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DOI:
https://doi.org/10.1007/s12549-023-00588-w

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Palaeobiodiversity and Palaeoenvironments (2024) 104:181–190
https://doi.org/10.1007/s12549-023-00588-w

SENCKENBERG

ORIGINAL PAPER

Where's dinner? Variation in carnivoran distributional responses to the mid-Vallesian faunal turnover

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Received: 27 April 2023 / Revised: 4 July 2023 / Accepted: 11 July 2023 / Published online: 13 September 2023

Abstract

The Catalan locality of Can Llobateres 1 (early Vallesian, MN9) shows a remarkably rich diversity just prior to the mid-Vallesian crisis, including 23 species of Carnivora. Similarity maps using the Raup-Crick index and covering the Middle to Late Miocene (16–5.3 Ma) show that the origin of this carnivoran chronofauna lies to the north of the Iberian Peninsula, gradually making its way south. The chronofauna built up through migrations during the Aragonian, but shows a major influx during the early Vallesian, leading to a biodiversity hotspot. At the end of MN9, the mid-Vallesian turnover, the chronofauna collapses. This is mainly because of the extinction of parts of the fauna, and the retraction of some species to the north, disappearing from Spain. Thus, the rich fauna is an amalgamation of persisting older elements, northern elements having a brief temporary presence and new elements coming in. All these were supported by the unique rich ecosystem of the Vallès-Penedès Basin during the early Vallesian.

Keywords Late Miocene · Palaeobiogeography · Carnivora · Vallesian Crisis · Mammals · Iberian Peninsula

Introduction

Large carnivorans, like lions, leopards, bears, and wolves, have some of the widest distributions among mammals (Nowell and Jackson 1996), although they have been greatly reduced by anthropogenic influence. Only a few decades ago, leopards, for instance, still roamed the hills of Anatolia (Baskaya and Bilgili 2004), and lions survived in the Atlas Mountains well into the last century (Black et al. 2013). Mythology and folklore make it clear that in historical times large carnivorans have disappeared from various areas. One only has to consider the role of the wolf in European fairy tales or the presence of lions in the Middle East and southern Europe, which were featured in classical mythology (Hercules) and the Bible (David, Daniel). Nowadays, particularly the large cats like the Asian lion and tiger, are severely threatened, and various subspecies have already gone extinct (IUCN 2021).

When considering the Late Pleistocene record, the distributions of the large carnivorans are even more impressive. (Sub)species of lion and spotted hyena roamed throughout Eurasia, the former even reaching the Americas (e.g. Rohland et al. 2005; King and Wallace 2014; Argant and Brugal 2017). Moreover, these large carnivorans were found during both glacial and interglacial cycles. Combined with the sizable present-day distribution, this suggests that these carnivorans are able to cope with a wide range of habitats and climatic conditions and hunt a wide variety of prey species. Even though some research suggests that hypercarnivorans may be more prone to extinction (Van Valkenburg et al. 2004; DeSantis et al. 2012), we may hypothesise that such

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ecological plasticity makes carnivorans more resilient than other groups to environmental changes and major faunal turnovers. To test this hypothesis, this paper focuses on the carnivorans during one of the most important faunal changes in the European Miocene, the mid-Vallesian faunal turnover.

Originally identified in the Vallès-Penedès Basin, the mid-Vallesian turnover known as the 'Vallesian Crisis' (Moyà-Solà and Agusti 1990; Agustí and Moyà-Solà 1990) started to be recognised throughout Europe and was considered as marking the change towards more seasonal climates and more open landscapes in Eurasia. The mid-Vallesian faunal turnover was also identified by Morales et al. (2015) as one of the major extinction events affecting Iberian Carnivora. However, recently the magnitude of the 'crisis' has come under scrutiny. Casanovas-Vilar et al. (2014, 2016) showed that, at least for the micromammals, the proposed sudden drop in diversity could be explained in part by sampling bias. Additionally, the geographic range of the Vallesian Crisis seems to be more limited than posed by some authors. Already within the confines of the Iberian Peninsula, inland basins show a quite different pattern of small mammal diversity change than the Vallès Penedès (Madern et al. 2018), the coastal basin that holds the type sections for the Vallesian European mammal age and in which the faunal turnover was first recognised. At the beginning of the Late Miocene the Vallès-Penedès hosted a remarkably rich mammal fauna (Madern and Van den Hoek Ostende 2015). This is particularly evident at the most famous of its fossil sites, the extensively sampled locality of Can Llobateres (Crusafont 1964; Begun et al. 1990; Moyà-Solà and Köhler 1995; Alba et al., 2011a, 2011b).

