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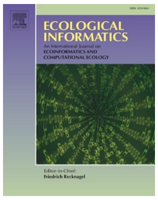

Modelling Mediterranean oak palaeolandscapes using the MaxEnt model algorithm: The case of the NE Iberia under the Middle Holocene climatic scenario

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ABSTRACT

The Mediterranean Basin is a global biodiversity hotspot, and oak tree species play an important role in it. Since the beginning of the Holocene (~11.4 kyr BP), the distribution of forests has not occurred uniformly, resulting in diverse types of vegetation landscapes. In this study, we used a maximum entropy algorithm (MaxEnt) to obtain the ecological niche model (ENM) of two sub-Mediterranean oak species, *Quercus pubescens* Willd. (pubescent oak) and *Quercus ilex* subsp. ilex (holm oak), both in the present day in the Iberian Peninsula and within a Middle Holocene (8.2–4.2 kyr BP) climatic scenario in the NE Iberian Peninsula. Moreover, we used the locations of Neolithic archaeological sites containing anthracological data to analyze the relationship between human occupations and oak habitats. Our results suggest that the two oaks have responded differently to the climatic conditions that have occurred, and show changes in both potential distributions. The palaeolandscape vegetation map shows a denser vegetation cover in the lowlands and a more open landscape in the highlands, with a higher dominance of *Quercus pubescens* in the septentrional areas, while *Quercus ilex* was more restricted to certain coastal areas. Temperature and precipitation factors, mainly seasonal climatic conditions, have had a greater impact on the distribution of vegetation than other factors. We found a good overlap between the ENM of the two oaks and the locations of the Neolithic sites analysed, and determined that the distribution of Neolithic archaeological sites is not random. The Neolithic populations in the study area depended heavily on the resources of the deciduous and evergreen sub- Mediterranean forest, although they also exploited the resources of the mountain pine forest. Neolithic sites distribution suggests that Neolithic human groups were aware of the potential of forests and probably gathered woody resources in their surroundings.

1. Introduction

The interaction between human activities and the natural environment has been of key importance in the Mediterranean area for millennia, and has therefore played a major role in shaping modern landscapes and ecosystems. The human impact on forests has occurred through the exploitation of forest resources over the course of millennia (e.g., Allué et al., 2017a, 2018; Allué and Mas, 2020; Coles et al., 1978; Mas et al., 2021; Smith, 1999; Théry-Parisot, 2002; Vidal-Matutano et al., 2017, among others). Wood has unquestionably been a resource of great value to humans, and wood gathering and forest management practices have often been the focus of attention in the literature (e.g., Alcolea et al., 2021; Asouti and Austin, 2005; Dufraisse et al., 2018; Euba et al., 2016; Marinova and Thiebault, 2008; Mas et al., 2022, among others). Despite evidence of forest exploitation since the Palaeolithic, it is widely accepted that the process of Neolithization increased the impact on local landscapes throughout the world (e.g., Banks et al., 2013; Feeser et al., 2019; Fyfe et al., 2019, among others). However, several authors have suggested both chronological and geographical differences in the establishment of Neolithic populations throughout the Mediterranean Basin (e.g., Bernabeu et al., 2018; Gkouma and Karkanas, 2018; Guilaine, 2018, 2019; Leroy et al., 2019; Li et al., 2013; Natali and

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Forgia, 2018; Oms et al., 2016), explained in terms of different environmental adaptation strategies (e.g., Weniger et al., 2019; Weninger et al., 2009) and innovations in farming technologies (e.g., Antolín and Jacomet, 2015; Halstead, 2018).

