; Sibly et al., 2012; Grady et al., 2014). Moreover, Hatton et al. (2015) showed that predator-prey abundances of large mammals in African ecosystems scale close to the ¾ power relationship according to the following equation:

$$C = c^{*}B^{k}, \tag{1}$$

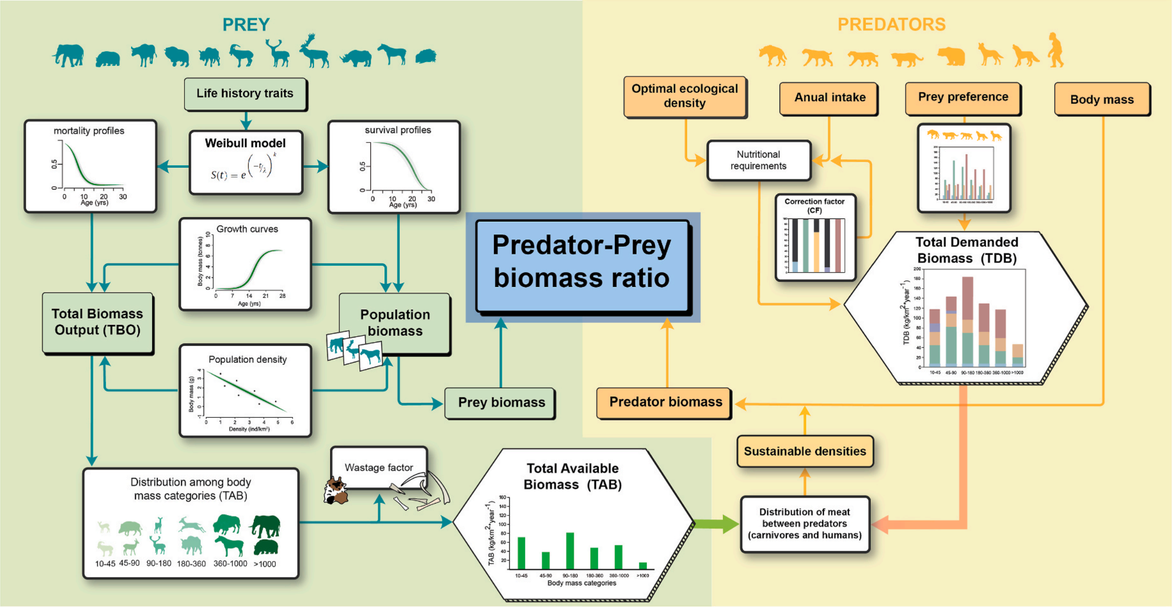

Fig. 1. Flowchart showing the different components of the PSEco model for estimating total available biomass (TAB) or meat availability, prey biomass and predator biomass (human and carnivore) supported by TAB. The carnivore silhouettes come from Palmqvist et al. (2008a, 2008b).

where C is the carnivore biomass, c is the predator-prey coefficient, B is the prey biomass, and $k \approx 3/4$. In addition, Hatton et al. (2015) also obtained this scaling law with exponents consistently close to ¾ when they analyzed trophic relationships and structures in different ecosystems and biomes around the World, from plankton to communities of large terrestrial mammals, both in predator-prey relationships and in production relationships for plant or aquatic communities. This pervasive pattern suggested that the relationships between trophic levels decreased significantly with increasing biomass (i.e., the structure of the biomass pyramid became increasingly bottom-heavy at higher biomass values). Given that the pattern is robust and is consistently observed in the living communities, Hatton et al. (2015) concluded that the trophic relationships do not depend on the particularities of ecosystem type but are inherent to the growth patterns and structures of the communities. For this reason, they proposed that the pattern suggests a greater degree of ecosystem-level organization than previously recognized, thus providing a more predictive approach to ecological theory (see Hatton et al., 2015).

PSEco is based on several theoretical assumptions (e.g., conditions of population stability and stationarity) that are difficult to meet for all species in the community. However, Palmqvist et al. (2022a, 2022b) showed that the reconstruction of the faunal assemblages from three sites from Orce (Guadix-Baza Depression, SE Spain) that are relevant for the study of the first hominin dispersal in Western Europe, Venta Micena, Barranco León and Fuente Nueva-3, was compatible with the predator-prey biomass ratios observed by Hatton et al. (2015).

This study aims to test whether the results obtained with PSEco for several faunal assemblages from the sites of Orce and Sierra de Atapuerca follow a predator-prey biomass ratio similar to that described by Hatton et al. (2015). If this were the case, it would support an increase of confidence on how PSEco reconstructs trophic relationships for paleocommunities of large mammals based on estimates of prey mortality profiles and meat availability for carnivores.

2. Materials and methods

The biomass of a population of large mammals per unit area can be estimated by multiplying the mean body mass of the individuals by the population density (Cyr and Pace, 1993):

$$B_i = M_i * D_i, \tag{2}$$

where B_i is the population biomass of prey species i, M_i is its mean body mass, and D_i is its population density. In this way, total prey biomass can be calculated by summing the biomasses of the populations of the prey species that make up an ecosystem. Following the nomenclature of Eq. (1), the prey biomass of a community is written as:

$$B = \sum_{i=1}^{n} (M_i * D_i) \tag{3}$$

Similarly, total predator biomass can be estimated as the sum of the populations of carnivore species. Following Eq. (1), we write the biomass of the predators (and scavengers) of a community as:

$$C = \sum_{j=1}^{n} (M_j * D_j) \tag{4}$$

Therefore, the body masses of prey and predator species and their population densities must be estimated before approaching the relationship between prey and predator biomass. In studies on living mammals, the average body mass of a population has been approached as three-quarters of the average female body mass (Owen-Smith, 1988; Hayward et al., 2007) or as female body mass (Hatton et al., 2015). However, Rodríguez-Gómez et al. (2022a) recently proposed the use of survival profiles for calculating the average body mass of a population as the best approach for estimating the carrying capacity of a paleocommunity. In addition, they estimated population density from an allometric equation that relates body mass to density (see below). In this study, we follow the approach of Rodríguez-Gómez et al. (2022a) to estimate the prey biomass of paleocommunities. In the case of carnivores and hominins, we estimate their population densities based on the amount of meat resources provided by the prey community, following the procedure of Rodríguez-Gómez et al. (2013, 2014b, 2016b) (see below).

2.1. *Faunal assemblages analyzed and their survival and mortality profiles*

In this study, we started from the material and methods used in previous analyses aimed to reconstructing the large mammal paleocommunities from the Orce and Sierra de Atapuerca sites (Fig. 2) (Rodríguez-Gómez et al., 2013, 2014b, 2016a, 2017a, 2017b). We focused here on the Orce sites of Venta Micena (VM), Barranco León, and Fuente Nueva 3 (BL-FN3), as well as on the Sierra de Atapuerca sites of Gran Dolina (levels TD3-TD4, TD6 1–2, TD8, and TD10-1) and Galería (levels GIII and GIIB) (Table 1). Following a similar criterion used by Rodríguez-Gómez et al. (2017c) to select faunal assemblages with a high degree of preservation completeness, all these sites preserve faunal assemblages that record at least seven prey species and four secondary consumers.

Apart from the information provided by the faunal lists, we used estimates on the life history traits of the prey species based on their modern analogues to reconstruct their survival and mortality profiles (Fig. 1). As commented above, survival profiles are useful for estimating the mean body mass of past populations of herbivores (see Rodríguez-Gómez et al., 2022a) and their estimated mortality profiles allow calculating meat availability for the secondary consumers (see Rodríguez-Gómez et al., 2013, 2014a, 2016b, 2022b). For doing that, we used values for several life history traits based on their modern analogues (see below), which include neonate and adult body mass (NBM and ABM, respectively), age at first birth (or sexual maturity + pregnancy) (AFB), number of litters per year (LY), litter size (LS), and longevity (L). Life history traits are parameters used by the Weibull model (Martín-González et al., 2016) for reconstructing stable and stationary survival and mortality profiles, which represent an average of population fluctuations over time (Rodríguez-Gómez et al., 2013; Martín-González et al., 2019). Estimates of mean adult body mass (ABM) were based on metric measurements taken on the specimens preserved in the fossil record (Rodríguez-Gómez et al., 2022a) (Table 2). Life history traits were estimated using information available for the extant species more related phylogenetically to the extinct ones in the databases PanTHERIA (Jones et al., 2009), Animal Diversity Web (Myers et al., 2020), and AnAge (Magalhães and Costa, 2009). Body masses of prey species of different age intervals (see growth curves in Fig. 1) were determined following Zullinger et al. (1984):

$$M\ (t) = A * e^{-e^{-K(t-I)}}, \tag{5}$$

where A is the asymptotic body mass (i.e., the adult body mass), M (t) is the mass (in g) at age t, K is the growth rate constant (days^{-1}), and I is the age at the inflection point (days). K relates to adult body mass following the equation:

$$\log(K) = -0.901 - 0.302 * \log(M) \tag{6}$$

The average mass for each age interval was estimated as the arithmetic mean of the two most extreme values within each age interval.

2.2. *Estimates of meat availability and densities of secondary consumers*

In order to estimate the biomass of humans and carnivores, we used PSEco (see Rodríguez-Gómez et al., 2013, 2014a, 2014b, 2016a, 2016b, 2017a, 2017b, 2017c, 2020; Domingo et al., 2017; Martín-González

