



# Latitudinal gradients and indicator species in ungulate paleoassemblages during the MIS 3 in W Europe



Diego J. Álvarez-Lao<sup>a,\*</sup>, Marcos Méndez<sup>b</sup>

<sup>a</sup> Departamento de Geología, Universidad de Oviedo, C/ Jesús Arias de Velasco s/n., E-33005 Oviedo, Spain

<sup>b</sup> Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, c/ Tulipán s/n., E-28933 Móstoles, Madrid, Spain

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## ABSTRACT

Studies of mammal assemblages for the European MIS 3 have focused on a regionalization using presence–absence data and traditional cluster analysis. Although this approach has revealed mammal assemblages with no modern analogs, it can easily miss two important dynamical aspects of the MIS 3 assemblages, namely, transitional regions and faunal mixtures. We revisited this regionalization using a complementary approach based on the study of quantitative data for ungulate species. The main aim of this work is to evaluate whether the MIS 3 climatic oscillations led to a mixture of faunas or a latitudinal gradient in faunal composition, as well as to identify indicator species for different areas in ungulate mammal paleoassemblages of Western Europe.

Ungulate faunal compositions of 86 fossil assemblages from 63 Western European sites of MIS 3 age were gathered from published sources. The distribution area was divided into four regions: central W Europe, S France, Cantabrian region and rest of the Iberian Peninsula. Chronologies of the assemblages were collected and calibrated. Multivariate ordination and indicator value analysis were carried out.

Our study provided four main results: (i) there was a latitudinal faunal turnover during the MIS 3 period consistent with a temperature gradient; (ii) the Cantabrian region hosted a transitional faunal assemblage between the northern cold faunas and the southern temperate faunas; (iii) it was possible to find indicator species of large herbivores for different geographical areas along that latitudinal gradient, although not all of them were linked to climate but to orography (mainly in Cantabrian and other Iberian sites); and (iv) within those indicator species, a signal of mixed temperate and cold faunas was discernible. Together, this evidence supports a scenario in which the succession of cold and warm episodes typical from MIS 3 left signals of mixed cold and temperate faunal assemblages but without totally blurring the latitudinal gradient in climatic conditions.

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## 1. Introduction

The distribution patterns of large herbivore mammals changed throughout the Pleistocene in response to glaciation-related climate changes. This led to the latitudinal assemblage of mammal faunas according to climatic tolerance of different species. Cold-adapted mammal faunas were predominant during the cold stages in middle and high latitudes of Eurasia and North America (Kahlke, 1999; Stewart et al., 2003; Markova et al., 2010), reaching southern latitudes only during the coldest events (Álvarez-Lao et al., 2009; Álvarez-Lao and García, 2011a, Sommer et al., 2014). Temperate mammal faunas, which were predominant in most of the Holarctic during the Pleistocene interglacial episodes (Kurtén, 1968; Stuart, 1982; Guérin and Patou-Mathis, 1996), persisted in southern glacial refugia (Iberian, Italian and Balkan peninsulas) during the cold stages (Hewitt, 2000; Sommer and Nadachowski, 2006; Jennings et al., 2011; Stewart and Stringer, 2011). However, a clear link

between mammal assemblages and climate could be blurred based on several paleoecological considerations. First, late Pleistocene faunal and environmental heterogeneity was greater than that of the Holocene and, consequently, many Late Pleistocene communities do not have modern analogs (Graham et al., 1996; Stewart, 2005, 2008). Second, due to vagaries of climate, migrating species responding individually to environmental change (Stewart, 2008) were mixed so that distinct assemblages could be obscured (Graham et al., 1996). Third, species, taken separately, could have a reduced value as indicators of climatic conditions (Stewart, 2005; De Cáceres et al., 2012).

