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Testing the hypothesis of an impoverished predator guild in the Early Miocene ecosystems of Patagonia: An analysis of meat availability and competition intensity among carnivores



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ABSTRACT

The lower Miocene Santa Cruz Formation (dated to ~18–16 Ma) of Southern Patagonia, Argentina, preserves rich vertebrate faunas, which are representative of communities that existed prior to the Great American Biotic Interchange (GABI). Some previous researchers have hypothesized that these pre-GABI faunas had a low richness of mammalian carnivores (an impoverished predator guild), while others argue for a predator/prey ratio similar to those of recent communities. In this paper, we analyze faunas from the lower part of the Santa Cruz Formation (FL 1–7) using a methodology that allows us to quantify (i) the meat resources that were available to the secondary consumers of the palaeocommunity; and (ii) the competition intensity for these resources. In our modeling, we considered different scenarios related to meat consumption, including the possibility that several taxa had a scavenging behavior, and also differences in mortality rates between young and adult prey. Our results provide estimates of the nutritional requirements from the predator/scavenger guild under maximum and minimum quantities of meat offered by the prey community, which indicate the presence of a well-balanced palaeocommunity. Moreover, the competition indices point to a relatively high level of competition for prey of small-to-medium size, although competition for resources from large mammal prey was rather low. This suggests that the predator/scavenger guild was not impoverished, although there were insufficient carnivore species to fully consume the megaherbivore biomass.

1. Introduction

Except for some non-permanent land connections with East Antarctica (Reguero et al., 2014), South America underwent considerable diversification and ecological specialization of its mammalian fauna in isolation from other continents through much of the Cenozoic Era (Simpson, 1980). This "splendid isolation", as designated by Simpson, was only interrupted by the arrival from Africa of caviomorph

rodents in the Middle Eocene (~41 Ma) (Antoine et al., 2011; Boivin et al., 2017) and platyrrhine primates in the late Middle Eocene or Late Eocene (Bond et al., 2015). Later, a more intense interchange of faunas took place at the beginning of the Late Miocene, when South America began to establish contact with Central and North America, an event known as the Great American Biotic Interchange (GABI) (Stehli and Webb, 1985; Cione et al., 2015).

The Santa Cruz Formation (SCF) outcrops along the Atlantic coast of

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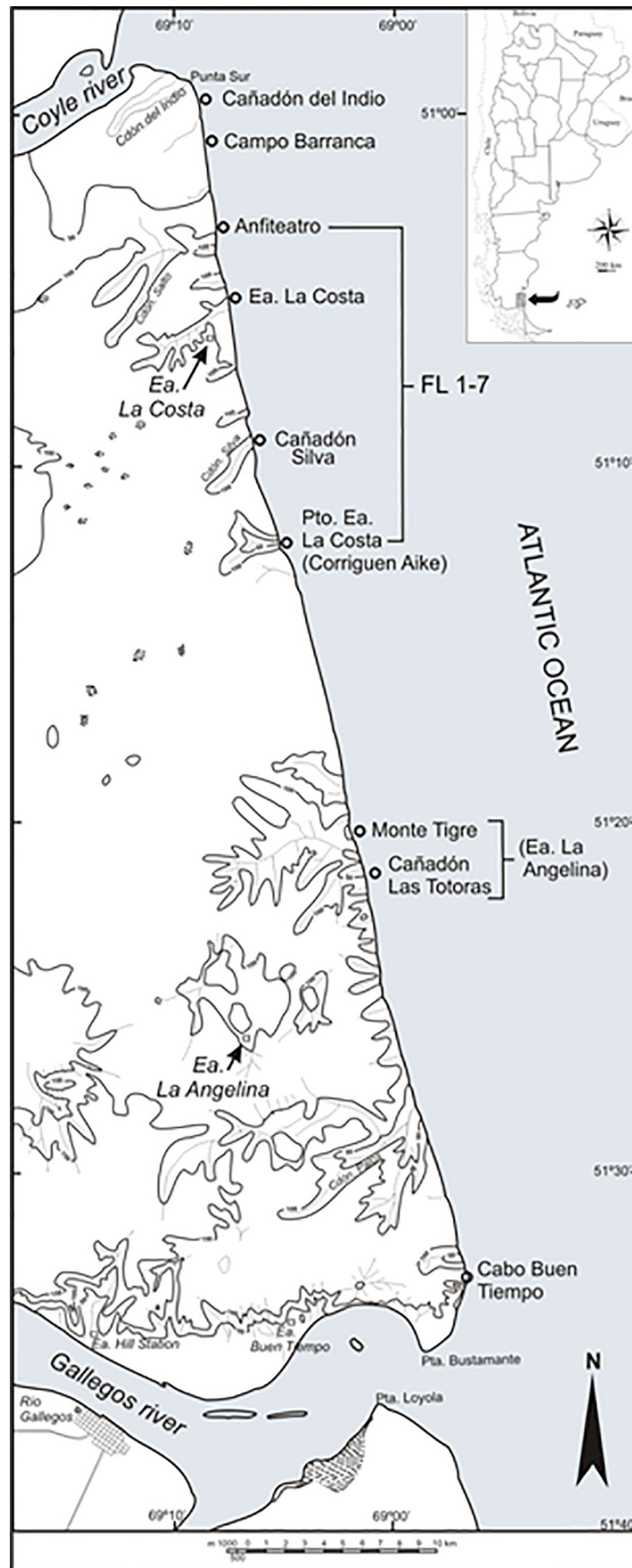


Fig. 1. Map showing the localities of the main outcrops of the Santa Cruz Formation at the Atlantic coast (modified from Cassini, 2013).

southernmost continental Patagonia (~18–16 Ma, lower Miocene; Cuitiño et al., 2016, 2019) and contains a rich vertebrate fauna characteristic of pre-GABI communities. This assemblage marks the peak of known species richness achieved by South American mammals after the arrival of primates and rodents, but before the later appearance of North American immigrants (Simpson, 1980; Marshall and Cifelli, 1990). According to Vizcaíno et al. (2012a), the South American Early-Middle Miocene fauna consists of a complex mixture of descendants of ancient mammalian lineages endemic to the continent (Marsupialia, Xenarthra, Litopterna, Notoungulata, and Astrapotheria) and immigrating from Africa (Rodentia and Primates), together with a rich assemblage of birds (Rheiformes, Tinamiformes, Gruiformes, Anseriformes, Pelecaniformes, Ciconiiformes, Falconiformes, and Carniiformes). No crocodylians are recorded in the SCF fauna, but there are remains of herpetofauna, including two anurans, *Calyptocephalella* and an indeterminate Leptodactylidae, and several squamates, the tupinambine teiid *Tupinambis* (*Salvator*) and some indeterminate pleurodont iguanians and colubrids (Fernicola and Albino, 2012). The mammalian fauna includes a wide array of forms, which comprises small paucituberculates and caenolestids, many carnivorous sparassodonts and rodents, some forms of protherotheid litopterns and a medium-sized macraucheniid, several small tyotheres, two medium-to-large toxodontids, a large homalodothera, a large astrapothera, several armadillos, some medium-sized glyptodonts, a large diversity of medium to heavy sloths, a small anteater, and a small platyrrhine monkey (Vizcaíno et al., 2010, 2012a). They are part of the “Santacrucian” South American Land Mammal Age (SALMA), which is an Early Miocene local stage used with SALMA classification in South America that corresponds to the Burdigalian. Additional information on these faunal assemblages is provided in the Supplementary information.

The specimens from these localities are often found in an excellent state of preservation, including partial or even complete articulated skeletons. For this reason, the fossils collected from the Atlantic Coast outcrops of SCF offer a unique opportunity to perform palaeobiological studies based on a form-function approach (see Vizcaíno et al., 2006; Bargo et al., 2009; Vizcaíno et al., 2011; Toledo et al., 2012, 2013; Prevosti and Martín, 2013; Toledo et al., 2015; Toledo, 2016; Cassini et al., 2017a, 2017b; Muñoz et al., 2017, 2019). Moreover, many of them come from stratigraphic levels that were deposited within a restricted time frame, which provides a narrow temporal window that allows performing reliable palaeoecological analyses (Perkins et al., 2012; Kay et al., 2012a).

Based on a comparison of predator and prey diversity for 385 modern mammal faunas, Croft (2006) analyzed the diversity of mammalian predators in South America during the Cenozoic before the GABI. He proposed that predator species richness causally limits prey richness, and that this effect is more pronounced in the faunas from open habitats than in those from closed ones. Croft (2006) observed an apparently low diversity of mammalian carnivores (marsupials were the primary predators) in the extinct pre-GABI faunas of South America, including the SCF assemblages, which led him to suggest that they show greater-than-expected numbers of medium-sized prey mammals. Later, Vizcaíno et al. (2010) analyzed the structure of the SCF mammalian palaeocommunity at two of the most important coastal localities and found that both showed low carnivore to herbivore ratios compared with modern faunas. Following Fariña (1996), Palmqvist et al. (2003) and Vizcaíno et al. (2004), Vizcaíno et al. (2010) used the relationship between population density and body size for estimating the on-crop biomass (in kg/km²) of the species of these palaeocommunities and calculated also the metabolic requirements of the carnivores. They reported a high diversity of coexisting herbivores at these sites, which suggested a strong competition for dietary resources and a fine partitioning of the herbivore niche. They also compared the distribution of body mass values and the diversity of predators and prey, which indicated that potential secondary productivity was at least three times higher than the metabolic requirements of the members of this

impoverished carnivore palaeoguild. In contrast, a similar analysis of the Early Pleistocene assemblage from Venta Micena in Orce (Baza Basin, SE Spain) showed a balance between the metabolic requirements of the carnivores, which included species without modern analogs such as two saber-toothed cats, and the estimate of secondary productivity obtained for the palaeocommunity (Palmqvist et al., 2003). However, Prevosti et al. (2012) analyzed the diversity of sparassodont marsupials of SCF compared to that of their potential prey and concluded that sampling bias could be behind the underestimation of the number of predators. Correcting for sampling bias, they found that the number of sparassodont taxa considered in the ratio presented by Croft (2001, 2006) fell within the observed range for placental faunas.