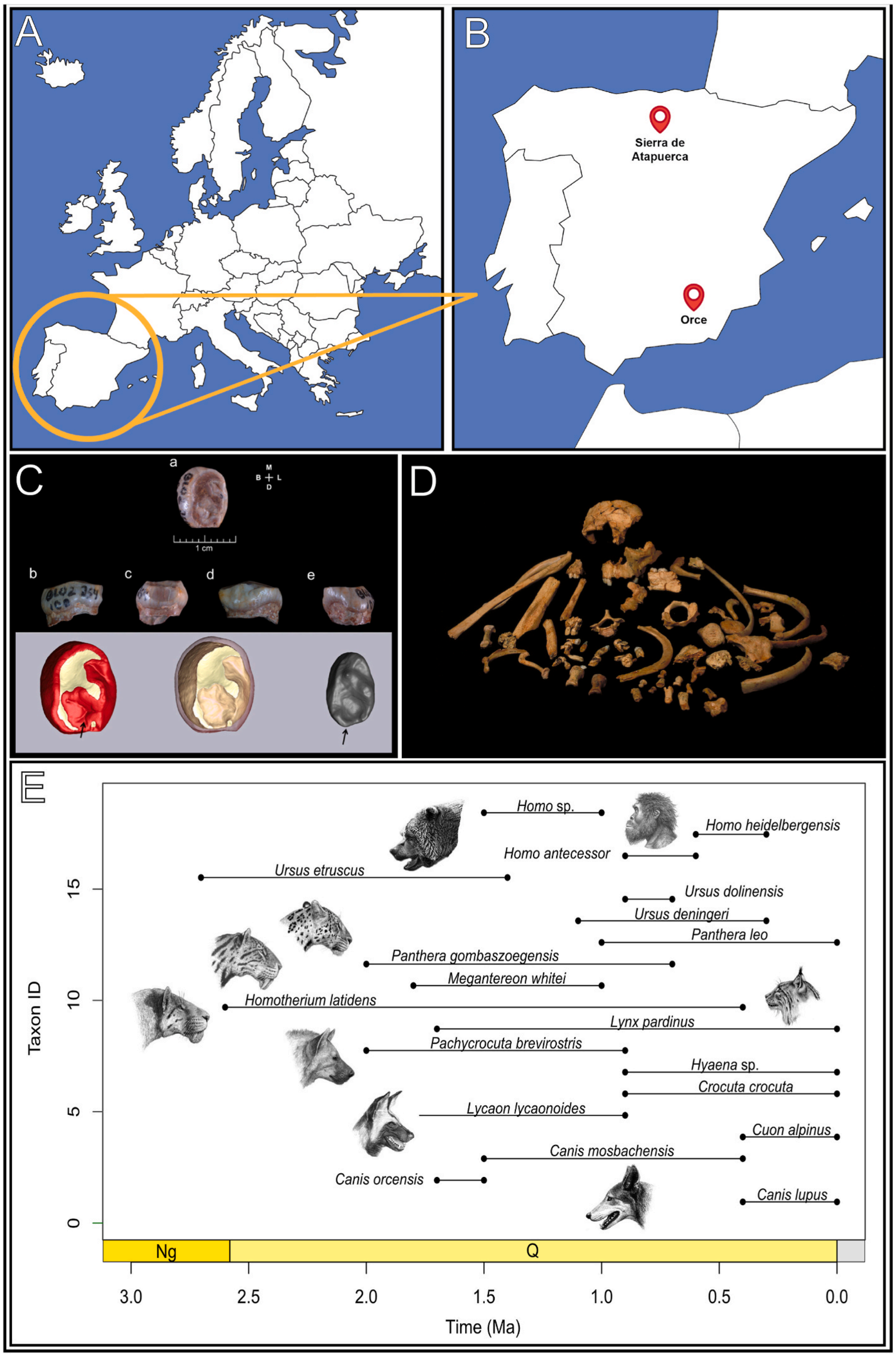

Fig. 2. Geographical location of the sites from Orce and Sierra de Atapuerca in Europe (A) and in the Iberian Peninsula (B); human deciduous tooth from Barranco León (BL02-J54-100) in occlusal (a), buccal (b), distal (c), lingual (d), mesial (e) view; below it is shown the computed tomography reconstruction of the enamel (left), dentin (center) and pulp cavity (right), with the arrow indicating the presence of a small hypoconulid (from Toro-Moyano et al., 2013) (C); human fossil remains recovered during the 1994–1996 field seasons from the Aurora Stratum, level TD6, of the Gran Dolina cave site in Sierra de Atapuerca (D); and representation of the temporal presence of large carnivores and humans in the Iberian Peninsula, estimated from the faunal assemblages analyzed using the R package 'paleoverse' (Jones et al., 2023), to which we have added species names and some carnivore silhouettes from Palmqvist et al. (2022b) (E).

et al., 2019), which allowed us to estimate their population densities based on the meat availability in the paleoecosystem (Fig. 1). In this way, PSEco uses the mortality profiles of the large herbivore species of a community to estimate the number of individuals that could die annually without causing their populations to collapse (see Rodríguez-Gómez et al., 2013; Martín-González et al., 2016, 2019). As mentioned above, PSEco uses faunal lists (Table 1), densities, and life history trait values (Table 2) of prey species in the paleoecosystems to provide estimates on the amount of prey biomass that can be extracted annually by the secondary consumers, including carnivores and hominins. The mortality profiles inferred with the Weibull model are used to distribute the dead individuals among body mass categories (Class 1: 10–45 kg; Class 2: 45–90 kg; Class 3: 90–180 kg; Class 4: 180–360 kg; Class 5: 360–1000 kg; Class 6: >1000 kg) (Fig. 1), as body size is the most relevant factor in the selection of prey by predators (Palmqvist et al., 1996; Carbone et al., 1999; Radloff and Toit, 2004; Ercoli et al., 2014). In addition, PSEco applies a "wastage factor" (Fig. 1), which estimates the percentage of biomass not used by the secondary consumers (e.g., skin, horns, and

Table 1

Faunal assemblages from Orce (Granade, Spain) and Sierra de Atapuerca (Burgos, Spain) analyzed in this study. Marked cells denote when species are present (X). Abbreviations: VM, Venta Micena; BL-FN3, Barranco León-Fuente Nueva 3; TD3-TD4, Trinchera Dolina 3–4; TD6 1–2, Trinchera Dolina 6 1–2; TD8, Trinchera Dolina 8; TD10-1, Trinchera Dolina 10–1; GIIb, Galería IIb; GIII, Galería III (Moyà-Solà et al., 1987; Martínez-Navarro, 1991; Martínez-Navarro and Palmqvist, 1995; Made, 2001; García García, 2003; Abbazzi, 2010; Martínez-Navarro et al., 2010; 2011, Martínez-Navarro et al., 2021; Rodríguez et al., 2011; Ros-Montoya et al., 2012; Medin et al., 2017; among others).[a], Martínez-Navarro (1991), Martínez-Navarro and Rook (2003), Martínez-Navarro et al., (2015);[b], Duval et al., (2012), Toro-Moyano et al., (2013), Álvarez et al., (2015);[c], Moreno et al., (2015), Álvarez-Posada et al., (2018);[d], Duval et al., (2018);[e], Falguères et al., (1999);[f], Falguères et al., (2013);[g], Falguères et al., (2013), Demuro et al., (2014).

Dating (Ma)	*c.* 1.60[a]	*c.* 1.50–1.2 (FN-3)[b] *c.* 1.4 (BL)[b]	*c.* 1.10–0.85[c]	*c.* 0.900–0.800[d]	*c.* 0.60[e]	*c.* 0.39–0.31[f]	0.27–0.22 [g]	0.28–0.21 [g]
Prey species	VM	BL-FN3	TD3-TD4	TD6 1-2	TD8	TD10-1	GIIb	GIII
Ammotragus europaeus		X						
Bison schoetensacki						X		
Bison sp. (S. de Atapuerca)							X	X
Bison sp. (Orce)	X	X						
Bison voigtstedtensis			X	X	X			
Bovidae indet-Caprinae	X							
Hemibos cf. *gracilis*	X							
Hemitragus albus	X	X						
Hemitragus bonali							X	X
Praeovibos sp.	X							
Soergelia minor	X							
Arvernoceros giulii			X	X	X			
Capreolus priscus						X		
Cervidae indet.	X							
Cervus elaphus			X	X	X	X	X	X
Dama clactoniana						X	X	X
Dama vallonnetensis			X	X	X			
Metacervocerus rhenanus	X	X						
Praemegaceros solilhacus					X		X	X
Praemegaceros cf. *verticornis*	X	X						
Hippopotamus antiquus	X	X			X			
Sus scrofa				X	X			
Equus altidens	X	X	X	X	X			
Equus ferus						X	X	X
Equus hydruntinus						X	X	X
Equus suessenbornensis		X						
Stephanorhinus etruscus			X	X	X			
Stephanorhinus hemitoechus						X	X	X
Stephanorhinus hundsheimensis	X	X						
Macaca sp.					X			
Mammuthus meridionalis	X	X						
Mammuthus sp.				X				
Castor fiber			X	X				
Hystrix refossa		X	X	X				
Hystrix sp.	X							
Hystrix vinogradovi							X	X
Secondary consumer species								
Canis lupus						X		
Canis orcensis	X							
Canis mosbachensis		X	X	X	X			
Cuon alpinus							X	X
Lycaon lycaonoides	X	X						
Crocuta crocuta			X	X	X			
Hyaena sp.					X			
Pachycrocuta brevirostris	X	X						
Lynx cf. *pardinus*	X	X						
Lynx pardinus							X	X
Lynx sp.			X	X	X	X		
Homotherium latidens	X	X						
Megantereon whitei	X	X						
Panthera gombaszoegensis	X		X		X			
Panthera leo						X	X	X
Ursus deningeri								X
Ursus dolinensis			X	X				
Ursus etruscus	X	X						
Ursus sp. (S. de Atapuerca)					X	X		
Homo antecessor				X				
Homo heidelbergensis								X
Homo sp. (Orce)		X						
Homo sp. (S. de Atapuerca)			X			X	X	

bones) (see Rodríguez-Gómez et al., 2013, 2014a, 2014b, 2020; Martín-González et al., 2016, 2019). The densities used as input for PSEco in this analysis are estimated with Damuth's equation (1981) for European mixed temperate forests:

$$\log(D) = -0.79 * \log(M) + 4.33;\ r^2 = 0.94 \tag{7}$$

where D is the population density (individuals/km^2), and M is the mean adult body mass (in g). The combination of the mortality profiles,

Table 2
Life history traits of prey species estimated from their living analogues using different databases: PanTHERIA (Jones et al., 2009), AnAge (Magalhães and Costa, 2009), and Animal Diversity Web (Myers et al., 2020). We mainly used the PanTHERIA database as a reference and completed the missing values with data from the others. Adult body mass (ABM) values are from Rodríguez-Gómez et al. (2022a). Adult body mass (ABM) (in kg); neonate body masses (NBM) (in kg); age at first birth (AFB) (in years (yrs)); litter size (LS); litters per year (LY); longevity (L) (in years (yrs)); Density (D) (ind/km^2).

Order	Family	Species	ABM	AFB	LS	LY	NBM	L	D[c]
Artiodactyla	Bovidae	Ammotragus europaeus	135	2.00	1.19	1.00	4.95	19.2	2.38
Artiodactyla	Bovidae	*Bison schoetensacki*	631	2.62	1.00	0.91	27.67	25.0	0.70
Artiodactyla	Bovidae	*Bison* sp. (S. de Atapuerca)	410	2.62	1.00	0.91	19.03	25.0	0.99
Artiodactyla	Bovidae	*Bison* sp. (Orce)	450	2.62	1.00	0.91	25.79	25.0	0.92
Artiodactyla	Bovidae	*Bison voigtstedtensis*	400	2.62	1.00	0.91	24.56	25.0	1.01
Artiodactyla	Bovidae	Bovidae indet-Caprinae	25	2.00	1.19	1.00	1.89	19.2	9.03
Artiodactyla	Bovidae	*Hemibos* cf. *gracilis*	300	2.50	1.00	0.96	14.50	22.4	1.27
Artiodactyla	Bovidae	*Hemitragus albus*	75	2.00	1.19	1.00	3.28	19.2	3.79
Artiodactyla	Bovidae	*Hemitragus bonali*	96	2.00	1.19	1.10	3.87	19.2	3.12
Artiodactyla	Bovidae	*Praeovibos* sp.	315	2.00	1.19	1.00	9.96	19.2	1.22
Artiodactyla	Bovidae	*Soergelia minor*	225	2.00	1.19	1.00	7.45	19.2	1.59
Artiodactyla	Cervidae	*Arvernoceros giulii*	276	2.86	1.00	1.10	13.64	20.8	1.35
Artiodactyla	Cervidae	*Capreolus priscus*	52	1.75	1.22	1.10	2.49	13.8	5.07
Artiodactyla	Cervidae	Cervidae indet.	25	2.86	1.00	1.10	1.82	20.8	9.03
Artiodactyla	Cervidae	*Cervus elaphus*	163	2.72	1.00	1.10	10.61	25.0	2.05
Artiodactyla	Cervidae	*Dama clactoniana*	110	2.86	1.00	1.10	6.30	20.8	2.80
Artiodactyla	Cervidae	*Dama vallonnetensis*	84	2.86	1.00	1.10	5.57	20.8	3.47
Artiodactyla	Cervidae	*Megaloceros giganteus*	646	2.86	1.00	1.10	27.85	20.8	0.69
Artiodactyla	Cervidae	Metacervocerus rhenanus	95	2.86	1.00	1.10	5.57	20.8	3.14
Artiodactyla	Cervidae	*Praemegaceros solilhacus*	383	2.86	1.00	1.10	19.40	20.8	1.05
Artiodactyla	Cervidae	*Praemegaceros* cf. *verticornis*	400	2.86	1.00	1.10	18.63	20.8	1.01
Artiodactyla	Hippopotamidae	*Hippopotamus antiquus*	3200	4.00	1.00	0.52	40.20	54.5	0.20
Artiodactyla	Suidae	*Sus scrofa*	85	0.85	4.52	1.59	0.81	21.0	3.43
Perissodactyla	Equidae	*Equus altidens*	350	3.50	1.00	0.67	30.70	38.8[a]	1.12
Perissodactyla	Equidae	*Equus ferus*	565	3.50	1.00	0.67	54.69	38.8[a]	0.77
Perissodactyla	Equidae	*Equus hydruntinus*	210	3.50	1.00	0.67	28.63	38.8[a]	1.68
Perissodactyla	Equidae	*Equus suessenbornensis*	565	3.50	1.00	0.67	54.69	38.8[a]	0.77
Perissodactyla	Rhinocerotidae	*Stephanorhinus etruscus*	1400	6.75	1.00	0.36	41.75	47.0	0.38
Perissodactyla	Rhinocerotidae	*Stephanorhinus hemitoechus*	1400	6.75	1.00	0.36	41.75	47.0	0.38
Perissodactyla	Rhinocerotidae	*Stephanorhinus hundsheimensis*	1000	6.75	1.00	0.36	41.75	47.0	0.49
Primate	Cercopithecidae	*Macaca* sp.	18	4.79	1.02	1.01	0.45	22.0	11.70
Proboscidea	Elephantidae	*Mammuthus meridionalis*	6000	11.25	1.13	0.24	101.00	65.0[a]	0.12
Proboscidea	Elephantidae	*Mammuthus* sp.	6040	11.25	1.13	0.24	101.00	65.0[a]	0.12
Rodentia	Castoridae	*Castor fiber*	22	2.50	2.95	1.00	0.55	25.0	9.99
Rodentia	Hystricidae	*Hystrix refossa*	20	1.46[b]	1.51	1.51	0.31	20.0	10.77
Rodentia	Hystricidae	*Hystrix* sp.	15	1.46[b]	1.51	1.51	0.31	20.0	13.52
Rodentia	Hystricidae	*Hystrix vinogradovi*	10	1.46[b]	1.51	1.51	0.31	20.0	18.62

