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Caves as archives of ecological and climatic changes in the Pleistocene—The case of Gorham's cave, Gibraltar

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Abstract

In this paper, we describe a new method for quantitative reconstruction of bioclimate using a combination of multi-scale ecological datasets of present-day distributions of species with fossil plant and bird data derived from cave deposits of known age. In the specific case of Gorham's Cave, Gibraltar, we make predictions as to the prevailing climate during the Last Glacial Maximum (LGM). Our results indicate only slight variations compared to present-day climate. The present-day climatic regime is encompassed by a wider regime during the LGM. The importance of caves as climate archives is highlighted and our results additionally give focus to the generally underestimated importance of small-scale refugia during glacials.

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1. Introduction

The persistence of a Mediterranean vegetation and mixed forest during oxygen isotope stages 3 and 2 (OIS 3 and 2) has been observed in a number of Iberian Mediterranean localities (e.g. Carrión, 1992a, b; Burjachs and Julia, 1994; Carrión et al., 1995; Carrión and Munuera, 1997). OIS 3, covering the period between 60 and 20 ka (van Andel et al., 2004), followed by the Last Glacial Maximum (LGM) (OIS 2), were the coldest and most unstable of the entire Pleistocene (Finlayson, 2003). Studies of vegetation based on pollen and charcoal data have gone a long way towards providing a better understanding of the palaeoenvironments of southern Iberia at this critical time. Bioclimatic interpretations from plant taxa have been largely qualitative. Bird taxa have not been used in such work in spite of their abundance in many cave sites (Sánchez Marco, 2004). This paper takes a step forward by quantifying extant bioclimatic patterns of plants and birds across a wide region of southern Iberia (Fig. 1) and applying the results to the species patterns obtained from a cave archaeological register.

2. Methods

2.1. *Regional study of extant vegetation and bird communities*

The study area was located in the south-western region of the Iberian Peninsula from 36° to 40°N, and from 8.5° to 2.35°W. Given the physiographic heterogeneity of the study area, a grid made up of 20,100 km^2 units was randomly drawn on a map of the Iberian Peninsula, centred on the southernmost region, and in order to ensure that a representative sample was surveyed over a broad geographical range, nine Regional Squares were selected at random from this grid. Each of these Regional Squares was then subdivided into 10,010 km^2, Landscape Squares, from which 49 were randomly selected, and within these, 9801-ha plots were sampled.

The latitudinal range covered in the study area was from 36° to 40° North, with the majority of the study plots

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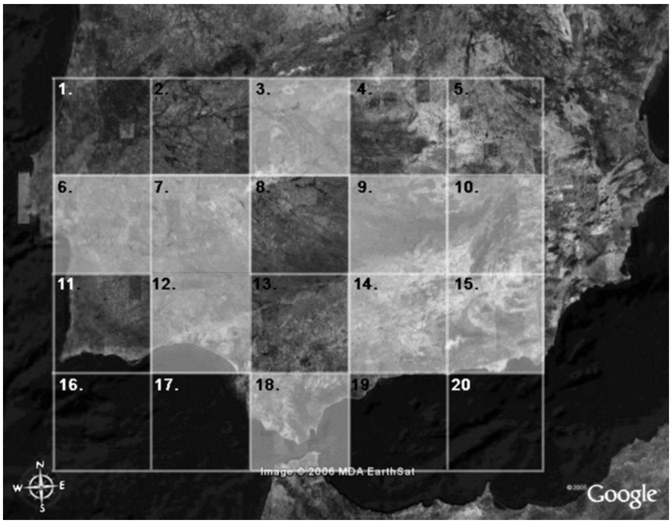

Fig. 1. Position of regional squares.

studied falling between 36.5°N and 38.0°N ($n = 537$). The longitudinal range of the study area covered from 8.5°W to 2.35°W, the majority of plots falling between 5.5°W and 5.0°W ($n = 164$) showing that the study sites are representative of a broad geographical area of the southern and western Iberian Peninsula, spanning 4° of latitude and 6 of longitude.

The altitudinal range of the entire dataset was between 0 and 2375 m above sea level, the majority of the plots ($n = 298$) falling between 200 and 400 m above sea level. The mean altitude for all the plots sampled ($n = 980$) was 500.09 m (474.55–525.63 m; 95% confidence limits). These geographical ranges were representative of the region (Finlayson, 2006).

2.2. Relationship between geographical, bioclimatic and ecological variables

Altitudinal zonation of vegetation particular to a biogeographical region, or groups of regions, can be attributed, in part at least, to the progressive descent of mean annual temperature with altitude. There are, furthermore, close correlations between climate, soil and communities of organisms that can be identified with changes in altitude. These observations are global and indicate a close association between biological organisms and climate, including temperature and rainfall. Rivas-Martínez (1987), correlating biotic and climatic factors, has pioneered the development of bioclimatic and plant community indicators in the Iberian Peninsula, and recognises two biogeographical regions within the Iberian Peninsula: the Mediterranean Region, and the Eurosiberian Region. Bioclimatic indices derived from temperature and rainfall data are used to assign bioclimatic regions. Variations in the thermic and ombrothermic values are identified to distinguish bioclimatic belts. The five main macrobioclimates identified in this way are: Tropical, Mediterranean, Temperate, Boreal and Polar. Only the Mediterranean bioclimate is relevant to this study.

