

Patterns of relative abundance among large Carnivora in western Eurasia during the Plio-Pleistocene

Otto Oksanen

Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland

ABSTRACT

Background: The present-day Carnivora metacommunity in western Eurasia is functionally impoverished of large hypercarnivores (animals that only eat vertebrate tissues). The interplay of climate change and interspecific competition in the decline of large hypercarnivores during the Plio-Pleistocene is not well understood. I estimated relative abundance trajectories for Plio-Pleistocene Canidae, Felidae, and Hyaenidae to infer competitive relationships within the families. I further examined how the family-level patterns influenced the proportion of hypercarnivores in the fossil metacommunity over time.

Data: Presence/absence data of Carnivora (>7 kg) belonging to the families Canidae, Felidae, Hyaenidae, and Ursidae from 124 fossil localities. The fossil localities were sampled within six temporal intervals, spanning the Pliocene up to the beginning of the Late Pleistocene. The intervals track long-term changes in global and regional climate. The study area included Europe, Anatolia, Caucasus, and the Levant.

Methods: Relative locality coverage (occupancy) within a sample was used as a proxy for relative abundance for individual taxa. For the community metrics, taxa were classified as hypercarnivores based on the morphology of the lower first molar.

Conclusions: The results indicate differences in coexistence potential within the different families. Large felids, including both sabre-toothed and conical-toothed forms, tend to have broadly overlapping occupancy trajectories. The occupancy trajectories of large bone-cracking hyaenids overlap less extensively, being generally restricted to only one common taxon at a time. The occupancy trajectories in the Canidae seem to be almost independent of each other. At the community level, both the number of common taxa and the proportion of hypercarnivores among them increased from the Pliocene to the Early Pleistocene. This trend reversed again during the Middle Pleistocene. The most common Middle Pleistocene taxa mainly belonged to different families, emphasizing their ecological differences in seasonally cold environments.

Keywords: Carnivora, climate, competition, hypercarnivore, metacommunity, Pleistocene, Pliocene, relative abundance.

Correspondence: O. Oksanen, Department of Geosciences and Geography, University of Helsinki, 00014 Helsinki, Finland. email: otto.oksanen@helsinki.fi

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INTRODUCTION

The present-day large Carnivora in western Eurasia are scarce due to Late Pleistocene extinctions (Dalerum *et al.*, 2009) and Holocene range contractions (Wolf and Ripple, 2017). This is especially the case for large hypercarnivores such as felids, the decline of which since the Late Pleistocene has been linked to modern humans (Johnson, 2002; Sandom *et al.*, 2018). In addition, the role of climate change in structuring Carnivora communities over time is not well understood. Changes in species distributions can affect biotic interactions, which in turn can alter community structure and ecosystem processes (Barton and Schmitz, 2009; Nogués-Bravo and Rahbek, 2011). Such mechanisms have been proposed as causes for Early and Middle Pleistocene changes in the large Carnivora in Europe (Turner and Antón, 1998; Raia *et al.*, 2007; Turner, 2009), before modern humans appeared. Other hominins, represented by Neanderthals and their close relatives, became widespread in Europe during the Middle Pleistocene (Roebroeks, 2001). Therefore, comparisons between these earlier changes and the more recent changes in the Carnivora are not simply comparing scenarios with vs. without humans.

Plio-Pleistocene changes in the diversity of large Carnivora in western Eurasia have previously been well-established (Turner, 1992; Raia *et al.*, 2007; Rodríguez *et al.*, 2012). However, there is uncertainty regarding the proportion of large hypercarnivores in the fossil metacommunity as a result of climate change. One way to address this is to examine changes in the relative abundance of individual taxa over time, which have not been studied at the metacommunity level. They provide a measure of evenness of abundance (Blois *et al.*, 2010), which should allow a more complete picture of community change when combined with functional traits.

Since abundance is difficult to estimate directly in the fossil record, I will use relative locality coverage (occupancy) as its proxy (Jernvall and Fortelius, 2002, 2004; Carotenuto *et al.*, 2010). Occupancy has previously been applied to Neogene herbivores (Jernvall and Fortelius, 2002), which, together with mean hypsodonty, showed that changes in herbivore community structure mainly involved common genera. The underlying process was interpreted not as *in-situ* evolution, but as habitat-tracking of species that were better adapted to utilize structurally demanding plant resources, which became more abundant as climate change occurred (Fortelius *et al.*, 2014). A similar process should also apply to Carnivora, albeit more indirectly because meat should always be available but the types of prey can influence the number and characteristics of coexisting predators.

An important aspect of occupancy is that individual taxa tend to have a single peak in their relative abundance, during which they are most widespread and abundant (Jernvall and Fortelius, 2004; Carotenuto *et al.*, 2010; Fortelius *et al.*, 2014). Recently, the occupancy peak was associated more with competition, whereas extinction was associated more with environmental change (Žliobaitė *et al.*, 2017). This may be especially relevant for Carnivora because aggressive interspecific competition (Palomares and Caro, 1999; Donadio and Buskirk, 2006) is a major potential limiting factor that can lead to local extinction (Carbone *et al.*, 2005a). Competitive interactions in the fossil record have not been the focus of previous studies on occupancy but here I will make inferences by comparing occupancy trajectories of individual taxa. This is similar in principle to comparing patterns of differential survival between taxa in the fossil record (Benton, 1987; Van Valkenburgh, 1999). This approach is of course more plausible for fossil taxa which have modern analogues because apparent patterns of replacement in the fossil record can also occur independently (Benton, 1987).

In this study, I will estimate occupancy of large Carnivora in western Eurasia to investigate changes in metacommunity structure in relation to climate change from the Pliocene until the beginning of the Late Pleistocene, with a particular focus on hypercarnivores. First, I will provide an overview of all well-studied families that include hypercarnivores (Canidae, Felidae, and Hyaenidae) in the study area based on the occupancy trajectories of individual taxa. I will

then summarize how the family-level patterns influence the proportion of hypercarnivores at the metacommunity level based on the morphology of the lower carnassial tooth, combining taxon-based and trait-based approaches.

MATERIALS AND METHODS

Study area and fossil localities

This study covers a total of 124 fossil localities across Europe, Anatolia, Caucasus, and the Levant (Fig. 1). Most of them are well-known reference localities that have been featured in previous overviews of the fossil record in the study area (e.g. Koenigswald and Heinrich, 1999; Van Kolfschoten, 2002; Rook and Martínez-Navarro, 2010; Kahlke *et al.*, 2011). Species lists for the localities were extracted from the NOW database (2020), supplemented by literature. Localities without definitive records of large Carnivora (Canidae, Felidae, Hyaenidae, and Ursidae) were excluded. The list of localities, their species lists, and references are available at evolutionary-ecology.com/data/3234Appendix.pdf.

I sorted the localities into six temporal intervals (Table 1), numbered from the oldest to the youngest. The intervals become shorter towards the present, but they remain coarse enough to include a sample of localities that are dated with different methods, ranging from absolute dates to mammalian biochronology. The purpose of the intervals is to track large-scale changes in global and regional climate, which are correlated with well-established chronostratigraphic markers in the fossil record.