[a] AnAge.
[b] Sexual maturity plus gestation period.
[c] Densities were estimated by Damuth's equation (1981) ($\text{Log}(D) = -0.97 \times \text{Log}(BM \times 1000) + 4.43$).

densities, distribution of individuals among size categories, and wastage factor provides the biomass available to the secondary consumers (in kg/km^2*year and kcal/km^2*year), which in PSEco is referred to as TAB (Total Available Biomass) (Fig. 1) (Rodríguez-Gómez et al., 2014a). Given that the Weibull model provides infinite mortality profiles, PSEco only considers the extreme values that correspond to the maximum and minimum subadult mortalities (Martín-González et al., 2016, 2019). In this way, TAB-min is the available biomass corresponding to maximum subadult mortality (and minimum adult mortality), while TAB-MAX refers to the opposite situation.

Once the meat offered in a paleoecosystem is estimated, the meat demands of secondary consumers must be calculated. The estimate of meat demands by each secondary consumer combined with its consumption profile is called as Total Demanded Biomass (TDB) (Fig. 1). In order to estimate it, PSEco uses as inputs the annual meat intake of the population, its optimal density, and the prey preferences (Fig. 1). Annual meat intakes of carnivores are estimated through the equation obtained by Farlow (1976), which relates meat intake (I) (kcal/day) to body mass (M) (in g):

$$\log I = (0.69686 \pm 0.01276)\log(M) + 0.27747;\ r^2 = 0.97 \qquad (8)$$

The maximum value of the slope (0.70962) was used for estimating maximum meat demands, and the body masses of carnivores estimated in previous works (Rodríguez-Gómez et al., 2016a, 2017a, 2017b) were also employed (see Table 3). In the case of humans, we assumed a mean daily requirement of 2750 kcal per individual, as in Rodríguez-Gómez et al. (2017b). Following Rodríguez et al. (2012) and Rodríguez-Gómez et al. (2012), we made some adjustments to the intakes of the extinct carnivores according to their prey preferences and applying a correction factor (CF) (Table 3 and Fig. 1) (see also Rodríguez-Gómez et al., 2016a, 2017a, 2017b). In this way, we considered that large mammal flesh accounted for 20% of the nutritional requirements of the medium-sized (~10 kg) dog *Canis mosbachensis* (Palmqvist et al., 1999, 2003; Rodríguez et al., 2012). In the case of the spotted hyena (*Crocuta crocuta*) and of the giant short-faced hyena (*Pachycrocuta brevirostris*: ~110 kg; Palmqvist et al., 2011), a reduction of 2% of the total nutritional requirements was applied, as these bone-cracking carnivores would have access to the bone marrow contents (Blumenschine and Madrigal, 1993; Outram and Rowley-Conwy, 1998). For *Hyaena* sp., we assumed 75% of consumption of large mammals by analogy with the modern striped hyaena (*Hyaena hyaena*), in which carrion from large mammals accounts for approximately two-thirds of its metabolic needs, with small vertebrates, invertebrates, and plant resources making up the remainder (Holekamp and Kolowski, 2009). In the case of lynx species, we considered a diet similar to that of the modern Iberian lynx (*Lynx pardinus*) (Delibes, 1980; Rodríguez, 2008; Rodríguez et al., 2012), although the energy requirements obtained from large mammals was increased to 10% given that the extinct species were slightly larger. We assumed that meat represented 10% of the nutritional requirements of

Table 3
Carnivore and hominin species identified in the paleocommunities analyzed in this study, with estimates of body mass (M, in kg) and densities (D, in ind/km^2) obtained from Damuth (1993) (African carnivores: log (D) $= -0.64 \times$ log (M (in grams) +2.23), and their nutritional requirements (NR, in kcal/km^2 per year) estimated from the Farlow (1976) equation (see text). NR values of carnivore species were corrected according to their dietary type with a correction factor (CF) that multiplies the total requirements. For each carnivore species, the last six columns represent the preferences for each prey body mass category (see text) expressed in percentage (a null percentage indicates that a prey body class category is not consumed).

Species of secondary consumers	BM	D	CF	NR	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6
Canis lupus	43	0.19	1.00	246,599	0.12	0.18	0.29	0.35	0.06	0.00
Canis orcensis	12	0.42	0.20	45,163	0.17	0.17	0.17	0.17	0.17	0.17
Canis mosbachensis (Orce)	12	0.42	0.20	45,163	0.17	0.17	0.17	0.17	0.17	0.17
Canis mosbachensis (S. de Atapuerca)	23	0.27	0.20	47,256	0.17	0.17	0.17	0.17	0.17	0.17
Cuon alpinus	18	0.33	1.00	231,827	0.38	0.31	0.25	0.06	0.00	0.00
Lycaon lycaonoides	30	0.23	1.00	240,691	0.13	0.38	0.25	0.25	0.00	0.00
Crocuta crocuta	65	0.14	0.98	248,922	0.15	0.30	0.25	0.15	0.10	0.05
Hyaena sp.	44	0.18	0.75	185,396	0.17	0.17	0.17	0.17	0.17	0.17
Pachycrocuta brevirostris	110	0.10	0.98	258,209	0.17	0.17	0.17	0.17	0.17	0.17
Lynx cf. *pardinus*	18	0.32	0.10	23,228	0.75	0.25	0.00	0.00	0.00	0.00
Lynx pardinus	14	0.38	0.10	22,825	0.75	0.25	0.00	0.00	0.00	0.00
Lynx sp.	18	0.32	0.10	23,228	0.75	0.25	0.00	0.00	0.00	0.00
Homotherium latidens	200	0.07	1.00	274,676	0.00	0.11	0.21	0.26	0.32	0.11
Megantereon whitei	100	0.11	1.00	261,736	0.06	0.19	0.25	0.31	0.19	0.00
Panthera gombaszoegensis	105	0.10	1.00	262,626	0.11	0.11	0.33	0.22	0.22	0.00
Panthera leo	170	0.08	1.00	271,586	0.14	0.29	0.24	0.19	0.10	0.05
Ursus deningeri	475	0.04	0.10	29,173	0.17	0.17	0.17	0.17	0.17	0.17
Ursus dolinensis	300	0.05	0.10	28,254	0.17	0.17	0.17	0.17	0.17	0.17
Ursus etruscus	300	0.05	0.10	28,254	0.17	0.17	0.17	0.17	0.17	0.17
Ursus sp. (S. de Atapuerca)	203	0.07	0.10	27,496	0.17	0.17	0.17	0.17	0.17	0.17
Homo antecessor	77	0.24	0.45	108,405	0.24	0.29	0.19	0.14	0.10	0.05
Homo heidelbergensis	77	0.24	0.45	108,405	0.24	0.29	0.19	0.14	0.10	0.05
Homo sp. (Orce)	53	0.24	0.30	72,270	0.17	0.17	0.17	0.17	0.17	0.17
Homo sp. (S. de Atapuerca)	77	0.24	0.45	108,405	0.24	0.29	0.19	0.14	0.10	0.05

ursids, as happens in the living populations of European brown bears (*Ursus arctos*) (Clevenger et al., 1992; Parde and Camarra, 1992; Bocherens et al., 2004; Purroy, 2017). In the case of hypercarnivores (i.e., sabertooth cats, pantherine felids, and pack-hunting canids), we assumed that meat represented 100% of their metabolic requirements (Table 3). We considered that large mammals provided 45% of the dietary needs of humans, which is the average proportion of animal resources consumed by the extant populations of hunter-gatherers (Jenike, 2001; Leonard et al., 2007). In the case of the FN3-BL sites, which preserve the oldest faunal assemblages of this analysis with human presence, we considered that these early hominins covered only 30% of their nutritional requirements with meat from large mammals, as in Rodríguez-Gómez et al. (2016a).

In order to estimate the energy demands of each carnivore population per km^2, we multiplied their annual intakes by their optimal ecological densities (Fig. 1), which were calculated using Damuth's equation (1993) for African carnivores:

$$\log(D) = -0.64 * \log(M) + 2.23;\ r^2 = 0.36 \tag{9}$$

where D is the population density, in number of individuals per km^2, and M is the body mass, in g. In the case of humans, we used the population density of Hadza, as in Rodríguez-Gómez et al. (2013, 2014a, 2016a, 2017a, 2017c), which is 0.24 individuals per km^2.

Finally, we defined the energy demands of each human and carnivore population following the consumption profiles of ungulates by carnivores according to body mass categories (Fig. 1), as proposed by Rodríguez-Gómez et al. (2017b). This approach was based on the observed behavior of the modern analogues of the Pleistocene carnivores as well as on the inferences obtained for the extinct taxa from ecomorphology and isotopic biogeochemistry (see Owen-Smith and Mills, 2008; Rodríguez et al., 2012; Palmqvist et al., 2003, 2008a, 2008b) (Table 3).

As mentioned above, PSEco distributes the meat offered annually to the members of the carnivore guild (predators and scavengers, including humans) according to their energy requirements and consumption profiles (i.e., TDB) (Fig. 1). This distribution of TAB considers the preferences of each carnivore for each prey body mass category as well as the intensity of consumption in each prey category as a function of the requirements of other carnivores (see Rodríguez-Gómez et al., 2013, 2014b, 2016a, 2016b, 2017b). This means that the distribution of TAB is dynamic, changing as the requirements of each carnivore species are met. TAB distribution ends when: (i) all meat is fully distributed; (ii) all species have met their energetic requirements; or (iii) there are no carnivore species with access to the body mass class in which meat remains unconsumed. Consequently, the distribution of TAB among carnivore species translates into those ecological densities that hold the ecosystem without risk of collapse. According to Eq. (4), the biomass of the secondary consumers is obtained by summing the multiplications of body mass and densities obtained with PSEco.

2.3. Prey biomass

As mentioned above, in order to estimate prey biomass in the paleocommunities (Eq. (3)) we used the approach of Rodríguez-Gómez et al. (2022a) to calculate the mean body mass of a population, which considers the relative proportion of individuals in each age interval (R_i) and the body mass for each interval (M_i) (see 2.1 section):

$$B = \sum_{i=1}^{n} R_i * M_i * D,\ i = 1, \ldots, n, \tag{10}$$

where D is the population density, which equals 1 in these analyses to know the average body mass of the population (see details in Rodríguez-Gómez et al., 2022a). In the latter, R_i was estimated as follows:

$$R_i = \frac{X_i}{\sum_{i=1}^{n} X_i},\ i = 1, \ldots n, \tag{11}$$

where X_i is the number of individuals in each age interval. The survival profiles and age structures provided by the Weibull model (Fig. 1) (Martín-González et al., 2016, 2019) for the different species are used to estimate the R_i values.

