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Exploring paleo food-webs in the European Early and Middle Pleistocene: A network analysis

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ABSTRACT

Food webs are networks of feeding (trophic) interactions among species. As any other network approach, research on food webs focuses its analysis on the structure of direct and indirect interactions among diverse species, rather than looking at the particularities of certain taxa. In recent times, scholars have collected an impressive amount of empirical food-web data to study present day terrestrial and aquatic habitats.

More restrictively, this approach has also been applied to trophic interactions represented in the fossil record of extinct ecosystems. Nevertheless, to our knowledge, none of them has addressed the role played by the different Pleistocene hominin species as part of such food-webs. In this work, we aim at filling this gap by focusing on the Early and Middle Pleistocene paleo-communities in Western Eurasia. Our goal is to improve our understanding on changes experienced by large mammals' interactions during this period, and shed some light on the influence of and on *Homo* species of those changes.

We have constructed up to 27 paleo food-webs from the archaeo-paleontological record of European assemblages, covering from the Middle Villafranchian to the Late Galerian. Only large mammals have been considered, including a couple of *Homo* species that are present in 8 food-webs. Then, we have developed a two-steps analysis. First, we have calculated the main structural features of all the networks, and have compared them across geographical areas, periods and cases with and without *Homo* species. Second, we have calculated different structural centrality measures in order to assess the relevance of *Homo* species in their corresponding food-webs.

The obtained results show that the Pleistocene food webs under study shared basic features with modern food webs, although differences in the values of some parameters might be significant. Moreover, when comparing the networks across periods, we found a marked change that could be related to the Mid-Pleistocene Revolution. Finally, our results also highlight the trophic position of hominins in the web as a central species that channeled energy fluxes.

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1. Introduction

Food webs are networks of feeding (trophic) interactions among species (Cohen et al., 1990). As any other network approach, research on food webs focuses its analysis on the structure of direct and indirect interactions among diverse species, rather than looking at the particularities of certain taxa. In recent times, scholars have collected an impressive amount of empirical food-web data to

study present day terrestrial and aquatic habitats (Martínez, 1991; Williams and Martínez, 2000; Dunne et al., 2002; Stouffer et al., 2005; Pascual and Dunne, 2006; Brose et al., 2006). Moreover, there is an increasing literature on the construction of theoretical models of food-web structure to understand dynamics of ecological communities like, for instance, their robustness to the extinction of certain species or the introduction of new ones (Allesina et al., 2008; Stouffer and Bascompte, 2011; Stouffer et al., 2012; Capitán et al., 2013).

Beyond its application to study ecosystems *in vivo*, the 'food web approach' has also been used to study trophic relationships as represented in the fossil record of extinct ecosystems. Since the pioneering work by Dunne et al. (2008), which constructs and

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analyses paleo food-webs from extraordinarily well preserved Cambrian records, some authors have contributed other case studies (Maschner et al., 2009; Roopnarine and Hertog, 2010; Lotze et al., 2011), and guidelines on how to deal with methodological specificity of paleo food-webs (Roopnarine, 2009). Nevertheless, to our knowledge, none of these works have applied food-web analysis to the fossil record in order to address long-term ecological processes and, specifically, interactions of different *Homo* species with other animal taxa along the first steps of human evolution. The closest reference we have found, analyzes structural changes on seed-dispersal interactions related to the late Quaternary mega-faunal extinction in America (Pires et al., 2014).

The general objective of this article is to explore the potential of food-webs generated from paleontological fossil records as a valid methodological approach to study dynamics in Pleistocene ecosystems. To this end, we have chosen as a case study the late Early Pleistocene and the Middle Pleistocene in Western Eurasia. A major climate and ecological event, known as the Mid-Pleistocene Revolution (MPR), driven by variations in the orbital forcing of the climate cycles occurred within this period (Maslin and Ridgwell, 2005). The effects of the MPR on the climate system were particularly evident in the period from 1.0 Ma to 0.8 Ma, when a substantial increment on global ice volume occurred at 0.94 Ma, the periodicity of the cycles changed from 41 ky to 100 ky and their amplitude increased (Head and Gibbard, 2005). These climate changes promoted a drastic reorganization of the European ecosystems, that affected both the fauna and the vegetation, and was characterized by an expansion of the open environments (Suc and Popescu, 2005; Bertini et al., 2010; Croitor and Brugal, 2010; Kahlke et al., 2011; Leroy et al., 2011; Palombo, 2014). These environmental changes undoubtedly affected the survival opportunities of the European humans because the new environments provided different qualities and quantities of trophic resources (Rodríguez et al., 2012; Palombo, 2014). Within that framework, our goal is twofold. First, to uncover possible changes on large mammals' trophic relationships along this period. Second, to analyze the role (either passive or active) played by different Pleistocene's *Homo* species in such changes.