Archaeological research in the NE Iberian Peninsula has evidenced the establishment of Neolithic populations during the Middle Holocene (8.2 to 4.2 ka BP) (e.g., Oms et al., 2021; Oms and Martín, 2018). Although archaeological data clearly provide a record of farming activities, including husbandry and crop cultivation, they do not offer enough information to assess the impact of human activities on the vegetation cover of the surrounding landscapes during the process of Neolithization. Thus, different palaeobotanical approaches have been applied to determine past plant communities. Data relating to the presence of plant communities come from published pollen records (e.g., Azuara et al., 2020; Carrión et al., 2007; Carrión et al., 2010a, 2010b; Fletcher et al., 2012; Fletcher and Sánchez, 2008; González-Sampériz et al., 2017; González-Sampériz et al., 2020; Iriarte-Chiapusso et al., 2016; Jalut et al., 2000, 2009; Leunda et al., 2020; Pérez-Obiol et al., 2011; Revelles, 2017; Revelles et al., 2022; Riera et al., 2007; Riera and Esteban, 1994; among others) and charcoal sequences (e.g., 2021; Allué et al., 2009; Allué and Mas, 2020; Mas et al., 2022; Piqué et al., 2018; Ros, 1998; Ros and Vernet, 1987; Uzquiano, 2018, among others). These have served as the primary sources of reference in research of this type. Pollen records provide palaeoecological data on a large geographical scale, whereas anthracological records have more local significance (e.g., Asouti and Kabukcu, 2021; Chabal, 1992, 1997; Chabal et al., 1999; Kabukcu, 2018; Kabukcu and Chabal, 2021). Some palaeobotanical researchers suggest that it is not possible to propose a single palaeoecological model of the Holocene for the NE Iberian Peninsula (e.g., Allué et al., 2009, 2017b; Burjachs and Riera, 1996; Carrión et al., 2010a; Piqué et al., 2021; Revelles et al., 2022; Riera and Esteban, 1994). Indeed, palaeobotanical data indicate the existence of a highly heterogeneous landscape. For example, anthracological sequences from the NE Iberian Peninsula have shown that deciduous oak woodland was clearly present during the Neolithic period (e.g., Allué et al., 2009; Mas et al., 2022; Mas and Allué, 2020; Piqué, 2005; Ros, 1995, 1996). However, deciduous oak woodlands were widespread in conjunction with sclerophyllous taxa, indicating mixed oak forests (deciduous and evergreen oaks) in some geographical locations (e.g., Allué et al., 2009, 2017b; Antolín et al., 2013; Daura et al., 2019; Martín and Piqué, 2008; Piqué, 2005; Ros, 1996; Senabre and Socias, 1993). Unfortunately, the distribution patterns of past forest formations are uncertain (e.g., Chabal and Heinz, 2021), indicating the need to expand upon our understanding of the ecological, geographical and human factors that influence species distribution.

Recently, several studies based on ecological niche models (ENMs), habitat suitability models (HSMs), and species distribution models (SDMs) have been used to explain current, past and future habitats suitable for different species (Dormann, 2007; Elith et al., 2011; Guisan and Thuiller, 2005; Sillero et al., 2021, 2023). The data most often used in ENMs are georeferenced species distribution records combined with geospatial datasets (raster maps) representing environmental and geographic parameters that may affect the occurrence of species. The ENM is an empirical approximation for evaluating the species-environment equilibrium, which can estimate the environmental predictors that influenced the expected distribution of species and how they did so (e.g., Bradie and Leung, 2017; Elith et al., 2006; Guisan et al., 2017; Sillero et al., 2021). The use of ENM is widespread in ecology research in several fields of interest, such as forest management (Jafarov et al., 2021; Sun et al., 2021; Vessella and Schirone, 2013) and studies of invasive species expansion (Carboni et al., 2018; MacDougall et al., 2009), the impacts of climate change (Boonman et al., 2020; Moor et al., 2015; O'Donnell et al., 2012; Santini et al., 2021), and local refugia (Roces-Díaz et al., 2018; Wolf et al., 2021), among others.

This study represents a first approach based on maximum entropy (MaxEnt) to examine current and past suitable habitats for sub-Mediterranean oak woodlands, including the deciduous *Quercus pubescens* Willd. (pubescent oak) and the evergreen *Quercus ilex* subsp. *ilex* (holm oak). The ENMs of the two oak species under current environmental conditions were generated within the region of the Iberian Peninsula, while the ENMs generated under the climatic scenario of the Middle Holocene were projected to the NE Iberian Peninsula. Therefore, we analysed the location of Neolithic settlements in relation to the predicted suitability habitats. Our aims were 1) to determine the factors which most influence the current distribution of both oak species in the Iberian Peninsula, 2) to map the realised ecological niches of both oak species under a Middle Holocene climatic scenario in the NE Iberian Peninsula, and 3) to evaluate the results using the Neolithic settlement locations which provided the anthracological data.

2. Study areas

We applied the current ENMs to the Iberian Peninsula, a region located in the western Mediterranean Basin (SW Europe) and geographically isolated from Europe by the Pyrenees. The Pyrenees are a mountainous region at the confluence of the Mediterranean and Central Europe. Thus, these mountains form a geographic barrier, which contributes to the isolation of the Iberian Peninsula. The elevations in the region vary widely, from valleys below 200 m a.s.l. to summits of 3404 m a.s.l. (Mount Aneto). The Pyrenees have a continental climate with great differences in temperature between the northern and southern slopes and the interior (Carreras and Ferré, 2014), which is explained by the orographic effect and the influence of the Atlantic Ocean. To define the modelling background area, we used the limits of the two main biogeographical regions (Eurosiberian region and Mediterranean region) as they work as closed systems, as recommended by Sillero et al. (2009). The Iberian Peninsula is distinguished by a great deal of orographic diversity, with an irregular elevation range extending from sea level to ≥3000 m a.s.l. This also results in a pronounced climatic gradient from the rainiest and coldest areas in the north and northwest (Eurosiberian region) to the driest and warmest areas in the south and southeast (Mediterranean region) (Fig. 1A). Mean annual precipitation can vary widely, ranging from 1800 mm to 215 mm (Fig. 1B), and mean annual temperatures can range from −3.1 °C in high elevation areas to temperatures exceeding 18 °C (Fig. 1C) (AEMet, 2021).