As commented previously, body mass at each age interval was calculated using Eq. (5), and prey density was calculated with Eq. (7)

(see sections 2.1 and 2.2).

2.4. Predator-prey biomass ratio

The estimated biomass values for prey and predators/scavengers allowed us to compare our results with those of Hatton et al. (2015) for present-day African ecosystems (Fig. 1). Moreover, we also included an analysis that considered only the fraction of predator biomass related to the proportion of meat consumed (FPB) in the predator's diet (i.e., once discarded the fraction of the diet based on resources other than large herbivores). This fraction was calculated multiplying each predator biomass by its Correction Factor (CF) (see Table 3). The arithmetic mean of the predator biomasses obtained with TAB-min and TAB-MAX estimates was used in these analyses.

3. Results

Mean body mass population values (BMP), TAB values, and sustainable densities for hominins and carnivores in each paleoecosystem were calculated before obtaining the biomass values of prey and predators (Tables 4–6). Our estimates reduce BMP to 70% of the adult mass (ABM) when subadults are considered, a percentage similar to that of Rodríguez-Gómez et al. (2022a). Prey density values (Table 2) and mean BMP values (Table 4) allowed to estimate the prey biomasses of each ecosystem (Table 7). These levels of prey biomass are those that could sustain the ecosystems over time, which Rodríguez-Gómez et al. (2022a) considered as the carrying capacity. We can see that there is a higher amount of prey biomass in the Orce sites than in those of Sierra de Atapuerca, with VM being the site with the highest amount (Table 7 and Fig. 3). Among the faunal assemblages from Sierra de Atapuerca, TD8 shows the highest prey biomass and TD10-1 the lowest one. The two Galería faunal assemblages (GIIa and GIII) show the same prey biomass values because they record the same prey species.

Table 4
Adult body mass (ABM, in kg) and mean body mass population (BMP, in kg) obtained for the prey species identified in the faunal assemblages from the Orce and Sierra de Atapuerca sites using the approach of Rodríguez-Gómez et al. (2022a).

Species	ABM	BMP
Ammotragus europaeus	135	89
Bison schoetensacki	631	405
Bison sp. (S. de Atapuerca)	410	276
Bison sp. (Orce)	450	305
Bison voigtstedtensis	400	275
Bovidae indet-Caprinae	25	20
Hemibos cf. *gracilis*	300	205
Hemitragus albus	75	54
Hemitragus bonali	96	66
Praeovibos sp.	315	191
Soergelia minor	225	142
Arvernoceros giulii	276	187
Capreolus priscus	52	37
Cervidae indet.	25	20
Cervus elaphus	163	117
Dama clactoniana	110	81
Dama vallonnetensis	84	64
Megaloceros giganteus	646	398
Metacervocerus rhenanus	95	71
Praemegaceros solilhacus	383	253
Praemegaceros cf. *verticornis*	400	261
Hippopotamus antiquus	3200	2015
Sus scrofa	85	22
Equus altidens	350	272
Equus ferus	565	429
Equus hydruntinus	210	172
Equus suessenbornensis	565	429
Stephanorhinus etruscus	1400	1084
Stephanorhinus hemitoechus	1400	1084
Stephanorhinus hundsheimensis	1000	801
Macaca sp.	18	15
Mammuthus meridionalis	6000	4486
Mammuthus sp.	6040	4506
Castor fiber	22	14
Hystrix refossa	20	13
Hystrix sp.	15	10
Hystrix vinogradovi	10	7

Table 5
Estimates of Total Available Biomass (TAB, in kg/km^2*year^{-1}) values according to minimum and maximum mortalities and the arithmetic mean for both values. Abbreviations: VM, Venta Micena; BL-FN3, Barranco León-Fuente Nueva 3; TD3-TD4, Trinchera Dolina 3–4; TD6 1–2, Trinchera Dolina 6 1–2; TD8, Trinchera Dolina 8; TD10-1, Trinchera Dolina 10–1; GIIb, Galería IIb; GIII, Galería III.

	VM	BL-FN3	TD3-TD4	TD6 1-2	TD8	TD10-1	GIIb	GIII
TAB-min								
Class 1	141	78	102	139	93	50	81	81
Class 2	73	65	52	54	67	36	44	44
Class 3	31	48	22	22	25	58	62	62
Class 4	83	53	42	43	48	17	28	28
Class 5	47	59	16	16	27	33	39	39
Class 6	26	26	13	29	23	13	13	13
Total TAB-min	400	328	248	303	283	208	267	267
TAB-MAX								
Class 1	142	65	106	141	71	27	62	62
Class 2	68	74	46	54	58	38	35	35
Class 3	56	67	48	48	48	82	102	102
Class 4	159	102	87	87	106	37	69	69
Class 5	67	96	22	23	44	63	70	70
Class 6	44	44	18	36	43	18	18	18
Total TAB-MAX	536	447	327	389	370	266	356	356
TAB-average	468	387	287	346	326	237	311	311

The base of PSEco for estimating human and carnivore densities is the TAB estimates deduced from the mortality profiles. Table 5 shows the TAB values for both the TAB-min and TAB-MAX scenarios and provides the arithmetic mean for both values. A similar pattern to that of prey biomass (see above) can be observed for TAB, although with smaller differences between the faunal assemblages (Table 5 and Fig. 3). VM is the faunal assemblage with the highest TAB value, followed by BL-FN3. Among the faunal assemblages from Sierra de Atapuerca, the one with the highest TAB value is TD6 1–2, closely followed by TD8. This is a difference with respect to prey biomass estimates, for which TD8 shows a higher value than TD6 (Table 7). As in the case of prey biomass, TD10-1 is the assemblage with the lowest TAB value, and the two Galería sites show the same TAB value (Table 5). A decreasing trend in prey biomass and TAB is recorded between the Early Pleistocene and the end of the Middle Pleistocene (Fig. 3). This trend is similar to the one previously observed by Rodríguez-Gómez et al. (2017c) for TAB at a continental scale, which they interpreted as resulting from changes in the composition of the community of primary consumers (see Raia et al., 2007; Meloro and Clauss, 2012; Rodríguez et al., 2012).

According to our results, TAB represents 11–14% of the prey biomass (Table 8 and Fig. 3), with the faunal assemblage from TD3-TD4 showing the highest percentage and the one from BL-FN3 the lowest value. Thus, TD3-TD4 would have the highest amount of available meat per unit of prey biomass. However, if the absolute values of prey biomass and TAB are considered separately, they do not stand out in the overall analysis. In this relationship, the composition of the prey species and the distribution of TAB among size classes are both relevant factors, because smaller prey can support higher mortality rates and their carcasses provide higher yields (Viljoen, 1993; Martín-González et al., 2019). The fact that BL-FN3 is the faunal assemblage that shows a lower TAB:prey biomass ratio is interesting for another reason: this assemblage preserves the oldest evidence of human presence in Western Europe (Fig. 2). The

Table 6
Estimates of sustainable carnivore densities (ind./km^2) in each faunal assemblage from the Orce and Sierra de Atapuerca sites obtained using the paleosynecological model of Rodríguez-Gómez et al. (2013) (PSEco). Density values for minimum (TAB-min) and maximum TAB (TAB-MAX) are provided. Abbreviations: VM, Venta Micena; BL-FN3, Barranco León-Fuente Nueva 3; TD3-TD4, Trinchera Dolina 3–4; TD6 1–2, Trinchera Dolina 6 1–2; TD8, Trinchera Dolina 8; TD10-1, Trinchera Dolina 10–1; GIIb, Galería IIb; GIII, Galería III.

Faunal assemblages	VM		BL-FN3		TD3-TD4		TD6 1-2		TD8		TD10-1		GIIb		GIII	
Species TAB	min	MAX	min	MAX	min	MAX	min	MAX	min	MAX	min	MAX	min	MAX	min	MAX
Canis lupus											0.07	0.11				
Canis orcensis	0.21	0.27														
Canis mosbachensis			0.19	0.24	0.15	0.20	0.27	0.27	0.16	0.21						
Cuon alpinus													0.19	0.22	0.18	0.21
Lycaon lycaonoides	0.11	0.13	0.09	0.12												
Crocuta crocuta					0.07	0.10	0.14	0.14	0.08	0.10						
Hyaena sp.									0.10	0.14						
Pachycrocuta brevirostris	0.05	0.06	0.05	0.06												
Lynx cf. *pardinus*	0.28	0.28	0.25	0.22												
Lynx pardinus													0.24	0.18	0.23	0.18
Lynx sp.					0.29	0.29	0.32	0.32	0.29	0.25	0.18	0.11				
Homotherium latidens	0.02	0.03	0.02	0.04												
Megantereon whitei	0.04	0.06	0.04	0.06												
Panthera gombaszoegensis	0.04	0.06			0.05	0.07			0.05	0.07						
Panthera leo											0.04	0.05	0.05	0.07	0.05	0.07
Ursus deningeri															0.03	0.04
Ursus dolinensis					0.03	0.04	0.05	0.05								
Ursus etruscus	0.03	0.03	0.02	0.03												
Ursus sp. (S. de Atapuerca)									0.04	0.05	0.04	0.05				
Homo antecessor							0.24	0.24								
Homo heidelbergensis															0.15	0.22
Homo sp. (Orce)			0.11	0.14												
Homo sp. (S. de Atapuerca)					0.14	0.17					0.12	0.14	0.16	0.23		

Table 7
Prey and predator biomass (kg/km^2) values obtained with PSEco. The predator biomass obtained with the model has a minimum and maximum interval, which correspond to the conditions of minimum (TAB-min) and maximum (TAB-MAX) biomass of available meat. We also include the fraction of predator biomass derived exclusively from the meat consumed (FPB). Abbreviations: VM, Venta Micena; BL-FN3, Barranco León-Fuente Nueva 3; TD3-TD4, Trinchera Dolina 3–4; TD6 1–2, Trinchera Dolina 6 1–2; TD8, Trinchera Dolina 8; TD10-1, Trinchera Dolina 10–1; GIIb, Galería IIb; GIII, Galería III.

Faunal assemblage	Prey biomass	Predator biomass		FPB	
		TAB-min	TAB-MAX	TAB-min	TAB-MAX
VM	3813	37	49	24	32
BL-FN3	3535	36	47	20	28
TD3-TD4	1987	38	48	16	22
TD6 1-2	2595	55	56	21	21
TD8	2618	31	39	15	20
TD10-1	1967	30	35	15	18
GIIb	2368	28	37	18	25
GIII	2368	39	53	18	25

distribution of TAB among prey size classes is shown in Table 5 and Fig. 4. These results show a similar trend for VM, TD3-TD4, TD6 1–2, and TD8, with classes 1 (10–45 kg) and 4 (180–360 kg) standing out. Among these sites, VM and TD6 1–2 show the highest values of TAB in the first size class, with estimates close to 140 kg/km^2*year^{-1}, while TD10-1 has the lowest one, <40 kg/km^2*year^{-1}. In the case of BL-FN3, TAB is distributed more homogeneously among body size classes, showing the highest values in classes 4 and 5 (360–1000 kg). Palmqvist et al. (2023) proposed that the differences between VM and BL-FN3 could be due to top-down forces, following Ripple and Van Valkenburgh (2010). In the case of TD10-1, GIIb and GIII, class 3 (90–180 kg) stands out. This distribution of TAB among body size classes influences meat distribution and consumption by carnivores and hominins.