2. Material and methods

2.1. Data compilation and network construction

A set of 27 European large mammal Local Faunal Assemblages (LFAs) dated from the middle Villafranchian to the late Galerian was selected from the literature (See Table 1 and Fig. 1). Five time periods, corresponding to the middle Villafranchian (2.6–1.8 Ma), late Villafranchian (1.8–1.2 Ma), early Galerian (1.2–0.78 Ma), middle Galerian (0.78–0.05 Ma), and late Galerian–early Aurelian (0.5–0.3 Ma) (Palombo, 2014) were distinguished, and local faunas were assigned to one of them according to biostratigraphic correlations and numerical ages provided by the original sources. Only reasonably complete LFAs were included in the database. Although it is extremely difficult to establish strong criteria to determine whether a LFA is reasonably complete, we established a rule of thumb based on the analysis of 1452 Pleistocene LFAs from Europe. We selected faunas with a number of primary and secondary consumers above the median of the 1452 LFAs. Thus, we selected a number of faunal assemblages with more than seven primary consumer species and more than four secondary consumers. This is a conservative criterion, based on selecting the richest LFAs on the confidence that they are reasonably complete, but it does not necessarily imply that poorer LFAs are incomplete. The dataset includes only large mammals, defined as species weighing more than 10 kg. This size is slightly below the threshold where predators

shift from small to large prey, which according to Carbone et al. (1999) is 21.5 kg. Setting the threshold at 10 kg avoids excluding medium-sized carnivores that occasionally include large prey in their diets.

Putative trophic relationships between the species in the LFAs were inferred on the basis of the information available about the characteristics and behavior of the prey and predators as explained in Rodríguez et al. (2012). Extrapolation of the behavior of recent relatives (see references in Rodríguez et al., 2012), isotopic (Palmqvist et al., 2008; García et al., 2009; Feranec et al., 2010; Bocherens et al., 2011), and paleontological or zooarchaeological evidence was taken into account to infer the trophic relationships. The evidence on the predatory behaviour and the potential prey of *Homotherium* sp, *Lynx issiodorensis*, *Lynx pardinus*, *Megantereon cultridens*, *Panthera gombaszoegensis*, *Panthera pardus*, *Puma pardoides*, *Acinonyx pardinensis*, *Chasmatorchetes lunensis*, *Pachycrocuta brevirostris*, *Crocota crocuta*, *Pliocrocuta perrieri*, *Canis arvensis*, *Canis etruscus*, *Canis mosbachensis*, and *Lycaon lycaonoides* was discussed in detail in Rodríguez et al., 2012. Here we review the information available to infer the predatory behavior of the other species included in the present work.

The lion (*Panthera leo*) arrived in Europe 0.7–0.6 Ma. to occupy the niche of a top predator, able to kill very large prey (Croitor and Brugal, 2008). Modern lions are certainly the best analog for the predatory behavior of Pleistocene *P. leo*. The sociability of lions allow them to kill very large prey in group hunting. Their cursorial abilities and social hunting make them very efficient in open country, while their strong constitution makes them good ambush hunters (Turner, 2009). Mean prey size of recent lions is around 130 kg (correcting by age and sex of the prey), but almost half of the prey weigh around 70 kg, while 40% of the kills are around 220 kg and the rest correspond to prey above 400 kg (Rapson and Bernard, 2007). Megafauna species like rhinos (Brain et al., 1999) or young elephants are opportunistically killed and there is practically not limit for the smaller prey (Sunquist and Sunquist, 2009). Isotopic studies confirm the role of Pleistocene lions as top predators, including in their diet significant amounts of megafauna species (Bocherens et al., 2015).

A medium sized hyaenid attributed to the genus *Hyaena* is present in the Untermassfeld LFA and some other Middle Pleistocene localities. It is usually identified as *Hyaena prisca*, although Arribas and Garrido (2008) consider *H. prisca* a synonym of *Hyaena brunnea* (= *Parahyaena brunnea*). Both the recent striped hyaena (*Hyaena hyaena*) and the brown hyaena (*H. brunnea*) are omnivorous and extremely efficient scavengers. They also consume significant amounts of vegetable matter and opportunistically kill small mammals and other vertebrates (Burgener and Gusset, 2003; Holekamp and Kolowski, 2009). Thus we consider that the European *Hyaena* was a scavenger, unable to kill ungulates.

Two large social canid species were present in Europe during the Middle and Late Pleistocene: *Cuon alpinus* and *Canis lupus*. The European representatives of the genus *Cuon* are considered by some authors as subspecies of the recent species *Cuon alpinus*, living in East Asia, while other specialists consider them a different species (Brugal and Boudadi-Maligne, 2011). In any case, they were hypercarnivorous canids closely related to the dhole (*C. alpinus*), which constitutes the better analog to infer their behavior. Modern dholes are group hunters. Males weigh 15–20 kg and females 10–12 kg. They hunt medium sized and large ungulates and occasionally eat carrion (Sillero-Zubiri, 2009). Preferred prey are in the size interval 15–50 kg and include fawns of *Cervus unicolor*, and *Axis axis* together with adults of *Muntiacus muntjak* and *Sus scrofa* (Venkataraman et al., 1995; Andheria et al., 2007; Wang and Macdonald, 2009). The European *Cuon* was larger in size than the dhole, specially the middle Pleistocene forms usually classified as

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