The most comprehensive study of the SCF faunas was performed by Kay et al. (2012a), who made an exhaustive palaeoecological analysis of a fossil assemblage from a set of localities that outcrop along the coastal Atlantic South of Río Coyle between about 50.3° and 51.6° S, identified as FL 1–7 (Fig. 1), which are well restricted chronologically (~17.6–17.3 Ma; ages revised by Trayler et al., 2020). Given that the palaeolatitude was similar to today, FL 1–7 was extratropical and had highly seasonal day lengths. Kay et al. (2012a) found that FL 1–7 was analogous to a single modern fauna of limited geographic and temporal scope, with an overall annual rainfall of 1000–1500 mm with cool/wet winters and dry/warm summers. This palaeofauna developed in a landscape consisting of a mosaic of open temperate humid and semi-arid forests, with ponds in some areas and seasonal flooding in others, which prompted the formation of marshlands with a mixture of grasses and forbs. In order to evaluate Croft’s (2006) hypothesis, Kay et al. (2012a) gathered data on the number of predators and the richness of medium-sized mammalian prey (0.5–250 kg) in those mammalian faunas with known annual rainfall and vegetation structure. They found that predator richness increased in parallel to the decrease of rainfall among the extant faunas of South America and that the predator to prey ratio in FL 1–7 agreed with the expectations from rainfall and latitude.

Finally, Spradley et al. (2019) applied an approach that combined ecological indices as predictors in two regression modeling techniques—Random Forest (RF) and Gaussian Process Regression (GPR)—to derive palaeoecological predictive models for FL 1–7 and one Miocene locality of Colombia. Their estimates of precipitation and temperature were in agreement with those previously reported by Kay et al. (2012a) and they provided also additional information on other climate/habitat variables. Similarly, Di Giacomo and Fariña (2017) developed allometric ecological models for comparing a huge number of Pleistocene faunas with a recent one (Serengeti) and a Miocene one (Patagonian Santa Cruz, the database used by Kay et al., 2012a). Their approach, which did not incorporate birds as predators, included the original model of Fariña (1996) plus other three with revised values of (i) predator population density, (ii) secondary productivity, and (iii) secondary productivity and population density, respectively. According to their results, only those models based on revised estimates of secondary productivity and revised values of both secondary productivity and population density rendered balanced reconstructions for the SCF fauna. The failure of the model based exclusively on estimates of population density was attributed to an underestimation of this parameter resulting from the low metabolic rate of xenarthrans and marsupials (Di Giacomo and Fariña, 2017).

Given these contradictory results, the aim of our study is to assess the hypothesis of an impoverished carnivore palaeoguild in the faunal assemblages of SCF, as first proposed by Croft (2006) and supported by Vizcaíno et al. (2010), but later contradicted by Prevosti et al. (2012) and Kay et al. (2012a). For doing so, we analyze the food web of the large mammals assemblage from FL 1–7 (for details, see the Supplementary Information) using a model that estimates the biomass of the primary consumers of the palaeoecosystem and the biomass required by the secondary consumers, which allows calculating the degree to which the dietary requirements of the latter are satisfied. The model distributes the biomass available to the secondary consumers among the

members of the carnivore palaeoguild according to their prey preferences, which in turn allows to estimate their sustainable densities (D_s) (see details in Rodríguez-Gómez et al., 2013, Rodríguez-Gómez et al., 2014a, and also in the Supplementary Information). This methodology has been previously applied to a number of Pleistocene sites of Europe that include human remains for measuring the level of competition intensity of their carnivore palaeoguilds, for example those from Sierra de Atapuerca (Burgos, Spain) (Rodríguez-Gómez et al., 2013, 2014b, Rodríguez-Gómez et al., 2017a) and Orce (Grenade, Spain) (Rodríguez-Gómez et al., 2016b, 2017b). In the case of FL 1–7, we test different scenarios in order to assess if competition within the carnivore guild was intense or, alternatively, the resources available were in excess of those expected for satisfying the nutritional requirements of all species of secondary consumers, which would be an argument in support of the interpretation of an impoverished predator guild for these palaeocommunities.

2. Materials

The SCF fossils studied here come from a number of coastal localities between the Coyle and Gallegos rivers, at about 51° South latitude (Anfiteatro: 51° 03' S, 69° 08' W; Estancia La Costa: 51° 05' S, 69° 08' W; Cañadón Silva: 51° 09' S, 69° 05' W; Puesto Estancia La Costa: 51° 11' S, 69° 05' W; see Vizcaíno et al., 2012b), ~100 km North from the Strait of Magellan (Fig. 1). The lower member of SCF (Estancia La Costa Member) bears a rich mammalian association, which, according to Tauber (1997a, 1997b), is distributed in some 20 fossiliferous levels (FL) that are differentially exposed along the coastal exposures (Matheos and Raigemborn, 2012). Based on tephrostratigraphic correlations, Perkins et al. (2012) proposed that several of Tauber's (1997a) lower fossiliferous levels (FL 1–7) can be considered penecontemporaneous, dated ~17.6 to 17.3 Ma (Perkins et al., 2012; Trayler et al., 2020).

Following Vizcaíno et al. (2010), only those prey species of mammals and birds from the FL 1–7 with body masses of > 10 kg were included in the analyses, in order to avoid preservation and sampling biases. Anurans and squamates were not included in our analyses because they weighted < 10 kg. This procedure resulted in the selection of twenty-two prey species with body masses ranging between 10 and 925 kg, and nine predator/scavenger species with mass estimates comprised between 8 and 95 kg (Table 1) (Kay et al., 2012a; Prevosti et al., 2012; Vizcaíno et al., 2012c). Two species with body masses of < 10 kg (a phorusrhacid bird, *Psilopterus lemoinei*, and a sparassodont mammal, *Cladosictis patagonica*) were included in the analyses because they presumably were able to prey on animals larger than 10 kg (Ercoli et al., 2014) and could have played a significant role in the food web (see Methods section). The species were placed in the prey and predator categories based on phylogenetic and anatomical information, as well as on palaeoautecological inferences (Table 1).

3. Methods

3.1. Food web reconstruction of FL 1–7

In order to reconstruct the food web of the SCF assemblages, information was gathered for their extant analogues on fertility and other life-history traits, including adult body mass (ABM), body mass at birth (NBM), age at first birth (AFB), gestation, litter size (LS), litters per year (LY), breeding interval, growth rate, sexual maturity, and lifespan (L) (Table 2). All time-dependent parameters were expressed in years. Adult body mass values were taken from Vizcaíno et al. (2012a) and the remaining life traits were estimated from recent mammalian species, using three databases: PanTHERIA (Jones et al., 2009), AnAge (Magalhães and Costa, 2009) and Kissling et al. (2014). Information from PanTHERIA was prioritized for adult body mass, body mass at birth, female age at first birth, gestation length, and litter size. When no

information for these parameters was available in PanTHERIA, data was gathered from AnAge. The latter database was prioritized for sexual maturity and longevity because it incorporates more information for both parameters. In the case of litters per year, the most accurate values (i.e., those with more decimal numbers) were used. If both PanTHERIA and AnAge coincided in number of decimal places, the values from the former were used. The sum of gestation and sexual maturity time was used as a proxy for estimating female age at first birth when this information was not available in the databases. The database compiled by Kissling et al. (2014) was also used to define population densities for prey species and predators/scavengers, checking this information with density data provided by PanTHERIA. Kissling et al. (2014) defined (i) a “carnivore” as a species that consumes vertebrate and/or invertebrates, without (or only occasionally) consuming plant species; (ii) an “omnivore” as a species that consumes animal and plant species; and (iii) a “herbivore” as a species that only consumes plant species and not (or only occasionally) animals. We only used “carnivore” species as defined by Kissling et al. (2014) to estimate the ecological densities of the predator/scavenger species from Santa Cruz, and we only used “herbivore” species in the case of prey species.

3.2. Defining the palaeobiology of the FL 1–7 species

The estimates of life traits derived from recent species were used to characterize the FL 1–7 prey guild (Table 2). Although the use of regression equations that relate fertility parameters with body mass is common, we did not find a good fit in the case of age of female age at first birth, average litter size and number of litters per year. In order to estimate these parameters, the median values of the extant clades that are ecologically equivalent were taken: (i) armadillos (Dasypodidae) for *Peltephilus pumilus*, *Proeutatus oenophorus*, *Cochlops muricatus*, and *Pro-palaeohoplophorus australis*; (ii) sloths (Bradypodidae and Megalonychidae) and anteaters (Myrmecophagidae) for *Hapalops* sp.1, *Hapalops* sp.2, *Pelecypodon cristatus*, *Hyperleptus* sp., *Eucholoaeops fronto*, *Eucholoaeops ingens*, and *Nematherium* sp.; (iii) porcupines (Erethizontidae) for *Steiromys duplicatus*; (iv) tapirs (Tapiridae) for *As-trapotherium magnum*; (v) camels and lamas (Camelidae) for *Theosodon gracilis* and *Theosodon lydekkeri*; (vi) deers (Cervidae) for *Anisolophus australis*, *Diadiaphorus majusculus*, *Tetramerorhinus cingulatum*, and *Thoatherium minusculum*; (vii) perissodactyls (Perissodactyla) for *Homalodotherium* sp. and *Nesodon imbricatus*; and (viii) bovids (Bovidae) for *Adinotherium ovinum* (Table 2). The toxodont *A. ovinum* was characterized as a medium sized grazer or a mix-feeder dwelling in open habitat (Cassini et al., 2011, 2012a, Cassini et al., 2012b; Cassini, 2013). We used artiodactyls (bovids) for estimating the life traits of *Adinotherium*. Body mass at birth (in kg) was estimated for neonates through regression with adult body mass, as both parameters show a tight correlation. Although longevity and adult body mass are well correlated, the latter scales at the one-third power of the former. For this reason, the cube root of adult body mass was used. In order to estimate prey density (expected densities, D_x), we used density values from PanTHERIA for those species defined as herbivores by Kissling et al. (2014). The correlations between \log_{10} -transformed values of population density and adult body mass allowed selecting the equation corresponding to the median quartile, which was coherent with the values selected for other parameters. These values were used as expected densities by regression (D_xR). However, these estimates do not match the richness and relative abundance of the fossils in the assemblages (Vizcaíno et al., 2012b), which probably reflects taphonomic biases. In order to adjust the D_xR values, a proportional representation of each prey taxa preserved in the FL 1–7 beds was computed using the relative frequency of specimens recovered in field works between the years 2003 and 2017. This was named as the “taphonomic proportion”. For doing so, the ratio of the total number of identifiable remains of all taxa over the number of taxa preserved in the assemblage was calculated. This ratio (4.5454), named as the taphonomic bias factor (TBF),

Table 1

Species recorded in FL 1–7 from the Atlantic coastal of the Santa Cruz Formation, with their estimated body masses (adult body masses, ABM) (in kg; values taken from Kay et al., 2012a; Prevosti et al., 2012; Vizcaíno et al., 2012c). This table includes also information on dietary categories and locomotor or substrate preferences (Kay et al., 2012a, Cassini et al. 2012 and Degrange et al., 2012) used for characterizing the Santacrucian fauna.