Concerning carnivore densities, a density interval for the conditions of minimum and maximum meat availability (i.e., TAB-min and TAB-MAX, respectively) in the environment was obtained for each paleoecosystem (Table 6). There is a consistent pattern in carnivore densities due to body mass differences: the smaller the carnivore species, the higher the density value it reaches (Table 6). This pattern mainly reflects the density ceilings used in PSEco, which are the carnivore densities derived from Damuth's (1993) allometric equation (Eq. 9) that are considered as optimal (Table 3). Thus, when the species and genera are analyzed considering all sites, lynxes and *Canis mosbachensis* are the species that reach the highest densities. At the same time, *Homotherium latidens* and ursids are the ones that reach the lowest ones (Table 6). *Lynx* is the only genus that is represented in all fossil assemblages studied, showing higher densities in the Early Pleistocene assemblages (VM, BL-FN3, TD3-TD4, TD6 1–2) and TD8 than in those of late Middle Pleistocene age (TD10-1, GIIb, and GIII) (Table 6). This is due to a combination of two factors: the lower TAB values in the latter sites, especially in the case of the two smaller prey size classes (10–90 kg), and the higher competition for meat from these size classes among the secondary consumers, as these size classes are the only ones from which lynxes consume meat (Table 3). The faunal assemblages with the lowest TAB values are GIIb, GIII, TD10-1, and TD3-TD4. Of these sites, the first three show the lowest TAB estimates in the first two prey size categories (Table 5). In addition, GIIb and GIII record the presence of *Cuon alpinus*, which preferred prey belong to these two size categories. For this reason, the presence of the dhole results in lower lynx densities (Table 5). In the case of hominins, our results provide minimum densities of 11 individuals per 100 km^2 in BL-FN3 for TAB-min conditions and maximum densities in TD6 1–2, with 24 individuals per 100 km^2, both for TAB-min and TAB-MAX conditions (Tables 5 and 6). In the faunal assemblages of Sierra de Atapuerca, human densities would be above 15 individuals per 100 km^2 if a hunting strategy is considered. The exception is TD10-1, the assemblage with the lowest available meat (Table 5), where the sustainable density of human groups would be of 13 individuals per 100 km^2 (Table 6).

Predator biomass (Table 7) was estimated from carnivore body mass values (Table 3), and carnivore densities calculated with PSEco (Table 6). We included as part of our analyses the biomass of predators obtained using the Correction Factor (CF) and discarding the fraction of the diet based on resources other than large herbivores (Table 3) to estimate the fraction of biomass that would depend exclusively on the

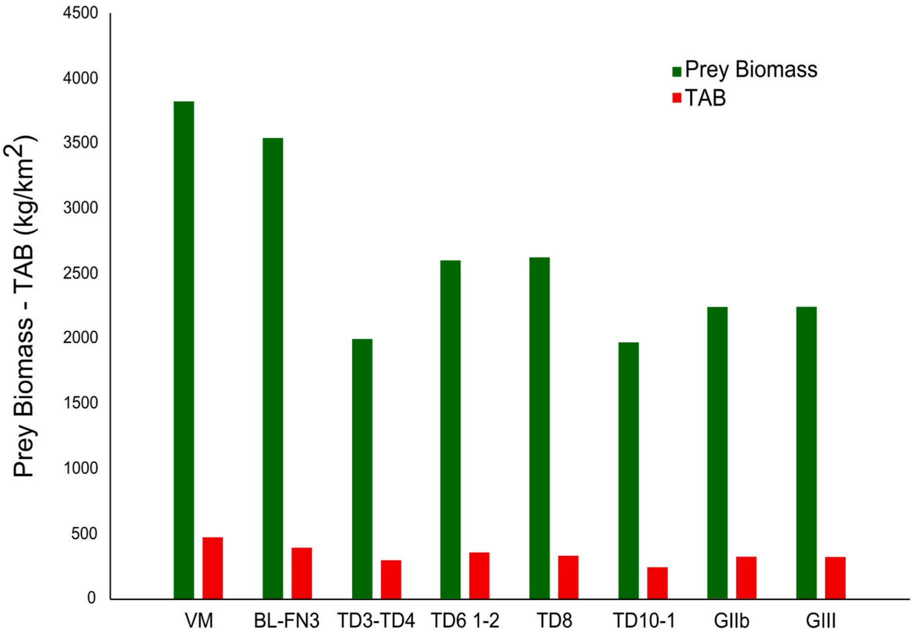

Fig. 3. Scatter plots of prey biomass and TAB (kg/km^2*year^{-1}) estimates for the paleocommunities of large mammals from the sites of Orce and Sierra de Atapuerca. TAB values are the arithmetic means of TAB-min and TAB-MAX estimates (Table 5). Abbreviations: VM, Venta Micena; BL-FN3, Barranco León-Fuente Nueva 3; TD3-TD4, Trinchera Dolina 3–4; TD6 1–2, Trinchera Dolina 6 1–2; TD8, Trinchera Dolina 8; TD10-1, Trinchera Dolina 10–1; GIIb, Galería IIb; GIII, Galería III.

Table 8
Prey Biomass (in kg/km^2), Total Available Biomass (TAB, in kg/km^2), relative percentage of TAB to PB, average predator biomass (in kg/km^2) for TAB-min and TAB-MAX and ratio of prey biomass to predator biomass for the faunal assemblages analyzed in this study. Abbreviations: VM, Venta Micena; BL-FN3, Barranco León-Fuente Nueva 3; TD3-TD4, Trinchera Dolina 3–4; TD6 1–2, Trinchera Dolina 6 1–2; TD8, Trinchera Dolina 8; TD10-1, Trinchera Dolina 10–1; GIIb, Galería IIb; GIII, Galería III.

	Prey biomass	TAB	Relative percentage	Predator biomass	Ratio of prey biomass to predator biomass
VM	3813	468	12.28	43	89
BL-FN3	3535	387	10.96	42	85
TD3-TD4	1987	287	14.46	43	46
TD6 1–2	2595	346	13.34	55	47
TD8	2618	326	12.47	35	75
TD10-1	1967	237	12.04	32	61
GIIb	2238	311	13.91	32	74
GIII	2238	311	13.91	46	52

availability of large herbivores (i.e., FPB; Table 7). Our results show the highest predator biomass values for TD6 1–2, followed by GIII and TD3-TD4. VM and BL-FN3 have similar values to TD3-TD4, but the former sites show significantly higher prey biomass estimates. GIIb depicts the opposite situation, showing the lowest predator biomass estimate. However, when the fraction of predator biomass derived exclusively from consumed meat (FPB) is considered, there is a more direct relationship with prey biomass. In this case, VM and BL-FN3 are the assemblages that show the highest predator biomass estimates, while TD10-1 is the one that provides the lowest one. Analyzing the values of the ratio of prey biomass to predator biomass among the faunal assemblages (Table 8), three groups can be distinguished: (i) those with values > 74 (VM, BL-FN3, TD8, and GIIb); (ii) those with values < 52 (TD3-TD4, TD6 1–2, and GIII); and (iii) the one with intermediate values (TD10-1) (Table 8 and Fig. 3A). The three faunal assemblages with the lowest prey-predator biomass ratios are those that show the highest values of predator biomass, the highest relative percentages of TAB to prey biomass, and the predator-prey biomass ratios furthest situated from the expectations of the Hatton et al. (2015) regression (Tables 7 and 8 and Fig. 3). In terms of FPB values, these three faunal assemblages are also characterized by higher predator biomass estimates than others with similar prey biomass values (e.g., TD6 1–2 and GIII with TD8, and TD3-TD4 with TD10-1) (Table 7 and Fig. 3B). This suggests that higher predator biomass values of these assemblages show are due to their higher proportions of TAB. However, other factors apart from the proportion of TAB in prey biomass may influence these reconstructions of predator-prey biomass ratios, for example the composition of the prey and predator guilds (see Discussion).

Given that the main goal of this study was to test whether the results obtained with PSEco for the Orce and Sierra de Atapuerca sites show predator-prey biomass relationships similar to those obtained by Hatton et al. (2015) for the African ecosystems, we have depicted graphically our results with those of Hatton et al. (2015). Fig. 5A shows that the Orce and Atapuerca paleocommunities have predator-prey biomass ratios that fit within the variance of African ecosystems, although all they plot above the values expected from the regression derived by Hatton et al. (2015) following Eq. (1) ($C = c \times B^k$), $C = 0.094 \times B^{0.73}$. The fossil assemblages that show a higher departure from the expectations of Hatton et al. (2015) are TD6 and TD3-TD4, which both scatter outside the upper 95% confidence limit of the bivariate regression (Fig. 5A). On the other hand, GIIb, VM and BL-FN3 are the paleocommunities with values closest to those expected. When predator-prey biomass ratios are analyzed considering FPB (Tables 3 and 7), the estimates obtained for the paleocommunities are lower than expected (Fig. 5B), with lower differences between them than those observed without considering FPB (Fig. 5A). In the latter analysis, TD8 was the paleocommunity furthest from the expectations of the regression of Hatton et al. (2015), while TD3-TD4 was the closest (Fig. 5B). When we included the paleocommunities to derive new least-squares regressions, a slight increase in the value of the Y-intercept (c) of Eq. (1) was observed in the approach that did not consider FPB [$C = (0.099 \pm 1.315)*B^{(0.727+0.035)}$, $r^2 = 0.891$] (Fig. 5A) and a minor decrease in the slope (k) in the one that used it [$C = (0.098 + 1.294)*B^{(0.716+0.033)}$, $r^2 = 0.898$] (Fig. 5B). In any