We tested our model under the Middle Holocene climatic scenario in the background area of the NE Iberian Peninsula. The NE Iberian Peninsula is also characterised by climatic and orographic diversity. Notable geographical features include the coastal (*litoral*) and pre-coastal (*prelitoral*) mountain ranges, which act as a barrier to the humid air masses of the Mediterranean Sea. Consequently, the two mountain ranges prevent more humid air from penetrating into inland areas. Mean annual temperature varies markedly from the coast to the mountainous areas, ranging from 18 °C to 1 °C, respectively (Meteocat data from 2021). Elevation is a relevant modifier of climatic conditions, especially precipitation, which tends to be more abundant and regular in mountainous areas. Thus, mean annual rainfall varies from 250 mm to 1450 mm (Meteocat data from 2021). The Eurosiberian and Mediterranean regions influence the NE Iberian Peninsula, determining different biogeographical stages or vegetation series (Carreras and Ferré, 2014; Rivas-Martínez, 1987) and ecoregions (Dinerstein et al., 2017; Olson et al., 2001).

3. Materials and methods

3.1. Occurrence data

We created an ENM of two tree species that are dominant in some Mediterranean landscapes: *Quercus pubescens* Willd. (pubescent oak) and *Quercus ilex* subsp. *ilex* (holm oak). The two oak species have different ecological and environmental requirements (Table 1). The holm oak (*Quercus ilex* subsp. *ilex*) is native to the central-western Mediterranean

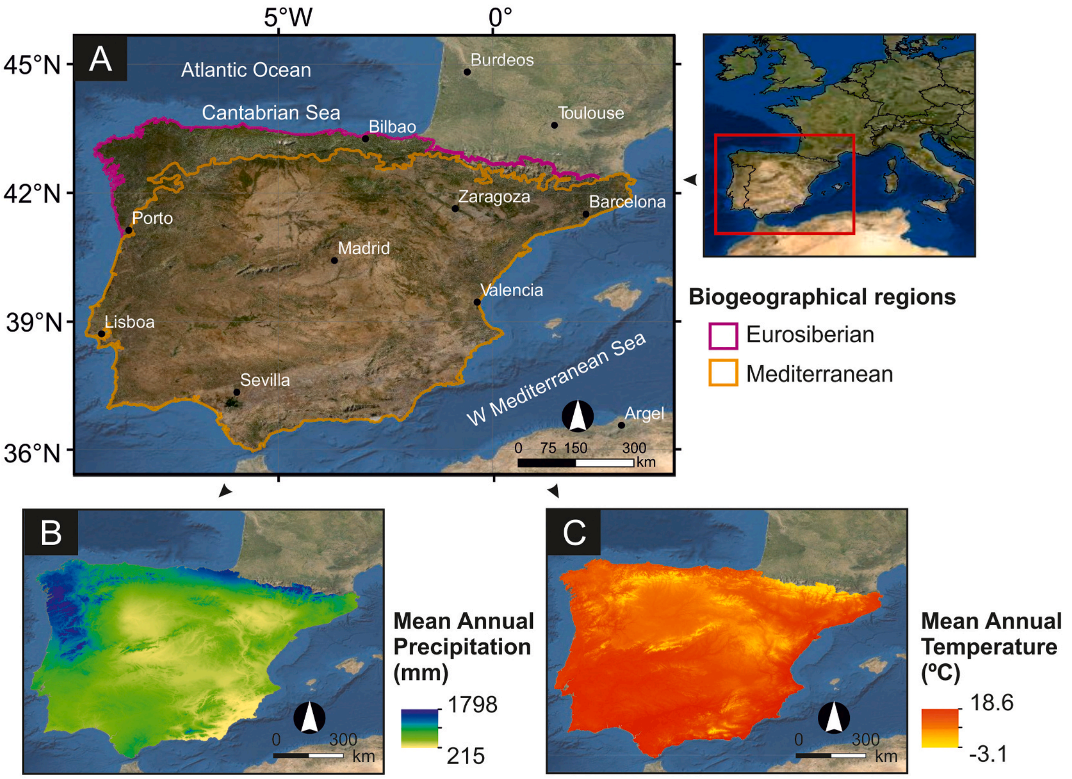

Fig. 1. A) Location map of the study area and biogeographical regions; B) Mean annual precipitation and C) Mean annual temperature maps of the Iberian Peninsula.