Class	Order	Family	Species	ABM	Diet category	Locomotor or substrate preference
Prey						
Mammalia	Xenarthra	Peltephilidae	<i>Peltephilus pumilus</i> (Ameghino, 1887)	11.00	Carrion and tubers	Terrestrial and fossorial
Mammalia	Xenarthra	Dasypodidae	<i>Proeutatus oenophorus</i> (Ameghino, 1887)	15.00	Carrion and browse	Terrestrial and fossorial
Mammalia	Xenarthra	Glyptodontidae	<i>Cochlops muricatus</i> (Ameghino, 1889)	82.99	Leaves	Terrestrial ambulatory
Mammalia	Xenarthra	Glyptodontidae	<i>Propalaeophlophorus australis</i> (Ameghino, 1887)	81.64	Leaves	Terrestrial ambulatory
Mammalia	Xenarthra	Megatherioidea	<i>Hapalops</i> sp. 1 (Ameghino, 1887)	46.29	Leaves	Scansorial
Mammalia	Xenarthra	Megatherioidea	<i>Hapalops</i> sp. 2 (Ameghino, 1887)	27.71	Leaves	Scansorial
Mammalia	Xenarthra	Megatherioidea	<i>Peleciodon cristatus</i> (Ameghino, 1891)	50.00	Leaves	Scansorial
Mammalia	Xenarthra	Megatherioidea	<i>Hyperleptus</i> sp. (Ameghino, 1891)	40.00	Leaves	Scansorial
Mammalia	Xenarthra	Megalonychiidae	<i>Eucholeops fronto</i> (Ameghino, 1891)	78.00	Leaves	Scansorial
Mammalia	Xenarthra	Megalonychiidae	<i>Eucholeops ingens</i> (Ameghino, 1887)	76.88	Leaves	Scansorial
Mammalia	Xenarthra	Mylodontidae	<i>Nematherium</i> sp. (Ameghino, 1887)	95.02	Grass	Scansorial
Mammalia	Rodentia	Erethizontidae	<i>Steiromys duplicatus</i> (Ameghino, 1887)	14.17	Leaves	Scansorial
Mammalia	Astrapotheria	Astrapotheriidae	<i>Astrapotherium magnum</i> (Owen, 1853)	921.32	Leaves/Grass	Terrestrial ambulatory
Mammalia	Litopterna	Macrauchenidae	<i>Theosodon gracilis</i> (Ameghino, 1891)	121.55	Leaves	Terrestrial cursorial
Mammalia	Litopterna	Macrauchenidae	<i>Theosodon lydekkeri</i> (Ameghino, 1887)	130.93	Leaves	Terrestrial cursorial
Mammalia	Litopterna	Protheriidae	<i>Anisolophus australis</i> (Burmeister, 1879)	41.61	Leaves	Terrestrial cursorial
Mammalia	Litopterna	Protheriidae	<i>Diadiaphorus majusculus</i> (Ameghino, 1887)	82.05	Leaves	Terrestrial cursorial
Mammalia	Notoungulata	Protheriidae	<i>Tetramerorhinus cingulatum</i> (Ameghino, 1891)	41.71	Leaves	Terrestrial cursorial
Mammalia	Notoungulata	Protheriidae	<i>Thoatherium minusculum</i> (Ameghino, 1887)	24.20	Leaves	Terrestrial cursorial
Mammalia	Notoungulata	Homalodotheriidae	<i>Homalodotherium</i> sp. (Flower, 1873)	405.08	Leaves	Terrestrial ambulatory
Mammalia	Notoungulata	Toxodontidae	<i>Adinotherium ovinum</i> (Owen, 1846)	100.29	Grass	Terrestrial ambulatory
Mammalia	Notoungulata	Toxodontidae	<i>Nesodon imbricatus</i> (Owen, 1846)	637.51	Grass/Leaves	Terrestrial ambulatory
Predator/scavenger						
Aves	Cariamiformes	Phorusrhacidae	<i>Psilopterus lemoinei</i> (Moreno and Mercerat, 1891)	8.00	Invertebrate/vertebrate	Flying cursorial
Aves	Cariamiformes	Phorusrhacidae	<i>Patagornis marshi</i> (Moreno and Mercerat, 1891)	26.00	Vertebrate	Terrestrial cursorial
Aves	Cariamiformes	Phorusrhacidae	<i>Phorusrhacos longissimus</i> (Ameghino, 1887)	93.00	Vertebrate	Terrestrial cursorial
Mammalia	Sparassodonta	Borhyaenidae	<i>Borhyaena tuberata</i> (Ameghino, 1887)	36.42	Vertebrate	Terrestrial cursorial
Mammalia	Sparassodonta	Borhyaenidae	<i>Arctodictis munizi</i> (Mercerat, 1891)	51.60	Vertebrate	Terrestrial ambulatory
Mammalia	Sparassodonta	Borhyaenidae	<i>Acrocyon sectorius</i> (Ameghino, 1887)	28.70	Vertebrate	Scansorial
Mammalia	Sparassodonta	Hathliacynidae	<i>Cladosictis patagonica</i> (Ameghino, 1887)	6.60	Vertebrate	Scansorial
Mammalia	Sparassodonta	Stem-Borhyaenidae	<i>Prothylacinus patagonicus</i> (Ameghino, 1891)	31.79	Vertebrate	Scansorial
Mammalia	Sparassodonta	Stem-Borhyaenidae	<i>Lycopsis torresi</i> (Cabrera, 1927)	19.40	Vertebrate	Scansorial

was used for dividing the relative abundance of specimens of each taxa and the result was multiplied by their DxR values, which provided a more balanced representation of the abundance of taxa in the fossil assemblage (see Supplementary Information, Table S2). The densities

obtained, corrected for taphonomic biases, were used as expected densities by regression with taphonomic adjustments ($DxTA$) (Table 2).

In the case of the predator/scavenger species, we defined them according to their estimated nutritional requirements and prey

Table 2

Prey guild of FL 1–7 from the Santa Cruz Formation, with indication of the life-history traits estimated from their living analogues. These traits are the inputs of the model that allow to obtain an estimate for FL 1–7. Adult and neonate body masses (ABM and NBM, respectively) are expressed in kg. Age at first birth (AFB) and longevity (L) are expressed in years (yrs). Expected densities by regression (DxR) and by regression with adjustment ($DxTA$) are expressed in individuals per square kilometer and year ($\text{ind}/\text{km}^2\text{yr}$). The table includes also estimates of litter size (LS) and litters per year (LY).

Species	ABM (kg)	AFB (yrs)	LS	LY	NBM (kg)	L (yrs)	DxR ($\text{ind}/\text{km}^2\text{yr}$)	$DxTA$ ($\text{ind}/\text{km}^2\text{yr}$)	Living analogues
<i>Peltephilus pumilus</i>	11.00	0.91	1.25	1.00	0.39	20.65	12.87	16.66	Cingulata
<i>Proeutatus oenophorus</i>	15.00	0.91	1.25	1.00	0.53	22.90	10.36	45.08	Cingulata
<i>Cochlops muricatus</i>	82.99	0.91	1.25	1.00	2.91	40.50	3.12	2.57	Cingulata
<i>Propalaeophlophorus australis</i>	81.64	0.91	1.25	1.00	2.87	40.28	3.15	3.71	Cingulata
<i>Hapalops</i> sp. 1	46.29	3.00	1.00	1.00	2.44	48.84	4.70	4.97	Folivora
<i>Hapalops</i> sp. 2	27.71	3.00	1.00	1.00	1.46	41.16	6.73	7.13	Folivora
<i>Peleciodon cristatus</i>	50.00	3.00	1.00	1.00	2.64	50.11	4.45	1.05	Folivora
<i>Hyperleptus</i> sp.	40.00	3.00	1.00	1.00	2.11	46.52	5.20	0.61	Folivora
<i>Eucholeops fronto</i>	78.00	3.00	1.00	1.00	4.11	58.12	3.26	1.72	Folivora
<i>Eucholeops ingens</i>	76.88	3.00	1.00	1.00	4.05	57.84	3.29	1.74	Folivora
<i>Nematherium</i> sp.	95.02	3.00	1.00	1.00	5.01	62.07	2.84	0.67	Folivora
<i>Steiromys duplicatus</i>	14.17	3.58	0.99	1.06	1.18	17.00	10.78	7.61	Erethizontoidea
<i>Astrapotherium magnum</i>	921.32	4.09	1.00	0.50	24.50	51.41	0.58	0.54	Tapiridae
<i>Theosodon gracilis</i>	121.55	3.56	1.00	0.70	11.52	27.40	2.39	0.14	Camelidae
<i>Theosodon lydekkeri</i>	130.93	3.56	1.00	0.70	12.41	28.09	2.26	0.13	Camelidae
<i>Anisolophus australis</i>	41.61	2.00	1.00	1.10	2.09	17.41	5.06	0.60	Cervidae
<i>Diadiaphorus majusculus</i>	82.05	2.00	1.00	1.10	4.13	21.83	3.14	1.85	Cervidae
<i>Tetramerorhinus cingulatum</i>	41.71	2.00	1.00	1.10	2.10	17.43	5.05	2.97	Cervidae
<i>Thoatherium minusculum</i>	24.20	2.00	1.00	1.10	1.22	14.53	7.40	7.84	Cervidae
<i>Homalodotherium</i> sp.	405.08	4.47	1.00	0.60	14.24	36.87	1.02	0.12	Perissodactyla
<i>Adinotherium ovinum</i>	100.29	2.00	1.00	1.10	7.02	22.73	2.73	12.53	Bovidae
<i>Nesodon imbricatus</i>	637.51	4.47	1.00	0.60	22.40	42.89	0.75	1.32	Perissodactyla

Table 3
 Carnivore guild of FL 1–7 from the Santa Cruz Formation, with indication of the body masses estimated for the species (BM, in kg; values taken from Kay et al., 2012a; Prevosti et al., 2012; Vizcaíno et al., 2012c) and their nutritional requirements (NR, kcal/km² per year). NR values were corrected according to diet with a correction factor (CF) that multiplies the total species requirements. Expected densities (Dx) (ind/km²yr) for carnivore species were estimated from regressions between adult body masses and densities for recent mammalian carnivores. The last six columns represent the preferences of size categories of prey species (see text) expressed in percentages (the percentage is zero when a body class category is not consumed by a carnivore). Two conditions were modeled for the carnivore guild according to the dietary abilities of the species, differentiating between a condition where scavenging behavior is allowed (yes) and other where it is not (no). This possibility was assumed for *Phorusrhacos longissimus*, *Borhyaena tuberata* and *Arctodictis munizi*, which resulted in a decrease of the prey size consumed by these species. The remaining predators were assumed as not able to consume carrion; therefore, this consideration did not influence their consumption. In order to show how we modeled this carnivore guild in both scenarios of scavenging behavior, we include consumption profiles for all species, even when their consumptions were not influenced.

