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# Resource partitioning among top predators in a Miocene food web

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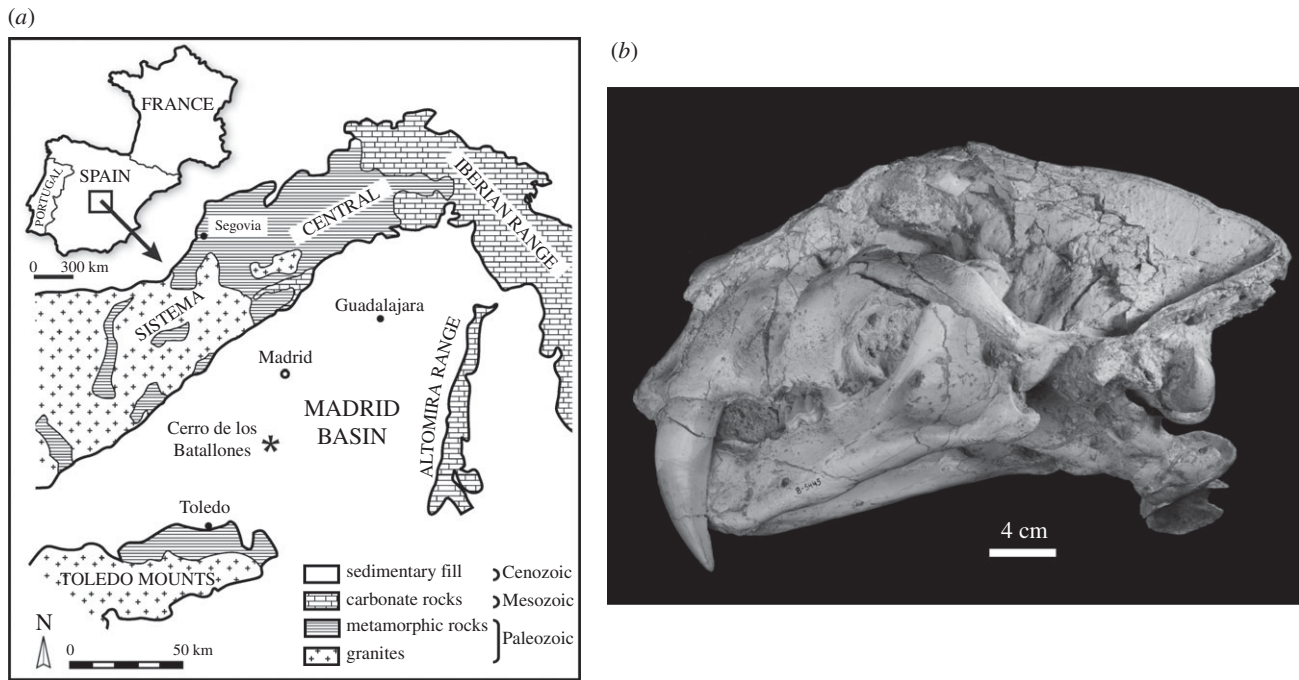
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The exceptional fossil sites of Cerro de los Batallones (Madrid Basin, Spain) contain abundant remains of Late Miocene mammals. From these fossil assemblages, we have inferred diet, resource partitioning and habitat of three sympatric carnivorous mammals based on stable isotopes. The carnivorans include three apex predators: two sabre-toothed cats (Felidae) and a bear dog (Amphicyonidae). Herbivore and carnivore carbon isotope ( $\delta^{13}\text{C}$ ) values from tooth enamel imply the presence of a woodland ecosystem dominated by  $\text{C}_3$  plants.  $\delta^{13}\text{C}$  values and mixing-model analyses suggest that the two sabre-toothed cats, one the size of a leopard and the other the size of a tiger, consumed herbivores with similar  $\delta^{13}\text{C}$  values from a more wooded portion of the ecosystem. The two sabre-toothed cats probably hunted prey of different body sizes, and the smaller species could have used tree cover to avoid encounters with the larger felid. For the bear dog,  $\delta^{13}\text{C}$  values are higher and differ significantly from those of the sabre-toothed cats, suggesting a diet that includes prey from more open woodland. Coexistence of the sabre-toothed cats and the bear dog was likely facilitated by prey capture in different portions of the habitat. This study demonstrates the utility of stable isotope analysis for investigating the behaviour and ecology of members of past carnivoran guilds.

## 1. Introduction

Apex predators occupy the peak of the trophic pyramid and, from that position, they are important regulators of the food web because they are partly responsible for limiting their prey populations, commonly herbivores, and, by controlling herbivory, they indirectly regulate vegetation [1]. The propagation of impacts by consumers on their prey through food webs was formalized in the concept of ‘trophic cascades’ [2]. The removal of apex predators from ecosystems, either from natural or anthropogenic causes, triggers reactions that cascade to the lowest trophic levels [3]. An intrinsic characteristic of species at the top of the consumer food web in terrestrial ecosystems is that they occur in low densities. In the fossil record, the common pattern is that herbivore remains far outnumber carnivoran remains [4]. Consequently, the scarce carnivoran remains have a particularly high value in systematic studies, and analyses that require destructive sampling (such as stable isotope analyses) are rarely permitted. Accordingly, ancient predator–prey systems remain understudied from the perspective of stable isotope geochemistry and this fact is more evident for older systems. Yet, in terms of stable isotope ecology, apex predators are particularly useful because their isotopic values typically represent multiple species of prey and, therefore, have the potential to convey an integrated environmental signal [5].