The sites for which data were obtained in this study were visited at specific times of the year; climatic data could not be obtained for them. Furthermore, as these sites were randomly chosen they did not necessarily coincide with meteorological stations. The variables available for the study plots were altitude, latitude and longitude and the suitability of these as predictors of climatic variables were investigated. This was done by regression analyses of the Rivas-Martínez (1987) dataset, using altitude as the independent variable and the climatic parameters as dependant variables. The analyses were carried out independently for each of the regional squares to minimise the effects of latitude and longitude.

The regression analyses of the Rivas-Martínez (1987) dataset, using altitude as the independent variable and each of the climatic variables as the dependant variables was carried out for the regional squares, and the resulting regression equations were used to predict the climatic variable in each of the 980 study plots, for which altitude data were available from the field. These were in the form of a mean value with 95% confidence limits. These figures now provided the likely range of values for each of the calculated variables in each regional square with a high level of statistical significance, giving the predictions high robusticity. These scores were then used to estimate the thermotype and ombrotype (Rivas-Martínez, 1987) categorisation of each of the 980 study plots and to estimate the proportion of each thermotype and ombrotype in each of the regional squares.

Using the definitions provided by Rivas-Martínez (1987), and the predicted values for each of the 980 study plots, the proportion of each thermotype and ombrotype for each of the regional squares was calculated. These results enable a classification of the study area, and its component regions, by bioclimate. Overall, Meso-Mediterranean, Subhumid regimes appear dominant followed by Thermo-Mediterranean, Dry (Table 1). These results will form the basis of bioclimate analysis in this paper.

Plant and bird species were recorded for each of the 980 study plots. From this it was possible to characterise the bioclimatic attributes of each species. Plants are listed in Appendix A. Similar results were obtained for bird species.

2.3. Gorham's Cave, Gibraltar

We selected the site of Gorham's Cave in Gibraltar as a case study in the application of the acquired field data.

There is a number of reasons for selecting this site:

(a) It has been the subject of detailed archaeological excavations since 1991 (Barton et al., 1999; Stringer, 2000);
(b) it has long stratigraphical sequences for the Last Glacial cycle; and

Table 1
showing the number study plots allocated to each thermotype and ombrotype

Cryoro-Mediterranean	0
Oro-Mediterranean	5
Supra-Mediterranean	53
Meso-Mediterranean	703
Thermo-Mediterranean	219
Infra-Mediterranean	0
Total	980
Hyperhumid	1
Humid	110
Subhumid	689
Dry	180
Semiarid	0
Arid	0
Total	980

Table 2
Woody plant taxa used in quantitative bioclimate, habitat and landscape reconstruction of Level III, Gorham's Cave

Taxon*	Charcoal	Pollen
Olea europaea	*	*
Pinus sylvestris/nigra	*	
Pinus pinaster/pinea	*	
Alnus		*
Fraxinus		*
Evergreen *Quercus*		*
Deciduous *Quercus*		*
Salix		*
Cistaceae—*Cistus/Halimium*	*	*
Erica		*
Juniperus	*	*
Phillyrea		*
Pistacia lentiscus		*

(c) the archaeological and palaeontological deposits are rich in plant and animal fossils.

The framework of the Gibraltar landscape during the Quaternary has been established through the study of the Rock's Geomorphological evolution (Rodríguez-Vidal et al., 2004). These authors have provided a detailed analysis of the Rock's sedimentary record (uplifted marine terraces, windblown sands, scree breccias and karstic sediments) and its erosional landforms (cliffs, wave-cut platforms, staircased slopes and endokarstic systems), which show that the Rock's evolution has proceeded through a combination of tectonic uplift and eustatic sea level change. The position of the present-day coastline is unusual, the sea level having been on average −80 m below the present position for the greater part of the Last Glacial cycle and reaching an extreme of −120 m at the LGM. This situation exposed a large plain on the shallow eastern (Mediterranean) coastline of the Rock, the shoreline being up to 4.5 km from its present position. It is this coastal plain that was immediately outside Gorham's Cave and would have been the principal component of the home ranges of the people that utilised these and other Gibraltar caves (Finlayson and Giles Pacheco, 2000). It is the habitats and landscapes of this coastal plain, along with that of the limestone Rock itself, that we will attempt to reconstruct quantitatively below.

Gorham's Cave is a large cavern with archaeological and palaeontological sediments that fill the cavity to a thickness of 18 m and which span a temporal sequence from the Last Interglacial (~125 ka) to the third century BC when the site's use, as a shrine by the Phoenicians and Carthaginians, ended.