Order	Family	Species	BM (kg)	NR (kcal/km ² per year)	CF	Dx (ind/km ² yr)	Scavenging	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)
Cariamiformes	Phorusrhacidae	<i>Psilopterus lemoinei</i>	8.0	23,628	0.060	0.97	yes	100.0	0.0	0.0	0.0	0.0	0.0
Cariamiformes	Phorusrhacidae	<i>Patagonis marshi</i>	26.0	233,238	1.000	0.25	no	100.0	0.0	0.0	0.0	0.0	0.0
Cariamiformes	Phorusrhacidae	<i>Phorusrhacos longissimus</i>	93.0	132,101	1.000	0.06	yes	80.9	19.1	0.0	0.0	0.0	0.0
Sparassodontata	Borhyaenidae	<i>Borhyaena tuberata</i>	36.4	200,684	1.000	0.17	no	21.0	21.0	21.0	18.5	18.5	0.0
Sparassodontata	Borhyaenidae	<i>Arctodictis munizi</i>	51.6	171,799	1.000	0.11	yes	63.0	37.0	0.0	0.0	0.0	0.0
Sparassodontata	Borhyaenidae	<i>Acrocyon sectorius</i>	28.7	223,183	1.000	0.22	no	77.2	4.6	4.6	4.6	4.6	4.6
Sparassodontata	Hathliacynidae	<i>Cladocitis patagonica</i>	6.6	16,384	0.038	1.21	yes	72.6	11.4	11.4	0.0	0.0	0.0
Sparassodontata	Stem-Borhyaenidae	<i>Prothylacynus patagonicus</i>	31.8	213,232	1.000	0.20	no	72.6	5.5	5.5	5.5	5.5	5.5
Sparassodontata	Stem-Borhyaenidae	<i>Lycopsis torresi</i>	19.4	265,781	1.000	0.35	yes	79.9	13.7	13.7	0.0	0.0	0.0
							no	20.1	20.1	0.0	0.0	0.0	0.0
							yes	100.0	0.0	0.0	0.0	0.0	0.0
							no	100.0	0.0	0.0	0.0	0.0	0.0
							yes	78.8	10.6	10.6	0.0	0.0	0.0
							no	78.8	10.6	10.6	0.0	0.0	0.0
							yes	83.7	16.3	16.3	0.0	0.0	0.0
							no	83.7	16.3	16.3	0.0	0.0	0.0

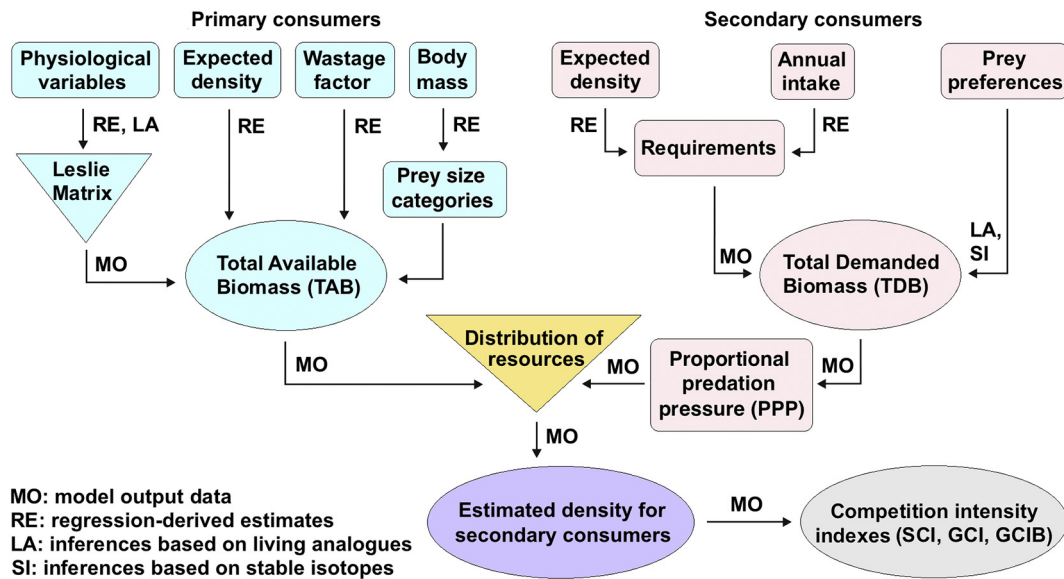


Fig. 2. Flowchart diagram showing the components of the model used to evaluate trophic resource availability of carnivores and competition intensity in the carnivore guild of FL 1–7 from the Santa Cruz Formation (modified from Rodríguez-Gómez et al., 2017b).

preferences (Table 3). Nutritional requirements (NR) of each species were obtained multiplying the estimated annual intake of one individual by the estimated density. Annual intakes were obtained from the allometric equation provided by Farlow (1976), which relates intake with body mass:

$$\log I = (0.684) \times \log(m) + 0.278; r^2 = 0.97 \quad (1)$$

where I is intake rate in kilocalories per day (kcal*day) and m is body mass in grams. Farlow (1976) provided also a confidence interval for the slope of this regression (0.697 ± 0.013). We used the minimum value of this range in order to test the most unfavorable condition for our working hypothesis, i.e. to assess if competition intensity for prey among the members of the FL 1–7 carnivore palaeoguild allowed them to maintain their populations under conditions of minimum nutritional requirements expressed in kcals per year.

It could be argued, however, that birds show higher standard metabolic rates than mammals. For this reason, to estimate the daily energy expenditure of the SCF phorusrhacids with an equation derived from modern mammals could result in lower estimates of meat intake for these terror birds. This would in turn result in lower estimates of competition intensity for the carnivore guild. Taken as a whole, it is true that birds show higher metabolic rates than mammals of their size, but this only applies to passerine birds. According to a study of Lasiewski and Dawson (1967), the Y-intercept of the equation for the weight-specific metabolic rate of passerine birds (kcal/day = $129 \cdot W^{0.724}$, with W in kg) is higher than the ones derived for non-passerine birds ($78.3 \cdot W^{0.723}$) and mammals ($70.5 \cdot W^{0.734}$). In fact, the latter two equations provide similar estimates of metabolic rate for a terror bird the size of *Phorusrhacos longissimus* (93 kg, Table 2), 2074.8 and 1963.5 kcal/day, respectively (i.e., a variation of ~5%).

Density values of predators/scavengers were estimated with the same approach used for prey species (i.e., obtaining one equation that correlated density with body mass and then selecting the equation of the median quartile). However, these densities were not adjusted taphonomically because, unlike that of prey species, the fossil record of predators is scarce (especially in the case of birds, due to the low preservation potential of their bones) and the adjustment could be biased. Prey preferences were defined according to Vizcaíno et al. (2012a, 2012b, 2012c) and Ercoli et al. (2014) (Table 3). Following Ercoli et al. (2014), we assumed that the range of typical prey mass (TPM) consumed by a predator/scavenger was equivalent to its primary prey

requirements (PPR). We also considered that each species had a size threshold, the mean estimated value of maximum prey mass (MPM). Using the proportion between the mean of TPM and the MPM value, we calculated the percentage of requirements consumed from secondary prey (RSP) as follows:

$$RSP = \text{mean TPM} \times 100/\text{MPM} \quad (2)$$

The higher the difference between TPM and MPM, the higher the consumption of secondary prey (RSP). We distributed the same prey preferences for body size categories in the range between maximum typical prey size and MPM. In the case of *Cladosictis patagonica* and *Psilopterus lemoinei*, their requirements were adjusted with a correction factor (CF) because we assumed that they could only consume a small fraction of the spectrum of prey size categories considered in our study (i.e., between 10 and 1000 kg; see the following section on the palaeoecological model), feeding mainly on prey of < 10 kg to fit their total requirements. This CF value was multiplied by their total nutritional requirements. According to this, we estimated that the nutritional requirements satisfied with species of body masses of 10–45 kg (Category I, see below) represented only 3.8% in *Cl. patagonica* and 6.0% in *Ps. lemoinei* (Table 3).

3.3. The palaeoecological model

The large mammal food web of FL 1–7 was reconstructed using the mathematical model of Rodríguez-Gómez et al. (2013, 2014a, 2016a), which distributes prey resources among the secondary consumers (predators and/or scavengers) of the ecosystem (Fig. 2). For doing this, the model considers: (i) the biomass of prey resources available in the palaeocommunity, which depends on the demographic structure of the prey species and their population densities; (ii) the ability of each secondary consumer to obtain and process these resources; and (iii) the level of competition intensity among the members of the carnivore palaeoguild. The model computes the biomass of herbivores in the ecosystem as the total available biomass (TAB) and the meat demanded by carnivore species as the total demanded biomass (TDB) (Fig. 2). Later, the distribution of meat resources among the predator/scavenger species is modeled, which provides an estimate of their sustainable densities (D_s). For a detailed and more formal description of this model, see Rodríguez-Gómez et al. (2013, 2014a, 2016a, 2016b), Martín-González et al. (2019) and the Supplementary Information. The model

was written in Matlab R2009b and executed in Matlab R2017b.