Exceptionally rich fossil sites present a unique opportunity to investigate trophic interactions in ancient ecosystems. The fossil sites of Cerro de los Batallones (Madrid Basin, Spain; figure 1a) contain abundant, diverse and well-preserved remains of Late Miocene vertebrates (approx. 10–9 Ma;



**Figure 1.** (a) Location of Cerro de los Batallones within the Madrid Basin. (b) Skull and mandible of *Machairodus aphanistus* (B-5445) from the fossil locality Batallones-1.

Vallesian European Land Mammal Age [6,7]). The nine fossil sites discovered thus far are concentrated in an area of 16 ha. Fossil remains occur in marls and siliciclastic sediments that discordantly cut across the three sedimentary units defined in the ridge, indicating that the fossil assemblages were deposited in cavities. Several independent chambers formed by erosion of the clay matrix [8].

The most remarkable feature of these fossil sites is that two of the nine assemblages are overwhelmingly dominated by mammalian carnivores [8]. In the other fossil sites, herbivore remains are far more abundant than carnivorous fossils. More than 92 per cent of the large-mammal specimens ( $n \approx 18\,000$ ) recovered from the lower-level assemblage of the locality Batallones-1 belong to 10 carnivorous taxa. These include four species of Felidae (cats): two sabre-toothed cats (*Promegantereon ogygia* and *Machairodus aphanistus*; figure 1b) and two felines (*Styriofelis vallesiensis* and an undescribed species). In addition, a bear dog (*Magericyon anceps*) from the extinct family Amphicyonidae, a primitive hyaena (*Protictitherium crassum*), an early relative of the red panda (*Simocyon batallieri*), a marten (*Martes* sp.) and two relatives of modern skunks (*Proputorius* sp. and *Sabadellctis* sp.) have been recovered [8–10]. Geological and taphonomic evidence suggests that the dominance of carnivores resulted from preferential entrapment of these taxa in the chambers [8,11].

The three carnivores analysed here, the two sabre-toothed cats and the amphicyonid, were apex predators in this ecosystem (i.e. taxa with virtually no predators of their own, except possibly each other). We evaluated their diet through comparison of their carbon isotopic values to those of relevant herbivore prey. Also, stable carbon isotope ( $\delta^{13}\text{C}$ ) analyses permitted us to investigate how these Miocene carnivores partitioned the resources and, therefore, provided further information on the ecology and behaviour of these members of ancient carnivorous guilds.

For mammals, the  $\delta^{13}\text{C}$  composition of tooth enamel tracks the values of their diet [12–14].  $\delta^{13}\text{C}$  values of herbivores reflect the values of ingested plants and in turn,  $\delta^{13}\text{C}$  values of carnivores reflect the values of ingested prey [15].

By extension,  $\delta^{13}\text{C}$  values from mammalian fossil enamel are an important tool for reconstructing the type(s) of habitat where the animals lived.

In modern ecosystems with diverse carnivorous mammals, the apex predators compete intensively over prey and carcasses [16]. Differential use of resources (i.e. resource partitioning) facilitates coexistence. Coexistence of predators is achieved through numerous strategies, such as targeting different types of prey in terms of species, size and age classes, temporal separation of predatory activity (diurnal versus nocturnal predators), mutual avoidance or differences in habitat use [17–19]. Here, we use stable isotope analyses to evaluate the predator–prey relationships and habitat partitioning of the three largest carnivores and their potential ungulate prey species in Late Miocene Cerro de los Batallones localities. We use a mixing-model for  $\delta^{13}\text{C}$  values of the predators and eight potential prey species to infer which herbivores were feasible prey for each predator. Because sample sizes of the three carnivores are relatively large, we also use the variance in  $\delta^{13}\text{C}$  values as a measure of the versatility of habitat use by the predators.  $\delta^{13}\text{C}$  values of the mammals are used to estimate gradients from open to closed habitats within the original Miocene ecosystem. Compared with analyses of mammalian herbivores, stable isotope analyses of modern and Pleistocene carnivores are infrequent (although increasing; [20–29]). Cerro de los Batallones localities offer a view into carnivorous guilds that is rarely available and, to the best of our knowledge, this study constitutes the first stable isotope analysis of mammalian predator–prey relationships for a Miocene fauna.

## 2. Material and methods

### (a) The carnivores

As previously indicated, the three carnivores analysed in this study were top predators. *Promegantereon ogygia* was a sabre-toothed cat the size of a leopard (table 1) and was the most abundant species from the lower-level assemblage of Batallones-1. The sabre-toothed cat *M. aphanistus* was the size

**Table 1.** Estimated body weight (kg) of taxa analysed in this study. Body weights were derived from measurements on Cerro de los Batallones skeletal remains except for *Microstonyx* sp. For *Microstonyx* sp., we used the mean body weight proposed by Liu [30]. For *Austroportax* sp., we complemented our estimates with those of Moyà-Solà [31].