In this study, we examine stratigraphic Level III, an Upper Palaeolithic level, situated in the upper part of Gorham's Cave. Level III has three horizons identified within it, two of which contain technology associated with Solutrean and a higher horizon corresponding to the Magdalenian. We have focused on the Solutrean horizon (16 420–18 440 BP) which is the first Upper Palaeolithic occupation horizon in Gorham's Cave corresponding to a period in OIS 2 (Finlayson, 2006).

Charcoal, sediment pollen and coprolite pollen have been successfully collected from this level (Carrión et al., 2005). The charcoal collected from the hearths made by humans occupying the cave came from plants that would have been collected in the vicinity of the cave. Pollen would have been derived from the wider landscape of the region. Plant woody taxa were identified from charcoal and pollen and compared with species for which present day data had been collected as part of this study. These plants formed the basis of the reconstruction. Throughout this paper, both for plants and for birds, the reconstruction is carried out on the basis of positive evidence derived from species known to have been present (Table 2). In this study, the pollen was taken to be comparable to the vegetation equivalent to the landscape scale and charcoal at the local, habitat, scale.

A number of explanatory comments are required before proceeding with the analysis. These concern the taxon attribution. *Pinus* species are difficult to separate from pollen, but they can be distinguished to a greater degree from charcoal. However, *Pinus nigra* and *Pinus sylvestris* are difficult to separate even then and are kept together. In this reconstruction, data from both species were used separately; in the case of *P. nigra* and *P. sylvestris* the two species show a very similar pattern and so there is a high degree of confidence on the reconstruction even though it cannot be certain which of the two species is in the archaeological level. The same applies for *Pinus pinaster* and *Pinus pinea*. In this latter case, the presence of pine cone fragments and seeds confirms that *P. pinea* is present in part, at least. This is the most abundant taxon. In other cases where identification has been made to the level of genus (e.g. *Alnus*, *Fraxinus*), the locally present species has been used. The same applies to genera divisible by other characteristics (e.g. evergreen vs. deciduous *Quercus* oaks). Those identified as deciduous *Quercus* were compared with

Quercus pyrenaica and *Quercus faginea*. Similarly, the pollen grains identified as being from evergreen *Quercus* were compared to *Quercus rotundifolia/ilex* and *Quercus suber*.

A reconstruction of bioclimate based on fossil plant data was carried out and then the exercise was repeated, also at two scales, using present-day bird data. It is interesting to note that there is a very high number of bird species detected from the fossil record in Gorham's Cave, with 141 species having been identified (Cooper, 1999; Sánchez Marco, in press).

The bird species were divided into two categories according to two spatial scales. Those birds recorded as breeding within the 1-ha study plots, and therefore directly linked to the plot's vegetation features, were referred to as s-species. Those bird species seen within a radius of 1 km of the study plots and which were breeding in the area though not necessarily within the 1-ha plots, were referred to as S-species and it was assumed that they would have found adequate habitat within the 10 × 10 km sampled.

3. Results

3.1. Bioclimatic predictions—plant data

The bioclimate of Gibraltar today is Thermo-Mediterranean, Subhumid. Charcoal and pollen data, in conjunction, with present-day data indicate very similar conditions at the height of the LGM. In between these periods, analyses of Bolling-Allerod macroremains of charcoal from CHA5 in the Chemtou profile (*Fraxinus* sp., *Ficus* sp., *Labiatea* and especially numerous *Olea* sp.) point to bioclimatic conditions which were already similar to the ones of today in the western Mediterranean (Zielhofer et al., 2004). The tendency towards Meso-Mediterranean especially at the landscape level, may indicate slight cooling.

3.1.1. Local scale (charcoal)

The species present indicate that the thermotype locally outside the cave would have ranged from Thermo- to Meso-Mediterranean. Supra- and Oro-Mediterranean are of low probability (Fig. 2(1)); ombrotype appears to be Subhumid to Dry with a low probability of Humid (Fig. 2(2)).

3.1.2. Landscape scale (pollen)

As would be expected from the larger scale, a greater bioclimate mosaic is apparent. Nevertheless, Meso-Mediterranean stands out (Fig. 2(3)) as having the highest probability of occurrence with a significant attribution to Thermo-Mediterranean. The Subhumid ombrotype (Fig. 2(4)) stands out as the most important at this scale.

3.2. Bioclimatic predictions—bird data

The results suggest slightly cooler and more humid conditions than at present with the most probable bioclimatic attribution being Meso-Mediterranean, Subhumid.

3.2.1. Local scale (S-species)

The results indicate Meso-Mediterranean conditions with a tendency towards Supra-Mediterranean (Fig. 3(1)). Ombrotype is predominately Subhumid with elements of Humid and Dry (Fig. 3(2)).

3.2.2. Landscape scale (S-species)

The results show a mosaic at the landscape scale with a predominance of Meso-Mediterranean (Fig. 3(3)). Subhumid to Humid conditions predominate at this scale (Fig. 3(4)).