The model assumes that population size and age structure tend to remain stable and stationary through time, as described by a survival model with fecundity as input data. This population dynamic is defined through Leslie matrices (Leslie, 1945, 1948), considering a stable and stationary dynamic from year to year. The Weibull distribution, a parametric model, is used to estimate survival and mortality profiles (Martín-González et al., 2016, 2019). This model is more powerful than the linear approaches previously used by Rodríguez-Gómez et al. (2013, 2014a, 2014b, 2016a, 2016b, 2016c, 2017a, 2017b) and Domingo et al. (2017). For an in-depth comparison and discussion of these models, see Martín-González et al. (2019). Survival and mortality profiles for the fossil species were obtained using fecundity and other life traits data from their closest living relatives or from their ecological analogues (Table 2), as explained in the section on parameter estimation. Mortality profiles provide the proportion of individuals by age class that must die to maintain a sustainable population, but their outputs do not depend on population size. For this reason, it is necessary to estimate the population density of each SCF prey species to estimate the number of individuals dead by each age class (see section on parameter estimation). Next, we estimate the total biomass output (TBO), which is the amount of biomass that can be subtracted from the ecosystem in the long term. In the model, a “wastage factor” (modified from Viljoen, 1993; see Rodríguez-Gómez et al., 2013, 2014a, 2016a) was applied for excluding non-edible tissues (i.e., horns, bones, hide, or carapace), using a different correction factor depending on prey body mass. The corrected value of prey biomass was distributed among six body mass categories according to Rodríguez-Gómez et al. (2013): 10–45 kg (Category I); 45–90 kg (Category II); 90–180 kg (Category III); 180–360 kg (Category IV); 360–1000 kg (Category V); and > 1000 kg (Category VI). These meat resources, distributed among size categories, constitute the total available biomass (TAB). Given that the model yields several population and mortality profiles for each species, we select the extreme values with maximum and minimum pressure on subadults (i.e., individuals that do not reach the adult size), which results in minimum and maximum TAB levels that correspond to maximum subadult (and minimum adult) mortality (TAB-m) and minimum subadult (and maximum adult) mortality (TAB-M), respectively. Therefore, we considered in the analysis a wide range of values that includes all population and mortality profiles for the species recorded in the FL 1–7 palaeo-community. In the calculation of TAB values, each size category includes adults and also subadults of the larger size categories. The model assumes for TAB-M values that a higher proportion of individuals reach the adult weight, which results in a displacement of biomass toward the higher body mass categories compared with TAB-m conditions, in which the greatest mortality occurs at a younger age.

TAB estimates are distributed among the members of the carnivore guild according to the biomass required by each species and its prey preferences. Given that prey size is a key factor for prey selection in most predators (see review in Palmqvist et al., 1996), prey preferences for the SCF carnivores were related to the six body mass categories of primary consumers. For doing so, we adjusted estimates of typical and maximum prey size in the six body mass categories and distributed the biomass demanded by each species of secondary consumers according to its prey preferences (see section on parameter estimation). Given that meat distribution among predator/scavengers considers the total amount of meat demanded from each body mass category, which ultimately depends on the meat demanded by each member of the carnivore guild, the model includes also an estimate of the level of competition among the secondary consumers. The assumption here is that a higher demand of meat by a species implies a higher rate of meat consumption by this species. The distribution of TAB in the model is complete if: (i) all predator/scavengers fulfill their energetic requirements; (ii) TAB is consumed completely; or (iii) there is no predator that can consume prey from a given mass category. The first and third situations imply that TAB is not consumed completely. The fraction of

meat not consumed is called the remaining total available biomass (RTAB). The distribution of TAB results in estimates of sustainable densities for each carnivore, which are named estimated densities (D_s) in the competition indexes (for a more detailed description of the computation of resource distribution, see Supplementary Information).

In addition to estimating the sustainable densities of carnivores in a palaeoecosystem, the model provides a number of competition indexes that allow a comparison of environmental conditions among different palaeoecosystems. Competition indexes assume an ideal condition in which all species would reach their optimal densities and/or maximum levels of population biomass. This ceiling value marks the expected densities (D_x) used as the starting point for estimating the values of the competition indexes (Table 3). These indexes, based on the densities estimated (D_s) and expected (D_x) for carnivores, measure the quantity of dietary requirements not satisfied at both the species level and the guild level. They include: (i) the species competition index (SCI), which compares the densities estimated with the model for each carnivore species with their expected densities (Table 3); (ii) the global competition index (GCI), which provides an overall estimate on the degree to which all members of the carnivore guild reach their expected densities; and (iii) the global competition index biomass (GCIB), which estimates the degree to which the members of the carnivore guild reach their expected biomasses in optimal conditions (i.e., with maximum population densities). The values of these indexes were obtained for TAB-m and TAB-M conditions (SCI-m, SCI-M, GCI-m, GCI-M, GCIB-m, and GCIB-M, respectively). An index value close to 1 means that the level of competition among carnivores is high. In contrast, index values close to 0 indicate a low degree of competition for prey biomass (for details on the mathematical calculation of these indexes, see Rodríguez-Gómez et al., 2016a, 2016b).

3.4. Studied scenarios

We considered several scenarios in this study to model FL 1–7. D_xR and D_xTA values (densities expected by regression with or without taphonomic adjustments) were used as expected densities of prey (Table 2 and Fig. 3). In the case of secondary consumers, a number of researchers have proposed that all members of the carnivore guild from SCF were primary predators (e.g., Degrange et al., 2012; Prevosti and Martín, 2013). In contrast, Ercoli et al. (2014) pointed out that the large sparassodonts could have scavenged carcasses. Based on their craniodental features, Prevosti et al., (2012) supported that at least *Arctodictis munizi* and *Borhyaena tuberata* could break bones. Moreover, we considered that *Phorusrhacos longissimus* could scavenge carrion because it

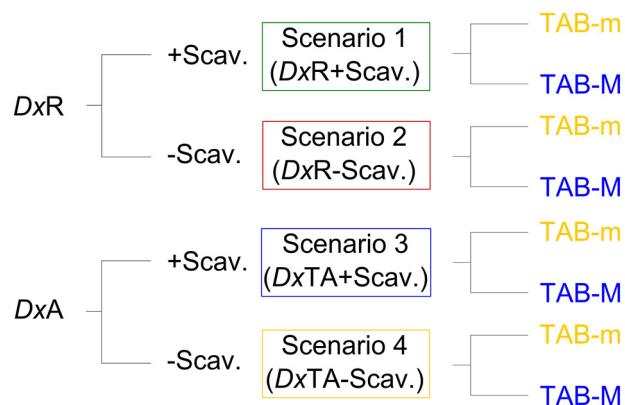


Fig. 3. Diagram showing the different ecological scenarios tested in this study, with indication for each scenario of the results obtained with minimum and maximum total available biomass (TAB-m and TAB-M, respectively). D_xR : prey expected densities estimated by regression; D_xTA : prey expected densities estimated by regression with taphonomic adjustments; +Scav.: carnivore guild with scavenging behavior; -Scav.: carnivore guild without scavenging behavior.

Table 4

Ecological indexes of the Santacrucian FL 1–7 in four different scenarios according to the expected densities (Dx , individuals per km^2) of prey and the possibility of scavenging behavior for some carnivores. Expected prey densities were estimated following two procedures: by regression (DxR) and by regression with taphonomic adjustment ($DxTA$). Two conditions were envisioned for the possibility of scavenging behavior in the predator/scavenger guild: with and without scavenging behavior (+Scav and -Scav, respectively) (see Fig. 2). Minimum and maximum values of total available biomass (TAB-m and TAB-M, respectively), values of total demanded biomass (TDB) and minimum and maximum estimates of remaining total available biomass (i.e., the fraction of prey biomass non-consumed: RTAB-m and RTAB-M, which correspond to TAB-m and TAB-M conditions, respectively) were measured in kilocalories per km^2 and year. GCI-m: global competition index with minimum total available biomass; GCI-M: global competition index with maximum total available biomass; GCIB-m: global competition index biomass with minimum total available biomass; GCIB-M: global competition index biomass with maximum total available biomass.

	$DxR + \text{Scav}$	$DxR\text{-Scav}$	$DxTA + \text{Scav}$	$DxTA\text{-Scav}$
	Scenario 1	Scenario 2	Scenario 3	Scenario 4
TAB-m	1.01×10^6	1.01×10^6	1.04×10^6	1.04×10^6
TAB-M	1.22×10^6	1.22×10^6	1.30×10^6	1.30×10^6
TDB	1.14×10^6	1.14×10^6	1.14×10^6	1.14×10^6
RTAB-m	5.61×10^3	1.19×10^5	1.99×10^4	1.28×10^5
RTAB-M	1.22×10^5	1.83×10^5	1.87×10^5	2.43×10^5
GCI-m	0.17	0.23	0.12	0.18
GCI-M	0.23	0.27	0.16	0.20
GCIB-m	0.13	0.22	0.10	0.19
GCIB-M	0.11	0.15	0.08	0.12

had a powerful bite force, based on the estimates of body mass by Degrange et al. (2012). For this reason, the level of competition intensity among the secondary consumers was evaluated including and excluding the possibility of scavenging behavior for these three species (Table 3, Fig. 3). To consider a scavenging behavior for them results in an increase of the upper range of prey size consumed. Given that we assume that the other predators could not consume carrion, this would only influence indirectly their consumption of meat. As a result, four scenarios were modeled (Fig. 3): (i) prey densities estimated by regressions with the possibility of a scavenging behavior for the three carnivorous species discussed above ($DxR + \text{Scav}$); (ii) prey densities by regressions without scavenging behavior ($DxR\text{-Scav}$); (iii) prey densities by regressions with taphonomic adjustment and with scavenging behavior ($DxTA + \text{Scav}$); and (iv) prey densities by regressions with taphonomic adjustment and without scavenging behavior ($DxTA\text{-Scav}$) (Fig. 3).

4. Results

In our analyses, we estimated TAB, TDB, RTAB, SCI, GCI, and GCIB values in FL 1–7 for four scenarios (see Material and Methods sections) (Table 4).

4.1. Total available biomass (TAB)

The model provided the range of TAB-m and TAB-M values available to the carnivore palaeoguild in the four FL 1–7 scenarios of our study (Fig. 3). The value of TAB-m for Scenarios 1 and 2 (i.e., DxR with and without scavenging, respectively) was 1,007,409 kcal/ km^2 per year (i.e., $\sim 672 \text{ kg}/\text{km}^2$ per year) (Fig. 4A). The corresponding value for Scenarios 3 and 4 (i.e., $DxTA$ with and without scavenging, respectively) was 2.75% higher, 1,035,843 kcal/ km^2 per year ($\sim 691 \text{ kg}/\text{km}^2$ per year) (Fig. 4B). TAB-M estimates were 1,223,716 kcal/ km^2 per year ($\sim 816 \text{ kg}/\text{km}^2$ per year) for Scenarios 1 and 2 (Fig. 4A) and 1,295,785 kcal/ km^2 per year ($\sim 864 \text{ kg}/\text{km}^2$ per year) for Scenarios 3 and 4 (Fig. 4B), which represents a difference of 5.56%.