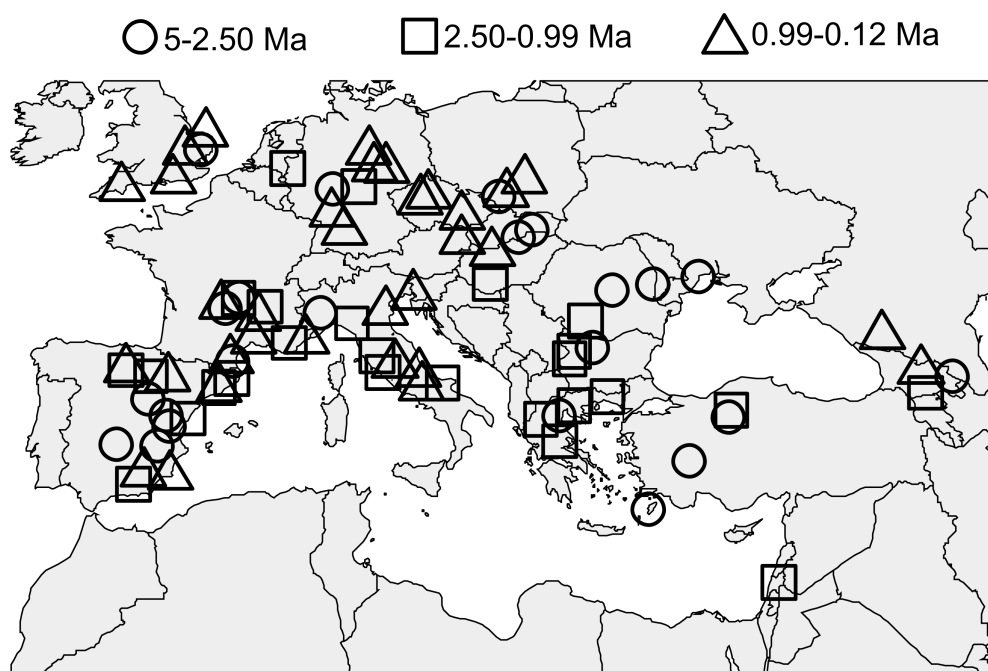


Fig. 1. Study area and the spatial extent of fossil localities included in the study. The localities are grouped within three coarse time intervals to show how different areas are represented in the fossil record over time. Some localities with overlapping coordinates were removed.

Table 1. The time intervals used for the sampling of fossil localities, and their temporal coverage

Interval	No. of localities	Time boundaries (Ma)	Duration (Ma)
1	12	5.00–3.55	1.45
2	12	3.55–2.50	1.05
3	25	2.50–1.80	0.70
4	16	1.80–0.99	0.81
5	31	0.99–0.42	0.57
6	28	0.42–0.12	0.30

The first two intervals are based on the MN 15 and MN 16 European Land Mammal Zones, respectively (time intervals as they are in the NOW database). Together they represent the Pliocene Series, which, for the most part, was considerably warmer than today with a weaker latitudinal gradient (Utescher *et al.*, 2000; Brierley *et al.*, 2009; Salzmann *et al.*, 2011). Reconstructed biomes for the Piacenzian Stage suggest a predominance of warm-temperate mixed forests throughout most of Europe (Salzmann *et al.*, 2011). More open and drier conditions occurred in the southeast Iberian Peninsula and parts of Anatolia (Salzmann *et al.*, 2011). Similar vegetational zonation had already been established since the beginning of the Pliocene, at least in the western Mediterranean area (Suc *et al.*, 1995; Fauquette *et al.*, 1999). Climatic cooling led to the impoverishment of subtropical tree taxa close to the Plio-Pleistocene boundary in northwest Europe (Donders *et al.*, 2007), while Mediterranean xerophytes became more abundant in the northwest Mediterranean province (Suc *et al.*, 1995). These environmental changes are assumed to partly overlap with MN 16, or alternatively, with the Early Villafranchian large mammal localities (Rook and Martínez-Navarro, 2010).

Interval 3 corresponds to the Gelasian Stage of the Early Pleistocene (Gibbard *et al.*, 2010; Head, 2019), chronostratigraphically constrained between the base of the Matuyama reverse magnetochron and the top of the Olduvai subchron. The climate of the Gelasian Stage was largely influenced by the establishment of permanent northern hemisphere glaciation, which fluctuated in size between cold glacial periods and relatively warm interglacial periods (e.g. Ravelo *et al.*, 2004; Mudelsee and Raymo, 2005). Vegetation changed along with the climate cycles, depending on latitude, altitude, and longitude. For example, a Late Pliocene pollen record from central Hungary indicates that the earliest glacials were marked by an expansion of boreal tree species (e.g. *Pinus*, *Picea*, *Betula*) at the expense of subtropical and temperate species (Willis *et al.*, 1999). Additional pollen records from Poland and the Netherlands suggest that non-arboreal plants, especially Ericaceae, also expanded during the glacial periods (e.g. Popescu *et al.*, 2010; Westerhoff *et al.*, 2020). Alternations between boreal and temperate forest elements also occurred in montane environments in the northwest Mediterranean province (Suc *et al.*, 1995). Low-altitude Mediterranean environments alternated between *Artemisia* steppes during glacials and deciduous forests during interglacials (Suc *et al.*, 1995). However, pronounced forest–steppe alternations mainly occurred close to a local humidity source in the generally warmer and drier southwest Mediterranean province (Suc *et al.*, 1995). The vegetation assemblages, especially the glacial ones, are consistent with increased seasonality in North Atlantic sea surface temperatures (SST) compared with the Pliocene (Hennissen *et al.*, 2015).

The remaining Pleistocene intervals are characterized by gradual changes in the global climate, which eventually led to longer and higher amplitude climate cycles (e.g. Ruddiman *et al.*, 1989;

Lisiecki and Raymo, 2007; Head and Gibbard, 2015). The changes in glacial–interglacial dynamics are linked to the Early–Middle Pleistocene Transition (EMPT), a complex state-shift in the global climate system around 1.4–0.4 million years (Ma) ago (Head and Gibbard, 2015). However, pronounced regional responses to climate change had already occurred before the onset of the EMPT, close to the Gelasian–Calabrian boundary.

The first major changes occurred about 2 Ma ago when modern thermocline conditions appeared in tropical and subtropical upwelling areas of the Atlantic and Pacific Oceans (Ravelo *et al.*, 2004). This seems to have roughly coincided with higher amplitude fluctuations in Mediterranean SST estimates compared with early Gelasian times (Herbert *et al.*, 2015). The changes in Mediterranean SSTs might reflect increased climate sensitivity (Herbert *et al.*, 2015), which was possibly influenced by enhanced long-distance teleconnections after 2 Ma ago (Ravelo *et al.*, 2004). Furthermore, during this time Mediterranean SST estimates fell to consistently lower values even during interglacials (Herbert *et al.*, 2015), suggesting a step towards present-day climatic conditions. This is corroborated by Gelasian pollen records from southern Italy, which indicate declining winter temperatures during younger interglacials, although they remained consistently warmer and more humid than they are today (Klotz *et al.*, 2006). As a result, subtropical trees (e.g. Taxodiaceae) survived during low-latitude interglacials in southern and southeast Europe until about 1 Ma ago (Suc *et al.*, 1995; Suc and Popescu, 2005). The changes in interglacial seasonality, along with the early stages of the EMPT, provide climatic context for Interval 4.

The later portion of the EMPT (Interval 5) is characterized by the switch from 41,000 year glacial–interglacial cycles to 100,000 year cycles around 0.9 Ma ago (e.g. Head and Gibbard, 2015). In addition to the onset of longer and colder glacials, this interval was also the time during which modern plant communities developed throughout Europe during subsequent interglacials (Tzedakis *et al.*, 2006). The EMPT culminated in the final amplification of the glacial–interglacial cycles, referred to as the Mid-Brunhes Event at the end of MIS 12 (Head and Gibbard, 2015). MIS 12, regionally correlated with the Elsterian or Anglian glacial, was a particularly harsh glacial stage, during which extensive continental glaciers formed prominent glaciogenic deposits in central and northwest Europe (e.g. Pawley *et al.*, 2008; Lauer and Weiss, 2018). The Elsterian/Anglian deposits provide regional chronostratigraphic markers for the end of the EMPT, as well as for Interval 5.