taxon	body weight in kg, median (min.–max.)	algorithm references	basis for estimate
carnivores			
<i>Promegantereon ogygia</i>	41 (28–97)	[32]	long bones
<i>Machairodus aphanistus</i>	153 (117–285)	[32]	long bones
<i>Magericyon anceps</i>	194 (175–195)	[33]	mandible, long bones
herbivores			
Rhinocerotinae indet.	2484 (1280–3573)	[34]	mandible, dentition
<i>Aceratherium incisivum</i>	1678 (788–2554)	[34]	mandible, dentition
<i>Hipparion</i> sp. 1	149 (92–265)	[35]	long bones
<i>Hipparion</i> sp. 2	238 (178–294)	[35]	long bones
Giraffidae indet.	902 (549–1102)	[36]	dentition
<i>Tetralophodon longirostris</i>	3905 (2060–6984)	[37]	long bones
<i>Microstonyx</i> sp.	330		
<i>Austroportax</i> sp.	105 (47–280)	[34,36]	dentition, long bones

of a tiger (table 1 and figure 1b) [38]. The amphicyonid *Magericyon anceps* was also tiger-sized (table 1) [9]. Modern felids are obligate carnivores and require a diet of fresh meat to survive. Their dentition displays hypercarnivorous traits, including reduced cheek teeth and blade-shaped carnassials. Similar traits in the dentition of the sabre-toothed cats suggest that their diet consisted exclusively of meat. The family Amphicyonidae is a monophyletic group of extinct carnivorans with a peculiar skeletal morphology that includes features shared by living canids (dog-like dentition) combined with characteristics of modern ursids (robust body plan); thus, they are popularly known as bear dogs [33]. Although the dentition of amphicyonids shows bone-crushing adaptations (robust cheek teeth, presence of zigzag Hunter–Schreger enamel bands [39]), the teeth of *M. anceps* exhibit hypercarnivorous traits (loss of premolars, reduction of cusps on premolars and molars, and lateral compression of upper canines) that imply a greater reliance on active predation and less reliance on scavenging [9,38].

The remaining carnivoran taxa from Batallones-1 were not examined because they are represented by very few individuals, their teeth are too small for isotopic sampling, or they were likely to have consumed food resources not represented in the fossil assemblage. For example, *Protictitherium crassum* was a small hyaena comparable in size to an African civet (*ca* 13 kg) that would have fed on small mammals, birds and insects [40].

## (b) Fossil teeth

We analysed tooth enamel from a total of 69 specimens for  $\delta^{13}\text{C}$  from the carbonate fraction of apatite (see the electronic supplementary material, table S1). Twenty-seven teeth belong to the three carnivoran species (*P. ogygia*, *M. aphanistus* and *Magericyon anceps*) and the remaining 42 teeth belong to eight herbivore taxa. Because herbivore specimens in Batallones-1 were rare, we also sampled teeth from the nearby fossil assemblage of Batallones-10. Faunal composition and isotopic results (almost identical  $\delta^{13}\text{C}$  mean values for the *Hipparion* species) suggest that the age difference, if any, was small [41] and that the habitat was similar for both localities.

We sampled all medium to large mammalian herbivores with available teeth. The herbivores analysed include two species of rhinoceros (Family Rhinocerotidae, *Aceratherium incisivum* and an undescribed species, *Rhinocerotinae* indet.), two hipparionine

horses (Family Equidae, *Hipparion* sp. 1 and *Hipparion* sp. 2), a proboscidean (Family Gomphotheriidae, *Tetralophodon longirostris*), a giraffe not yet described (Family Giraffidae, Subfamily Sivatheriinae), a pig (Family Suidae, *Microstonyx* sp.) and an antelope (Family Bovidae, *Austroportax* sp.). The estimated adult body weights of these species range from 105 to 3905 kg (table 1).

*Hipparion* sp. 1 refers to the equid from Batallones-1 and *Hipparion* sp. 2 to the equid from Batallones-10. The latter may include two different species. Both Batallones-1 and Batallones-10 also contain remains of three species of musk deer (Family Moschidae) [11] but the scarcity of their teeth and their small size (all < 10 kg) required that we exclude them from this analysis. The teeth analysed in this study were from adult individuals. All fossil material sampled is housed in the Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain).

## (c) Isotopic methods

Four to 5 mg of enamel powder was obtained from each tooth, using a rotary drill with a diamond-tipped burr. In order to obtain samples representing the time span of tooth formation, the enamel was generally sampled from the base to the crown of each tooth, although this was not possible for some broken teeth. Enamel pre-treatment followed the methods of Koch *et al.* [42] (see the electronic supplementary material). Isotopic analyses were performed on a Thermo MAT253 dual-inlet isotope-ratio mass spectrometer coupled to a Kiel IV Carbonate Device at the Stable Isotope Laboratory of the Department of Earth and Environmental Sciences, University of Michigan.

$\delta^{13}\text{C}$  results are reported in  $\delta$ -notation,  $\delta^{13}\text{C}_{\text{sample}} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , where  $X$  is the element,  $H$  is the mass of the rare, heavy isotope and  $R = {}^{13}\text{C}/{}^{12}\text{C}$ . The isotopic reference standard for carbon is Vienna Pee Dee Belemnite (VPDB). The analytical standard was NBS-19 ( $n = 36$ ) which yielded a mean value of 1.95‰ and a s.d. of 0.03‰, VPDB.

The  $\delta^{13}\text{C}$  composition of herbivores reflects the range of plant resources in their diets [12–14]. Along modern climatic gradients, as vegetation becomes more forested, the  ${}^{13}\text{C}$  of plants becomes depleted ('canopy effect' [43]) so  $\delta^{13}\text{C}$  values also reflect the existing canopy cover in the habitats where these animals lived.