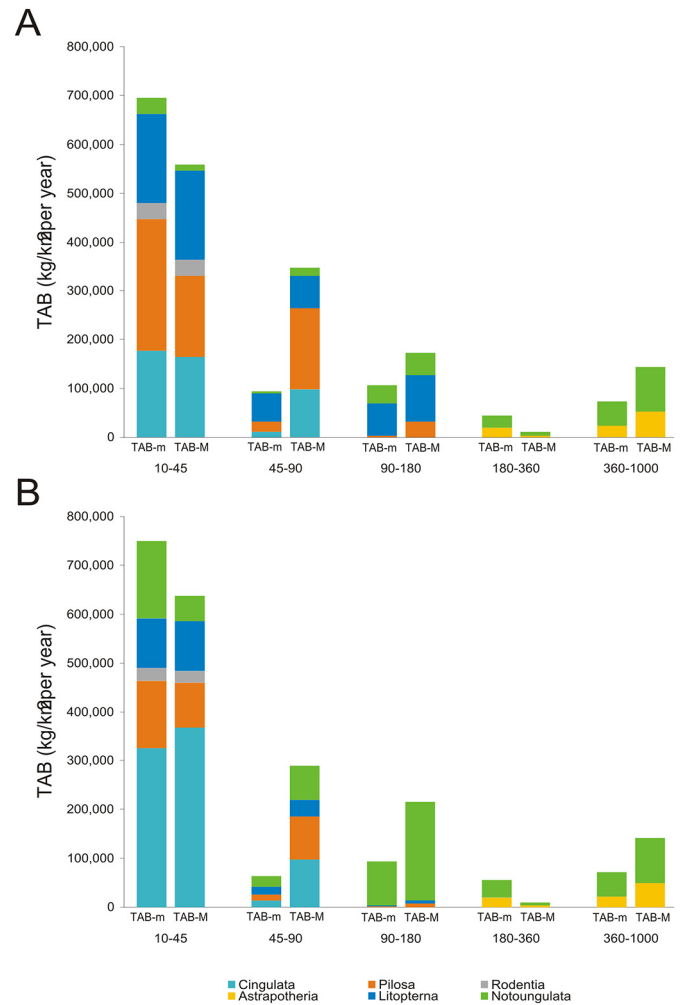


Fig. 4. Values of total available biomass (TAB) distributed among five body mass categories of prey (see text) obtained for maximum and minimum sub-adult mortality rates for all prey species (TAB-m and TAB-M, respectively). There are two scenarios for each TAB condition according to the procedure used for estimating the expected densities of prey (Dx): A: regressions (DxR); B: regressions with taphonomic adjustments ($DxTA$). The colors in each column correspond to different taxa: Cingulata, Pilosa, Rodentia, Astrapotheria, Litopterna, and Notoungulata.

Table 5

TAB values distributed by body mass categories (see text) for TAB-m and TAB-M conditions (in kcal/ km^2 *year) in scenarios with expected densities estimated by regressions (DxR) and in scenarios with densities estimated by regressions with taphonomic adjustments ($DxTA$).

	DxR	$DxTA$
TAB-m		
10–45 kg	6.90×10^5	7.50×10^5
45–90 kg	9.36×10^5	6.48×10^5
90–180 kg	1.05×10^5	9.35×10^5
180–360 kg	4.67×10^5	5.60×10^5
360–1000 kg	7.27×10^5	7.19×10^5
TAB-M		
10–45 kg	5.53×10^5	6.37×10^5
45–90 kg	3.43×10^5	2.89×10^5
90–180 kg	1.73×10^5	2.17×10^5
180–360 kg	1.31×10^5	1.03×10^5
360–1000 kg	1.42×10^5	1.42×10^5

The distribution of biomass among body mass categories was similar for DxR and $DxTA$ values (Table 5, Fig. 4A and B, respectively). Biomass tends to concentrate in Category I (10–45 kg), showing a greater value for TAB-m than for TAB-M in both cases. For TAB-m estimates, the biomass available from the other size categories is strikingly lower and not in excess of 110,000 kcal/km² per year. However, in TAB-M conditions there is a more gradual decrease from Category I to Category IV (180–360 kg) and it is also evident an increase in Category V (360–1000 kg). Category IV shows the lowest amounts of TAB-m and TAB-M with both DxR and $DxTA$ estimates. As expected, the comparison of TAB-m and TAB-M values shows that the increase in the survival of sub-adult individuals results in a displacement of biomass toward the largest size categories due to the higher proportion of sub-adults that reach their adult body mass.

The most important differences between the DxR and $DxTA$ scenarios are found in the first three size categories, because the $DxTA$ scenarios show a greater abundance of cingulates (*Proeutatus*) and notoungulates (*Adinotherium*) and a lower representation of pilosans and litopterns compared to the DxR ones. Overall, these differences are most remarkable in the Category III (90–180 kg) (Fig. 4).

4.2. Total demanded biomass (TDB) and remaining total available biomass (RTAB)

The same TDB estimate was obtained in the four scenarios, 1,136,212 kcal/km² per year (~757 kg/km² per year), because the dietary requirements of species do not vary depending on whether or not scavenging behavior is considered. Given this value, TDB is 12.8 and 9.7% higher than TAB-m in the DxR and $DxTA$ scenarios, respectively, but 9.3 and 12.3% lower than TAB-M (Table 4). This means that the members of the carnivore palaeoguild do not reach their maximum expected densities in FL 1–7 with TAB-m because the prey biomass available is lower than the requirements of carnivores.

The value of RTAB (i.e., the fraction of TAB not consumed) is derived from the interaction among TAB, TDB and the consumption profiles of predators and/or scavengers. In general terms, the lowest RTAB values were obtained with TAB-m (RTAB-m). Considering the same condition of TAB (i.e., TAB-m or TAB-M) and the same prey density source (i.e., DxR or $DxTA$), RTAB values are lower in the scenarios with scavenging behavior than in those without it. This was expected, as three species would access to more prey species if a scavenging behavior is modeled for them. For example, the RTAB-m values in the scenarios 1 ($DxR + Scav$) and 3 ($DxTA + Scav$) are 5605 kcal/km² and ~20,000 kcal/km², respectively, which represent less than 0.6 and 2% of their TAB-m values, respectively (Table 4). In

contrast, the RTAB-m values for scenarios 2 and 4 (both without scavenging behavior) are quite similar, ~120,000 and ~130,000 kcal/km², values that are close to 12% of TAB-m in both cases. RTAB-M values are between 12.5% (Scenario 3) and 3.1% (Scenario 2) greater than RTAB-m values. This increase is higher in the scenarios with scavenging behavior, which represent more opportunities for meat consumption. Another interesting pattern is that the scenarios in which prey densities are adjusted with the taphonomic bias factor provide RTAB values that are 4–5% higher than those without this adjustment (Table 4).

Although TDB is higher than TAB-m in all scenarios, there is a fraction of biomass that is not consumed (RTAB-m). The reason is that no predator/scavenger species can consume these body mass categories due to the limitations considered in their consumption abilities. Similarly, although TAB-M is higher than TDB, the carnivore guild is not able to consume all these resources and 2.13–7.79% of meat is not consumed. This effect is more evident when the consumption of carrion is not considered, which means that the biomass of the higher body mass categories (180–360 and 360–1000 kg) is left over (see RTAB values in Table 3).

4.3. Competition intensity indexes

4.3.1. Global competition index (GCI) and global competition index Biomass (GCIB)

The GCI and GCIB values are lower than 0.30 in all scenarios (Table 4). In the case of the GCI index, the highest values are found in Scenario 2 ($DxR + Scav$), 0.23 for GCI-m and 0.27 for GCI-M, and the lowest ones in Scenario 3 ($DxTA + Scav$), 0.12 for GCI-m and 0.16 for GCI-M. In the absence of scavenging behavior, competition indexes are higher in all cases except GCI-M, in which Scenario 1 ($DxR + Scav$) shows a higher value (0.23) than Scenario 4 ($DxTA + Scav$) (0.20). This is due to the difference of TAB-M values between DxR and $DxTA$ conditions. Regarding the GCIB index, Scenario 2 shows also the highest values, both for TAB-m (0.22) and TAB-M (0.15) (Table 4). In addition, Scenario 3 has the lowest values of competition intensity for both TAB conditions (GCIB-m = 0.10; GCIB-M = 0.08). However, this pattern changes between the GCIB and GCI indexes, as GCIB-m shows higher values than GCIB-M in all scenarios (Table 4).

4.3.2. Species competition index (SCI)

According to the SCI values, nearly all carnivore species show a percentage of satisfaction of their dietary requirements of > 60% in all the scenarios considered in this study, with SCI values below 0.40 (Fig. 5). In almost all species, the most adverse conditions are found in

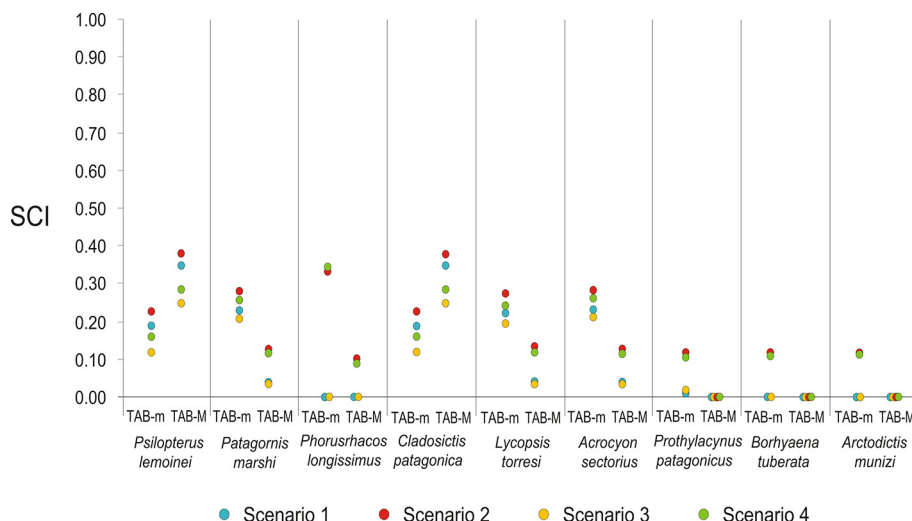


Fig. 5. Values of the species competition index (SCI) for the species of predators/scavengers identified in FL 1–7 under four scenarios: Scenario 1: $DxR + Scav$; Scenario 2: $DxR + Scav$; Scenario 3: $DxTA + Scav$; Scenario 4: $DxTA + Scav$. There are two conditions of total available biomass (TAB) for all prey species: minimum (TAB-m, left columns) and maximum (TAB-M, right columns). Abbreviations as in Fig. 3.