Interval 6 represents the aftermath of the EMPT, from MIS 11 until the Eemian interglacial (MIS 5e). This interval documents iterative faunal exchange of large mammal taxa that were better adapted to either glacial or interglacial habitats, which alternated between the climate cycles (Koenigswald, 2011). However, this faunal exchange was less pronounced in the areas south of the Alps and Pyrenees, which provided refugia for the interglacial mammals as the climate became more continental in central and northwest Europe (Koenigswald, 2011). From a temporal perspective, the upper boundary of this interval precedes not only the beginning of Late Pleistocene large mammal extinctions, but also the expansion of modern humans in the study area (e.g. Stuart and Lister, 2012). So modern humans are effectively ruled out as potential agents of faunal change for the timespan of the present study.

Relative locality coverage (occupancy) and taxonomic units of analysis of Carnivora included in this study

Following Jernvall and Fortelius (2002, 2004), I used ‘the number of localities where a taxon is present divided by the total number of localities in the sample’ as a proxy for occupancy over time. I analysed occupancy for all Canidae, Felidae, Hyaenidae, and Ursidae >7 kg, following

Van Valkenburgh (1989). The taxonomic units of analysis within these families are variable, yet consistent in terms of what species and genera they contain throughout all the samples. The units are – in a broad sense – groups of closely related taxa that resemble each other morphologically more than members of other units. Their purpose is to provide long-term estimates of the relative abundance of distinct, relatively monotypic forms (i.e. morphotaxa) in the metacommunity.

The morphotaxa are inclusive enough to encompass occasional nomenclatural inconsistencies in the literature and accommodate gradual evolutionary changes that might take place within a timespan of over 4 Ma. They do not, however, assume explicit ancestor–descendant relationships; they are in many cases unclear and beyond the scope of this study. In general, most of the morphotaxa are straightforward in the sense that they include species that are referred to the same genus. However, there are species that either lack taxonomic consensus at the genus level or differ considerably from other members of the same genus which overlap both spatially and temporally. These are here grouped together as morphogenera and morphospecies, respectively.

The morphogenera in this study correspond to large hypercarnivorous canids that formed a so-called *Xenocyon* clade in a previous cladistic analysis (Tedford *et al.*, 2009). These include the extant *Cuon alpinus* (dhole) and *Lycaon pictus* (African wild dog), as well as their fossil relatives. However, the evolutionary relationships within this clade are unclear (see Wang *et al.*, 2015 and references therein). This is reflected in particular in the taxonomy of Early Pleistocene representatives of this clade, *Canis falconeri* and *Xenocyon lycaonoides*, placed in separate genera by Tedford *et al.* (2009). Both species are occasionally referred to a subgenus of *Canis* (e.g. Sotnikova, 2001), or to the genus *Xenocyon* (e.g. Petrucci *et al.*, 2012) or *Lycaon* (Martínez-Navarro and Rook, 2003). In this study, I group together the fossil occurrences of these canids with fossil *Cuon*, for relative locality coverage. They have limited spatial and temporal overlap with each other, providing a taxonomically conservative estimate of the relative abundance of hypercarnivorous canids in the study area over time.

The morphospecies in this study belong to two genera from different families: *Panthera* (Felidae) and *Ursus* (Ursidae). These genera tend to have relatively high interspecific variation in body size and, to some extent, in craniodental morphology. Body size is a fundamental functional trait for Carnivora and vertebrates in general. For example, it scales with range size (e.g. Gittleman and Harvey, 1982; Carbone *et al.*, 2005b; Tamburello *et al.*, 2015), prey size (e.g. Rosenzweig, 1966; MacArthur, 1972, pp. 65–68; Gittleman, 1985), and fasting endurance (Lindstedt and Boyce, 1985). The morphospecies included here (see below) are not necessarily species in a phyletic sense because fossil material of Carnivora tends to be scarce and fragmentary, thus limited in diagnostic features. They are, however, expected to reflect the size of the animal in question.

The smallest Pleistocene pantherines in Europe are referred to the extant leopard (*Panthera pardus*). A medium-sized pantherine, the so-called European jaguar is usually referred to *Panthera gombaszoegensis* (O'Regan and Turner, 2004), but it is occasionally considered as a fossil subspecies of the extant jaguar, *Panthera onca* (e.g. Hemmer *et al.*, 2001). These are here considered as *Panthera gombaszoegensis s.l.* *Panthera gombaszoegensis* was roughly the size of a large jaguar, the largest individuals being comparable in size to female lions (O'Regan and Turner, 2004). The largest members of the genus *Panthera* are represented by animals closely related to the extant lion (*Panthera leo*). Although these Pleistocene lions are often referred to the extant species in the literature, they are evolutionarily distinct from modern lions based on ancient DNA (Burger *et al.*, 2004; Barnett *et al.*, 2016; Stanton *et al.*, 2020). This supports species-level separation of Pleistocene lions from modern lions. Their intra-clade taxonomic status is unclear, however, because some of the Middle Pleistocene specimens in Europe are occasionally referred to *Panthera fossilis* (e.g. Barnett *et al.*, 2016), whereas *Panthera spelaea* is commonly used for Late Pleistocene specimens. They are all considered here as *Panthera spelaea s.l.* More

importantly, the Pleistocene lions in western Eurasia were on average considerably larger than extant lions (e.g. Kurtén, 1968, pp. 85–87; Lewis *et al.*, 2010).

In the case of *Ursus*, I analysed occupancy separately for relatively small, black-bear-sized forms (*Ursus minimus* and *U. thibetanus*), larger generalized forms (*Ursus etruscus* and *Ursus arctos*), and the herbivorous cave bears, including *U. deningeri* and *U. spelaeus* (Kurtén, 1968, pp. 124–125; Mazza and Rustioni, 1994; Bocherens, 2015; van Heteren *et al.*, 2019; Pérez-Ramos *et al.*, 2020). The taxonomy follows Mazza and Rustioni (1994).

Hypercarnivorous phenotypes in fossil Carnivora

Compared with many other mammalian orders, members of the order Carnivora tend to have a highly differentiated post-canine tooth row in which certain teeth have a specific masticatory function, including slicing, crushing, and grinding (Ewer, 1973; Van Valkenburgh, 1989). The primary slicing apparatus is formed by the carnassial teeth: the fourth upper premolar and the first lower molar. The molars behind the carnassials are the main crushing and grinding teeth in relatively unspecialized, mesocarnivorous taxa (Van Valkenburgh, 2007). Relatively high heterodonty in Carnivora provides a versatile toolkit for processing food items with different structural properties, which is beneficial for species with flexible diets. At the macroevolutionary scale, heterodonty also provided a flexible template for dietary specialization within the order. As a result, many extant and extinct species deviated from the more generalized carnivore tooth row during their evolution, emphasizing one masticatory function over others (e.g. Ewer, 1973; Martin, 1989; Van Valkenburgh, 2007). Particularly contrasting functional trade-offs occurred between hypercarnivores (vertebrate specialists) on the one hand and plant-dominated omnivores on the other hand. The latter expanded the crushing/grinding surfaces of their molars at the expense of the carnassial blades (Ewer, 1973; Martin, 1989). Hypercarnivores in turn emphasized the slicing function of the carnassials, while the post-carnassial molars became reduced or disappeared completely (Ewer, 1973; Van Valkenburgh, 1989, 2007).

When only a single tooth is considered, the above-mentioned dietary adaptations are particularly well-reflected in the morphology of the lower carnassial (m1). Because of the interlocking nature of tooth occlusion, m1 is a dual-function tooth in relatively unspecialized Carnivora due to its position on the lower tooth row (Ewer, 1973, p. 36). The principal slicing crests are located anteriorly, formed by the paraconid and protoconid cusps on the trigonid, whereas the posterior cusps on the talonid form a crushing/grinding basin. Because these separate functional units are organized consistently, dietary specializations in extant and fossil Carnivora are inferable based on their relative proportions.