In this paper, we compare the carnivoran assemblage of Can Llobateres (Table 1) with the other European assemblages of the Middle and Late Miocene. We compute faunal similarity to assess to what extent the assemblage was part of the southward diversity trend noted by Madern and Van den Hoek Ostende (2015) or that it was a unique assemblage in itself.

Table 1 Fauna list Can Llobateres 1 (CL1); carnivoran chronofauna

FAMILY	GENUS	FAMILY	GENUS
Ailuridae	*Protursus*	Mephitidae	*Mesomephitis*
Amphicyonidae	*Magericyon*	Mephitidae	*Promephitis*
Amphicyonidae	*Thaumastocyon*	Mustelidae	*Circamustela*
Barbourofelidae	*Albanosmilus*	Mustelidae	*Eomellivora*
Felidae	*Machairodus*	Mustelidae	*Marcetia*
Hyaenidae	*Protictitherium*	Mustelidae	*Martes*
Ursidae	*Indarctos*	Mustelidae	*Sabadellictis*
Ursidae	*Ursavus*	Mustelidae	*Trocharion*
Viverridae	*Semigenetta*	Mustelidae	*Trochictis*

Material and Methods

Palaeobiogeography

The methods used stem from the concept of chronofauna developed by Olson (1952). A chronofauna refers to a regionally limited assemblage of animal populations that has maintained its structure over a significant period of time. Analytically, the chronofaunas are represented by a set of localities distinguished by its similarity to a locality of interest (here Can Llobateres 1) (Ataabadi et al. 2013).

The basis of this palaeobiogeographic analysis is a dataset downloaded from the New and Old World database of fossil mammals (NOW) on February 19th, 2023 (NOW Community 2023). The area under investigation for the Vallesian carnivoran chronofauna ranges from Europe to Anatolia and excludes North Africa; longitude between 10° W and 50° E; latitude between 15° and 55° N. Before filtering, the dataset contained 1434 specimen records (occurrences), from 332 Miocene localities. From the initial dataset, we applied several thresholds to filter out most single occurrences. We follow the updated Mammal Neogene units (MN) by Hilgen et al. (2012). We acknowledge the possible diachrony in MN unit boundaries (Van der Meulen et al. 2011, 2012), but since the biogeographic analysis relies on non-overlapping time bins, they are recognised as the best option. Localities with greater accuracy than MN unit level are lumped into the corresponding MN unit. Localities that cannot be confidently assigned to a unique MN unit are omitted from the dataset.

All analyses in this paper are carried out at the genus level. Genus-level data are considered more taxonomically robust than species-level data (Alroy 1996, 2003; Madern and Van den Hoek Ostende 2015), albeit these may introduce generalised assumptions about the ecology of the species within a genus (Martín-Suárez et al. 2001). Use of genus-level data holds more consensus (Peláez-Campomanes and Van der Meulen 2009) and is a widely-used taxonomic level at which specimens are identified (Forcino et al. 2012).

The biogeography of the Carnivora present in the early Vallesian Vallès-Penedès is analysed using the faunal resemblance index (GFRI) to Can Llobateres 1 based on Raup-Crick similarity indices (Raup and Crick 1979; Eronen 2009). The data was transformed into a presence-absence matrix using the sample2matrix function (Webb et al. 2008) from the picante library (Kembel et al. 2010) in R (R Core team, 2023). Can Llobateres 1 was chosen as a reference locality, being the best documented fauna in the Vallès-Penedès (Alba et al., 2011a, b) and, additionally, the reference locality for MN9 (De Bruijn et al. 1992; Hilgen et al. 2012). Similarity indices were calculated using the vegan library (Oksanen 2023) in R (R Core team 2023). These were computed using the raupcrick function with 1000 randomizations of the dataset (Chase et al. 2011). An advantage of the Raup-Crick similarity index is that it takes the genus frequencies into account. Thus, localities sharing rare genera will score a higher similarity than communities sharing the same number of common genera. Calculated GFRI values per locality are given in the Supplementary Material.

Because the study addresses a terrestrial ecosystem, marine genera (Pinnipedia) were excluded. Occurrences of marine carnivorans are generally restricted to coastal areas and therefore do not contribute to the expected signal.

From the initial dataset, genera that were present in less than 10% of the sites in each MN unit were filtered out. The filtering threshold was empirically determined, by running analyses with a 0%, 5% and 10% filter, the latter providing the most consistent results (Braumuller 2019). Out of 332 localities and 133 genera, a total of 283 localities and 50 genera were retained, covering European mammal units MN4 to MN13 (around 17 to 5.3 Ma). In order to work out the relationship between distribution and extinction, carnivoran similarity was mapped.