Scenario 2 for both TAB conditions, with the only exception of *Ph. longissimus*, a species that shows its highest SCI value in Scenario 4 with TAB-m. In most cases, the SCI values of each species are higher with TAB-m than with TAB-M, but the pattern is reversed for *Ps. lemoinei* and *Cl. patagonica*, being TAB-M conditions less adverse for them than TAB-m ones. Both species never satisfy > 90% of their meat requirements, even in their most favorable scenarios. On the contrary, the sparassodonts *Prothylacynus patagonicus*, *B. tuberosa* and *A. munizi* always satisfy at least 90% of their requirements in their most adverse scenarios (Fig. 5). The most favorable conditions for most species are found in Scenario 3 for TAB-m and TAB-M, and four species reach also the minimum value of competition intensity in Scenario 1: *Ph. longissimus*, *Pr. patagonicus*, *B. tuberosa*, and *A. munizi*. DxTA scenarios (3 and 4) show more meat available than DxR ones (1 and 2), both with TAB-m and TAB-M conditions. This facilitates that the carnivore species reach lower SCI values, but the scavenging behavior also allows to decrease the level of competition intensity in the smallest prey mass categories, with only some species consuming prey beyond 180 kg.

The terror bird *Ph. longissimus* is the most affected by the difference between considering a scavenging behavior or not. This species consumes all prey categories in the scavenging scenarios. However, if we consider a strict predatory behavior it only consumes prey from the first two size categories. The other two species that may have behaved as scavengers, *B. tuberosa* and *A. munizi*, may also consume in the third size category when scavenging is not considered. For this reason, they do not suffer the change of scenario to the same extent than *Ph. longissimus*. We have also analyzed the percentages of biomass consumed by each species (see Supplementary Information).

5. Discussion

The idea that the extinct South American faunal assemblages had a splendid herbivore community subject to a low predator pressure is common in the literature (e.g., Marshall, 1978; Flannery, 1994; Croft, 2001, 2006; Croft et al., 2020). This relates to the assumption that pre-GABI faunal assemblages, like those of SCF in Southern Patagonia, were dominated by marsupials, which were sub-optimal predators compared to placental mammals (Croft, 2006). The four scenarios modeled in our study show that (i) the predator guild could satisfy to a large extent their metabolic requirements with the meat provided by their prey; and (ii) to consider the possibility of scavenging behavior for some taxa results in a greater degree of satisfaction of the dietary demands of the carnivore guild. The differences between considering a carnivore guild composed exclusively of primary predators and one with predators and scavengers are more conspicuous under conditions of maximum subadult mortality (TAB-m) than of minimum subadult mortality (TAB-M). In addition, although birds are less well preserved in the fossil record, the inclusion of terror birds whose remains have been conclusively identified in the assemblages results in a more balanced predator guild.

The aim of this work was to quantify the competition intensity of FL 1–7 in order to test if this palaeocommunity showed an impoverished carnivore guild, a working hypothesis that results from the two conflicting interpretations on the predator/prey ratio of mammals in these assemblages: on the one hand, Croft (2006) and Vizcaíno et al. (2010) reported on the low abundance of predators in relation to the expectations from the richness of the herbivore guild; on the other, Prevosti et al. (2012) estimated in these palaeocommunities a predator/prey ratio similar to that of recent faunas and Kay et al. (2012a) suggested that the predator richness of FL 1–7 fell within the expectations of mean annual rainfall estimated from recent mammalian faunas of South America. To evaluate this disagreement, we tested if the carnivore palaeoguild of SCF was in optimal condition and quantified their competition intensity using the model developed by Rodríguez-Gómez et al. (2013, 2014a), which was previously applied to a number of Pleistocene European communities of large mammals. This model is based on concepts already used by Prevosti and Vizcaíno (2006) in their

study of the palaeocommunities of Río Luján and the Lujanian of the Pampean Region in Argentina (Late Pleistocene-Early Holocene). Our results show a perspective that lays midway between the proposals of Croft (2006) and Vizcaíno et al. (2010), on the one side, and those of Kay et al. (2012a) and Prevosti et al. (2012), on the other: all the scenarios tested in our study show a low to moderate level of competition intensity in the carnivore palaeoguild, because the predators and scavengers would not consume all the biomass offered due to their consumption profiles, which do not allow their access to all prey size categories. More specifically, we have detected a lack of carnivore species that could consume the largest prey sizes, which supports in part the proposal of Croft (2006) and Vizcaíno et al. (2010).

The inclusion of consumption profiles is a relevant aspect of the model: compared to predator/prey ratios, it provides more accurate information on the distribution of meat resources and on the level of competition intensity among carnivores (Rodríguez-Gómez et al., 2016a). In this way, the model generates sheds light on how this food web worked and its results open some possible interpretations. Below, we discuss on several aspects of our results and their modeling.

5.1. Offered biomass for predator species (TAB)

The distributions of prey biomass available for the secondary consumers are similar in the scenarios with densities of prey expected by regression with or without taphonomic adjustments (DxTA and DxR, respectively). In fact, there are only minor differences in the percentages of each prey size category, but they have no effect on the distribution of meat among the members of the carnivore palaeoguild or on the level of competition intensity. Moreover, our results show a prey guild without individuals larger than 1000 kg. This did not occur when we modeled the Pleistocene communities of Europe, which included hippos, rhinos or mammoths (Rodríguez-Gómez et al., 2013, 2014b, Rodríguez-Gómez et al., 2016b, Rodríguez-Gómez et al., 2017a, 2017b, 2017c; Domingo et al., 2017). These large mammalian herbivores occur at low densities and are primarily top-down regulated by predators (Ripple and Van Valkenburgh, 2010). In the case of FL 1–7, although some individuals of *A. magnum* reached a body mass of > 1000 kg (see Cassini et al., 2012c), the average mass estimated for this species was 921 kg (Table 2). In spite of that, its inclusion in part within the Category VI (> 1000 kg) would have no noticeable effects in the level of competition intensity, as this would represent a minor drop of biomass in the Categories IV and V, which would lead to a minimal change in the distribution of TAB values. Specifically, the inclusion of Category VI in the scenarios with scavenging behavior would result in a decrease of the consumption by *B. tuberosa* and *A. munizi* from Categories IV and V, which would translate in a greater consumption by *Ph. longissimus* from the latter two categories, while in those scenarios without scavenging behavior there would be no effects (see the Supplementary Information).

5.2. Competition intensity and factors that may influence it

In relation to the level of competition intensity, our results show that the SCF carnivore palaeoguild obtained more than two-thirds of the meat required under optimal ecological conditions (i.e., those in which they would reach their maximum population densities). This contradicts the hypothesis of an impoverished carnivore guild for FL 1–7, because the meat available was not enough to maintain a predator guild free of stress, even in the scenario with the lowest level of competition intensity (Scenario 3, with prey densities estimated by regressions with taphonomic adjustments and a carnivore guild that includes scavengers).

Several factors may affect our results. Firstly, the model distributes TAB as a function of the biomass offered by each prey and demanded by each carnivore. The patterns of meat consumption modeled in this study are the most parsimonious, as they show the lowest competition

Table 6

Ecological indexes for the faunal assemblages of the Orce, Sierra de Atapuerca (SA) and Santa Cruz FL 1–7 sites under maximum values of demanded biomass by the secondary consumers. Minimum and maximum total available biomass (TAB-m and TAB-M, respectively) and total demanded biomass (TDB) in kilocalories per km² and year; GCI-m: global competition index with minimum total available biomass; GCI-M: global competition index with maximum total available biomass; GCIB-m: global competition index biomass with minimum total available biomass; GCIB-M: global competition index biomass with maximum total available biomass; scenarios 1 and 2: indexes derived from prey expected densities estimated by regression in a carnivore guild with or without scavenging behavior, respectively; Scenarios 3 and 4: indexes derived from prey expected densities estimated by regression with taphonomic adjustments in a carnivore guild with or without scavenging behavior, respectively.

	VM (Orce)	FN-3-BL (Orce)	TD3-D4 (SA)	TD6-2 (SA)	TD8 (SA)	TD10-1 (SA)	GIIB (SA)	GIIIa (SA)	FL 1-7 Scenario 1	FL 1-7 Scenario 2	FL 1-7 Scenario 3	FL 1-7 Scenario 4
TAB-m	5.84×10^5	4.11×10^5	4.22×10^5	4.88×10^5	5.02×10^5	3.93×10^5	4.41×10^5	4.43×10^5	1.01×10^6	1.01×10^6	1.04×10^6	1.04×10^6
TAB-M	7.80×10^5	5.75×10^5	5.41×10^5	5.97×10^5	6.28×10^5	5.16×10^5	5.88×10^5	5.90×10^5	1.22×10^6	1.22×10^6	1.30×10^6	1.30×10^6
TDB	1.21×10^6	1.05×10^6	7.19×10^5	4.56×10^5	7.71×10^5	6.77×10^5	6.35×10^5	6.64×10^5	1.48×10^6	1.48×10^6	1.48×10^6	1.48×10^6
GCI-m	0.39	0.58	0.33	0	0.26	0.3	0.34	0.36	0.36	0.41	0.32	0.37
GCI-M	0.28	0.5	0.2	0	0.16	0.22	0.26	0.26	0.38	0.43	0.32	0.37
GCIB-m	0.48	0.59	0.38	0	0.32	0.36	0.28	0.28	0.33	0.4	0.3	0.38
GCIB-M	0.32	0.45	0.22	0	0.17	0.21	0.09	0.07	0.25	0.33	0.2	0.28

intensity. However, it is always possible that not all prey biomass was used by the secondary consumers (e.g., because some was hidden in natural traps or loss by microbial degradation).

Secondly, we estimated minimum values of meat intake by the carnivores because we wanted to assess if the resources available were enough to maintain their populations. However, given that the slope of Farlow's eq. (Farlow, 1976), 0.69686 ± 0.01276 , provides a range of meat intake estimates for each carnivore species, if we take the mean or even the maximum estimates this would result in higher levels of competition intensity. This provides additional evidence for rejecting the hypothesis of an impoverished carnivore guild. In order to compare our analyses with those conducted in Pleistocene ecosystems, we reconstructed their food web using the maximum values of demanded biomass by the secondary consumers (see below). This resulted in an increase of competition intensity indexes (see Table 6) and the absence of remaining total available biomass (RTAB) when TAB was distributed among the predators and scavengers.