Table 1
Environmental features of holm oak (*Quercus ilex* subsp. *ilex*) and pubescent oak (*Quercus pubescens* Willd.). The ecological and environmental requirements of both tree species were gathered from specialized vegetation atlases (Serrada et al., 2008).

	Quercus ilex subsp. *ilex*	*Quercus pubescens* Willd.
Temperature (C°)		
Average Annual Temperature	10–18	5–15
Average Temperature in coldest month	>10	-3 - 7
Average Temperature in warmest month	< 25	15–25
Pluviometry (mm)		
Mean Annual Rainfall	>500	600
Average Rainfall during summer	>150	150
Geographical distribution		
Bioclimate (Rivas-Martínez, 1987)	meso-Mediterranean	supra-Mediterranean, Montane
Altitude range (m.a.s.l.)	0–1.000	(0) 200–1.600
Climate	Drier conditions	Temperate conditions

Basin and is a dominant evergreen sclerophyllous species, mainly integrated with Mediterranean pines and mesic shrubs in open and disturbed areas in some locations of the western Mediterranean (Reille and Pons, 1992; Terradas, 1997). It grows in the Atlantic valleys of the Eurosiberian region and in coastal areas with a temperate and mildly humid Mediterranean climate conditions, mainly from the Cantabrian region to the NE Iberian Peninsula. The subspecies *rotundifolia* (*ballota*) is distinguished from subsp. *ilex* by the fact that it grows in the innermost areas of regions with drier and warmer Mediterranean climate conditions (Castroviejo et al., 1990: 20), and its hybridisation with *Quercus coccifera* is recurrent (Castroviejo et al., 1990: 35). The pubescent oak (*Quercus pubescens* Willd.) is frequently hybridised with other sympatric eciduous oaks (*Q. faginea*, *Q. petraea*, *Q. humilis* or *Q. pyrenaica*) San-Miguel-Ayanz et al., 2016) and represents the predominant tree species in the large temperate forests of southern Europe. The pubescent oak is a thermophilous and sub-Mediterranean species primarily found in the NE Iberian Peninsula (Fig. 2).

Occurrence data refers to sets of coordinates (X-Y) where species have been observed. We used the location points from the GBIF-Global Biodiversity Information Facility (https://www.gbif.org/) online database to obtain the coordinates of the two oak species in the Iberian Peninsula. The database indicated a total of 3308 occurrences of *Quercus ilex* subsp. *ilex* and 6739 of *Quercus pubescens* Willd. Based on the work of Hijmans (2012), in order to reduce the potential location biases in the species records, we applied filters to narrow the datasets, such as removing the occurrences of *Quercus ilex* subsp. *rotundifolia*, and deleting duplicates and outliers using R and ArcGis programs. The ocurrences of the two oak species were standarized in 10 km grids as a way to obtain a homogeneous sample for use in modelling. In total, 298 locations were selected for *Quercus pubescens* Willd. and 288 for *Quercus ilex* subsp. *ilex* (Fig. 3).

3.2. Selecting variables

To generate the ENM of the two oak species, we used current bioclimatic variables (raster maps) from the Worldclim.org project (Fick and Hijmans, 2017). From the 19 bioclimatic variables available, we excluded the variables bio3 ‘Isothermality (bio2/bio7) (x100)’, bio14 ‘Precipitation of wettest month’ and bio15 ‘Precipitation seasonality (Coefficient of variation)’ as they are biased when projected to past climate scenarios (Bedia et al., 2013). Furthermore, we generated three geographic variables (elevation, slope and aspect) from a DEM (digital elevation model) of the Iberian Peninsula using the ArcGis program. To calculate the aspect variable, we followed that described in Sillero et al. (2021), who recommend using radians. All of these variables were in GeoTIFF format with 1 km^2 resolution (30 s). They were then transformed into ASCII files so that they could be worked on in MaxEnt.