The analysis and visualisation were performed in QGIS 3.26, using the IDW interpolation tool featured in the Spatial Analyst toolbox (QGIS.org 2023). The GFRI Raup-Crick values per locality were analysed separately for each MN unit with an inverse distance weighted distance coefficient P set at 3.0 (~300km) and pixel size 0.005. The interpolation areas were masked with an influence radius of 3 degrees buffer zone around each point (again ~300km) and plotted on the map per MN unit.

Results

Similarity maps

The map of MN4 (Fig. 1a) shows still little overall similarity with the Vallesian chronofauna. The highest similarity is found in the Swiss locality of Ober Schriberschwändili (0.66), but this is based on its sole carnivoran, *Trochictis*, being part of the chronofauna. Well-defined French carnivoran assemblages from the MN unit, like Bézian (twelve genera) and Artenay (15 genera), show much lower similarities (0.16 and 0.29, respectively), and have respectively three and four taxa in common with the chronofauna. One of these is *Martes*, a genus name that has been used as a waste-basket for many Miocene mustelids (Valenciano et al. 2022), and therefore should be treated with caution. Notably, it is also the only taxon of the chronofauna that is recorded from the Iberian Peninsula in MN4 and only in two out of the ten localities, El Canyet (also in the Vallès-Penedès, 0.45) and Artesilla (0.11).

In MN5 (Fig. 1b), the highest similarity is again found north of Spain, but this time it is much higher, reaching over 0.95. The assemblages with the highest indices are clustered in the Loire region. Most evident is Contres, France, (0.96), which shares four out of six genera with the Vallesian chronofauna. Contres is, however, an exception. Seven central European localities have a similarity between 0.55 and 0.75. This includes well-defined carnivoran assemblages such as Noyant-sous-le-Lude (5 out of 12 chronofauna genera shared; 0.68) and Pontlevoy (6/15; 0.67). Other larger assemblages from central Europe have much lower similarities, such as those from Göriach (1/9; 0.05) and Sandelzhausen (1/9; 0.02). Only two out of twelve Iberian MN5 assemblages in our analysis contain elements from the chronofauna, viz. La Retama (1/6; 0.06) and els Casots (2/7; 0.47).

The MN6 map (Fig. 1c) suggests relatively high similarities with central Europe, but this is caused by the three closely set Swiss localities of Oeschgraben, Uzwil-Nutzenbuech, and Sagentobel, which all represent single occurrences of *Trocharion*, resulting in the highest similarities in MN6 (0.65-0.68). Overall, similarities are somewhat lower than in the preceding unit, but more equitably distributed. This more equitable distribution is also evident from the higher proportion of the Iberian assemblages containing elements from the chronofauna, namely four out of ten. The highest similarity on the peninsula is found in the assemblage of Arroyo del Val (3/9; 0.36). A notable feature of the MN6 map is the very low similarity of the reference locality of the unit, Sansan (2/20; 0.01), in southernmost France.

MN7+8 (Fig. 1d) is the first unit with the highest similarity found inside Spain, in the assemblages of Escobosa de Calatañazor (3/5; 0.89) and Sant Quirze (3/5; 0.89). Even though the latter is located in the Vallès-Penedès Basin, in the *Democricetodon crusafonti* - *Hippotherium* interval zone, representing the latest part of MN unit 7+8, the basin appears as an area of low similarity on the map. The low value of the small assemblage of Barranc de Can Vila 1 (0/2; 0.0) visually obscures the highest similarity of the MN unit at San Quirze, in fact one of the highest overall similarities (Fig. 1d). Apart from having the highest similarity, the Iberian Peninsula shows for the first time a majority of assemblages containing an element from the chronofauna (five out of nine).

Similarities for well-defined assemblages in central Europe are moderate, such as those from La Grive M (0.63; 6/18), Steinheim am Albuch (0.65; 5/15), and Anwil (0.67; 3/6). The latter two display as areas of higher similarity in southern Germany and Switzerland, but, as was the case in the Vallès-Penedès, the area of La Grive in southwestern France appears as an area of low similarity. Here, the value of La Grive M is overshadowed by those of other La Grive