Thirdly, in spite of the variable levels of competition intensity calculated for all scenarios, the TAB estimates would not have been fully consumed in neither of them, which would result in RTAB values (Table 4). The reason is that not all prey biomass was available for all predators and scavengers, because some members of the carnivore palaeoguild could not consume meat from the largest prey size categories (Table 3). As commented above, this is an interesting aspect of the methodology used, which considers the abilities of the species of secondary consumers to obtain and process prey of different size and the influence of this in the competition intensity, an aspect not considered in previous studies. If we consider the meat demands of predators and scavengers (TDB: total demanded biomass) under optimal conditions (i.e., when they reach their maximum expected densities), these demands are balanced in the long term with the biomass offered by their prey. The reason is that the TDB estimates are comprised between the TAB-m and TAB-M values. However, not all carnivores would have access to the whole spectrum of prey biomass offered. Moreover, our TAB-m estimates are close to those derived with the mortality profiles of modern species, while our TAB-M estimates consider the same mortality rate for all age classes (Martín-González et al., 2016, 2019). However, given that we defined the consumption profiles based on inferences from the fossil record, some aspects not considered in the study could allow for a better use of the meat resources available. This would in turn result in a decrease of competition intensity. For example, RTAB values vary according to each scenario. In the case of Scenario 1, the RTAB estimate is the lowest (0.6% of TAB-m) while the RTAB values of scenarios 3 and 4 are the highest (> 14% of TAB-M in both cases). This increase takes place when the consumption of carrion is not considered, which means that the biomass from the largest prey size categories is not consumed (Table 3). The influence of the consumption profile in the results obtained for each scenario can be observed for *Ps.*

lemoinei and *Cladosictis patagonica*: in overall terms, although the scenarios with TAB-m provide less biomass than those with TAB-M, the latter are more adverse for both species because they provide less biomass from Category I (10–45 kg), the only size class that they can consume with TAB-M. In this study we assumed that these species only consumed part of their meat requirements from prey species weighting > 10 kg (see correction factor (CF) in Table 3) and that the remaining requirements were consumed from smaller prey species. In all the scenarios considered, however, TAB-M results in a decrease of biomass from Category I compared to TAB-m, which translates in an increase of biomass from Category II (45–90 kg).

A fourth factor that may affect our estimates of competition intensity is that we only considered meat consumption by cariamiforms and sparassodonts. However, it should be acknowledged that extant armadillos usually feed on carrion when it is abundant, and this situation could also apply to the SCF fauna. Thus, we should consider that the TDB estimate could be higher, which would increase the level of competition intensity in the carnivore guild.

Finally, another factor that could affect the results obtained is that our model does not consider environmental preferences for the species (e.g., open, closed or mixed habitat). However, prey availability by predators and competition for carcasses by scavengers probably varied among the environments inhabited by the primary consumers, which would affect the level of competition intensity for these resources among carnivores, as recorded in modern ecosystems (Lewis, 1997; Domínguez-Rodrigo, 2001).

5.3. Competition indexes as a mean to deduce the characteristics of a food web

Apart from estimating the level of competition intensity in a palaeocommunity, competition indexes provide complementary information on the food web. For example, the differences between the values of the GCI and GCIB indexes show the effect of the distribution of meat resources among carnivores: when GCI and GCIB take the same value, this indicates a homogenous distribution of meat resources; if $GCI < GCIB$, more meat resources are consumed by the small carnivores; in contrast, if $GCI > GCIB$, large carnivores consume larger amounts of meat (Rodríguez-Gómez et al., 2016a). GCIB values in FL 1–7 are lower than their corresponding GCI values in all cases except in Scenario 4 with TAB-m. This indicates a trend for greater consumption of meat by the large carnivores, which is more evident with TAB-M than with TAB-m. $GCIB > GCI$ in Scenario 4 with TAB-m, which implies a higher relative consumption by the small carnivores. This results from differences in the distribution of TAB from the lowest prey size categories between the scenarios for D_xR (1 and 2) and D_xTA (3 and 4) (Table 5).

The SCI index shows the scenarios with greater influence on each

species. In general terms, the presence of scavenging behavior has the largest effect on the SCI values. However, TAB conditions have more influence on *Ps. lemoinei* and *Cl. patagonica* (see Table 3 and Fig. S2). As noted above, these species show their highest SCI values in Scenario 2 with TAB-M (Fig. 5). In the D_xR scenarios (1 and 2), the biomass available for carnivores is greater with TAB-m than in the D_xTA scenarios (3 and 4) with TAB-M (Table 5). This difference allows *Ps. lemoinei* to follow a pattern similar to most carnivore species (Table 3). There are other cases in which the SCI general patterns were not achieved. For example, the SCI values of *Prothylacynus patagonicus* do not fully agree with the general pattern obtained for TAB-m conditions (Fig. 5): this species shows a SCI value that is slightly lower for Scenario 1 than for Scenario 3. Given that there is less biomass available from Categories II and III for D_xTA than for D_xR scenarios with TAB-m (Table 5), *Pr. patagonicus* shows lower SCI values for Scenario 1. Another example is *Ph. longissimus*, which has lower SCI values for Scenario 2 than for 4, in contrast to the other species. This result reflects also an increase in the competition intensity for the meat available from the first three prey size categories in the scenarios 2 and 4, where *B. tuberosa* and *A. munizi* would compete for these resources. This information is further explained by the percentages of consumption (see Supplementary Information, Figs. S2 and S3).

5.4. Comparing our results with the Pleistocene food webs

In this study we used minimum estimates of prey intake by the SCF carnivores because they depict the scenario most opposed to the null hypothesis (i.e., that these palaeocommunities were not impoverished in carnivores; see the unbalanced models obtained with minimum predator densities by Di Giacomo and Fariña, 2017). However, our studies of Pleistocene food webs using this methodology were based on maximum estimates. According to Catena and Croft (2020), the SCF community had an ecological structure similar to those of recent Palaeartic communities of mammals. For this reason, it could be interesting to compare it with the Pleistocene palaeocommunities. For doing that, we repeated our analyses using maximum meat intakes (Table 6). A comparison with the results obtained in the Early and Middle Pleistocene sites of Sierra de Atapuerca and Orce (Rodríguez-Gómez et al., 2016b, 2017a, 2017b) shows that the TAB estimates for the SCF assemblages double those obtained in all these sites except Venta Micena (VM) in Orce (Table 6). The TDB value is also higher, two times on average, than the values of all the sites of Atapuerca. It is worth noting that in all cases except Trincheras Dolina TD6-2 (Atapuerca), the TDB values were higher than the TAB-m and TAB-M estimates obtained with maximum values of meat intake by the carnivores. This suggests that the members of the predator/scavenger guild of the SCF assemblages could not reach their optimal population sizes. However, this did not occur in our Pleistocene analyses with TAB-M, as the TDB estimates were lower than the meat available from the prey species. Concerning the competition indexes, those that measure competition intensity at the level of the whole carnivore palaeoguild of FL 1-7 (GCI-m, GCI-M and GCIB-M) show that the most unfavorable scenario for the SCF carnivores (Scenario 2, D_xR-Scav) shows the highest values, only behind the estimates of Fuente Nueva-3 and Barranco León (FN-3/BL) in Orce (0.58, 0.50 and 0.45, respectively). In the case of the GCIB-m index, the Scenario 2 shows the third highest value, although it is also lower than those measured in FN-3/BL (0.59) and VM (0.48). Scenario 3 (D_xTA + Scav) shows the lowest competition intensity (i.e., the most favorable condition for the whole carnivore guild), with similar values to those of the Sierra de Atapuerca sites for GCI-m, GCIB-m and GCIB-M. In the case of the GCI-M index, the closest site is VM (Table 6). These results indicate that the competition indexes of the SCF carnivores are close to those estimated for the Pleistocene sites of Western Europe, which argues against an impoverished carnivore guild in South America during Late Miocene times. These results support the proposal by Catena and Croft (2020) on the similarities between the ecological

structure of the SCF and Palaeartic communities.

5.5. Future perspectives

Modeling past ecosystems is a useful tool for testing hypotheses in palaeoecology, which allows visualizing past life conditions and helps to understand the relationships among extinct species. The information obtained depends on the accuracy of input data and the mathematical refinement of each model. Our model provides a global view of the food web of the FL 1-7 assemblages for prey species of > 10 kg. In order to refine this approach, further efforts will be invested in differentiating among the habitat adaptations of the SCF species. In addition, it will be interesting to model the species of < 10 kg, which would provide a more complete view of the palaeoecosystem, although these species may be more subject to taphonomic bias given their small size. Another aspect to consider in future studies is the comparison between FL 1-7 and other SCF assemblages. Finally, a complementary research line will be to expand the analyses to other South American assemblages of younger age, in order to know how the GABI, which started in Late Miocene times, affected their food webs.

6. Conclusions

Several interpretations of predator-prey relationships have been proposed for the SCF palaeocommunities: a number of researchers have suggested that these faunal assemblages had fewer carnivorous species than expected on the basis of the number of medium and large mammalian herbivores, while others found a predator/prey ratio similar to those of some recent communities, even when predatory birds are not considered in the palaeocommunities. In our analysis we have considered mammals and birds as potential predators, both with and without the possibility of scavenging, which provides a more realistic view of the food web. According to our results, the carnivore guild was not impoverished, as the biomass demanded by the carnivores (TDB) falls between the minimum and maximum estimates of available biomass (TAB-m and TAB-M). Moreover, we have estimated a variable level of competition intensity for meat resources, depending on the scenario considered. In general terms, our results show a community with a high competition for small- to medium-sized prey, in which the secondary consumers would not fully satisfy their meat requirements. However, competition seems to have been less severe for larger prey, which supports in part the impoverishment of predator/scavenger species in this palaeocommunity.

Our analysis refines previous studies on the SCF assemblages because it (i) considers meat availability from the whole prey community; (ii) assumes a palaeocommunity that was stable and stationary in the long term; and (iii) estimates consumption profiles for each predator/scavenger species. This heuristic approach allows obtaining more realistic results than in previous analyses, which provides new avenues of research on predator-prey relationships in these palaeocommunities of the South American Cenozoic.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2020.109805>.

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