The correlation between the set of variables was measured using

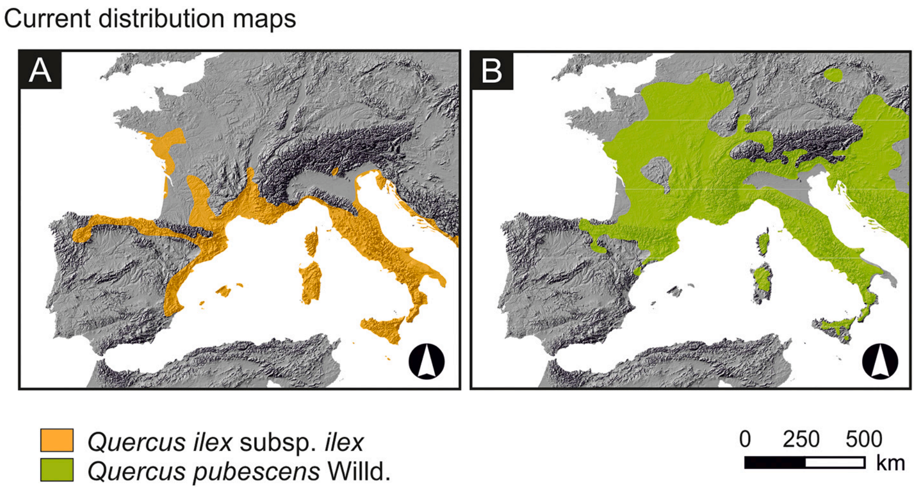

Fig. 2. Current distribution map of A) *Quercus ilex* subsp. *ilex* and B) *Quercus pubescens* Willd. in the western Mediterranean (Caudullo et al., 2017).

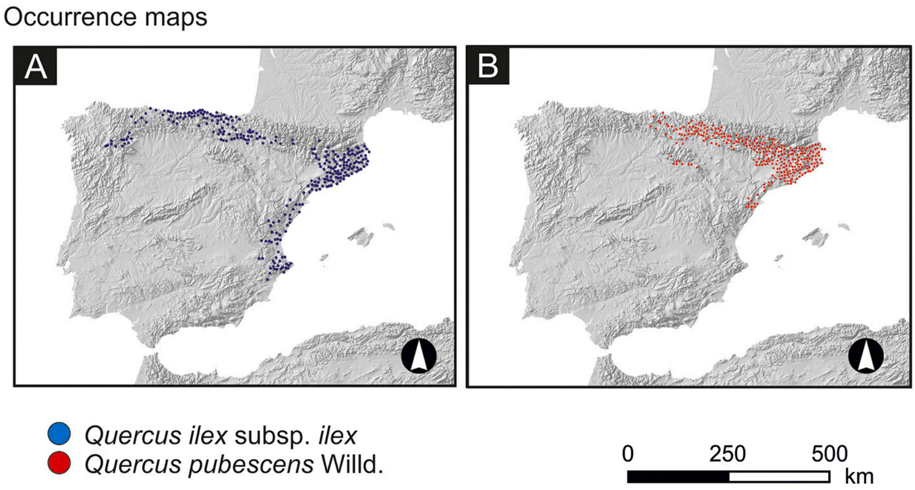

Fig. 3. Current observations of A) *Quercus ilex* subsp. *ilex* and B) *Quercus pubescens* Willd. used by MaxEnt ENMs.

parametric (Pearson) and non-parametric (Kendall and Spearman) coefficients (Field et al., 2012) (see Supplementary Material 1A). Then, we used the variance inflation factor (VIF) to measure the multicollinearity or non-independence of each variable with a combination of all the other variables in the model together (Sillero et al., 2021) (see Supplementary Material 1B). Furthermore, we selected the variables that were least correlated with one another and with the VIF value below as 3 (Bedia et al., 2013; Braunisch et al., 2013; Merow et al., 2013; Sillero et al., 2021). We also selected the six variables with least correlation among them: 1) bio4, 'Temperature seasonality', indicates the amount of temperature variation over a given year based on the standard deviation *100 of monthly temperature averages (degrees Celsius); 2) bio8, 'Mean temperature of wettest quarter', is a quarterly index of mean temperatures that occur during the wettest season (degrees Celsius); 3) bio9, 'Mean temperature of driest quarter', is a quarterly index that approximates the mean temperatures that occur during the driest quarter (degrees Celsius); 4) bio13, 'Precipitation of wettest month', is the index that identifies the total precipitation that occurs during the wettest month (millimetres); 5) bio19, 'Precipitation of coldest quarter', is a quarterly index that indicates the total precipitation that occurs during the coldest quarter (millimetres); and 6) 'Slope' in % values of the Iberian Peninsula (see Supplementary Material 1C). Finally, we used clamping maps of MaxEnt to project the same set of environmental variables used to perform the current models but expressing other time frame (Middle Holocene) and also different range of values. To do this, we downloaded the bioclimatic variables for the Middle Holocene climatic scenario from the CCSM4 set (National Center for Atmospheric Research, USA) from Worldclim.org (Fick and Hijmans, 2017). This datafile is the most accurate set for the Mediterranean region (sensu McSweeney et al., 2015).