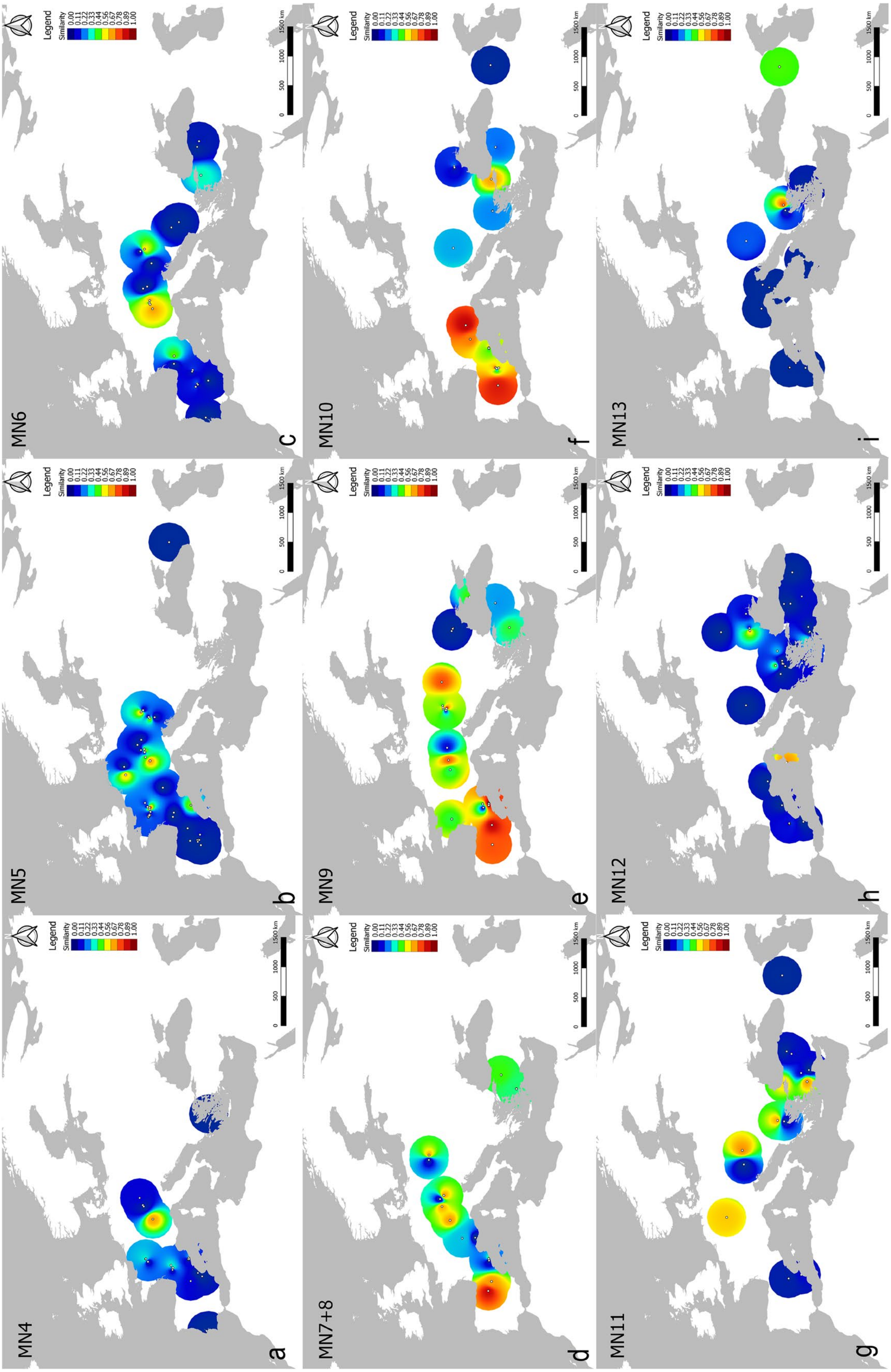

Fig. 1 **a** MN4, **b** MN5, **c** MN6, **d**, MN7+8, **e** MN9, **f** MN10, **g** MN11, **h** MN12, **i** MN13. Maps of Eurasia, colours indicate Genus Faunal Resemblance Index (GFRI), based on Raup-Crick similarity per locality to Vallesian locality Can Llobateres 1, in order to identify the carnivoran Vallesian chronofauna

fissures, with similarities ranging from 0.00 (La Grive CD 14; 0/1) to 0.50 (La Grive L3; 5/14).

As the analysis is based on the MN9 (Fig. 1e) chronofauna of the Vallès-Penedès, it is not surprising that the highest similarities are found in that basin. Apart from the reference fauna of Can Llobateres 1, with a similarity of 1 per definition, four other carnivoran assemblages (Can Poncic I (7/11), Can Poncic (6/11), Castell de Barberà (4/5), and Santiga (3/3)) have similarities exceeding 0.95. All 15 Iberian assemblages except for one, that of la Teuleria del Firal (0/1), contain elements of the chronofauna. Unfortunately, this single occurrence causes, together with the nearby assemblage from Bellestar (0.18; 1/4) an apparent spot of low similarity in the north of Catalonia on the map (Fig. 1e).

Similarities in central Europe are generally higher than in other MN units. The highest scores are found for the localities of Götzendorf (0.90; 3/5) and Rudabánya (0.76; 5/12). Notably, the overlap with the reference fauna Can Llobateres is not that large, and the high similarity is presumably based on shared rare taxa, such as *Mesomophitis* in the former and *Protursus* in the latter. In fact, Can Llobateres and Rudabánya are the only two localities that have a record of *Protursus*.