These considerations were potentially prevalent during the Marine Isotope Stage (MIS 3), an episode of the Late Pleistocene from 60 to 27 ka, placed between the two cold maxima of the last glaciation (MIS 4 and 2) (van Andel, 2002; Roucoux et al., 2005, Clark et al., 2009). Climatically, MIS 3 was characterized by several sharp oscillations between cold stadials and temperate interstadials (Dansgaard et al., 1993; Barron and Pollard, 2002; North GRIP Members, 2004; Van Meerbeeck et al., 2011). In most cases, rapid decadal warming episodes of 8–16 °C were followed by several centuries of gradual cooling,

\* Corresponding author. Tel.: +34 985103143; fax: +34 985103103.  
E-mail address: [dalao@geol.uniovi.es](mailto:dalao@geol.uniovi.es) (D.J. Álvarez-Lao).

reaching stadial temperature values (North GRIP Members, 2004; Huber et al., 2006; Van Meerbeeck et al., 2011).

Although MIS 3 is considered a climatically mild episode by some authors (van Andel, 2002), the fossil record of large herbivore mammals from North and Middle Europe shows a predominance of cold-adapted mammals (e.g. *Rangifer tarandus*, *Mammuthus primigenius* and *Coelodonta antiquitatis*) during most of this episode (Delpech, 1983, 1984; Turner, 2000; Münzel and Conard, 2004a, 2004b; David et al., 2005; Schreve, 2006). In addition, cold-adapted mammals were detected throughout MIS 3 even as far South as the Iberian and Italian peninsulas (García and Arsuaga, 2003; Palombo and Ferretti, 2005; Álvarez-Lao et al., 2009; Álvarez-Lao and García, 2010, 2011a, 2012; Álvarez-Lao, 2014). In fact, during MIS 3, the woolly mammoth reached its southernmost geographical distribution both in Europe (Álvarez-Lao et al., 2009) and Asia (Takahashi et al., 2007). Therefore, mixed faunal assemblages seem to have occurred during MIS 3, potentially obscuring a paleoecological reconstruction of this period.

Studies of mammal assemblages for the European MIS 3 (Stewart et al., 2003; Markova et al., 2010) have focused on a regionalization using traditional presence–absence based cluster analysis (Kreft and Jetz, 2010). This approach offers valuable insights into the composition of the mammal assemblages, including those with no modern analogs. However, it can easily miss two important dynamical aspects of the MIS 3 assemblages, namely, transitional regions and faunal mixtures. Dynamics of faunal assemblages has been shown for North America (Graham et al., 1996), or for single species in Europe (Sommer et al., 2011, 2014). Current regionalization of W Europe during MIS 3 considers that the Cantabrian region in northwestern Spain belongs to the same assemblage than the rest of the Iberian Peninsula (Markova et al., 2010; see, however, Stewart, 2005). This assessment ignores the biogeographical peculiarity of this area during this period. The Cantabrian region is a belt of land of nearby 300 km long and 30–50 km wide where short river valleys run perpendicular to the coast. Topography is highly rough and, consequently, large fluvial plains are lacking. While the Iberian Peninsula is relatively isolated from continental Europe by the Pyrenees, which acted as a barrier limiting faunal dispersals, a corridor west of the Pyrenees, that opened during the Late Pleistocene's coldest stages, allowed the entrance of large mammal faunas from continental Europe into the Cantabrian region (Álvarez-Lao and García, 2011a, 2011b). In addition, this region has relative isolation from the Iberian areas further south by the Cantabrian Mountain Range, which also acted as a barrier for large mammal faunas (Álvarez-Lao and García, 2011a). Consequently large mammal faunas from this area are highly influenced, not only by latitude, but also by topography. Moreover, pollen and marine isotope data indicate that environmental conditions recorded in at NW Iberia were significantly cold and dry during the MIS 3 coldest events (Lézine and Denèfle, 2003; Roucoux et al., 2005). The recent improvement in the Cantabrian MIS 3 archaeo-paleontological record (Altuna, 1996, 2004; Altuna and Mariezkurrena, 2000, 2010, 2011; Castaños, 1996; Castaños and Castaños, 2007; Castaños et al., 2009; Álvarez-Lao and García, 2010, 2011a, 2011b, 2012; Álvarez-Lao, 2014) currently allows a reassessment of the Cantabrian region faunal assemblages.