3.3. Running the ENM and evaluating accuracy and importance values

To calculate both ENMs, we used MaxEnt v.3.4.4. free software with the high-performing machine-learning algorithm Maximum Entropy (MaxEnt) (Phillips et al., 2006). MaxEnt compares the conditions of the background with the conditions of species presences using the localities of the occurrence (X and Y coordinates = by observed sample) of the sample species (Dudík et al., 2007; Guillera-Arroita et al., 2015; Phillips et al., 2006, 2009, 2017; Phillips and Dudík, 2008). MaxEnt estimates the range of species with the constraint of the expected value of each pixel. The algorithm weights each variable by means of a constant and estimates the probability distribution by exponentiating the sum of the weighted variables. This probability distribution is then divided by a scaling constant to ensure that the probability values range from 0.0 to 1 (Phillips et al., 2006). We ran 10 replicates of both ENMs using 500 maximum iterations with the subsample run type and a 30 random test percentage. The MaxEnt model's output was analysed, and the contribution and permutation importance of each variable used to develop the model (Pearson et al., 2007; Warren and Seifert, 2011) were calculated using the jackknife test (n−1) (Cameron, 2014), included in the MaxEnt software. Then, the probabilistic binomial threshold test with clog-log function was applied to estimate the probability of species presence (Phillips et al., 2017). Finally, using clamping maps of MaxEnt, we projected both models under the Middle Holocene climatic scenario in the NE Iberian Peninsula. Then, we reclassified the predicted suitability values of each pixel (0 to 1) of both projected models. We considered 0 as not suitability distributions, suitability distributions below 0.28 as the lowest probability of species occurrence, between 0.28 and 0.70 as moderately suitable, and over 0.70 as most suitable.

Many techniques have recently been developed for statistically evaluating species distribution models (e.g., Elith et al., 2006, 2011; Hijmans, 2012; Sillero et al., 2021, 2023). We used a variety of methods to evaluate and compare the results of our MaxEnt models. Firstly, the accuracy of both current ENMs was evaluated using the ROC curve and the AUC value (Lobo et al., 2008; Peterson et al., 2008; Phillips et al., 2006), both of which are included in MaxEnt. Moreover, we used the marginal response curves of MaxEnt to view how the habitat suitability varies as each environmental variable is changed while keeping all other environmental variables at their average value. Finally, based on that described in Sillero et al. (2021), we calculated 100 null models to compare the evaluation metrics (AUC value) between our real models and null models using *t*-test (one-way ANOVA test if variables were parametric and Kruskal Wallis test if variables were non-parametric) (Field et al., 2012). This is necessary because in presence-background methods, the metrics are relative and not absolute (absences are not available) (Bohl et al., 2019).

3.4. Middle Holocene anthracological data available for the NE Iberian Peninsula

We analysed anthracological data from Neolithic sites in the NE Iberian Peninsula to explore any possible associations between the location of archaeological sites and the potential distribution of the two oak species in a Middle Holocene climate scenario. The establishment of Neolithic cultural phases in the study area during the Middle Holocene (8.2 to 4.2 ka BP) has been extensively analysed (e.g., Martín et al., 2010; Oms et al., 2016; Oms and Martín, 2018, among others), but anthracological studies are currently scarce (Mas et al., 2022; Revelles et al., 2022). Given the diverse topographical characteristics of the study area, the anthracological data were taken from several geographical locations in order to provide a broader palaeolandscape analysis (Supplementary Material 2A). We revised all the available anthracological data, and two main criteria were used to select the sites. To avoid statistical bias, we only included sites that had >30 identified charcoal fragments, and we selected the layer from each site that had the highest number of identified taxa. The anthracological data included in this work came from 23 sites, both in rock shelters/caves and in the open air, stemming from 27 archaeological layers (Table 2) (Supplementary Material 2B).

It is important to mention that a continuous sequence of human occupation throughout the Neolithic period has not been documented in any of the archaeological sites discussed here, although Cova Colomera (Mas et al., 2022), Bauma del Serrat del Pont (Piqué, 2005), Cova 120 (Piqué, 2005; Ros, 1995) and Cova de la Guineu (Allué et al., 2009) have the most complete anthracological sequences of the Middle Holocene sub-epoch.