Similarities on the Iberian Peninsula remain high during MN10, but overall, they seem to be more localised (Fig. 1f). Ten out of the twelve highest Raup-Crick values are located in Spain, the other two being the localities of Soblay (0.91; 4/7) and Montredon (0.71; 3/7), both in southern France. In fact, only one locality in Spain has no similarity to the chronofauna, and this concerns a single occurrence in Masía del Barbo 2B (0/1). The map shows that there is a clear separation, with similarities in the west being higher than those in the east. The only light spot in the east on the map is caused by the Turkish locality of Yulafli (CY), which is again based on a single similar genus, in this case of *Indarctos*.

The map of MN11 (Fig. 1g) shows a marked decrease in similarities. Notably, only 16 carnivoran assemblages are available for this unit, with the two larger assemblages (Csákvár, (0.69; 4/11) and Dorn-Dürkheim (0.61; 7/18) suggesting the highest similarities with central Europe. Within the Iberian Peninsula, similarities are markedly low (Crevillente 2, 0.10; 1/5; Puente Minero, 0.07; 1/7). As on the map of MN10, lighter spots in the east are mainly caused by single occurrences (Kemiklitepe D in Anatolia and Kocherinovo 1 in Bulgaria), although the locality of Küçükçekmece also gives a relatively high similarity (0.58; 2/6).

Similarities remain low in MN12 (Fig. 1h). Out of the 50 carnivoran assemblages, 29 have no elements from the chronofauna. Higher similarities all concern assemblages with one or two carnivorans only, the highest being Samos (PMAS) (0.90; 2/2). Because of its isolated position, Fiume Santo (0.68; 1/1) creates a light spot on Sardegna/Corsica, but this is clearly an artefact. Large carnivoran assemblages such as those of Pikermi (0.06; 3/17) and Los Mansuetos (<0.01; 1/13) confirm the general lack of similarity with the Vallesian fauna. In MN13 (Fig. 1i), only four out of twenty-one assemblages contain elements from the chronofauna. The higher similarity for Maramena (0.75; 2/5), giving a peculiar light spot to the east, can be attributed to the presence of *Promephitis*, a rarer element in the Late Miocene assemblages, and a species of *Martes*, which we already recognised as a contentious taxon for the Miocene.

Rise and fall of the chronofauna

Figure 2 shows the temporal ranges of Carnivora genera of the chronofauna in Eurasia, first (FO) and last occurrences (LO), as well as their FO/LO on the Iberian Peninsula.

Only a few elements of the Vallesian carnivoran chronofauna appeared in Europe as early as MN4, accounting for the low similarities in western Europe and the Aegean region. The carnivorans that are already present are the hyenid *Protictitherium*, the viverrid *Semigenetta*, the ursid *Ursavus* and the mustelids *Trochictis* and *Martes*. One has to bear in mind, however, that the latter genus name is used as a waste basket for multiple Miocene species (Valenciano et al. 2022). Therefore, we should not attach much value to *Martes* being the only element of the chronofauna present on the Iberian Peninsula in MN4.

Not counting *Martes*, *Protictitherium* is the first element to enter the Iberian Peninsula in MN5. *Thaumastocyon* and *Trocharion* make their first appearance in Europe, bringing the total number of chronofauna elements up to seven. In MN6, only one element is added, the barbourofelid *Albanosmilus*, which immediately also appears in Spain. However, there are no records of *Thaumastocyon* as of yet in that unit.

Three small carnivorans make their first appearance on the Iberian Peninsula during MN7+8; the viverrid *Semigenetta* and the mustelids *Trochictis* and *Trocharion* (Alba et al. 2021). The major pulse comes in MN9. The ursid *Ursavus,* already present in Europe, now makes its way onto the Iberian Peninsula, as does the felid *Machairodus*. The entrance date of *Thaumastocyon* cannot be determined by the lack of records from MN6 and MN7+8, but it is also present on the Iberian Peninsula in MN9. Eight taxa appear for the first time: the amphicyonid *Magericyon*, the mustelids *Marcetia*, *Circamustela*, and *Sabadellictis*, the mephitids *Mesomephitis* and *Promephitis*, the ursid *Indarctos*, and the ailurid *Protursus*.