4. Discussion

Taken together the plant and bird data appear to provide a very similar signal to the present. The conditions at the height of the LGM are, surprisingly, at worst only slightly cooler than at present, locally and at the landscape level. Rainfall regimes are similar, or slightly more arid, than at present. This result contradicts the generalised view that severe changes affected southern Iberia at times during the Last Glacial cycle, and supports instead the view of the existence of localised refugia even during the most severe moments. From our results (and comparing with the Rivas-Martínez datasets) we can tentatively suggest that mean annual temperatures ranged between 13 and 19 °C, contrasting with a present day range of 17–19 °C. The winters may have been slightly cooler. Predicted monthly winter minima ranged between −1 and +10 °C, contrasting with a range of 4–10 °C today. The rainfall regime appears in the range 350–1000 mm per annum, compared to 600–1000 mm at present.

The vegetation cover in the region of Alborán, within which Gorham's Cave is situated, supposedly shifted drastically from a dominance of steppe plants in Dansgaard/Oeschger (D/O) stadials to forest during D/O interstadials (Combourieu Nebout et al., 2002; Sánchez Goñi et al., 2002; d'Errico and Sánchez Goñi, 2003; Moreno et al., 2005). Moreno et al. (2005) also show that the D/O stadials were not only characterised by enhanced aridity in the pollen signal but that there was a concomitant intensification of Saharan winds. The message is reinforced by Bárcena et al. (2001) who conclude, from an examination of the freshwater diatom record in Alborán cores during the Last Glacial–Interglacial transition, that the assemblage is wind-transported from North Africa. They add that river runoff in Alborán is insignificant and cite the importance of dust storms in North Africa with southern Algeria as a likely source. Bárcena et al. (2001) also comment on the regular presence of "red snow" over the Iberian coast. This widely described phenomenon of dust transport is related to south-westerlies generated by low pressures over the Gulf of Cádiz and appears to originate in north-west Africa. During glacials the Inter-tropical Convergence Zone (ITCZ) is known to