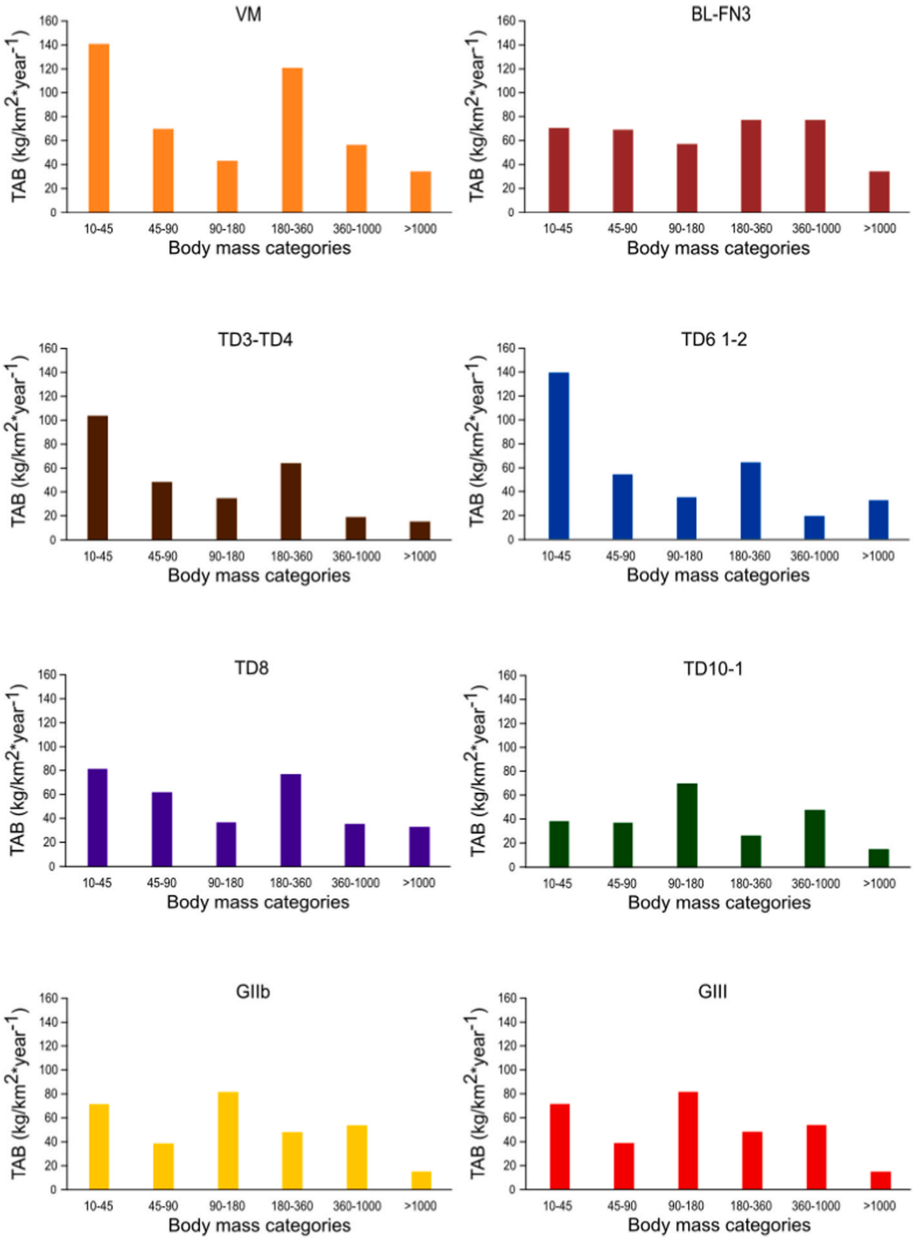

Fig. 4. Distribution of TAB (Total Available Biomass, in kg/km^{2}*year^{-1}) estimates according to prey body mass categories (class 1: 10–45 kg; class 2: 45–90 kg; class 3: 90–180 kg; class 4: 180–360 kg; class 5: 360–1000 kg; class 6: >1000 kg) for the different faunal assemblages analyzed in this paper. The arithmetic mean of TAB-min and TAB-MAX was used for each body size class. Abbreviations: VM, Venta Micena; BL-FN3, Barranco León-Fuente Nueva 3; TD3-TD4, Trinchera Dolina 3–4; TD6 1–2, Trinchera Dolina 6 1–2; TD8, Trinchera Dolina 8; TD10-1, Trinchera Dolina 10–1; GIIb, Galería IIb; GIII, Galería III.

case, these differences are not statistically significant according to a *t*-test ($p = 0.096$ for the comparison of slopes and $p = 0.997$ for the Y-intercepts). Similarly, these slopes and Y-intercepts do no differ significantly from those obtained using exclusively the data from Hatton et al. (2015). Therefore, our results indicate that the reconstruction of trophic relationships for Pleistocene faunal assemblages using PSEco provides similar results to those observed in contemporary African ecosystems.

4. Discussion

Reconstructing the relationship between ancient species and the paleoenvironments where they evolved is one of the major goals of paleosynecology. For this reason, deciphering the conditions and circumstances in which our lineage evolved is of great interest to many disciplines related to human evolution, such as archaeoecology (Revelles, 2021; Crabtree and Dunne, 2022). Almost a decade ago, a study was published that presented a paleosynecological model (PSEco) aimed at reconstructing the trophic relationships of the European communities of large mammals where humans lived during the Pleistocene (Rodríguez-Gómez et al., 2013). The model was grounded on several theoretical assumptions for the paleocommunities: for example, to consider conditions of stability and stationarity for the prey species, as proposed by other researchers for averaging population fluctuations (e.g., Gage, 1998; Gurven and Kaplan, 2007). Although there are populations of large mammals that exhibit conditions of stability, even stability and stationarity (Caughley, 1970; Simmons et al., 1984; Rolley, 1985), it is nearly impossible to observe a whole community under these conditions. However, Hatton et al. (2015) argued that the African large mammals' ecosystems that have censuses of population over the past 50 years are close to stationarity. Even though these ecosystems show some fluctuations in their components, these fluctuations compensate for each

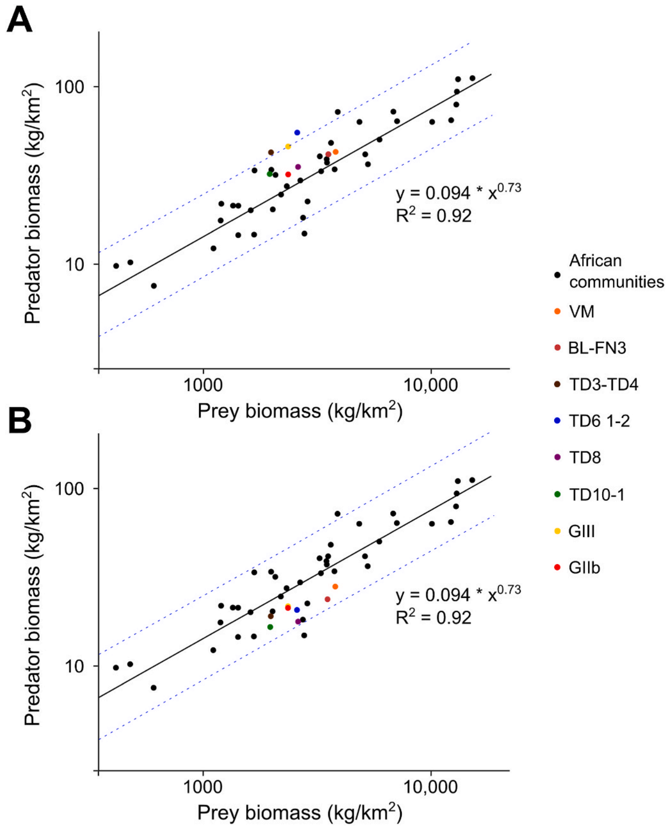

Fig. 5. Scatter plots of predator-prey biomass ratios (kg/km^2*year^{-1}) in the Orce and Sierra de Atapuerca faunal assemblages analyzed in this paper (Table 1), as well as in the African large mammal communities studied by Hatton et al. (2015). The black line is the regression obtained by Hatton et al. (2015) for the different African ecosystems (black circles), and the dashed lines show the 95% confidence limits above and below the regression line. A: predator-prey biomass ratio according to the densities obtained with PSEco. B: predator-prey biomass ratio considering only the fraction of predator biomass derived from the meat consumed (FPB) (i.e., discarding the fraction of the diet based on resources other than large herbivores). Abbreviations: VM, Venta Micena; BL-FN3, Barranco León-Fuente Nueva 3; TD3-TD4, Trinchera Dolina 3–4; TD6 1–2, Trinchera Dolina 6 1–2; TD8, Trinchera Dolina 8; TD10-1, Trinchera Dolina 10–1; GIIb, Galería IIb; GIII, Galería III.

other, and the ecosystems tend to be stationary at the community level. For this reason, the analysis of Hatton et al. (2015) can be used as a frame of reference for evaluating the goodness of fit of the PSEco model.

Previous studies have shown that PSEco outputs for Pleistocene sites provide results that are close to the predator-prey ratios of Hatton et al. (2015). Examples of this are the Orce sites in the Guadix-Baza Depression, SE Spain (Rodríguez-Gómez et al., 2016a, 2017b), which are key for studying early hominin dispersal in Western Europe (Espigares et al., 2013, Espigares et al., 2019, 2023; Toro-Moyano et al., 2013; Palmqvist et al., 2022a, 2022b, 2023). Prey and predator biomass estimates obtained in these studies for the paleocommunities of VM and BL-FN3 (Palmqvist et al., 2022a, 2022b) fell within the confidence interval of the regression of Hatton et al. (2015). This led us to consider the possibility of reproducing predator-prey biomass estimates with the model.

Our study has shown that PSEco provides values that are close to those observed by Hatton et al. (2015) (Fig. 5). This means that the model results in valid paleosynecological reconstructions, both in terms of predator-prey biomass relationships, on the one hand, and of meat availability and resource distribution among the carnivore guild of the paleocommunity, on the other. It must be noted that predator biomass is estimated by PSEco using an indirect approach that is completely different from the one used by Hatton et al. (2015). In our study, predator biomass is estimated according to the sustainability of the ecosystem, considering the resources available to the secondary consumers. PSEco achieves sustainable carnivore and human densities by estimating meat availability according to prey size classes and the distribution of this dietary resource among the species of secondary consumers. However, the estimates of available meat are derived from mortality profiles reconstructed from life traits of potential prey species, not from other more direct sources of information such as measured prey biomass (which is only possible in living ecosystems). Our results are close to those obtained by Hatton et al. (2015), although they differ slightly from the ones expected from their regression, being higher when total predator biomass is considered (Fig. 5A) and lower when FPB estimates are used (Fig. 5B).

Given that PSEco provides values similar to those of Hatton et al. (2015), it can be assumed that the mathematical assumptions and procedures of the model (i.e., the reconstruction of mortality profiles, the estimation of meat availability and the distribution of meat resources among carnivores) are close to reality. Fig. 6 shows two scatter plots that relate prey biomass to TAB (Fig. 6A) and TAB to fraction predator biomass (FPB) (Fig. 6B). In the latter case, predator biomass resulting from resources other than large mammals is not considered (see Table 7). Fig. 6A shows that prey biomass relates to the 0.76 power of TAB for the faunal assemblages analyzed in this study. In the case of TAB and FPB, the slope obtained is 0.74 (Fig. 6B). These values are close to

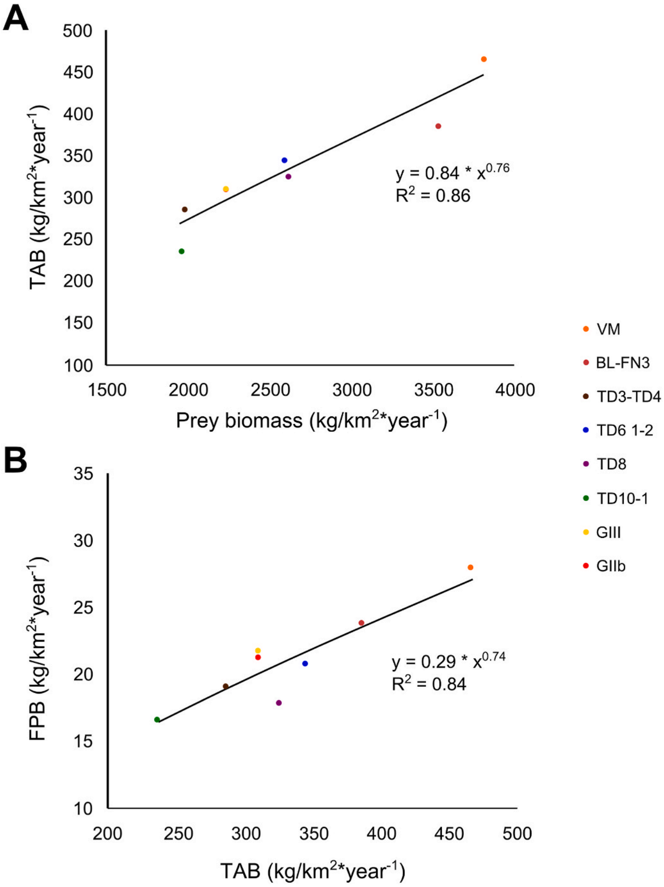

Fig. 6. Scatter plots of prey biomass on TAB (kg/km^2*year^{-1}) (A) and TAB on fraction of predator biomass (FPB) (kg/km^2*year^{-1}) (B) in the faunal assemblages of Orce and Sierra de Atapuerca analyzed in this paper, discarding biomass from other meat resources other than large mammals (see Table 7). Abbreviations: VM, Venta Micena; BL-FN3, Barranco León-Fuente Nueva 3; TD3-TD4, Trinchera Dolina 3–4; TD6 1–2, Trinchera Dolina 6 1–2; TD8, Trinchera Dolina 8; TD10-1, Trinchera Dolina 10–1; GIIb, Galería IIb; GIII, Galería III.

the ¾ ratios found by Hatton et al. (2015) in their analyses, being particularly close to the one obtained for predator-prey biomass ratios in African ecosystems. Therefore, the relationship between prey biomass and TAB may be the basis for scaling predator biomass relative to prey biomass found by Hatton et al. (2015). This result supports that the model estimates meat availability close to those present in the extant ecosystems and, consequently, that predator biomass estimates are reasonably accurate. However, there is room for improvement in PSEco to achieve a better fit of the model outputs to the values expected by the predator-prey ratios of Hatton et al. (2015), e.g., estimates of prey densities and aspects that influence resource distribution and predator-prey ratios.