The relative length of the trigonid (i.e. relative blade length) of the m1 is a useful metric for distinguishing hypercarnivores from other Carnivora, both within and between different families (e.g. Van Valkenburgh, 1989; Friscia *et al.*, 2007). Hypercarnivores generally have a long trigonid relative to the talonid, characterized by a well-developed and elongated slicing blade. The elongation of the trigonid in hypercarnivores is associated with increased height difference between the trigonid and the talonid cusps (Crusafont-Pairó and Truyols-Santonja, 1956; Meloro and Raia, 2010). However, there are notable differences in how far hypercarnivorous dental adaptations have progressed between different families. The most derived hypercarnivores (e.g. felids) have almost, if not completely, eliminated the talonid of the m1 during their evolution. Other Carnivora tend to retain a functional talonid on the m1 (Fig. 2). In such groups, hypercarnivores are distinguished from more omnivorous species by a relatively elongated trigonid, an absent or reduced metaconid, and a trenchant talonid characterized by an enlarged and more centrally positioned hypoconid (Ewer, 1973, p. 41; Van Valkenburgh, 1991). All fossil Carnivora that have either of these two morphologies

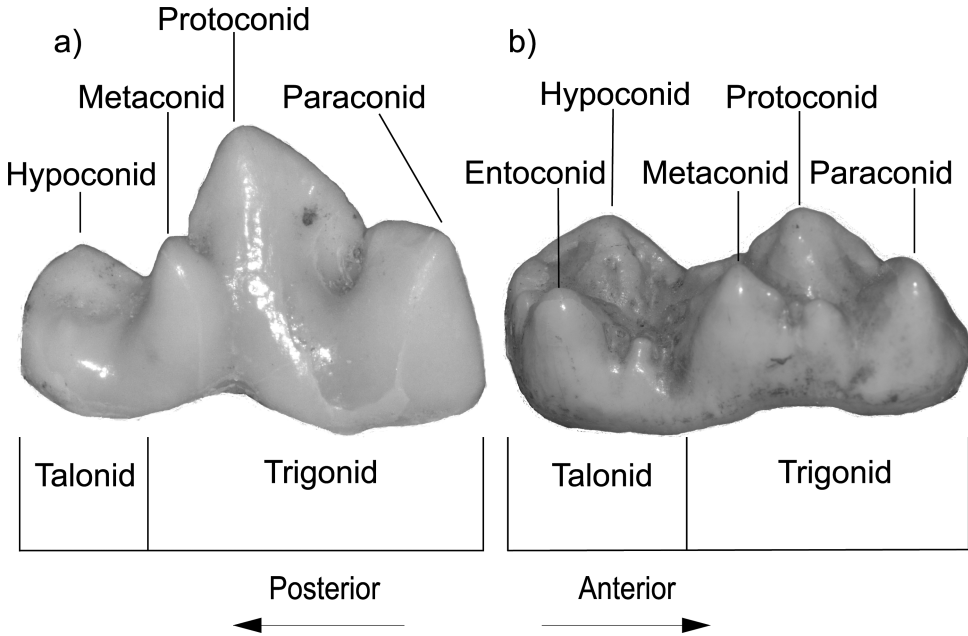


Fig. 2. Lingual view of the left lower carnassial tooth of (a) *Lycaon pictus*, a hypercarnivore and (b) *Ursus arctos*, an omnivore that eats mostly plants. Not to scale.

are here considered hypercarnivores. In the Plio-Pleistocene of western Eurasia, these essentially include all felids and hyaenids, but only the *Xenocyon* clade in the Canidae.

RESULTS AND DISCUSSION

Felidae

The felids have been diverse and well-represented hypercarnivores in Eurasian large mammal communities since at least Late Miocene times. But the family underwent major taxonomic and ecological changes during the Plio-Pleistocene. At the forefront of these is the eventual extinction of sabre-toothed forms belonging to the subfamily Machairodontinae. Almost exclusively they represented large felids for millions of years, but the situation changed during the Pliocene with the emergence of large-sized relatives of modern conical-toothed felids (Werdelin *et al.*, 2010). Interestingly, according to Werdelin *et al.* (2010), abundance data from some African fossil sites could indicate that machairodonts had a competitive advantage in some palaeoenvironmental settings. However, the competitive relationships between Machairodontinae and Felinae, and the felid guild as a whole, are poorly understood. This is especially so in Eurasia, where machairodonts disappeared later than in Africa (Turner and Antón, 1998).

There is evidence of a long coexistence between Machairodontinae and Felinae in the occupancy trajectories of individual taxa (Fig. 3), which show considerable overlap. There is no clear dichotomy between machairodonts (*Homotherium* and *Megantereon*) and other felids. In fact, the whole felid guild seems to have expanded during the Late Pliocene (Interval 2) and Early Pleistocene (Intervals 3 and 4), past the Plio-Pleistocene transition. Nevertheless, there

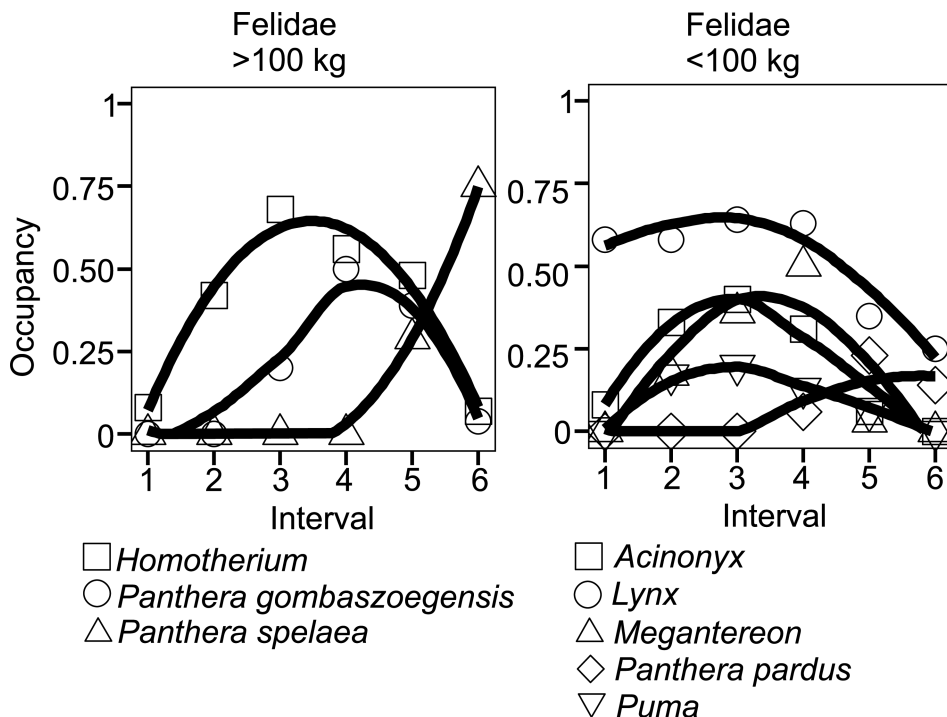


Fig. 3. Occupancy trajectories of Plio-Pleistocene Felidae in western Eurasia from the Early Pliocene (Interval 1) to late Middle Pleistocene and the Eemian interglacial (Interval 6). The occupancy trajectories are local regression (LOESS) curves (span = 1), calculated with the `geom_smooth` function of the R package `ggplot2`.

are interesting differences in the occupancy trajectories, which indicate that the felids responded individually to environmental changes.

The individual taxa tend to peak at different times, indicating an asynchronous end to their expansion (Žliobaitė *et al.*, 2017). And those taxa that do peak at the same interval share some similarities. For example, both *Homotherium* and *Acinonyx* peak during the Gelasian Stage of the Early Pleistocene (Interval 3 in Fig. 3). Both are, in their own way, relatively cursorial felids (Antón *et al.*, 2005; Hemmer *et al.*, 2011), suggesting an affinity for open areas. *Megantereon*, which was likely ill-suited for chasing prey over long distances – based on its relatively short, stocky limbs (Christiansen and Adolfsen, 2007) – peaks later. This is also the case with fossil representatives of *Panthera*, whose extant relatives tend to emphasize strength over speed and jumping ability in their postcranial morphology (Gonyea, 1976; Morales and Giannini, 2013; Polly, 2020). Apart from these differences, the broadly overlapping occupancy trajectories, and relatively gradually declining occupancy after the peak in most felid taxa (Fig. 3), suggest that these felids were buffered ecologically against competitive exclusion.