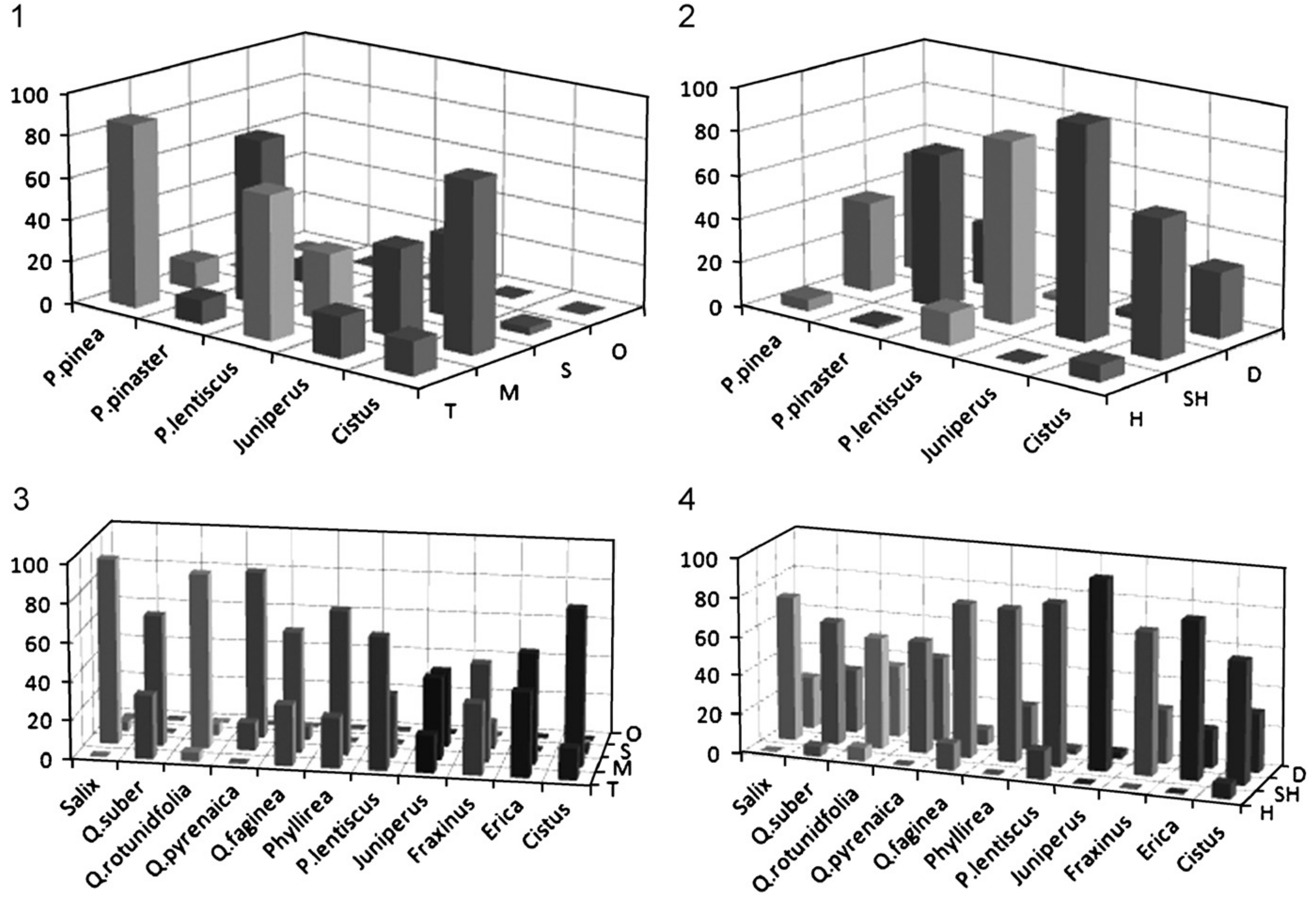

Fig. 2. (1) Gorham's Cave, charcoal—thermotypes predicted from vegetation data. Thermotypes (*x*-axis): T = Thermo-Mediterranean; M = Meso-Mediterranean; S = Supra-Mediterranean; O = Oro-Mediterranean. (2) Gorham's Cave, charcoal—ombrotypes predicted from vegetation data Ombrotypes (*x*-axis): D = Dry; SH = Subhumid; H = Humid. (3) Gorham's Cave, pollen—thermotypes predicted from vegetation data (axes as in Fig. 2(1)). (4) Gorham's Cave, pollen—ombrotypes predicted from vegetation data (axes as in Fig. 2(2)).

migrate south in Africa and this favours the localisation of a low-pressure system over the Mediterranean and prevailing westerlies which would favour this input of dust from Africa at times when maximum wind intensity is known to have occurred (Bárcena et al., 2001). Thus, it becomes very difficult to differentiate between two alternatives in this region as causes of the increase in arid species pollen during D/O stadials, as argued by Finlayson et al. (2004): (a) it reflects intense aridity in southern Iberia; or (b) it simply reflects a change in prevailing winds and the transport of arid plant pollen from the arid zones to the south, in North Africa. The latter alternative appears increasingly the most likely. In cold episodes, decreasing evaporation as a result of decreasing temperatures, may have additionally resulted in environmental conditions becoming more arid. On balance, the picture may be a combination of the two—increased aridity during D/O stadials, without this meaning that southern Iberia becomes a virtual desert. This scenario would reflect the observations made in this paper that show oscillations in the Gibraltar area between humid and dry scenarios, without intensification towards semi-arid.

Sánchez Goñi et al. (2000, 2002) and d'Errico and Sánchez Goñi (2003), using pollen analyses from two Iberian cores (MD95-2043 in Alborán and MD95-2042 off south-west Portugal) oversimplify a picture that is complex. For these authors, the vegetation of southern Iberia shows blanket shifts from, (a) cold/dry, desert-steppe, vegetation dominated by *Artemisia*, Chenopodiaceae and *Ephedra* to, (b) mild/wet open *Pinus* and *Quercus* forest with Mediterranean species, such as evergreen *Quercus, Olea* and *Pistacia*. They admit to the probable existence of localised refugia but add that cold events "drastically reduced plant and animal resources typical of the Mediterranean regions." They estimate that during cold HEs annual precipitation was 400 mm below present values and winter temperature ranged between 6 and 13 °C below present figures. As we have shown in this paper, the shifts in temperature and humidity were never of this order in Gibraltar, which suggests that the Iberian picture, with its topographic heterogeneity, was too complex to be simplified in the manner that these authors propose. They add that during temperate phases annual precipitation would have been around 600–800 mm and winter temperatures