In order to estimate prey biomass and meat availability for humans and carnivores, a set of allometric equations relating density values of prey species with their body masses were used. This is a very interesting topic in ecology and macroecology (Blackburn et al., 1993; Blackburn and Gaston, 1997; Currie and Fritz, 1993; Damuth, 1981, 1987, 1991, 1993; McGill, 2008; Silva and Downing, 1994, 1995; Silva et al., 1997, 2001; Santini et al., 2021; White et al., 2007). However, size-abundance relationships can be influenced by the ecological conditions of each ecosystem (Carbone and Gittleman, 2002; Currie and Fritz, 1993; Hatton et al., 2015; Pettorelli et al., 2009; Santini et al., 2018). To reconstruct prey paleocommunities, PSEco uses allometric approaches between body mass and density (Damuth, 1981, 1993), as previously employed in other models that analyzed trophic relationships in communities of large mammals (e.g., Bermúdez de Castro et al., 1995; Fariña, 1996; Vizcaíno et al., 2004, 2010). Some researchers have suggested that these approaches provide maximum values of ecological density (Blackburn and Gaston, 1997; White et al., 2007; but see also Blackburn et al., 1993; Lawton, 1990; Marquet et al., 1995). Thus, we assumed that PSEco depicts optimal conditions for the prey community, which means that prey abundances (and, indirectly, also carnivore ones) should be considered as ceiling values (Rodríguez-Gómez et al., 2013, 2016a, 2017b, 2022a). Increased information and methodological improvements, such as the recent studies of Santini et al. (2018, 2022), will allow refinement of the prey density estimates obtained with PSEco, thus improving the reconstructions of trophic relationships and bringing them closer to real situations. Given that the use of allometric equations for estimating prey abundances may translate into optimal ecological densities, this may be one of the reasons why predator values tend to be slightly higher with PSEco compared to those expected by Hatton et al. (2015). However, although the use of optimal densities affects the absolute values of prey and predator biomasses, this should not bias our estimated predator-prey biomass ratios compared to the expectations from the regression of Hatton et al. (2015). Our results tell us that predators yield more from prey than expected. Logically, these values relate to our assumptions on how predators satisfy their nutritional requirements. As shown in Fig. 5B, if we only consider the FPB derived from meat, our results are slightly lower than expected from the Hatton et al. (2015) regression. One of these assumptions of our model is that no prey biomass is lost (i.e., that all biomass is accessible to carnivores under optimal conditions), a situation that is not always true: for example, carcasses decompose over days without being fully utilized, especially in the case of megaherbivores.

Several aspects may influence our results: (i) differences in prey biomass and meat availability; (ii) composition of the prey community; and (iii) composition of the community of secondary consumers and their dietary preferences. As mentioned above, meat availability (TAB) represents between 11% and 14% of total prey biomass (Fig. 5, Table 8), and these proportions may influence predator biomass. The higher the ratio of TAB to prey biomass, the greater the predator biomass that can be sustained, as shown in our study for TD6 1–2, TD3-TD4 and GIII (see Results). The faunal assemblages compared show higher differences in prey biomass than in TAB estimates. It is even the case that faunal assemblages with lower prey biomass than others have higher TAB, as in the case of TD6 1–2 compared to TD8 (Table 8). TAB values are influenced by prey species composition because those prey species with low reproductive rates cannot support high mortality rates, as happens in the case of species with higher reproductive rates (see Martín-González et al., 2019). Thus, it can be observed that the distribution of TAB among the different body mass categories varies from one faunal assemblage to another (Table 5 and Fig. 4). Although TD6 1–2 and TD8 have similar TAB distribution patterns, the major difference between them is the amount of available meat from the first two prey size categories (class 1: 10–45 kg; class 2: 45–90 kg), which is > 30 kg higher in TD6 1–2 than in TD8 (Table 5 and Fig. 4). A similar situation can be observed between TD3-TD4 and TD10-1, which both have similar prey biomass estimates (20 kg of difference) (Table 7), but the difference in the amount of meat available (50 kg) is greater (Table 5). These differences increase when TAB values for the first two prey size categories are analyzed, being 68 kg higher in TD3-TD4 than in TD10-1 (Table 5). As mentioned above, the youngest faunal assemblages, TD10-1, GIIb and GIII, show a similar distribution of TAB and the lowest values, except for TD3-TD4 (Table 5 and Fig. 5). In an analysis of competition intensity between carnivores and humans in the Sierra de Atapuerca, an increasing trend of competition for meat was observed from the Early Pleistocene to the end of the Middle Pleistocene (Rodríguez-Gómez et al., 2017a). TAB values and their distribution can explain in part this trend. However, this is not observed at a European scale, with higher TAB values and lower competition intensities at the beginning of the Middle Pleistocene than at the end of both the Early and Middle Pleistocene (Rodríguez-Gómez et al., 2017c).

In terms of species composition and diet type of secondary consumers, there is only one species in Hatton et al. (2015) with an omnivorous diet, the brown hyena (*Hyaena brunnea*). This carnivore is predominantly a scavenger of all types of vertebrate carcasses, supplementing its diet with insects, fruits, bird eggs, and small vertebrates (Mills, 1982; Mills and Hofer, 1998; Holekamp and Kolowski, 2009). In our case, we considered *Canis mosbachensis*, *Hyaena* sp., lynx species, ursids, and humans as secondary consumers with a diet that included resources other than meat from large mammals. This is probably the main factor that explains why our values are slightly higher than those expected. Our estimates of predator biomass are derived from the estimates of species body mass (Table 3) and sustainable densities calculated by PSEco (Table 6) (Eq. (4)). In the case of those secondary consumers that supplement their nutritional requirements with resources other than large mammals, PSEco estimates their densities considering only the meat demands of large mammals, thus assuming that all other resources are fully consumed. This means that variations in meat consumption can have a relatively large effect on the sustainable densities of these species and, therefore, on predator biomass estimates. Another factor that influences the estimates on predator biomass is species body mass, as in the case of bears. This is more obvious when GIIb and GIII are compared. Both assemblages show the same values of prey biomass and TAB, and their distribution among body mass classes is identical. The only difference between them is the presence of *Ursus deningeri* in GIII, a species not recorded in GIIb (in this case, the differences in the human groups do not affect the modeling) (Table 1). This difference causes GIII to be farther from the value expected from the regression of Hatton et al. (2015) than GIIb, which is very close to it (Table 7 and Fig. 5A). "The bear effect" can also be observed when comparing other sites with close prey biomass and TAB values, for example: (i) TD3-TD4 and TD10-1; (ii) and TD6 1–2 and TD8 (Tables 5 and 6, Fig. 5A). In both cases, those assemblages with higher predator-prey biomass ratios have bear species that are larger than in the other assemblages, where bears are also present (Table 3). Thus, when considering only carnivore densities relative to the availability of meat resources from large mammals (i.e., if the analyses are focused on FPB), which cancels out factors such as "the bear effect", the predator-prey biomass ratios obtained decrease and fall within the confidence interval of the regression of Hatton et al. (2015) (Table 7 and Fig. 5B). With this in mind, it is relevant to refine the parameters associated with the meat demands of the members of the carnivore guild, to obtain results closer to those expected by Hatton et al. (2015).

Another aspect that may influence the results obtained with PSEco is the preservation completeness of the faunal assemblages. Given that the secondary consumers use to be the species less represented in the assemblages due to their low ecological densities in the paleocommunities, this may translate into a lower than expected predator-prey biomass ratio. However, this is not the case in our analysis, even though it has been proposed that the faunal assemblage of Gran Dolina level TD6 2 lacks at least one species of large felid (Rodríguez-Gómez et al., 2017a). In fact, it should be noted that if a large felid with a diet strictly based on large mammal meat were to have been present in TD6 1–2, the predator-prey biomass ratio would be closer to that expected because mesocarnivores and humans would have less access to these resources.

A possible option to avoid the problems of preservation completeness derived from the taphonomic biases that commonly affect the faunal assemblages of most sites is to analyze regional faunal assemblages, which faunal lists are usually more comprehensive. The late Early Pleistocene carnivore guild of Europe was composed of a diverse array of predators and scavengers, including (Palmqvist et al., 2022b: Fig. 4): (i) two machairodontine cats, the large (~200 kg; Anyonge, 1993) scimitar-tooth *Homotherium latidens* and the medium-sized (~100 kg; Palmqvist et al., 2007) dirk-tooth *Megantereon whitei*; (ii) four felines, the medium-to-large pantherine *Panthera gombaszoegensis* (~150 kg; Marciszak and Lipecki, 2022), usually referred to as the European jaguar, the giant (~80 kg; Cherin et al., 2014) cheetah *Acinonyx pardinensis*, a potential meat supplier for kleptoparasites like the hyenas and hominins (Hemmer et al., 2011), the puma (~52 kg; Cherin et al., 2013) *Puma pardoides*, and the lynx (~18 kg; Rodríguez-Gómez et al., 2016a) *Lynx pardinus;* (iii) a bone-cracking hyaenid, the giant (~110 kg; Palmqvist et al., 2011), short-faced *Pachycrocuta brevirostris*; (iv) two canids, the hypercarnivorous *Lycaon lycaonoides* (~30 kg; Palmqvist et al., 1999) and the mesocarnivorous *Canis mosbachensis* (~10 kg; Palmqvist et al., 2002); and (v) a large (~375 kg; Palmqvist et al., 1996), omnivorous ursid (Medin et al., 2017). Apart from these species, there are three small carnivores (Ros-Montoya et al., 2021), two mustelids (*Martellictis ardea* and *Meles meles*) and a fox (*Vulpes alopecoides*). These hypocarnivorous species, which probably had no access to ungulate prey and limited their consumption of flesh to small vertebrates, were not considered in the model (Rodríguez-Gómez et al., 2013, 2016a).

The carnivore guild described above includes ambushers from mixed and closed environments (*M. whitei* and *P. gombaszoegensis*) as well as cursorial predators adapted to hunting in open plains (*A. pardinensis*, *H. latidens* and *L. lycaonoides*). This suggests that scavenging opportunities were available for the hominins and hyenas in a variety of habitats (Palmqvist et al., 2022a). However, we must consider here the question of regional as opposed to local faunas, because not all species of this carnivore guild were present at each European site of late Early Pleistocene age (Palmqvist et al., 2022b). This means that regional species lists are expected to be longer than local ones, although there may be some exceptions to this rule. For example, the site of Venta Micena has been interpreted as a breeding den of *P. brevirostris*, a bone-cracking hyena that relied heavily on prey hunted by other predators (Palmqvist et al., 1996, 2011; Arribas and Palmqvist, 1998). Recent bone assemblages collected by hyenas usually show a high diversity of species, covering a wide range of body masses (Palmqvist and Arribas, 2001). The reason is that hyenas forage long distances searching for scavengeable carcasses, thus accurately sampling the large mammal communities from different environments. In the case of *P. brevirostris*, this species shows shortened distal limb segments compared to the living hyenas, which represents an adaptation for long-distance transport of ungulate carcasses without dragging (Turner and Antón, 1996; Palmqvist et al., 2011). Moreover, the lower canines are comparatively more developed in *P. brevirostris* than in the spotted hyaena (*Crocuta crocuta*), which behaves both as a predator and as a scavenger and was the species responsible for the accumulation of large vertebrate remains from level TD8 at the Gran Dolina site from the Sierra de Atapuerca (Blasco et al., 2011). In contrast, the two truly scavenging hyenas, the striped hyena (*Hyaena hyaena*) and the brown hyena (*Parahyaena brunnea*), show enlarged lower canines, like in *P. brevirostris*. This represents an adaptation to carry heavy loads to the denning site, as reflected in the longer mean distance of transport of the remains by the brown and striped hyenas compared to the spotted hyena (Pérez-Claros and Coca-Ortega, 2020). For this reason, it is expected that Venta Micena is more spatially averaged than other sites of Orce, showing a higher preservational fidelity of the fauna that inhabited the regional environments of the basin, and probably even than level TD8 of Gran Dolina, whose accumulating agent was *C. crocuta*. In contrast to Venta Micena, the upper archaeological level of Fuente Nueva-3 in Orce has been interpreted as a death trap for megafauna that became stuck in quicksand and whose carcasses were scavenged by the hominins and hyenas (Espigares et al., 2023). Something similar to Fuente Nueva-3 occurs at the Galería site in the Sierra de Atapuerca, which has been interpreted as a natural trap due to the formation of a chasm where humans and carnivores used to exploit the carcasses of the fallen animals (Cáceres, 2002; Huguet et al., 2001; Ollé et al., 2005). These aspects suggest that the degree of fidelity in representing the fauna of the environment of the bone assemblages unearthed at these sites was probably lower than at Venta Micena.