There is a potentially interesting relationship between the body size of the felid and its occupancy value. The size cut-off at 100 kg in Fig. 3 is arbitrary and is done for visualization purposes, for there certainly was size overlap between many of the felid taxa even across these two size categories, especially between *Acinonyx*, *Megantereon*, and *Panthera gombaszoegensis*.

Acinonyx was represented exclusively by the extinct *A. pardinensis*, which was considerably larger than the extant *A. jubatus*, large males weighing close to 100 kg (Hemmer *et al.*, 2011; Cherin *et al.*, 2014). *Megantereon* was the size of a large leopard or jaguar based on body mass estimates (Christiansen and Adolfsen, 2007). But, it would appear that both the largest (*Homotherium* and later *Panthera spelaea*) and the smallest felids (*Lynx*) have consistently higher occupancies compared with all other felids. This result can be linked to interspecific competition: the largest animals at the top of the dominance hierarchy have fewer enemies and are therefore relatively free to expand to new areas if environmental conditions are suitable for them. On the other hand, *Lynx* can mitigate competition with larger felids by being better able to persist on relatively small prey (e.g. lagomorphs). Overall, the results for felids resemble the case of diffuse competition, where multiple species are more likely to outcompete another species (MacArthur, 1972, p. 29). Furthermore, in a functionally similar group of single-resource specialists, where size is one of the most important functional traits in niche differentiation (e.g. Rosenzweig, 1966; Sicuro and Oliveira, 2011), persistence of species that are intermediate in size compared with others is difficult (MacArthur, 1972, pp. 44–45). Here, *Puma* and later *Panthera pardus* seem to have ended up in that role.

One major pattern in the felid occupancy trajectories stands out towards the Middle Pleistocene: *Panthera* is the only genus with a continuously rising occupancy trend after its first appearance during the Gelasian Stage. Part of this success no doubt stems from the high interspecific variation in body size, therefore at least one species is more likely to occur in any given environment. However, the occupancy results show that the expansion of *Panthera* during the Pleistocene was driven by the largest species at the time because the leopard (*Panthera pardus*) has a comparatively low occupancy over time (Fig. 3). This is in line with previous occupancy studies with fossil mammals, according to which the expansion of a genus generally involves a few wide-ranging species (Jernvall and Fortelius, 2004), which also tend to be relatively large (Carotenuto *et al.*, 2010). Although variable in size due to high sexual dimorphism (O'Regan and Turner, 2004), *P. gombaszoegensis*, the most frequent Early Pleistocene pantherine, was already one of the largest felids in western Eurasia. However, the expansion of *Panthera* during the Middle Pleistocene was continued by Pleistocene lions (*P. spelaea*) gradually replacing the smaller *P. gombaszoegensis*. Pleistocene lions were also larger than *Homotherium*, which itself was comparable in size to extant lions (Antón *et al.*, 2005). The Early–Mid Pleistocene Transition (Interval 5 in Fig. 3) was a time during which these large felids coexisted to some extent. Gradual replacement is evident, however, for even though both *Homotherium* and *P. gombaszoegensis* still have a comparatively high occupancy (Fig. 3), *P. spelaea* surpassed them both at some localities based on specimen numbers. This is the case, for example, with the Middle Pleistocene locality of Vertésszölös 2 (Jánossy, 1986).

After the Mid-Brunhes Event (Interval 6), *Panthera spelaea* was essentially the sole dominant large felid predator. Although not extinct, *Homotherium* and *Panthera gombaszoegensis* were extremely rare (Fig. 3), which suggests little more than a marginal presence until their extinction. In fact, these major changes in the felid guild also involve other taxa. Apart from the increasing dominance of Pleistocene lions, all other felids either disappeared completely or became extremely rare during the Middle Pleistocene. Even *Lynx* declined considerably over time (Fig. 3), suggesting a severe contraction of the felid guild.

Hyaenidae

Compared with the felids, Plio-Pleistocene hyaenids not only have lower diversity, but they also demonstrate relatively rapid patterns of expansion and decline over time (Fig. 4). It is especially striking that the occupancy trajectory of *Pachycrocuta*, exclusively represented by the giant

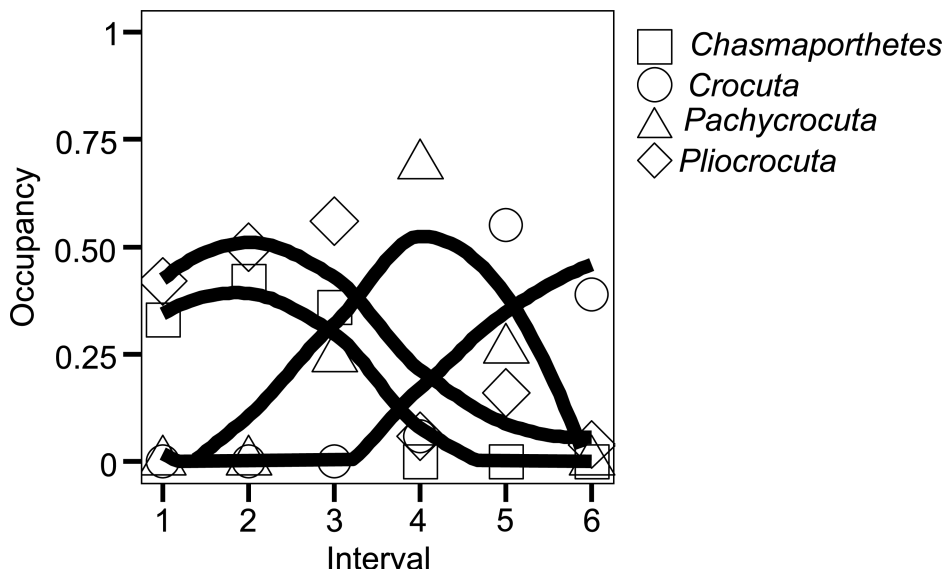


Fig. 4. Occupancy trajectories of Plio-Pleistocene Hyaenidae in western Eurasia from the Early Pliocene (Interval 1) to late Middle Pleistocene and the Eemian interglacial (Interval 6). The occupancy trajectories are local regression (LOESS) curves (span = 1), calculated with the `geom_smooth` function of the R package `ggplot2`.

Pachycrocuta brevirostris (Turner and Antón, 1996; Werdelin, 1999), shows the opposite trend compared with all other hyaenids. The opposite trajectories and the relatively low diversity in general indicate that coexistence potential in the Hyaenidae was very limited during this time, the reason for which is not yet clear.

Apart from the aardwolf (*Proteles*), all extant hyaenids are excellent scavengers, capable of utilizing vertebrate tissues better than all other extant Carnivora. They even consume the long bones of large ungulates. Yet, while bone is an important fallback food for these animals based on the feeding ecology of the spotted hyaena, *Crocuta crocuta* (Kruuk, 1972; Mills, 1990), meat is their preferred food item. Despite being able to thoroughly break and digest large bones, spotted hyaenas can ignore them completely during periods of high prey abundance (Kruuk, 1972, p. 73). The preference for meat enables a limited degree of niche partitioning based on active hunting and scavenging (Mills, 1990, p. 268). However, because modern large hyaenids are fundamentally scavengers, the niche partitioning between them is precarious because it depends on the degree of carcass utilization by individuals that kill their prey. That in turn depends on the abundance of scavengers relative to prey (Kruuk, 1972, p. 116).