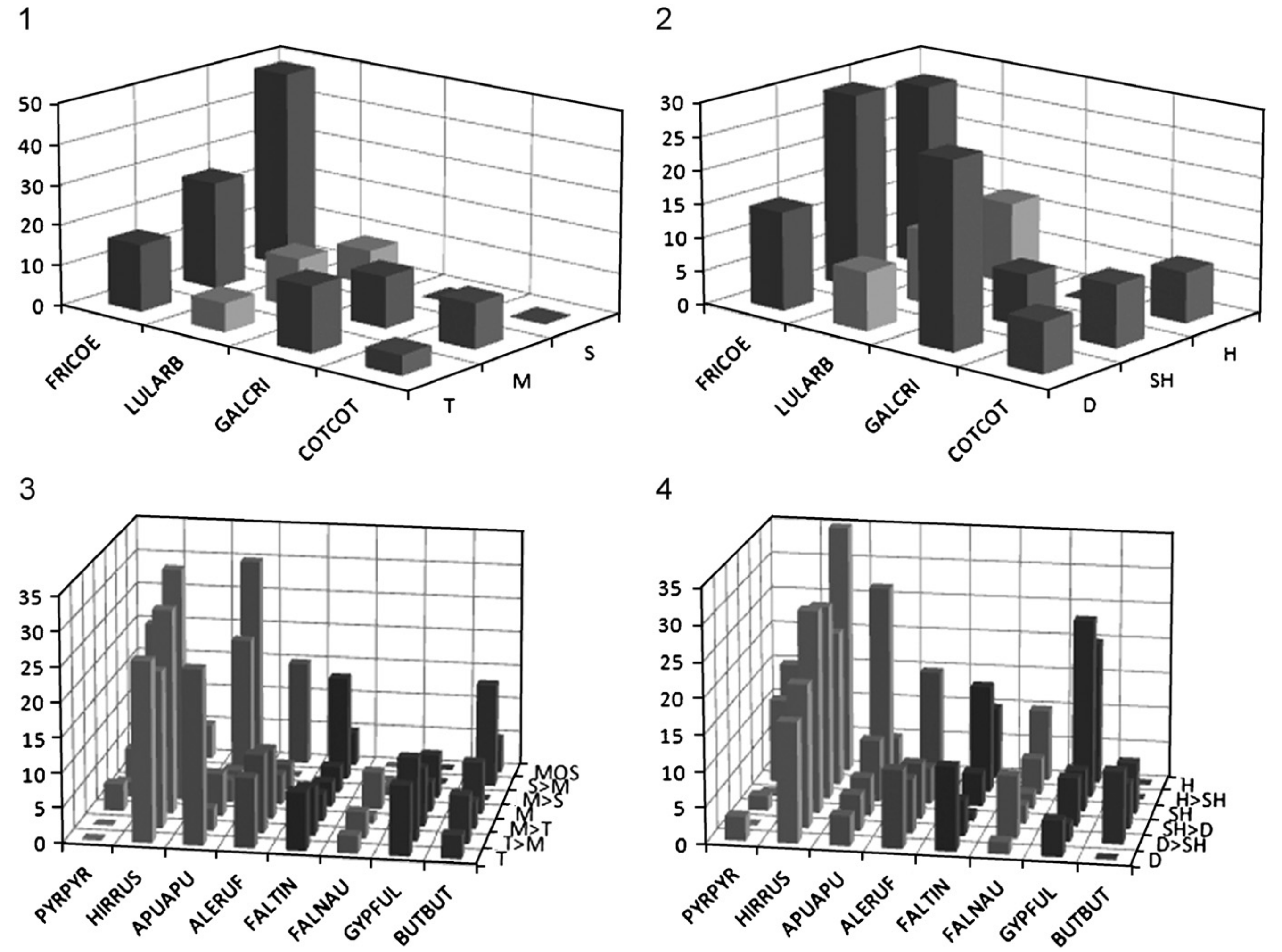

Fig. 3. (1) Gorham's Cave, S-species birds—thermotypes predicted from bird data (axes as in Fig. 2(1)). Species legend: FRICOE *Fringilla coelebs*; LULARB *Lullula arborea*; GALCRI *Galerida cristata*; COTCOT *Coturnix coturnix*. (2) Gorham's Cave, S-species birds—ombrotypes predicted from bird data (axes as in Fig. 2(2)). Species legend as Fig. 3(1). (3) Gorham's Cave, S-species birds—thermotypes predicted from bird data (axes as in Fig. 2(1)). Species legend: PYRPYR *Pyrrhocorax pyrrhocorax*; HIRRUS *Hirundo rustica*; APUAPU *Apus apus*; ALERUF *Alectoris rufa*; FALTIN *Falco tinnunculus*; FALNAU *Falco naumanni*; GYPFUL *Gyps fulvus*; BUTBUT *Buteo buteo*. (4) Gorham's Cave, S-species birds—ombrotypes predicted from bird data (axes as in Fig. 2(2)). Species legend as Fig. 3(3).

around 5–10 °C, not dissimilar to present-day values. This is another blanket generalisation, knowing the present-day variability of south-western Iberia.

There is an even greater source of concern in the interpretations of pollen sequences presented by these and other authors (e.g. Combourieu Nebout et al., 2002). These refer to the allocation of plant taxa to very specific, and often incorrect, climatic types. Part of the problem appears to stem from interpretation of the literature regarding present-day requirements of plant species. The following examples illustrate the point: Combourieu Nebout et al. (2002) state that for the Alborán area "Modern environments range from a Thermo-Mediterranean belt, with *Olea*, *Pistacia* and some steppe or semi-desert representatives (*Artemisia*, Chenopodiaceae, *Ephedra*), to a Meso-Mediterranean belt, represented by a sclerophyllous oak forest to a humid–temperate oak forest (mainly *Quercus* associated with Ericaceae), to a Supra-Mediterranean belt with a cold–temperate coniferous forest (*Pinus*, *Abies*, *Cedrus*) at higher altitudes." Sánchez Goñi et al. (2000), interpreting the MD95-2042 pollen record include *Quercus suber* as Eurosiberian and Ericaceae as "steppics". Such interpretations are not infrequent and the generalisation of *Quercus* and *Pinus* to specific conditions is prevalent. In Appendix A, we show the bioclimatic distribution of certain taxa from the 980 plot survey of south-western Iberia. Two aspects are worth noting:

(a) There is a great range of bioclimatic tolerance among different *Quercus* and *Pinus* species so that it becomes impossible to ascribe pollen at the genus level to particular conditions. In fact, it is clear from Appendix A that these genera range from typically warm bioclimate species (*P. pinea* and *Q. suber*) to cool ones (*P. nigra* and *Q. pyrenaica*). Similarly there is a range from humid bioclimate species (*Q. faginea*) towards dry ones (*P. sylvestris* and *Q. pyrenaica*). In general, *Pinus* are more confined to drier ombrotypes than *Quercus*. The separation of *Pinus* species is largely along a thermic gradient and *Quercus* along thermic and ombro gradients. *Pistacia* is usually allocated to Thermo-Mediterranean without distinction. It is clear that *P. lentiscus* tends towards warmer conditions than *P. terebinthus* with both occupying a similar ombroclimatic position so specific-level distinction makes a difference in this case.

(b) The allocation of ''Mediterranean'' taxa (usually meaning thermophillous) to very specific bioclimates is risky as these taxa span a range of thermotypes and ombrotypes. Thus, *Olea*, *P. lentiscus*, *Rhamnus alaternus* and *Phillyrea angustifolia* (Appendix A) predominate in the Thermo-Mediterranean but are not confined to it and cannot be considered exclusive indicators of Thermo-Mediterranean. Such distinctions also apply at the genus level, for example with *Erica* and *Cistus-Halimium*, which are often cited as indicators of very particular conditions.

In this paper, we have used frequencies of occurrence of plants and birds in bioclimates as indicators of probability and have shown the south-western Iberian picture to be a mosaic and not one of clearly defined belts of vegetation. The tolerance to a range of bioclimates (with preference to particular ones) seems to be a feature of many southern Iberian organisms, in particular reptiles, amphibians but also mammals and birds (Finlayson et al., 2005) and may reflect taxa that have avoided extinction during glaciations by their ability to shift position along a bioclimatic gradient.

Our results give a very clear picture of bioclimatic conditions outside Gorham's Cave around the LGM. They indicate that the bioclimatic changes were relatively minor compared to today. They highlight the importance of cave archives in our understanding of past climatic and environmental change at small to medium scales.

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Appendix A

Table A1 shows the number of study plots allocated to each thermotype and ombrotype.

Table A1
Showing the number of study plots allocated to each thermotype and ombrotype

Species	Thermotype				Ombrotype			
	Oro-Mediterranean ($n = 5$)	Supra-Mediterranean ($n = 53$)	Meso-Mediterranean ($n = 703$)	Thermo-Mediterranean ($n = 219$)	Hyper-humid ($n = 1$)	Humid ($n = 66$)	Subhumid ($n = 577$)	Dry ($n = 336$)
Olea europaea ($n = 361$)	0.00	0.00	28.03	81.28	0.00	60.61	43.67	20.54
Quercus rotundifolia($n = 306$)	0.00	33.96	38.98	6.39	0.00	31.82	30.16	33.04
Cistus spp. ($n = 234$)	0.00	15.09	26.74	17.35	0.00	27.27	25.30	20.83
Lygos sphaerocarpa ($n = 216$)	0.00	1.89	23.49	22.83	0.00	27.27	24.03	27.68
Quercus suber ($n = 216$)	0.00	0.00	15.22	49.77	0.00	12.12	27.12	15.18
Rubus ulmifolius ($n = 181$)	0.00	30.19	15.22	26.48	0.00	24.24	21.32	12.50
Pistacia lentiscus ($n = 143$)	0.00	0.00	7.40	41.55	0.00	25.76	17.16	8.04
Pinus pinaster ($n = 133$)	0.00	26.42	14.79	6.85	0.00	3.03	16.12	11.31
Ulex spp. ($n = 119$)	0.00	7.55	9.67	21.46	0.00	16.67	13.17	9.52
Crataegus monogyna ($n = 100$)	0.00	47.17	6.97	11.87	100.00	31.82	10.57	5.06
Pinus pinea ($n = 87$)	0.00	0.00	0.71	37.44	0.00	3.03	11.09	6.25
Juniperus spp.($n = 85$)	0.00	22.64	1.85	27.40	0.00	0.00	14.56	0.30
Genista spp. ($n = 75$)	0.00	22.64	7.40	5.02	0.00	3.03	6.10	14.33
Quercus faginea ($n = 74$)	0.00	9.43	6.54	10.50	0.00	15.15	10.05	1.79
Ficus carica ($n = 68$)	0.00	0.00	6.83	9.13	0.00	9.09	7.11	6.25
Erica spp. ($n = 67$)	0.00	0.00	5.41	13.24	0.00	0.00	12.22	8.61
Calicotome villosa ($n = 66$)	0.00	0.00	4.69	15.07	0.00	7.58	15.55	5.48

Table A1 (*continued*)