The main goal of this work is to compare the ungulate assemblages along the latitudinal gradient from Central Western Europe and South France to the Cantabrian region and the rest of the Iberian Peninsula during the MIS 3. Our specific questions are: (1) Did the climatic oscillations during MIS 3 lead to a mixture of faunas or was a latitudinal (temperature) gradient still recognizable in faunal composition? We predict that this gradient should be detected, with Cantabrian sites showing an intermediate faunal assembly compared to northern and southern sites. (2) Can some species be considered as indicators of some faunal assemblages along this latitudinal gradient? We predict that faunal mixture would decrease the value of single species as indicators of particular areas along the latitudinal gradient. We take advantage of new statistical tools from community ecology to assess indicator

value, which can be more powerful than subjective expert assessment or previous statistical tools in these scenarios of mixed assemblages. Moreover, quantitative data are used since they provide a more accurate expression of the faunal differences between nearby geographical areas than mere presence–absence records.

## 2. Material and methods

### 2.1. Study sites and species

A total of four regions were considered in this study. Following Stewart (2005), we considered Central Western Europe, a transition zone including Southern France and the Cantabrian region of the Iberian Peninsula, and a Southern region including the rest of the Iberian Peninsula. For our analysis, we treated the Cantabrian region and Southern France separately, to take into account the differences in topography among these two regions. Using a literature search, we compiled 86 faunal assemblages of MIS 3 age from 63 sites: 19 assemblages from 14 sites in Central Western Europe, 17 assemblages from nine sites in Southern France, 34 assemblages from 25 sites in the Cantabrian region, and 16 assemblages from 14 sites in the rest of the Iberian Peninsula (see Appendix A in Supporting Information). These sites covered a wide latitudinal gradient from central Western Europe to southern Spain (Fig. 1).

The studied species are associated with different environments based on paleontological and current ecological evidences: *R. tarandus*, *Saiga tatarica*, *Ovibos moschatus*, *C. antiquitatis* and *M. primigenius* are considered indicative of cold conditions and open landscapes; *Capra ibex/C. pyrenaica* and *Rupicapra rupicapra* indicate rocky environments; *Capreolus capreolus*, *Dama dama* and *Sus scrofa* are normally associated with forested landscapes while *Megaloceros giganteus*, *Equus caballus*, *Equus hydruntinus* and *Stephanorhinus hemitoechus* indicate open and herbaceous areas; *Cervus elaphus* and the bovines (*Bison priscus* and *Bos primigenius*) are flexible species in their palaeoclimatic parameters and not specifically indicative of any particular landscape (Kurtén, 1968; Corbet and Ovenden, 1980; Guthrie, 1982; Vereschagin and Baryshnikov, 1982; Guérin and Patou-Mathis, 1996; Kahlke, 1999, 2014).

In previous studies on MIS 3 faunal assemblages, presence–absence analyses have been mainly utilised (Stewart et al., 2003; Markova et al., 2010). However, ignoring differences in abundance between assemblages leads to loss of valuable information. Therefore, we took a quantitative approach using percentages of species, based on the number of identified specimens (NISP). Controversy exists on the suitability of NISP compared to MNI (minimum number of individuals) as quantitative estimates in paleoassemblages (Lyman, 2008). Both units show advantages and drawbacks. First, NISP is an observed or direct measure while MNI is a derived measure that can be calculated by different (more or less comprehensive) methods and, therefore, more subjective and less comparable across studies (see a detailed discussion in Lyman, 2008). Second, MNI data are not always provided in the literature. Finally, Lyman (2008) showed that there is a strong correlation between NISP and MNI. In our case, MNI data were available for only 33 assemblages (6 from W Europe, 1 from S France, 21 Cantabrian and 5 from other Iberian sites). A high correlation was found among total NISP and total MNI across sites ( $r = 0.70$ ,  $p < 0.001$ ). From 13 species, for which both NISP and MNI were available, a significant correlation was found for nine species present at nine or more sites ( $r \geq 0.65$ ,  $p \leq 0.003$ ). The remaining four species had nine or less data and therefore correlations were nonsignificant due to low sample sizes. Overall, we preferred to use NISP, which was available for a broader set of assemblages.

Within each site, we selected faunal assemblages from layers with NISP higher than 100. When sites had several layers containing faunal assemblages meeting this criterium, two or three layers were considered, in order to capture temporal variation in faunal assemblages. In

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