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INTRODUCTION

Trophic resource availability is one of the main constraints for the survival and dispersal of any species and it is generally accepted that animal resources were also essential to Pleistocene hominins. Resource availability and competition with carnivores have been repeatedly proposed to be a main limiting factor for the migration and settlement of Early Pleistocene European populations. The ability of hominins to obtain animal resources from their environment is conditioned by the abundance of prey, their ecological characteristics and the intensity of the competition with other secondary consumers. We present a model which includes the prey-predator interactions in a community and quantifies the available biomass for secondary consumers and the intensity of intraguild competition.

MODELING TROPHIC RELATIONSHIPS

A model for a Pleistocene palaeocommunity

Several factors should be taken into account to evaluate food resource availability for a hunter-gatherer population:

- 1) the amount of biomass that can be extracted from the prey populations.
- 2) the intensity of competition within the carnivore guild.
- 3) the human strategies to obtain the food resources.

The computational model based on Leslie Matrix

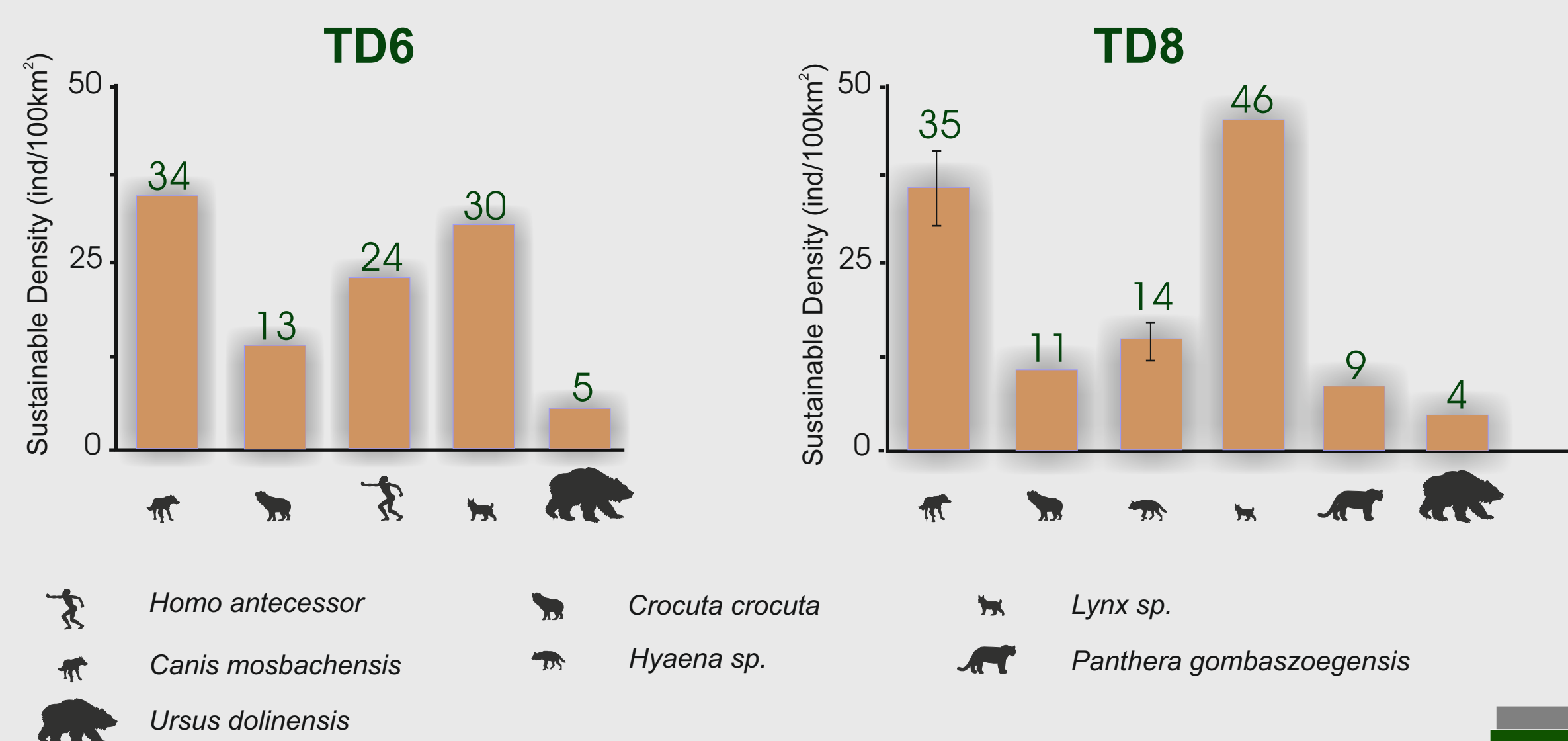
We developed a model using Leslie matrices (Leslie, 1945, 1948), a tool currently used in population dynamic studies. Our model determines the age structures that make the populations of primary consumers stable, the average biomass that can be sustainably extracted in the long term and its distribution in body size. It is developed under the assumption that all the variations in population size and composition may be taken as oscillations around a mean value that is constant through time, an assumption widely accepted in population dynamics research. We represent the average long term condition of every population, following the matrix:

$$X_{t+1} = \begin{bmatrix} a_1 & a_2 & \dots & a_n \\ b_1 & 0 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & \dots & b_{n-1} & 0 \end{bmatrix} X_t$$

$$\max_{0 \leq x_i \leq 1} \left[\sum_{i=1}^{n-1} (1 - b_i) \cdot x_i \cdot m_i \right] \quad \text{with } (a_1 + a_2 b_1 + a_3 b_1 b_2 + \dots + a_n b_1 \dots b_{n-1} = 1)$$

A detailed description of this model is provided in Rodríguez-Gómez, G., Rodríguez, J., Martín-González, J.Á., Goikoetxea, I., Mateos, A., 2013. Modeling trophic resource availability for the first human settlers of Europe: The case of Atapuerca TD6. J. Hum. Evol. 64, 645-657.

RESOURCE AVAILABILITY AND INTRAGUILD COMPETITION IN TD6 AND TD8



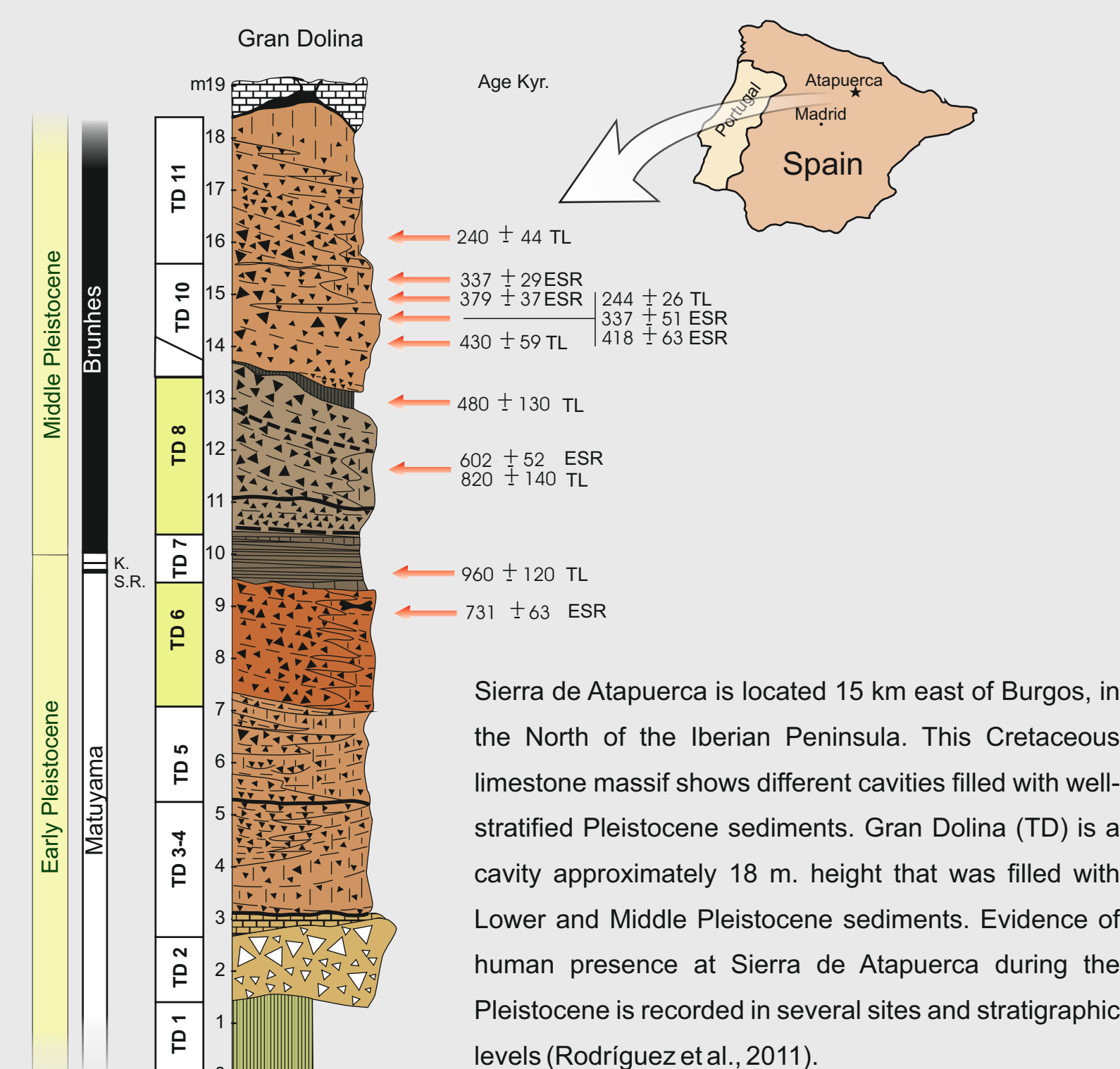
We model both the TD6 population (*Homo antecessor*) and an hypothetical human population at TD8 (*Homo* sp.) as species that cover a significant amount of its energetic requirements (3,000 kcal/day) with large mammals. Two different levels of animal food in the diet of *Homo* were tested to represent either a diet with a low (30%), or high (60%) meat component. It should be retained that given the key role of animal food in the human diet, hominins were highly carnivorous omnivores and only as members of the carnivore guild they were able to maintain high population densities.