Species	Thermotype				Ombrotype			
	Oro-Mediterranean ($n = 5$)	Supra-Mediterranean ($n = 53$)	Meso-Mediterranean ($n = 703$)	Thermo-Mediterranean ($n = 219$)	Hyper-humid ($n = 1$)	Humid ($n = 66$)	Subhumid ($n = 577$)	Dry ($n = 336$)
Lavandula spp. ($n = 66$)	0.00	9.43	6.83	5.94	0.00	3.03	11.00	2.09
Daphne gnidium ($n = 59$)	0.00	3.77	6.54	5.02	0.00	4.55	8.84	11.18
Populus nigra ($n = 59$)	0.00	9.43	6.40	4.11	0.00	1.52	5.55	7.74
Halimium spp. ($n = 56$)	0.00	0.00	3.13	15.53	0.00	0.00	6.24	5.95
Tamarix africana ($n = 55$)	0.00	0.00	2.56	16.86	0.00	3.03	3.99	8.93
Arbutus unedo ($n = 53$)	0.00	0.00	4.98	8.22	0.00	0.00	6.24	5.06
Rosmarinus oficinalis ($n = 51$)	0.00	18.87	4.55	4.11	0.00	0.00	8.15	1.19
Nerium oleander ($n = 44$)	0.00	0.00	2.99	10.50	0.00	7.58	5.60	2.99
Fraxinus ($n = 44$)	0.00	11.32	3.13	7.31	0.00	0.00	5.55	3.57
Salix spp. ($n = 42$)	0.00	3.77	5.69	0.00	0.00	0.00	5.37	3.27
Smilax ($n = 38$)	0.00	0.00	1.56	12.33	0.00	6.06	8.40	3.57
Phillyrea angustifolia ($n = 37$)	0.00	1.89	3.56	5.02	0.00	0.00	5.20	2.08
Chamaerops humilis ($n = 37$)	0.00	0.00	1.14	13.24	0.00	15.15	15.09	21.43
Pinus halepensis ($n = 36$)	0.00	24.53	2.84	1.37	0.00	0.00	4.68	2.68
Salicornia ($n = 28$)	0.00	0.00	0.00	12.79	0.00	0.00	4.85	0.00
Cytisus spp. ($n = 27$)	0.00	3.77	2.99	1.83	0.00	3.03	3.79	7.39
Thymus ($n = 25$)	0.00	1.89	2.84	1.83	0.00	0.00	0.00	7.44
Castanea sativa ($n = 23$)	0.00	13.21	2.28	0.00	0.00	0.00	2.25	2.98
Pistacia terebinthus ($n = 23$)	0.00	1.89	2.99	0.46	0.00	4.55	2.43	1.79
Rhamnus alaternus ($n = 16$)	0.00	0.00	1.28	3.20	0.00	3.03	4.61	5.26
Quercus coccifera ($n = 16$)	0.00	7.55	1.56	0.46	0.00	0.00	1.91	1.49
Rosa spp. ($n = 16$)	0.00	3.77	1.85	0.46	0.00	0.00	1.39	2.38
Pinus sylvestris ($n = 14$)	0.00	18.87	0.57	0.00	0.00	0.00	0.69	2.98
Quercus pyrenaica ($n = 14$)	0.00	22.64	0.28	0.00	0.00	0.00	1.39	1.79
Pinus nigra ($n = 13$)	40.00	18.87	0.14	0.00	0.00	0.00	1.91	0.60
Hedera ($n = 12$)	0.00	3.77	1.14	0.91	0.00	4.55	1.51	0.75
Spartium junceum ($n = 11$)	0.00	7.55	1	0.00	0.00	0.00	0.52	2.38
Populus alba ($n = 10$)	0.00	0.00	.57	2.74	0.00	0.00	1.04	1.19
Ceratonia siliqua ($n = 9$)	0.00	0.00	0.28	3.20	0.00	3.03	1.21	0.00
Astragalus ($n = 9$)	100.00	7.55	0.00	0.00	0.00	0.00	1.39	0.30
Ulmus spp. ($n = 7$)	0.00	0.00	0.85	0.46	0.00	0.00	0.69	0.89
Acer granatensis/monspessulanum ($n = 6$)	0.00	3.77	0.57	0.00	0.00	0.00	1.04	0.00
Viburnum tinus ($n = 6$)	0.00	0.00	0.71	0.46	0.00	0.00	0.69	0.60
Alnus glutinosa ($n = 3$)	0.00	0.00	0.00	1.37	0.00	0.00	0.52	0.00
Abies pinsapo ($n = 3$)	0.00	0.00	0.43	0.00	0.00	0.00	0.35	0.30
Buxus spp. ($n = 2$)	0.00	0.00	0.28	0.00	0.00	0.00	0.35	0.00

The species are listed in order of the percentage abundance within the entire study area. The number of study plots in which the species are present is indicated next to the species name. Only the Thermotypes and Ombrotypes present in the study area are shown in the table. The number of study plots (out of 980) to which these bioclimatic variables are ascribed is indicated under the bioclimate. Table figures are percentage attribution of each species to each bioclimate. For example, *Olea europaea* occurred in 81.28% of all plots ascribed to thermo-Mediterranean, etc.

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