Much like the modern large hyaenids, most of the fossil taxa in this study (*Pliocrocuta*, *Pachycrocuta*, and *Crocuta*) were also excellent bone-cracking hypercarnivores based on their ecomorphology (Turner *et al.*, 2008). *Chasmaporthetes*, on the other hand, likely killed its own prey more regularly based on its relatively trenchant cheek teeth, straight post-canine tooth row, and cursorial limbs (e.g. Kurtén, 1968, p. 68; Kurtén and Werdelin, 1988; Werdelin *et al.*, 1994; Antón *et al.*, 2006). This suggests that large hyaenids used to be more organized for niche partitioning on the hunting/scavenging spectrum. In support of this hypothesis, the occupancy trajectories of *Chasmaporthetes* and *Pliocrocuta* overlap extensively, although they peak at different intervals (Fig. 4). This

contrasts with the trajectories of Pleistocene bone-cracking hyaenids after the expansion of *Pachycrocuta* (Fig. 4). Typically, the record shows but one common hyaenid at a time, implying that the coexistence potential of large bone-cracking forms was very limited due to high niche overlap. The competitive advantage of efficient bone cracking is to gain access to additional nutrients that are mostly beyond the reach of other large predators, providing more options for a carnivore to persist and maintain a stable population in an environment with limited availability of prey. However, this advantage is compromised in the presence of another scavenger that has access to the same resources and can monopolize them due to larger size. My interpretation is supported by interactions of sympatric hyaenids in modern African ecosystems.

In the Serengeti plains, where *Crocuta crocuta* coexists with the smaller striped hyaena (*Hyaena hyaena*), Kruuk (1976) reported differences in habitat use between these species despite their overlapping geographic ranges. According to Kruuk (1976), *Crocuta*, the more common of the two, prefers open grasslands, whereas *Hyaena* mainly uses the more densely vegetated patches in the same area. *Hyaena* avoided *Crocuta* during most of their encounters, while the latter nearly always approached the former (Kruuk, 1976). Nevertheless, the two species were occasionally attracted to the same carcasses; in most instances, *Hyaena* was chased away by *Crocuta* before it could get any food (Kruuk, 1976).

Similar observations of spatial avoidance and interspecific aggression come from the Kalahari Desert, where *Crocuta* coexists with the brown hyaena (*Parahyaena brunnea*) (Mills, 1990). Generally, *Parahyaena* was almost invariably chased away by *Crocuta* whenever the two species met (Mills, 1990, pp. 265–267). A major difference to Serengeti, however, is that *Crocuta* is the less abundant of the two species in the Kalahari (Mills, 1990, p. 12), reducing the frequency of such antagonistic interactions. There, *Crocuta* mainly forages near riverbeds where large ungulates usually concentrate, while *Parahyaena* occurs more frequently in less productive dune habitats (Mills, 1990, p. 152). However, *Parahyaena* was more likely to discover a carcass first and eat uninterrupted in areas that were less frequented by *Crocuta* (Mills, 1990, pp. 261, 268). Overall, it seems that the smaller hyaenids are pushed into more marginal niches in areas of high *Crocuta* activity, where they are forced to eat more small food items, including small vertebrates, insects, and fruits (Kruuk, 1976; Mills, 1990).

The strongly antagonistic interactions in modern hyaenids suggest that the potential for the coexistence of bone-cracking hypercarnivores depends on the population density of the larger, more aggressive species. Applying that pattern to the Pleistocene of Eurasia, I suggest it is likely that *Crocuta* was lower down the dominance hierarchy than *Pachycrocuta*, which is in line with their opposite occupancy trajectories (Fig. 4). As a relatively large and robust carnivore, it would be difficult for *Crocuta* to establish and maintain a population in an area where access to carcasses is not guaranteed. Of course, possible differences in foraging group size can, to some extent, compensate for differences in individual body size during aggressive interactions. However, populations start small, which gives an advantage to the larger species. On the other hand, an initial decline in *Pachycrocuta* can provide a window of opportunity for *Crocuta*, as suggested by the Kalahari example above. The re-expansion of *Pliocrocuta* during the Middle Pleistocene (Turner *et al.*, 2008) is also interesting in this context, although this hyaenid was very rare when compared with *Crocuta* (Fig. 4).

Canidae

One of the most interesting aspects of the canid fossil record in western Eurasia is the ‘Wolf’ event (Sardella and Palombo, 2007). It was originally characterized by the first occurrence of the genus *Canis* in Europe, which was chronologically close to the old Plio-Pleistocene boundary (Azzaroli,

1983). Although we now know that the fossil record of *Canis* in Europe extends to the Pliocene (Sotnikova and Rook, 2010), the ‘Wolf’ event retains palaeoecological significance. It can represent a tipping point, after which *Canis* became almost ubiquitous in the fossil record (Interval 4 in Fig. 5). But how does the ‘Wolf’ event look in relation to other canids?

Despite the ‘Wolf’ event, the occupancy trajectories of *Canis* and the other canids, apart from the closely related *Eucyon*, appear to be quite independent of each other (Fig. 5). They either expand together with *Canis* (*Xenocyon*) or show no consistent decline over time (*Nyctereutes*). The rather marked extinction of *Nyctereutes* within Interval 3 (Fig. 5) is a major change, however, as it was one of the most common canids – perhaps the most common – before the ‘Wolf’ event. The competitive relationships between these canids are not well understood; perhaps they depended largely on local conditions, which is how some modern canids avoid competition with each other.

Niche differentiation among canids is relatively flexible because it not only incorporates differences in prey size, but also differences in the relative importance of different food items (Johnson *et al.*, 1996). These dietary differences can also relate to distinct habitat preferences. One example is the coexistence of jackals in East Africa (Kingdon, 1977; Johnson *et al.*, 1996). The side-striped jackal (*Canis adustus*) avoids encounters with other jackals by mostly frequenting areas of dense undergrowth. It is also the most omnivorous jackal; most of its diet is composed of insects and fruits (Kingdon, 1977, p. 25). A preference for dense vegetation has also been reported for the extant raccoon dog, *Nyctereutes procyonoides* (Kowalczyk and Zalewski, 2011; Drygala and Zoller, 2013), which has a flexible diet based on small vertebrates, invertebrates, and various plant parts (Hunter, 2011). In addition, there are also differences in the size of the lower second molar (m2) relative to m1 in extant and extinct *Nyctereutes* populations (Asahara and Takai, 2017). A relatively enlarged

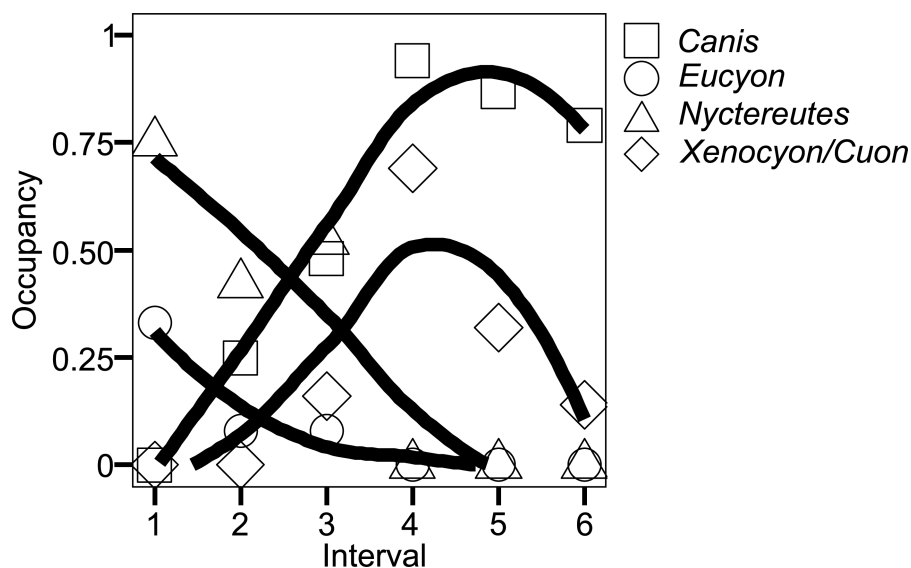


Fig. 5. Occupancy trajectories of Plio-Pleistocene Canidae in western Eurasia from the Early Pliocene (Interval 1) to late Middle Pleistocene and the Eemian interglacial (Interval 6). The occupancy trajectories are local regression (LOESS) curves (span = 1), calculated with the `geom_smooth` function of the R package `ggplot2`.

m2 is characteristic for regions where *Nyctereutes* individuals tend to include fewer vertebrates in their diet (Kauhala *et al.*, 1998).