Application of the model to TD6 shows that the environment was able to sustain the expected population densities of a diverse predatory guild including *Homo antecessor*. In contrast, when the model is applied to TD8 the higher values of the competition index (Rodríguez-Gómez et al., 2013) suggest an environment poorer in resources and with higher intraguild competition. In TD8 assemblage, without *Homo*, the total biomass output is insufficient to satisfy the secondary consumers requirements. The competition in TD8 was high in comparison to TD6, even when *Homo* is included in the computation with high meat consumption requirements. This last scenario is the one with the highest competition in the predatory guild.

This model is relevant to:

1. Understand the human role in a palaeocommunity.
2. Test whether there available was niche space for a hominin with a relevant proportion of meat in its diet.
3. Evaluate hypothesis relating the presence/absence of human settlement with low/high resource availability.

THE ATAPUERCA HOMININ POPULATIONS



Gran Dolina Cave (Burgos, Spain) at Sierra de Atapuerca is one of the best sites to address the study of resource availability for an Early Paleolithic population. The results will provide us information about the main features of the palaeoecosystem and the survival opportunities for human populations inhabiting Sierra de Atapuerca during the Pleistocene.

We selected two assemblages from Gran Dolina: TD6 and TD8 (aprox. 0.8 Ma. and 0.6 Ma.). The TD8 level is chronologically situated on around 600 kyr (602 ± 52 kyr, Falguères et al., 1999). From an archaeological point of view, evidence of human presence was not documented at TD8. The TD6 unit has a reversed polarity, interpreted as post-Jaramillo (0.99 - 0.780 Ma.) (Parés and Pérez-González, 1999). It includes the subunit TD6-2, also known as "Aurora stratum", which yielded a remarkable collection of human remains attributed to *Homo antecessor*, associated to numerous stone tools and abundant faunal remains (Carbonell et al., 2005; Carbonell et al., 1995).

CONCLUSIONS

- ✓ High food availability at TD6 (0.8 Ma.) implies a low to moderate level of competition for resources between carnivores and humans. An empty niche for a highly carnivorous omnivore existed in Europe during the Early Pleistocene and it was successfully exploited by *Homo*. In contrast, an ecosystem poorer in resources and with higher intraguild competition at TD8 suggests a more hostile environment at Atapuerca 600 kyr ago.
- ✓ Human ecodynamics in the late Early Paleolithic was constrained by the structure of the mammalian palaeocommunity and the intensity of competition among the secondary consumers.
- ✓ Hominin population densities could be constrained by the composition of carnivore guild but the abilities of human predation may help them to sustain the viability of these populations.
- ✓ Mathematical modeling of palaeocommunity trophic relationships is a useful tool for investigating food resource availability for Palaeolithic populations.

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