Some taxonomic categories of species used in anthracological studies conducted in the 1990s are currently no longer in use (Heinz and Vernet, 1995; Ros, 1996, 1998), and these have been updated. For example, *Crataegus* sp., *Amelanchier ovalis*, *Sorbus* sp. and *Malus sylvestris* are classified as Rosaceae-Maloideae, as most of the time this is the most common taxon identification level. To unify nomenclature, taxa of the same families were included in a genus “sp.” or regrouped “/”. In accordance with Schweingruber (1990), some anatomical features are difficult to identify, and species-level taxonomy of some genera is not always achieved (*Acer* sp., *Fraxinus* sp., *Prunus* sp., *Ulmus* sp., *Populus/Salix* or *Rhamnus alaternus/Phillyrea*). *Quercus* hybridisations make it difficult to identify them at the species level using anatomical features. Thus, Mediterranean oaks are often grouped into two categories: *Quercus* sp. evergreen (including *Quercus ilex/coccifera*) (Uzquiano et al., 2016) and *Quercus* sp. deciduous (including *Quercus faginea, Q. pubescens,* and *Q. pyrenaica*). Finally, *Pinus sylvestris*-type includes *Pinus sylvestris*, *P. nigra* and *P. uncinata*. *Pinus uncinata* has only been identified at

Table 2
Archaeological sites included in this paper.

Archaeological period	Site	Aspect	m a.s.l.	Vegetation stages	Layer	Reference
Early Neolithic	Barranc d'en Fabra	Open air	100	Termo-Mediterranean	–	Ros, 1996
	La Serreta	Open air	123	Meso-Mediterranean	E61	Allué, 2010
	La Draga	Open air	178	Meso-Mediterranean	Sector A	Piqué, 2005
	Cova d'en Pau	Cave	187	Meso-Mediterranean	III	Ros, 1996; Piqué, 2005
	Plansallosa	Open air	273	Supra-Mediterranean	II	Ros, 1995; Piqué, 2005
	Bauma del Serrat Pont	Rock shelter	300	Meso-Mediterranean	III.4	Piqué, 2005
	Cova Bonica	Cave	402	Meso-Mediterranean	IV2	Daura et al., 2019
	Can Sadurní	Cave	420	Meso-Mediterranean	18	Antolín et al., 2013
	Cova de l'Avellaner	Cave	430	Montane	–	Ros, 1996
	Cova 120	Cave	460	Meso-Mediterranean	III	Piqué, 2005
	Cova Colomera	Cave	670	Meso-Mediterranean	CE14	Mas et al., 2022
	Cova de la Guineu	Cave	734	Meso-Mediterranean	Ie	Allué et al., 2009
	Cova del Toll	Cave	745	Montane	C5, C4, C3	Mas and Allué, 2020
	Cova del Frare	Cave	942	Meso-Mediterranean	C6	Ros, 1996
	Balma Margineda	Rock shelter	970	Sub-Alpine	C3b	Heinz and Vernet, 1995
	Cova del Vidre	Cave	1100	Supra-Mediterranean	2 central	Alcolea, 2017
	Camp del Colomer	Open air	1385	Sub-Alpine	FS29	Piqué et al., 2015
	Coves del Fem	Cave	530	Supra-Mediterranean	UE 104	Alcolea, 2017
Late Neolithic	Roques del Sarró	Open air	196	Meso-Mediterranean	–	Vila and Piqué, 2012
	Santa Maria dels Horts	Open air	215	Meso-Mediterranean	–	Senabre and Socias, 1993
	Bauma del Serrat Pont	Rock shelter	300	Meso-Mediterranean	III.3	Piqué, 2005
	Cova Gran de Santa Linya	Rock shelter	385	Meso-Mediterranean	Fumier 3Nb	Allué, unpublished
	Auvelles	Rock shelter	417	Meso-Mediterranean	–	Martín and Piqué, 2008
	La Prunera	Open air	458	Montane	–	Piqué, 2005
	Cova 120	Cave	460	Meso-Mediterranean	II	Ros, 1995; Piqué, 2005
	Cova Colomera	Cave	670	Meso-Mediterranean	CE9	Mas et al., 2022
	Cova de la Guineu	Cave	734	Meso-Mediterranean	Id	Allué et al., 2009

the site of Balma Margineda (Heinz and Vernet, 1995) and is included in the *Pinus sylvestris*-type category.

The classification of Neolithic sites was based on the frequencies of the woody taxa (plant association) using a cluster analysis with the Manhattan distance (Supplementary Material 2C). This, in turn, allowed us to gain a deeper insight into the dynamics of landscape transformation during the Neolithic period.

4. Results

4.1. Accuracy of the two oak ENMs and current suitable distributions

The average training AUC value for the 10 replicated runs and 500 iterations of *Quercus ilex* subsp. *ilex* was 0.9261 and the average test AUC 0.9168. For *Quercus pubescens* Willd., these values were 0.932 and 0.9281, respectively. According to Phillips et al. (2006), these AUC results are very close to the value of 1, so the maximum entropy algorithm provided a valid estimation for both oak ENMs. These results indicate that both MaxEnt models were successfully performed and demonstrated high accuracy (Fig. 4).