While nine taxa of the chronofauna make their first appearances in MN9, the unit records the last occurrences of six. Four of these are elements that were already present in the Middle Miocene, the amphicyonid *Thaumastocyon*, the barbourofelid *Albanosmilus*, and the mustelids *Trochictis* and *Trocharion*. The two other taxa, *Marcetia* and *Protursus*, are, in fact, restricted to MN9. In addition, both the mephitid *Mesomephitis* and the ursid *Ursavus* have their last

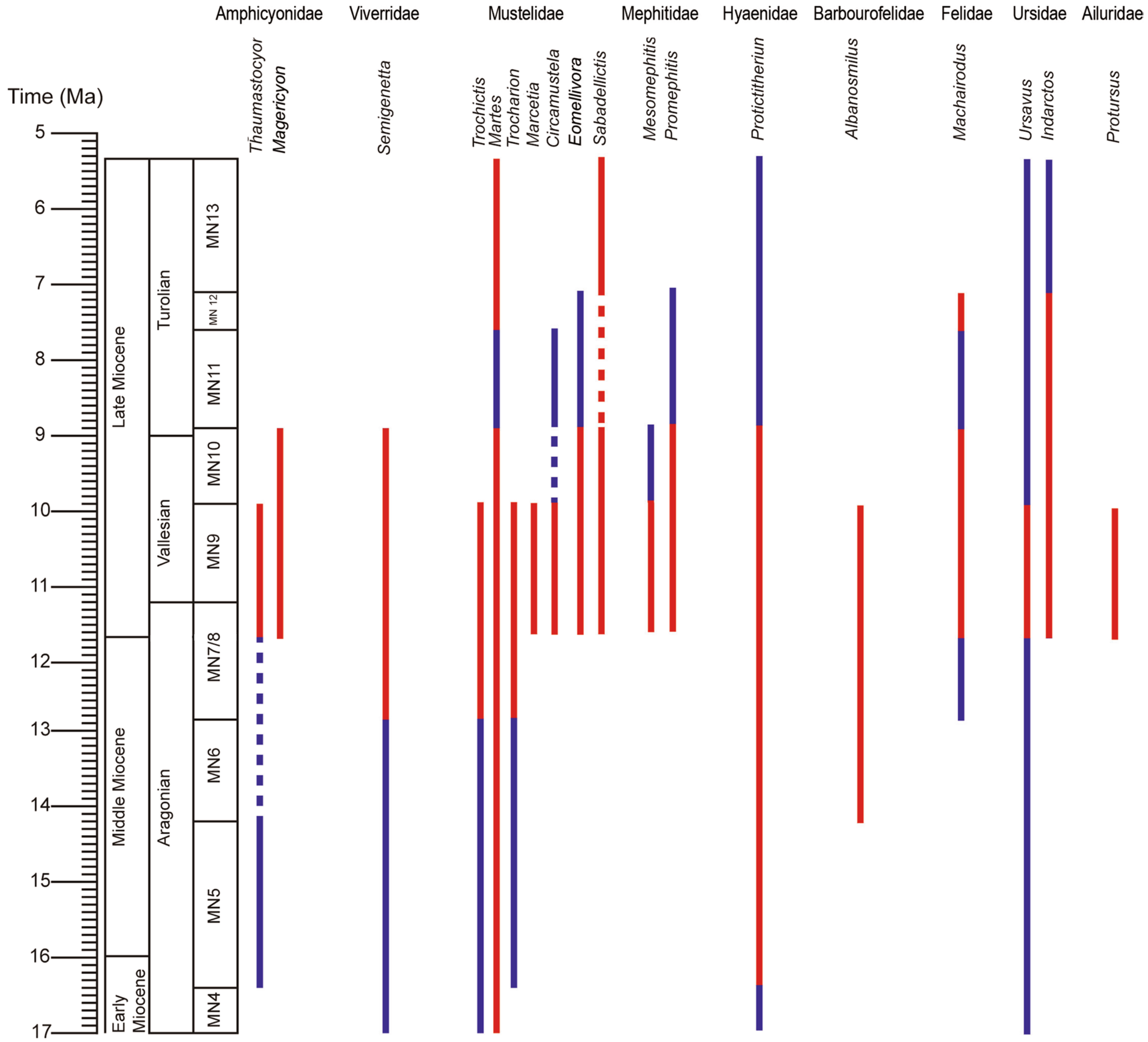

Fig. 2 Temporal ranges per genera in Europe (*blue*) and in Iberia (*red*) per MN unit

occurrence on the Iberian Peninsula. This holds also true for the mustelid *Circamustela*, but, in the absence of an MN10 record, the true time of its extirpation in Spain is unclear.

Two of the surviving genera into MN10*, Magericyon* and *Semigenetta* disappear during that unit. The presence of *Martes* and *Machairodus* on the Iberian Peninsula is interrupted during MN11, but as we noted above, fewer assemblages are available for this time unit, which may account for the temporary regional absence. All in all, eight taxa from the chronofauna are present in the Turolian, half of which are only found north of Spain. Notably, five out of the eight Turolian taxa made their first appearance at the beginning of MN9, representing true Late Miocene elements. *Protictitherium* and *Ursavus* are long ranging taxa. *Martes* also appears as such, but, as mentioned above, there are doubts to what extent the Miocene representatives can truly be attributed to the extant genus (Valenciano et al. 2022).