In order to compare the Miocene  $\delta^{13}\text{C}$  values with those documented for modern vegetation, it was necessary to adjust for changes in the  $\delta^{13}\text{C}$  of the atmosphere ( $\delta^{13}\text{C}_{\text{atmCO}_2}$ ) owing



to both geohistorical changes in  $\delta^{13}\text{C}$  of  $\text{CO}_2$  since the Miocene and the increase in light carbon released by the burning of fossil fuels in the last 200 years [44,45]. For the Late Miocene age of the Cerro de los Batallones fossil sites, based on the work of Tipple *et al.* [46], the  $\delta^{13}\text{C}_{\text{atmCO}_2}$  value was approximately  $-6\text{‰}$ , a difference of  $2\text{‰}$  relative to modern  $\delta^{13}\text{C}_{\text{atmCO}_2}$  (approx.  $-8\text{‰}$ ). Accounting for these shifts in baseline, the ranges of  $\delta^{13}\text{C}$  used to infer types of vegetation and canopy cover from fossil teeth from Cerro de los Batallones are (i) closed-canopy forest  $\delta^{13}\text{C}$  values would range from  $-20\text{‰}$  to  $-14\text{‰}$ , (ii) open-canopy woodland from  $-14\text{‰}$  to  $-9\text{‰}$ , (iii)  $\text{C}_3$  wooded grassland from  $-9\text{‰}$  to  $-6\text{‰}$ , (iv) mixed  $\text{C}_3$ – $\text{C}_4$  grassland from  $-6\text{‰}$  to  $-1\text{‰}$  and (v) pure  $\text{C}_4$  grassland from  $-1\text{‰}$  to  $+7\text{‰}$ . According to the UNESCO classification of African vegetation [47], (i) closed forest is a continuous stand of trees at least 10 m tall with interlocking crowns, (ii) woodlands have trees with canopy heights of 8–20 m; their crowns cover at least 40 per cent of the land surface but do not overlap extensively, (iii) wooded grassland has a cover of grasses and other herbs, with woody plants covering between 10 and 40 per cent of the ground and (iv) grassland is covered with grasses and other herbs, with woody cover less than 10 per cent.

#### (d) Statistical analysis and characterization of diet

Differences among species in  $\delta^{13}\text{C}$  values were evaluated with analysis of variance and *post hoc* Tukey tests [13,14,28]. These tests were performed separately for herbivores and carnivores to account for differences in their dietary resources. The significance level was  $p = 0.05$ .

To evaluate the relative contribution of different herbivore species to carnivore diets, we used the stable isotope mixing-model software IsoSOURCE v. 1.3.1. [48]. For a specified number of isotopic systems and isotopic values of carnivores and potential prey, IsoSOURCE finds the combinations of prey proportions that are mathematically feasible solutions for the data [48]. Here, for one isotope system ( $\delta^{13}\text{C}$ ) and more than two diet sources, the equations yielded a range of source proportions. In a preliminary approach, we attempted our dietary analysis using the software IsoERROR [49], a method that incorporates data such as the standard deviations or sample size of the species in the analysis; however, the nature of our data did not allow us to use this model (see the electronic supplementary material).

To reconstruct carnivoran diets, it is necessary to account for the trophic fractionation between the predator and its prey. Trophic fractionation is the isotopic partitioning between a consumer and its diet and involves a systematic  $\delta^{13}\text{C}$  offset of consumer tissue and diet [50]. Trophic fractionation of carbon isotopes between mammalian carnivores and their prey results in slightly lower  $\delta^{13}\text{C}$  values in carnivoran tooth enamel relative to that of their prey [27–29]. To account for this trophic fractionation, we adjusted carnivoran  $\delta^{13}\text{C}$  values by  $+1.3\text{‰}$ , following the trophic discrimination factor proposed by Clementz *et al.* [27]. Because the carnivoran teeth analysed here were found as isolated fossils in Batallones-1 and it was not possible to group the teeth by individuals, we treated each carnivoran tooth as a different individual and compared their  $\delta^{13}\text{C}$  values to the average  $\delta^{13}\text{C}$  values of feasible prey in terms of body size (see below). In IsoSOURCE, it is desirable that dietary sources exhibit distinctly different  $\delta^{13}\text{C}$  values in order to obtain clear discrimination among potential prey [48,51]. Although our results show considerable overlap among potential prey species, the IsoSOURCE analysis was useful in estimating the proportional contributions of each prey species to a particular carnivoran diet [51].

The relationship between predator and prey body size must be considered when evaluating a predator's diet because body size directly affects the predator's ability to run down, seize and kill prey [52,53] (see the electronic supplementary material).