Present-day raccoon dogs from the Honshu, Kyushu, and Shikoku islands of Japan tend to have a higher molar ratio than those from Hokkaido and continental Eurasia (Asahara and Takai, 2017). This finding is comparable with other omnivorous Carnivora, which tend to eat more meat in more seasonally cold environments (Vulla *et al.*, 2009). Interestingly, Pliocene and Pleistocene *Nyctereutes* specimens from Europe seem to have a comparable or slightly higher m2/m1 size ratio than the southern Japanese raccoon dogs (Asahara and Takai, 2017), suggesting a similar emphasis on invertebrates and plants in their diet. These comparisons can give context to the eventual replacement of *Nyctereutes* by *Canis* as one of the most frequent large canids as climate and biomes changed in western Eurasia. Increased seasonality during the Pleistocene likely limited the availability of invertebrates and edible plants, which, in turn, would have led to greater niche overlap with *Canis*.

The second half of the Early Pleistocene is also characterized by the expansion of the *Xenocyon* clade, whose members overlapped extensively, both geographically and temporally, with *Canis* (Sotnikova, 2001; Sotnikova and Rook, 2010). Both canids have relatively high occupancy during the early Calabrian Stage (Interval 4 in Fig. 5), although *Canis* has consistently higher values. *Canis* was also more common than *Xenocyon* based on specimen numbers at some localities, such as Untermassfeld (Kahlke and Gaudzinski, 2005) and Pirro Nord (Pavia *et al.*, 2012). Furthermore, the decline of the *Xenocyon* clade is also more extreme than that of *Canis* after its discernible peak during Interval 4 (Fig. 5). The decline coincided with the replacement of *Xenocyon* by fossil forms similar to modern *Cuon alpinus*, characterized by the most advanced dental adaptations to hypercarnivory (e.g. Tedford *et al.*, 2009; Petrucci *et al.*, 2012). This was accompanied by a size reduction from *Xenocyon* to *Cuon* [based on dental measurements (Petrucci *et al.*, 2012)]. *Canis*, on the other hand, shows the opposite trend as the grey wolf (*Canis lupus*) expanded to Europe during the late Middle Pleistocene. The early wolves of Europe were comparable in size to modern northern wolves (Flower and Schreve, 2014; Flower, 2016). Earlier Pleistocene *Canis* species (e.g. *C. etruscus* and *C. mosbachensis*) were invariably smaller (Flower and Schreve, 2014), roughly comparable to modern wolves in southern Asia and the Middle East (Kurtén, 1968, pp. 109–110; Sotnikova and Rook, 2010). The expansion of large wolves may have increased competition in the Canidae because both *Canis lupus* and *Cuon alpinus* depend on ungulate prey. However, *Canis lupus* still has a more flexible diet than *Cuon*, including more small prey and other food items during summer, while large ungulates are the mainstay during winter (Hunter, 2011). A relatively pronounced decline of the more specialized canids during the Middle Pleistocene reflects overall changes in the metacommunity structure of Carnivora in western Eurasia.

Patterns at the metacommunity level

Previous reviews (Barnosky, 2001; Liow *et al.*, 2011) established that the interplay of competition and environmental change in community evolution depends on the spatiotemporal scale of the analysis. This interplay has both advantages and challenges for interpreting the results of this study. Competition is only relevant in areas where the taxa in question are likely to co-occur and potentially interact with one another (Barnosky, 2001; Liow *et al.*, 2011). Such areas do not generally span entire continents (Barnosky, 2001), and that is also the case here. Competitive abilities of individual taxa in turn depend on local environmental conditions, which are likely to change more profoundly over larger spatial and temporal scales (Jablonski and Sepkoski, 1996; Barnosky, 2001; Jablonski, 2008). Taxon-specific responses to environmental change are informative in this context, but they are more easily identifiable at the millennial-scale temporal resolution of the Late Pleistocene

(Jablonski and Sepkoski, 1996). They are nevertheless also reflected here in the occupancy trajectories, but they manifest themselves in a more diffuse manner, such as in the tendency for individual taxa to peak asynchronously. Consequently, the metacommunity at a given time is composed of taxa at different phases of their trajectories; some are still expanding, whereas others, presumably, have already lost their competitive advantage. This arrangement recalls the incumbency effects discussed by Jablonski and Sepkoski (1996), where long-term persistence of community structure may depend on the ability of resident taxa to resist newly established invaders. The results of this study further suggest that some niches or guilds are more accommodating than others, influencing coexistence potential among ecologically similar taxa. Compare, for example, large cat-like hypercarnivores to hyaena-like bone-crackers.

How does the metacommunity of large Carnivora change over time in the background of all the waxing and waning of individual taxa? If the total diversity of different taxa present at a given time were considered, not much. However, when I exclude all the rare taxa, taxa which occur only in a few localities, a different picture emerges (Fig. 6).

After an initial increase from the Early Pliocene, the number of common taxa over time remained remarkably stable until the Middle Pleistocene (Fig. 6). The number of taxa that became extinct or rare during subsequent intervals was offset or exceeded by the number of new successful invaders. On the other hand, the distribution of dental functional traits in the community changed substantially, as shown by the proportion of hypercarnivores over time (Fig. 6).

Evidently, hypercarnivores increasingly dominated the metacommunity during the Early Pleistocene. Interestingly, this domination partly coincided with relatively high predator/prey ratios in regional Mediterranean faunas during the Early Pleistocene (Raia *et al.*, 2007; Rodríguez *et al.*, 2012). A combination of a high proportion of hypercarnivores and a relatively low prey diversity would inevitably mean limited options for prey partitioning among the predators. Therefore, competition intensity among the Carnivora must have been high. Rodríguez *et al.* (2012) came to a similar conclusion about prey size estimates for Early Pleistocene Carnivora in Europe. Low prey diversity does not necessarily indicate low abundance, however, as few especially abundant prey animals could have helped sustain the rich hypercarnivore component of the fauna. A present-day example is the Kruger National Park in South Africa, where most

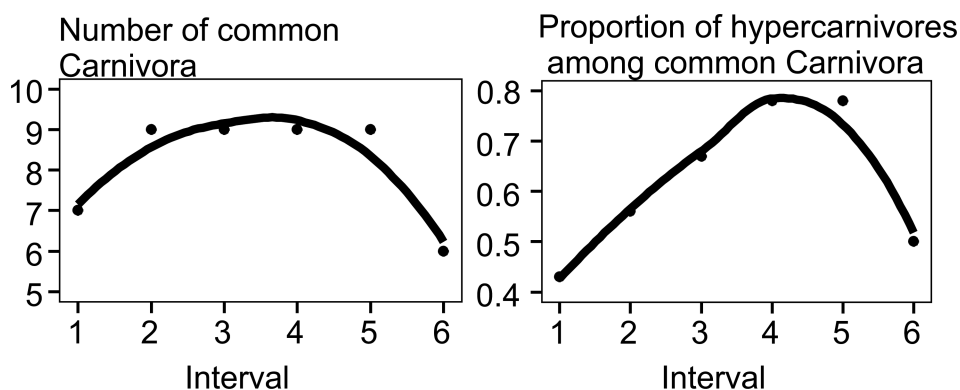


Fig. 6. The number of common Carnivora [occupancy ≥ 0.25 (following Jernvall and Fortelius, 2002)] and the proportion of hypercarnivores among them from the Early Pliocene (Interval 1) to late Middle Pleistocene and the Eemian interglacial (Interval 6). The trajectories are local regression (LOESS) curves (span = 1), calculated with the `geom_smooth` function of the R package `ggplot2`.

large Carnivora prey extensively on impala (*Aepyceros melampus*) despite having distinct prey preferences (Owen-Smith and Mills, 2008). Nevertheless, if similar conditions occurred in our study area during the Early Pleistocene, they did not remain stable in the long term. Both the number of common taxa and the proportion of hypercarnivores collapsed during the Middle Pleistocene (Fig. 6). At least for the Carnivora, this was already a step towards the modern impoverished fauna, which has prevailed since the Late Pleistocene megafaunal extinctions.