Discussion

Methodology

Similarities between localities and the early Vallesian chronofauna for the carnivorans from the Vallès-Penedès were calculated using the most complete fauna from the basin: Can Llobateres 1. Out of the four highest similarities found, three are from MN9 localities in the Vallès-Penedès (all >0.98), which indicates that Can Llobateres 1 is indeed a representative fauna for that time and region. However, some of the faunas from the basin in our analysis gave low similarities. This shows that we have to be careful with our interpretation of the maps, since particularly small faunas may show a similarity deviating from the overall pattern. Whereas the low similarities in the Vallès-Penedès can be considered a false negative, poor faunas in the Turolian and early Middle Miocene, particularly single occurrences, can lead to false positives. They appear like dots of high similarity in a region of low similarity. This is enhanced if the single occurrence happens to be a rarer element, even in larger assemblages such as the MN13 locality of Bazaleti. The relatively high number of deviant values is doubtlessly related to the general rarity of carnivorans in mammal assemblages. This enhances the effect of chance occurrences.

Although the carnivorans of Can Llobateres 1 are clearly representative of the early Vallesian fauna of the Vallès-Penedès, it is important to realise that they do not comprise the entire faunal community of the time and region. The chronofauna is clearly dominated by mustelids (Tab. 1, Fig. 2), but contains only one hyaenid, *Protictitherium*, and one felid, *Machairodus*. However, two more felids, *Styriofelis* and *Pseudaelurus,* and two more hyaenids, *Hyaenictitherium* and *Thalassictis*, were present in the early Vallesian of the Vallès-Penedès (e.g. Robles et al. 2013). As such, our analyses are partly influenced by the local conditions at Can Llobateres, and the similarities of localities containing these faunal elements would be higher when considering the Vallès-Penedès MN 9 carnivoran assemblage as a whole.

Biogeography

The Miocene is a period with large climatic changes, including the Mid Miocene Climatic Optimum, the Mid Miocene Cooling, and the increased seasonality in the Late Miocene (Zachos et al. 2001; van Dam 1997; Steinthorsdottir et al. 2021). Together with large-scale geographic changes, such as the closing of the Mediterranean and the gradual retreat of the Parathetys, these climatic events resulted in the shift of the distribution of mammals. Pickford and Morales (1994) already noted that changes in faunal similarity are connected to latitudinal shifting of zoogeographic realms. The southward trend of the area of highest diversity through the Middle and early Late Miocene, as suggested by Madern and Van den Hoek Ostende (2015), might represent the shifting of the border between two such realms. The Iberian Peninsula was open and arid during the Middle Miocene (Meulen and Daams 1992; Maridet and Costeur 2010), a situation that started to change towards the beginning of the Late Miocene. According to Van der Meulen and Daams (1992), humidity started to increase at the end of the Aragonian towards the humid conditions of the early Vallesian. This is, for instance, clear from the reappearance of beavers in the inland basins of the Iberian Peninsula, and supported by palaeobotanical evidence (e.g. Barrón et al. 2010; Jiménez-Moreno et al. 2010).

MN7+8 sees a marked increase in similarity between the Iberian faunas and the chronofauna (Fig. 1d). As discussed above, the apparent low similarity in the Vallès-Penedès in the figure is a mapping artefact, the highest similarity of the unit actually being found in this basin. Morales et al. (2015) identified the late Aragonian as a period in which many carnivorans migrated to the Iberian Peninsula. Abella et al. (2014) linked the migration of the Ursidae into Iberia to these humid conditions and the dense forests of the early Vallesian. Indeed, Ailuridae and Ursidae enter only at the beginning of the Vallesian, with *Indarctos* being the only genus that remains after MN9. *Ursavus*, by contrast, is only present in Spain during MN9. As such, the taxon is a transient in the sense of Van der Meulen et al. (2005). However, it is not the only genus that only appears in MN9 in Spain. *Marcetia* and *Protursus* have a range restricted to MN9, the former even being known from Can Llobateres 1 only, the latter only appearing in Rudabánya in our dataset, and recently identified in Hammerschmiede (Kargopoulos et al. 2022). Like *Ursavus*, possibly amphicyonid *Thaumastocyon* has a more northern occurrence before entering Spain in MN9 and becomes extinct at the mid-Vallesian turnover. The mustelids *Sabadellictis,* and *Circamustela*, as well as the skunks *Promephitis* and *Mesomephitis*, have their first overall occurrence. Of these four, only *Sabadellictis* continues into the Spanish Turolian. *Circamustela* and *Promephitis* seem to retract their ranges to the north, although the latter continues in Spain in the late Vallesian. *Mesomephitis* is no longer found in Spain after MN9, and becomes extinct at the beginning of the Turolian. As such, *Circamustela*, *Promephitis* and *Mesomephitis* should also be considered Vallesian transient taxa on the Iberian Peninsula