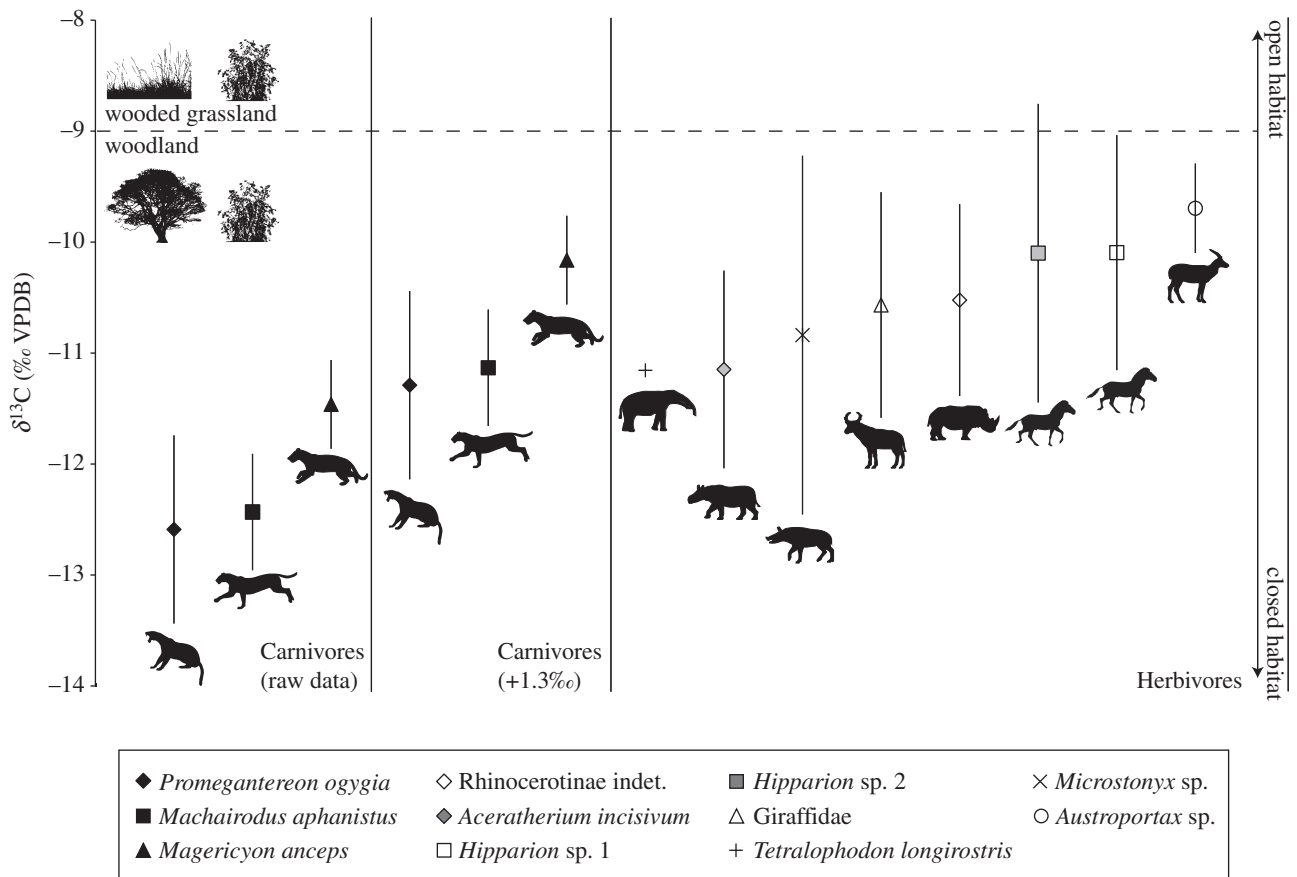
The large-bodied adults of Rhinocerotidae, Giraffidae and *T. longirostris* (all  $>900$  kg) would have been improbable prey for all three carnivores (table 1), particularly if we consider that a solitary lifestyle has been inferred at least for the two sabre-toothed cats [38]. The social behaviour of *M. anceps* has not been evaluated but, by analogy with other amphicyonines, it might have been a solitary hunter as well (see the electronic supplementary material). In modern ecosystems, megaherbivores rarely experience predation as adults and only infrequently as juveniles [53]. For active predators, scavenging of carcasses of large herbivores is not a common practice because carrion is a relatively unreliable food resource. Following these considerations, we performed one IsoSOURCE analysis with the  $\delta^{13}\text{C}$  values of the hipparionine horses, the suid and the bovid, which were considered the main prey species in terms of body size. We performed a separate IsoSOURCE analysis of the megaherbivores in order to evaluate the feasibility of their contribution to the diets of the three apex predators under special circumstances (preying on sick, young or old individuals, feeding on their carrion).

All feasible dietary combinations derived from IsoSOURCE solutions in increments of 1 per cent of different prey combinations were reported as minimum and maximum contributions of each prey species to the diet of each carnivore. On the basis of these estimates, we established a scoring system to rank the potential contribution of each herbivore to the carnivoran diet. When the maximum contribution from IsoSOURCE was less than 33 per cent, we considered that herbivore to be a 'less feasible' diet source. If the maximum was more than 33 per cent and the minimum was less than 33 per cent, the herbivore was considered a 'moderately feasible' prey. If the minimum contribution was more than 33 per cent, the herbivore was regarded as a 'highly feasible' diet source. The estimated diet combinations resulted in predicted  $\delta^{13}\text{C}$  values for the predator (i.e. the  $\delta^{13}\text{C}$  value of each carnivore tooth). If the predicted values were within  $\pm 0.2\text{‰}$  (i.e. the mass balance tolerance) of the observed predator value, then the prey combinations were considered feasible solutions [48].

For some carnivoran teeth, the  $\delta^{13}\text{C}$  values fell off the dietary mixing line (i.e. outside the line formed by the mean  $\delta^{13}\text{C}$  values of the prey species considered here), representing a failed solution in IsoSOURCE. However, when the  $\delta^{13}\text{C}$  value of a predator falls off of the mixing line, it does not directly imply that the predator was feeding on a non-measured prey. For those unresolved cases, an approach that uses the variability of the  $\delta^{13}\text{C}$  values of the herbivores, in the form of  $\pm 1$  standard deviation (s.d.) of the mean, was used to determine whether to some extent the herbivores could contribute to the predator diet. If the  $\delta^{13}\text{C}$  value of the carnivoran tooth was within  $\pm 1$  s.d. of the mean  $\delta^{13}\text{C}$  value of the herbivore, then we considered that the herbivore could have contributed to some extent to the predator diet and, therefore, it was regarded as a feasible prey species. If the  $\delta^{13}\text{C}$  value of the carnivoran tooth was greater than  $\pm 1$  s.d., then we considered that herbivore as less feasible prey. This approach was outlined by Fox-Dobbs *et al.* [25] to resolve predator dietary behaviour in their work on the Pleistocene megafauna of Beringia. In IsoSOURCE, we determined three feasibility categories for the contribution of the herbivores to the predator diets while in the s.d. approach only two alternatives were possible. Thus, the s.d. approach has less resolving power than IsoSOURCE. Nevertheless, the s.d. approach permitted us to evaluate teeth that otherwise would have remained unresolved.