The decline of large hypercarnivores over time happened alongside a progressive increase in cold seasonality. This culminated with the appearance of modern interglacial plant communities in Europe during the Middle Pleistocene (Tzedakis *et al.*, 2006). Formerly widespread tree taxa that became extinct or relictual were generally less tolerant of cold winters than the ones that remain widespread today (Svenning, 2003). However, the changes in the proportion of hypercarnivores over time did not track climate in a straightforward way, as the number of common taxa and the proportion of hypercarnivores eventually returned to values more comparable to those of the Pliocene (Fig. 6). The Pliocene climate was drastically different from that of the Middle Pleistocene: warmer and less seasonal (e.g. Utescher *et al.*, 2000; Mosbrugger *et al.*, 2005; Hennissen *et al.*, 2015). This does not necessarily indicate that the decline of large hypercarnivores during the Pleistocene had nothing to do with climate change. On the contrary, from the perspective of resource availability, the development of the seasonality regime during the Pleistocene can potentially explain the non-linear changes in the Carnivora metacommunity structure.

Large hypercarnivores tend to spend a large proportion of their active time in search of prey that are similar in size or larger than them (Carbone *et al.*, 1999). Long-term persistence of a diverse hypercarnivore fauna would require that prey remain accessible enough to maintain the populations of all the individual taxa. Seasonality may be relevant here because ungulates, an important food source for most of the large hypercarnivores, can potentially accumulate more biomass in moderately seasonal climates. This seems to be the case in sub-Saharan Africa based on historical biomass estimates, which indicate that the total ungulate biomass, excluding elephants, is generally higher in areas where mean annual rainfall is between 500 and 1000 mm/year (Hempson *et al.*, 2015). The total ungulate biomass is comparatively less in both rainforests and semi-arid areas (Hempson *et al.*, 2015). Although it is unclear how ungulate biomass varies in temperate latitudes and how it did so in the past, ungulate biomass does not correlate linearly with climate. Of course, prey biomass alone does not guarantee resource availability for hypercarnivores: the prey must die.

The long-term shift from the warm Pliocene climate to the seasonally cold Middle Pleistocene climate likely caused greater annual contrasts in resource availability. Herbivores living in seasonally cold environments must build fat reserves during the relatively short growing season to survive the winter or else they must migrate. At the same time, the nutrient quality of plants tends to increase towards high latitudes (Guthrie, 1990, p. 264). Both diet quality and fasting endurance select for large body size in herbivores, especially in ruminants (Guthrie, 1990, p. 265; Geist, 1998, pp. 14, 30; Saarinen, 2014). A clear trend in Pleistocene herbivore community evolution in Europe is that some species which appeared after 1 Ma ago were considerably larger than their predecessors (e.g. Azzaroli *et al.*, 1988; Raia *et al.*, 2007; Meloro and Clauss, 2012). This is especially so for bovids (e.g. *Bison* and *Bos*) and some cervids, such as *Cervalces* (Azzaroli *et al.*, 1988). Therefore, a major proportion of total ungulate biomass may have been concentrated in very large prey. Larger herbivores tend to have fewer numbers of shared predators (Sinclair *et al.*, 2003; Owen-Smith and Mills, 2008) and should be more difficult to kill. This in turn could have increased resource stress for large hypercarnivores during the Middle Pleistocene, especially if smaller prey became seasonally scarce (e.g. due to migration).

Table 2. List of large Carnivora in western Eurasia during the late Middle Pleistocene and their occupancy values (the five most common taxa are in bold)

Family	Taxon	Occupancy
Canidae	<i>Canis</i>	0.79
Canidae	<i>Cuon</i>	0.14
Felidae	<i>Homotherium</i>	0.07
Felidae	<i>Lynx</i>	0.25
Felidae	<i>Panthera gambaszoegensis</i>	0.04
Felidae	<i>Panthera pardus</i>	0.14
Felidae	<i>Panthera spelaea</i>	0.75
Hyaenidae	<i>Crocuta</i>	0.39
Hyaenidae	<i>Pliocrocuta</i>	0.04
Ursidae	<i>Ursus arctos</i>	0.50
Ursidae	<i>Ursus deningeri/spelaeus</i>	0.46
Ursidae	<i>Ursus thibetanus</i>	0.11

What can the large Carnivora themselves tell us about their community structure in western Eurasia before the onset of the Late Pleistocene megafaunal extinctions? For one thing, at a regional scale, most of the common taxa were members of different families (Table 2). The ursids are the only exception, being relatively well-represented by the modern brown bear (*Ursus arctos*) and the extinct cave bear (*Ursus spelaeus*). They are also less carnivorous than all the other taxa. The community composition of Carnivora is in line with Hanski's (1982) core-satellite hypothesis, according to which regionally common and locally abundant taxa (i.e. core species) tend to be ecologically differentiated from each other. The relative dominance of ecologically distinct core species in the metacommunity suggests that interspecific competition is an important modifier of community structure (Hanski, 1982). In other words, competition militates against ecological similarity. The likely importance of competition in structuring the Middle Pleistocene carnivore community is corroborated by temporal variation in British Pleistocene wolves, which were both larger and more hypercarnivorous in the absence of *Crocuta* and *Panthera* (Flower and Schreve, 2014). Some previous authors (Turner, 1992; Rodríguez *et al.*, 2012) have implied that competition among Carnivora in Europe was reduced after some taxa disappeared during the Early and Middle Pleistocene. The conclusion based on the core-satellite hypothesis does not negate this interpretation but refines it. Competition does not operate independently from the environment. Instead, it should be more severe during times of resource shortage, promoting ecological differences between coexisting taxa. Thus, I propose that because of climate change, interspecific competition became more consequential during the Middle Pleistocene. Only the most resilient taxa remained relatively common in seasonally cold environments, characterized by a different combination of functional traits to fall back on as resources became scarce during winter.

CONCLUSION

The large Carnivora of western Eurasia underwent major taxonomic and ecological changes during the Plio-Pleistocene. Asynchronous peaks in the relative abundance of individual taxa suggest that they generally responded individually to long-term climate changes. As a result, the

fossil metacommunity at a given time was composed of taxa at different phases of their expansion and decline. Long-term community structure was likely influenced by the ability of resident taxa to resist competition from new invaders. Family-level patterns of relative abundance suggest that some families were more sensitive to interspecific competition than others, depending on their ecology. Large felids, including both sabre-toothed and conical-toothed forms, attained a particularly high diversity and relative abundance during the Early Pleistocene, as reflected in their broadly overlapping abundance trajectories. Abundance trajectories for large bone-cracking hyaenids tend to indicate the presence of only one relatively common taxon at a time, suggesting strongly antagonistic interactions similar to those of their living relatives in Africa. Abundance trajectories for the Canidae appear more independent than those of the other families.

At the metacommunity level, the number of common Carnivora and the proportion of hypercarnivores among them increased from the Pliocene to the Early Pleistocene. Both measures of community structure declined once again during the Middle Pleistocene, as the regional climate became seasonally colder. Furthermore, the most regionally common taxa were members of different families (apart from ursids). This indicates a strong role for interspecific competition among large hypercarnivores before the beginning of the Late Pleistocene megafaunal extinctions.

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