All in all, the Vallesian turnover event for the carnivorans is an amalgamation of Aragonian relics, an influx of new taxa in late MN7+8/early MN9, combined with extinctions in MN9 (Fig. 1e; Casanovas et al. 2010; Morales et al. 2015). The build-up of the chronofauna on the Iberian Peninsula was apparently gradual, with two elements being present in MN4, one entering in MN5, one in MN6 and three in MN7+8 (Fig. 2). However, the time of entrance of *Thaumastocyon* is uncertain because of the lack of latest Middle Miocene records both inside and outside the Iberian Peninsula.

We also noted that the chronofauna lacks two hyaenids and two felids that are present in other early Vallesian localities in the basin. Of these, *Hyaenictitherium* is indeed an MN7+8 immigrant, whereas the other hyaenid, *Thalissictis*, enters only in MN9. Both genera continue into the Turolian. By contrast, the two felids are long-term residents on the Iberian Peninsula and were already present in the early Aragonian. Neither survives into the Turolian, *Pseudaelurus* having its last Iberian record in MN9 and *Styriofelis* in MN10 (Robles et al. 2013).

Conclusions

Plotting the similarity of carnivoran assemblages to that of our MN9 reference fauna, Can Llobateres 1, reveals a southward trend with the highest similarities in the Middle Miocene, accumulating in Spain in the early Vallesian, followed by a collapse in MN10. Whereas our study confirms the plotting of Raup-Crick values as a valuable tool for recognising patterns, it also shows the importance of looking behind the data. Anomalies in the pattern can be as important as the pattern itself. Although many of these anomalies are, even after filtering, the result of single occurrences or small sample sizes, larger assemblages may not fit the pattern. In our case, this could in part be traced back to some of the early Vallesian genera from the Vallès-Penedès not appearing in the reference fauna, namely the hyaenids *Hyaenictitherium* and *Thalassictis*, and the felids *Pseudaelurus* and *Styriofelis*. A second caveat that became clear from our analyses, is that high similarity may be obscured on the map, stressing the importance of looking beyond the visualisation and considering the data itself.

The stratigraphic ranges of the individual elements of the chronofauna show that older elements entered Spain gradually throughout the Middle Miocene. Their earlier presence at higher latitudes accounts for the higher similarities being found to the north of the Iberian Peninsula. The early Vallesian sees an increased influx of northern elements, the most notable of which are the bears, in line with the forested, humid conditions of the period. At the same time, new elements arrive, including the Mephitidae and Machairodontines.

The extinction of several lineages in the chronofauna, including the mustelids bearing the heaviest of the loads, marks the end of MN9 as a true turnover. However, a number of genera appear to be Vallesian transients, only appearing in Spain at a time when conditions were optimal, but retracting their ranges to the north afterwards.

To sum up, the early Vallesian carnivoran community of the Vallès-Penedès is an amalgamation of varying signals. It is a culmination of Middle Miocene elements entering Spain at various times, combined with new elements and northern taxa making a temporary appearance on the Iberian Peninsula. The optimal conditions in the basin led to a short-lived, real biodiversity hotspot. The role of the transient taxa certainly has bearing on the discussion about the range and extent of the 'Vallesian Crisis', as their disappearance from Spain enhanced the regional signal. The carnivorans thus emphasise the unique conditions of the early Vallesian in its type area.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12549-023-00588-w.

Acknowledgements We thank the teams of the NOW database, its contributors and coordinators, as well as David Harper and Øyvind Hammer for their help with the analyses, together with our colleagues Salvador Moyà Solà and David M. Alba. We express gratitude to Rutger van den Hoek Ostende, who assisted in making Fig. 2, and Marianne Dillen, Luc Rongen, Ruud van Hirtum and Adwin van Gerven for their overall support and encouragement. The comments provided by Juan Abella and Michael Morlo as reviewers helped improve not only our paper, but also provided an update for the NOW database, for both of which we are thankful.

Funding This article is part of the R+D+I project PID2020-117289GB-I00, funded by the Agencia Estatal de Investigación of the Spanish Ministerio de Ciencia e Innovación (MCIN/AEI /10.13039/501100011033/), and has also been supported by the Agència de Gestió d'Ajuts Universitaris i de Recerca of the Generalitat de Catalunya (2001 SGR 00620) and the Generalitat de Catalunya/CERCA Programme.

Data availability My manuscript has data included as electronic supplementary material.

Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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