### 3. Results

As expected, carnivoran tooth samples yielded  $\delta^{13}\text{C}$  values lower than those of the herbivores (see figure 2 and electronic supplementary material, tables S1 and S2). After adjustment



**Figure 2.** Mean  $\pm 1$  s.d. of  $\delta^{13}\text{C}$  from tooth enamel for the species analysed in this study. For the carnivorans, we present raw data and data adjusted (by  $+1.3\text{‰}$ ) to account for trophic fractionation [27]. Note that the adjusted carnivoran values show greater overlap with the herbivore  $\delta^{13}\text{C}$  values. The dashed line indicates the transition between woodland and wooded grassland in  $\delta^{13}\text{C}$  of diet. Profiles of the animals are not to scale.

for trophic fractionation, the carnivore  $\delta^{13}\text{C}$  values showed a high overlap with herbivore values (figure 2). Even though  $\delta^{13}\text{C}$  values indicated that some herbivores were feeding in more open habitats than others, their  $\delta^{13}\text{C}$  values did not differ significantly ( $F = 0.652$ ;  $p = 0.710$ ; electronic supplementary material, table S3a). By contrast, the carnivoran  $\delta^{13}\text{C}$  values differed significantly ( $F = 7.273$ ;  $p = 0.003$ ). The Tukey *post hoc* test found no significant differences between the  $\delta^{13}\text{C}$  values of the two sabre-toothed cats (*Promegantereon*–*Machairodus*:  $p = 0.845$ ; electronic supplementary material, table S3b). But the  $\delta^{13}\text{C}$  values of the two sabre-toothed cats differed from the  $\delta^{13}\text{C}$  values of the amphicyonid (*Promegantereon*–*Magericyon*:  $p = 0.004$ ; *Machairodus*–*Magericyon*:  $p = 0.01$ ). This result implies that the diet of *M. anceps* differed from the diets of the sabre-toothed cats. No significant differences in variance of  $\delta^{13}\text{C}$  values were found among the three carnivorans (Levene test = 1.357;  $p = 0.277$ ).

The IsoSOURCE model yielded solutions for about half ( $n = 13$ ) of the carnivoran teeth (table 2). For the remaining specimens ( $n = 14$ ), the s.d. approach indicated which of the four medium-sized prey species made a feasible contribution to each predator's diet (see table 2 and electronic supplementary material, figure S1 and table S4). Both approaches yielded similar results (table 2). Hipparionine horses had moderately feasible contributions to the diets of all three carnivorans. In some cases, the maximum contribution of both equids was very high, but the minimum contribution was 0 per cent in all cases. Therefore, although under some combinations, hipparionine horses were a very feasible diet source for the three carnivorans our scoring system indicated that their contribution was

moderate. The suid *Microstonyx* sp. was a highly feasible diet source for all three carnivorans according to both approaches. The bovid *Austroportax* sp. was an important dietary source only for *M. anceps* according to both approaches.

In the analysis of the megaherbivores, no differences were evident and each species could have contributed to the diet of the three carnivorans (see the electronic supplementary material, tables S5 and S6). In the s.d. approach, low scores for *T. longirostris* might be related to its small sample size ( $n = 2$  teeth).  $\delta^{13}\text{C}$  values of *T. longirostris* (figure 2) indicate that this proboscidean might have contributed more to the diet of the two sabre-toothed cats and possibly less to the diet of *M. anceps*.

The  $\delta^{13}\text{C}$  values of herbivore teeth imply that a  $\text{C}_3$  woodland ecosystem dominated the Cerro de los Batallones region in the Late Miocene (mean =  $-10.4\text{‰}$ , minimum =  $-12.6\text{‰}$ , maximum =  $-8.2\text{‰}$ ). Some teeth had values slightly higher than  $-9\text{‰}$ , suggesting that these herbivores fed in areas with fewer trees and more open grassland (see figure 2 and electronic supplementary material, tables S1 and S2).

## 4. Discussion

The vegetation surrounding Cerro de los Batallones was dominated by  $\text{C}_3$  plants according to the  $\delta^{13}\text{C}$  values of the mammals from these localities (figure 2). The range of herbivore  $\delta^{13}\text{C}$  values implies a predominantly woodland habitat with some open patches of  $\text{C}_3$  vegetation. Although the herbivores did not differ greatly in their average diets,

**Table 2.** Results of IsoSOURCE and s.d. approaches expressed as the feasibility of incorporation of each prey to the diet of each carnivoran. For IsoSOURCE: single asterisks denote less feasible (maximum contribution <33%), double asterisks denote moderately feasible (maximum >33% and minimum <33%) and triple asterisks denote highly feasible (minimum contribution >33%). For s.d. approach (unresolved samples in IsoSOURCE): plus symbols denote feasible ( $\delta^{13}\text{C}$  value of the carnivoran tooth is within  $\pm 1$  s.d. of the mean  $\delta^{13}\text{C}$  value of the herbivore) and minus symbols denote less feasible ( $\delta^{13}\text{C}$  value of the carnivoran tooth is greater than  $\pm 1$  s.d. of the mean  $\delta^{13}\text{C}$  value of the herbivore). Sample numbers as in the electronic supplementary material, table S1. IsoSOURCE maximum and minimum contributions are given in the electronic supplementary material, table S4.