In the case of carnivores, their low ecological densities and small population sizes compared to the herbivores imply that the former are usually worse sampled in the fossil assemblages (death traps are the exceptions to this rule, for example the Late Pleistocene Rancho La Brea tar seeps, where prey animals were trapped in asphalt and attracted large numbers of carnivores who became trapped in turn; Spencer et al., 2003). The vagaries of the fossil record of carnivores mean that the list of carnivore species recorded at a given site uses to be more biased than the list of herbivores. For example, >24,000 skeletal remains of large mammals have been unearthed during the last decades in Venta Micena from a surface of only ~400 m^2. Of these remains, ~8000 can be determined anatomically and taxonomically (Palmqvist et al., 2022c: Table 1). Each of the three ungulates better represented in the bone assemblage, horse (*Equus altidens*), bison (*Bison* sp.), and megacerine deer (*Praemegaceros* cf. *verticornis*), are represented by hundreds of fossil specimens. In contrast, carnivores account for only 5.7% of the NISP, and one species, *P. gombaszoegensis*, has been identified from one isolated hemimandible. The consequence of the rarity of carnivores means that our predator-prey biomass ratios can be underestimated and must therefore be considered as minimum estimates. As commented above, the exceptions to this rule are those sites that can be interpreted as death traps, where the remains of carnivores can account for >90% of the assemblage, as happens in the Late Pleistocene Rancho La Brea tar seeps (Spencer et al., 2003).

Apart from these taphonomic considerations, we must take into account that regional faunas are composed of species that are part of local assemblages within a region that has characteristics that make it a unit, such as net primary production (NPP) values and their evolution over time (e.g., Vidal-Cordasco et al., 2023). Thus, as expected, we find local faunal assemblages in present-day ecosystems that do not contain the whole regional fauna, as observed by Hatton et al. (2015). In this paper, parks and game reserves from the East (Ethiopia, Kenya, Tanzania, and Uganda) to the Southeast (Zimbabwe), South (Botswana and South Africa), and Southwest (Namibia) of the African continent are analyzed. Even the less common species (e.g., brown hyena, bushpig, springbok, oribi, dik-dik, white rhino, sable, nyala, and grysbok) have a wide distribution, so the species in the analysis can be considered part of the regional fauna. Looking at the ecosystem with the highest diversity, Kruger National Park in South Africa, there are species that are not present in the region (brown hyena, bushpig, springbok, oribi, dik-dik, kongoni, Thomson's gazelle, Grant's gazelle, oryx, and baboon), and even species from neighboring areas, such as the baboon, which is present in the Nwaswitshaka River and Sabie River ecosystems. As might be expected, this could result from a variety of factors, not just community structure. Given that we are interested in analyzing predator-prey interactions in our work, we believe that local faunal assemblages provide us with more certainty of true interactions than analyzing regional assemblages. Moreover, they inform on aspects that are specific to each local assemblage, which could be omitted in an analysis at a regional scale. In order to limit the effects of taphonomic biases, faunal assemblages with a high degree of preservation completeness were selected. Following an approach similar to Rodríguez-Gómez et al. (2017c), the sites studied record at least 11 species, with seven prey and four secondary consumers.

It should also be noted that our working perspective was similar to that of Hatton et al. (2015): these authors considered each local assemblage by the census year conducted, even though fact that sometimes species disappeared (e.g., wild dog in Etosha National Park and Nairobi National Park) or appeared (e.g., black rhino in Kruger National Park and Masai Mara National Reserve) throughout the censuses. In this way, Hatton et al. (2015) approached their study without attempting to cover the effects that may have influenced the presence or absence of species in the different censuses, analyzing the predator-prey biomass relationships observed in the different censuses. Although our study focused on local faunal assemblages, the model can of course estimate dietary interactions with a regional perspective and with an open system that allows the analysis of multiple scenarios. For example, by considering those species of secondary consumers not recorded at the sites but that were likely to have inhabited the region (Rodríguez-Gómez et al., 2013, 2014a, 2017a; Domingo et al., 2017) or hypothesizing different strategies for obtaining meat resources (Rodríguez-Gómez et al., 2016a, 2020).

Considering all the issues discussed above, the predator-prey biomass ratio values obtained with PSEco are mainly the result of the distribution of available meat among the secondary consumers, which is influenced by: (i) differences in the ratios between prey biomass and meat availability (TAB); (ii) the composition of prey species, which affects the distribution of TAB among size classes and the amount of resources (especially in the first two size classes) consumed by humans and carnivores (Table 8 and Fig. 4); (iii) the composition and subsistence strategies of the members of the predatory guild, which determines that the highest ratios of predator biomass to prey biomass are found in those communities with more mesocarnivorous and omnivorous species, as well as those hypercarnivorous species for which large mammals (>10 kg) represent a secondary resource (e.g., lynx) (Table 8 and Fig. 4); and (iv) sampling biases, which mostly affect predators (see above), because they can lead to very low values of predator biomass; this also happens if prey diversity is underrepresented, because PSEco evaluates predator biomass from estimates of meat availability. However, these situations did not occur in our analysis, since we selected faunal assemblages that at least record four species of secondary consumers. All these local predatory guilds required more meat than that available in the paleoecosystems, except in the case of TD6 1–2 (Rodríguez-Gómez et al., 2013, 2014a, 2016a, 2016a, 2017a, 2017b). Thus, the faunal assemblages TD3-TD4, TD6 1–2, and GIII stand out from the rest by showing values further away from the regression of Hatton et al. (2015). This is due to (i) their high TAB estimates relative to prey biomass; (ii) the distribution of TAB towards lower size categories; and (iii) the presence of secondary consumers with an important part of their diet based on resources other than large mammals (>10 kg). All this leads to higher-than-expected predator biomass values (Fig. 5). On the contrary, the situation characterized by low values of TAB relative to prey biomass, by a more displaced distribution of TAB towards larger size classes, and by a higher representation of large hypercarnivores leads to values that are closer to those expected. This is the case of BL-FN3, although a greater effect of the composition of secondary consumers is perceived in this assemblage than in VM (Table 8, Fig. 5A and B).

Taking all these issues into account from a temporal perspective, we observe in the faunal assemblages from Orce and Sierra de Atapuerca a trend towards a reduction in prey biomass and TAB from the end of the Early Pleistocene to the end of the Middle Pleistocene, with the exceptions of TD3-TD4 and TD10-1 (Tables 5 and 7 and Fig. 4). Thus, our results indicate that more resources were available in the Early Pleistocene than in the late Middle Pleistocene, because the faunal assemblages of the latter preserve lower numbers of prey species. However, when we analyze the amount of meat relative to prey biomass (Table 8 and Fig. 5B), these trends are reversed: a greater amount of meat per unit of prey biomass is estimated in the faunal assemblages from Sierra de Atapuerca than in the Orce sites. The only exception is the comparison of TD10-1 with VM (Table 8). Despite the fact that the absolute values of prey biomass and TAB are higher in the Orce assemblages, there are sites in the Sierra de Atapuerca showing FPB values that are closer to the expectations of the Hatton et al. (2015) regression line if we consider only the predator biomass produced by TAB. This is the case of TD3-TD4, TD6 1–2, and GIII (Fig. 5B). When all predator biomass is included, VM and BL-FN3 are the faunal assemblages with the lowest predator biomass relative to prey biomass (Table 8), and their values are the closest to the Hatton et al. (2015) regression line (Fig. 5A). These results may indicate an impoverishment of the community of secondary consumer from the Early Pleistocene to the end of the Middle Pleistocene. This may be related to the faunal turnover that took place at the Early-Middle Pleistocene transition, characterized by a profound renewal of the predatory guild (Konidaris, 2022). Konidaris (2022) indicated a slight increase in the diversity of the carnivore guild at the beginning of the Middle Pleistocene, from 10 to 11 species. However, these species do not co-occur at any site, unlike what he observed in the Early Pleistocene. Carnivores are scarce in both number of species and specimens, especially in archaeo-paleontological sites (Martínez-Navarro, 2018; Konidaris and Tourloukis, 2021). The richest sites show at the most five to seven species of large carnivores (Konidaris, 2022), as happens in the sites of Sierra de Atapuerca (Table 1). Konidaris (2022) proposed that the most profound changes in the carnivore guild of Europe occurred with the appearance of humans by late Early Pleistocene times. This may have led to a reduction in carnivore diversity as part of the carnivore niches vanished in the Late Pleistocene. Martínez-Navarro (2018) distinguished between sites with Oldowan and Acheulean industry. In the former sites, carnivores are better represented and more abundant, but the opposite situation occurs in those sites with Acheulean technology. Martínez-Navarro (2018) suggests that there was a change in the subsistence strategy of hominins from passive scavenging to active hunting, with a first phase in which the Oldowan hominins did not play a dominant role in the ecological scenario: this situation changed with the appearance of the Acheulean technology, when humans became the dominant predator, and this would lead to a more reduced presence of carnivores. It will be interesting conduct future analyses on predator-prey biomass relationships with PSEco at the Eurasian scale to explore the main factors operating behind these interactions in the carnivore guild.

Our results show that PSEco is a valuable approach for estimating meat availability in paleoecosystems, which allows reconstructing past large mammal food webs, and that it can also be useful in present-day ecosystems because it recreates conditions of stability and stationarity. When these conditions are met, the communities of large mammals can be sustainable over time. For this reason, it would be interesting to evaluate in future studies the predictive ability of PSEco in modern large mammal communities, such as those analyzed by Hatton et al. (2015). If PSEco is able to reproduce results close to reality, we would have a useful tool for explaining many of the factors that may influence predator-prey relationships.

5. Conclusion

Those models that provide inferences on the paleoecological conditions under which humans evolved during the Pleistocene are of great interest. We have developed a paleosynecological model (PSEco) that analyzes trophic relationships in the Pleistocene communities of large mammals, with the main goal of understanding the ecological conditions surrounding human evolution during this epoch. The model estimates the amount of meat available to the community of secondary consumers, carnivores and hominins, starting from the large herbivores. The application of this model to a number of Pleistocene faunal assemblages confirms that PSEco provides results similar to those observed in modern African ecosystems. This suggests that PSEco provides reasonable estimates on prey meat availability and also on its distribution among the members of the carnivore guild. Nevertheless, there is much room to improve PSEco in order to provide results closer to those expected for modern ecosystems, especially in terms of defining more accurately the dietary preferences and consumption profiles of carnivores and humans.

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Author contributions

GRG wrote the main manuscript text and all co-authors made contributions. GRG, PP, and InkScience developed the flowchart in Fig. 1. GRG, JAMG JMBC, BMN, PP, and InkScience made Fig. 2. The rest of the figures were made by GRG. All authors read and approved the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data and methods used in this study have been published in previous papers by our team.

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