	<i>Hipparion</i> sp.1 (n = 7)	<i>Hipparion</i> sp.2 (n = 9)	<i>Microstonyx</i> (n = 4)	<i>Austroportax</i> (n = 2)
IsoSOURCE				
<i>Promegantereon</i> S5	*	*	***	*
<i>Promegantereon</i> S19	*	*	***	*
<i>Promegantereon</i> S36	**	**	**	**
<i>Machairodus</i> S6	**	**	***	**
<i>Machairodus</i> S7	*	*	***	*
<i>Machairodus</i> S15	*	*	***	*
<i>Machairodus</i> S17	**	**	***	*
<i>Magericyon</i> S11	**	**	*	***
<i>Magericyon</i> S28	**	**	**	**
<i>Magericyon</i> S29	*	*	***	*
<i>Magericyon</i> S38	*	*	*	***
<i>Magericyon</i> S39	**	**	***	**
<i>Magericyon</i> S40	**	**	**	**
s.d. approach				
<i>Promegantereon</i> S1	+	+	+	—
<i>Promegantereon</i> S2	—	—	+	—
<i>Promegantereon</i> S3	+	+	+	—
<i>Promegantereon</i> S18	—	—	+	—
<i>Promegantereon</i> S20	—	—	—	—
<i>Promegantereon</i> S37	—	+	+	—
<i>Machairodus</i> S8	+	+	+	—
<i>Machairodus</i> S9	—	—	+	—
<i>Machairodus</i> S10	—	—	+	—
<i>Machairodus</i> S12	—	—	+	—
<i>Machairodus</i> S13	—	+	+	—
<i>Machairodus</i> S14	—	—	+	—
<i>Machairodus</i> S16	—	+	+	—
<i>Magericyon</i> S41	+	+	+	+

the  $\delta^{13}\text{C}$  values of the antelope *Austroportax* sp. and some of the hipparonine horses indicated a preference for feeding in more open areas, whereas other herbivores, including the rhino *A. incisivum* and the proboscidean *T. longirostris*, consumed plants from more closed woodland. On the basis of affinities between *Microstonyx* and modern wild boars [40], its large range of  $\delta^{13}\text{C}$  values could be related to an omnivorous diet or to herbivory over a wide spectrum of the habitat.

The adjusted  $\delta^{13}\text{C}$  values of the three carnivorans all fell below the  $-9\text{‰}$  threshold, indicating a diet of woodland herbivores. The  $\delta^{13}\text{C}$  values of the two sabre-toothed cats were statistically indistinguishable; it does not necessarily follow that they preyed on the same species but rather that they were feeding on prey in a similar habitat. The coexistence of carnivoran species with similar morphology and hunting

methods (such as these two sabre-toothed cats) is facilitated in part by differences in body size, with larger species incorporating larger prey [52,53]. Although some dietary overlap most likely occurred, it is possible that *M. aphanistus* systematically incorporated larger prey than *P. oxygia* did, as occurs for modern sympatric felids of different sizes [18,19]. Salesa *et al.* [38] suggested by analogy with extant sympatric felids (e.g. leopards and lions or leopards and tigers) that the coexistence of the two sabre-toothed cats was facilitated by widespread tree cover, which the smaller species could have used as a refuge from encounters with the larger species. This mode of habitat use is consistent with the inferred prevalence of woodland in the Cerro de los Batallones area.

IsoSOURCE failed to resolve the most feasible diet sources for several specimens of *P. oxygia* (see table 2 and electronic

supplementary material, table S4), because  $\delta^{13}\text{C}$  values of its teeth were outside the mixing line generated by the average  $\delta^{13}\text{C}$  values of the four herbivores considered. In the s.d. approach, most  $\delta^{13}\text{C}$  values of *P. ogygia* overlapped the mean  $\pm 1$  s.d. of *Microstonyx* sp., with one extreme case (S20) that was completely unresolved. However, based on the large estimated adult size of *Microstonyx* sp. (table 1), we consider this herbivore less feasible as prey of *P. ogygia* than suggested by the results. Rather, *P. ogygia* may have incorporated one or more unmeasured sources in its diet. These unmeasured prey would have occupied dense woodland according to the  $\delta^{13}\text{C}$  values of *P. ogygia*. The habitat of Cerro de los Batallones sites may not have been the common environment for these herbivores, and this could explain their absence from the assemblages. Cervids (deer), which commonly occupied wooded habitats and were present in contemporaneous fossil sites of Spain (e.g. *Amphiprox* and *Euprox* from the Vallès-Penedès Basin), could be that missing diet source [40]. Other herbivore groups cannot be ruled out as prey of *P. ogygia*, although isotopic data are not available for evaluating them.

The bear dog *M. anceps* and the larger sabre-toothed *M. aphanistus* were similar in size (table 1), so despite likely differences in hunting methods, they could have preyed on herbivores with similar body sizes. The  $\delta^{13}\text{C}$  values of these carnivorans suggest that their coexistence was possible because they partitioned the resources. Significant differences between *M. anceps*  $\delta^{13}\text{C}$  values and those of both sabre-toothed cats imply consumption of prey that occupied different portions of the habitat. According to both ISO SOURCE and s.d. approaches, the sabre-toothed cats fed on prey from denser woodland, whereas *M. anceps* fed on prey from more open woodland, such as the bovid *Austroportax* sp. (see table 2 and electronic supplementary material, figure S1).

Domingo *et al.* [11] concluded that a mammalian carnivore was responsible for the moschid assemblage in Batallones-1, based on bone corrosion owing to digestion, patterns of bone breakage and size of the recovered remains. The small body size of moschids and the dental adaptations of the three carnivorans analysed in this study suggest that musk deer were unlikely prey of the three apex predators. Nevertheless, based on the scavenging capabilities of the amphicyonid and the features of the moschid sample, this predator was considered a potential consumer of musk deer, not as prey but as carrion. Moschid species have been typically considered as forest dwellers [40]. However, hypsodont (high-crowned) teeth are relatively common in Miocene moschids from Spain and have been observed in the species from Cerro de los Batallones as well [54]. Hypsodonty is correlated with feeding in more open habitats where grasses or grit are prevalent. Although an isotopic analysis would shed more light on the musk deer diets from Cerro de los Batallones, the crown heights of their teeth are consistent with the habitat described in this study for this area (in fact, it would have been difficult to understand the presence of three different species in these localities, had the musk deer been dwellers of a forested habitat) and corroborate the fact that *M. anceps* was potentially responsible for the accumulation of the musk deer from Batallones-1.

Because of their very large size, the four megaherbivores were not common prey for any of the three carnivorans (table 1). Yet, they might have been consumed either as carrion or as prey under particular conditions (e.g. injured, juvenile or old individuals). No preferential feeding on specific

megaherbivores was found for any of the three carnivorans so we infer that the four large herbivores could have made a minor contribution to the diet of the three carnivorans (see the electronic supplementary material, table S6). Although the sample size of *T. longirostris* was low, the  $\delta^{13}\text{C}$  values of this proboscidean imply that this species inhabited more closed woodland, so this large herbivore might have contributed more to the sabre-toothed cats' diet than to the diet of *M. anceps*.

The variability of  $\delta^{13}\text{C}$  values has been used in other studies as a measure of dietary breadth under the assumption that consumers of a wide range of prey species or diet sources exhibit greater variation in their tissue isotopic signatures than consumers of a narrow range of prey items [22,55]. However, the use of variance as a measure of dietary variation has been questioned, because dispersion of the isotopic values of a population depends not only on the number of species consumed but also on variation in the isotopic values of the food sources [56,57]. Consequently, consumers feeding on only two resources that exhibit highly divergent isotopic composition could have broader isotopic values than consumers feeding on a greater number of diet sources with less divergent isotopic composition. Still, we consider the comparison of variance of sympatric carnivorans useful as a measure of the flexibility of predators to use different habitats rather than as a measure of the variety of prey consumed. A wide range of  $\delta^{13}\text{C}$  values for a carnivore, regardless of whether its diet is based on a diverse array or a small set of prey with divergent  $\delta^{13}\text{C}$  compositions, suggests a greater versatility of this carnivore to hunt in different habitats. Likewise, a carnivore with low variability of  $\delta^{13}\text{C}$  values suggests feeding from a more restricted portion of the habitat, regardless of whether its diet is based on a large or small number of prey with similar  $\delta^{13}\text{C}$  values. In this respect, the absence of significant differences in variance among the three carnivorans from Cerro de los Batallones suggests that none was more versatile than the others in habitat use and occupation. Rather, though the  $\delta^{13}\text{C}$  values from Cerro de los Batallones represent a woodland habitat with some wooded grassland, none of these three carnivorans used the entire habitat range. Rather, they hunted in particular areas with the felids more selective of closed woodland and the amphicyonid more selective of open woodland. Ecological studies of modern carnivoran guilds suggest that selectivity of habitats is common among mammalian predators. A study of 18 carnivoran species from Serengeti (Tanzania) demonstrated that coexistence is favoured through different habitat selection of these species [58]. In Hwange National Park (Zimbabwe), Loveridge & MacDonald [59] found that when the jackals *Canis mesomelas* and *Canis adustus* live in sympatry, they partition the habitat so that *C. mesomelas* uses grassland habitat to a greater extent than *C. adustus*.

## 5. Conclusion

The exceptional abundance and preservation of fossiliferous remains from the Cerro de los Batallones fossil sites have provided the opportunity to investigate, from a stable isotope perspective, how three medium to large sympatric carnivorans partitioned the available resources in a 9 million-year-old food web.

The  $\delta^{13}\text{C}$  values of all the taxa imply the dominance of  $\text{C}_3$  woodland with patches of wooded grassland. We inferred a



different use of prey and habitat from significant differences in the  $\delta^{13}\text{C}$  values of the sabre-toothed cats *P. oxygia* and *M. aphanistus* when compared with the amphicyonid *M. anceps*. The two sabre-toothed cats consumed herbivores with similar  $\delta^{13}\text{C}$  values from more dense woodland, a habitat that would have allowed the smaller cat to hide from the larger one. On the basis of their different body sizes, it is likely that these two cats avoided competition for prey by hunting herbivores of different size. Mixing-model analyses indicated that hipparionine horses and *Microstonyx* sp., were moderately to very feasible prey of these cats. The small sabre-toothed cat probably incorporated additional prey species from more dense woodland. The  $\delta^{13}\text{C}$  values of the amphicyonid implied prey acquisition from open woodland. This use of different portions of the habitat facilitated coexistence of this amphicyonid with the sabre-toothed cat *M. aphanistus* of similar size. In fact, diet preferences of the amphicyonid indicate that it was the only predator commonly consuming *Austroportax* sp., a bovid that occupied more open woodland.

Stable isotope analysis constitutes an insightful tool to evaluate various aspects of the ecology of sympatric carnivorans in modern predator guilds, although its use for this purpose is still uncommon. Further stable isotope analyses of modern sympatric predators would greatly enhance our understanding of their trophic relationships and behaviour and would provide analogues to better understand ancient predator guilds.

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