The AUC values of the 100 null models and our empirical models were not normally distributed (Saphiro-Wilk p = value 6.952e-16 and *p*-value = 4.026e-15, respectively) and there was no equality between groups (Kruskal-wallis p-value = 2.383e-13).

4.2. Important variables and response curves

Table 3 shows the percentage contribution and the permutation importance results for the current environmental and geographical variables that affect the geographical distribution of both oak species, according to the threshold test.

The variables 'Temperature seasonality' (bio4), 'Mean temperature of driest quarter' (bio9) and 'Precipitation of wettest month' (bio13) obtained a total percent contribution of 82.50% for *Quercus pubescens*. This result indicates that these three variables contain more information that other variables do, and that they contribute more information to the model of *Quercus pubescens*. Thus, the main factors that affected the pubescent oak ENM were the temperature factors bio4 and bio9, and the precipitation factor bio13. The geographical variable 'Slope' contributed only 4.6% to the model.

In addition, the variables 'Temperature seasonality' (sd*100) (bio4), 'Mean temperature of wettest quarter' (bio8), 'Precipitation of wettest month' (bio13) and 'Precipitation of coldest quarter' (bio19) had the highest contribution values for the *Quercus ilex* subsp. *ilex*., yielding a total percent contribution of 94%. The geographical variable 'Slope' had lowest contribution value (1.3). For instance, the main factors affecting the distribution of the current potentially suitable habitat for holm oak were temperature factors (bio4 and bio8) and precipitation factors (bio13 and bio19).

The response curves in Fig. 5 demonstrate how the two oak species responded to the six variables. The variables bio4 and bio13 were found to be significant contributors to both models. The results showed that the most ideal range for bio4 and bio13 was higher for *Quercus pubescens* than for *Quercus ilex* subsp. *ilex*.

4.3. Vegetation formation types according to the anthracological data

The cluster plots (Fig. 6) show the anthracological association and the configuration of five types of landscape or vegetation scenarios during the Middle Holocene.

In the first group (Fig. 6 in red), the anthracological data documented in the Early-Middle Neolithic layers (7.5 to 5.6 cal ka BP) of Cova Colomera (Mas et al., 2022), Cova del Toll (Mas and Allué, 2020), Cova de l'Avellaner (Ros, 1996), Bauma del Serrat del Pont (III.4) (Piqué, 2005), Cova de la Guineu (Allué et al., 2009), Can Sadurní (Antolín et al., 2013), Cova d'en Pau III, Plansallosa, La Draga and Cova del Frare (Piqué, 2005; Ros, 1995, 1996) indicate a landscape dominated by deciduous oak (20–71%) together with sub-Mediterranean mesophilous taxa, mainly *Buxus sempervirens* and *Acer* sp. Conversely, *Pinus sylvestris* type, *Taxus baccata*, evergreen oaks (*Quercus ilex/coccifera*) (<23%) and Mediterranean trees and shrubs yielded very low values (see Supplementary Material 2B). The frequency values of deciduous oak, boxwood (*Buxus sempervirens*) and maple (*Acer* sp.) are similar among the sites. However, some differences can be observed, especially in the values of conifers such as the yew (*Taxus baccata*) and mountain pines (*Pinus sylvestris*-type). Moreover, boxwood was not documented in either Can Sadurní or Cova de la Guineu. The anthracological data from the Late Neolithic layers (5.6 to 4.2 cal ka BP) of La Prunera and Bauma del Serrat Pont (III.3) (Piqué, 2005), Cova Gran de Santa Linya (Allué, unpublished) and Cova Colomera (Mas et al., 2022) show a a plant community that is very similar in composition to the Early-Middle Neolithic first group (see Supplementary Material 2C).

The second group (Fig. 6 in ochre) consists of the Early-Middle Neolithic anthracological data from Cova 120 (III) (Piqué, 2005) and Cova Bonica (Daura et al., 2019), and the Late Neolithic anthracological data from Cova de la Guineu (Ic) (Allué et al., 2009), Auvelles (Martín and Piqué, 2008) and Santa Maria dels Horts (Senabre and Socias, 1993). This Early-Middle Neolithic group indicates a mixed oak forest formation (deciduous and evergreen oaks) with montane pines (*Pinus sylvestris* type), Mediterranean pines (*Pinus halepensis/pinaster*) and *Juniperus* sp., and a marked presence of sclerophyllous and sub-Mediterranean shrubby vegetation, such as the strawberry tree (*Arbutus unedo*), and evergreen buckthorn (*Rhamnus alaternus/Phillyrea*). This second group seems to have a more open vegetation cover than that determined for the first group.

The third group (Fig. 6 in green) includes the Early-Middle Neolithic

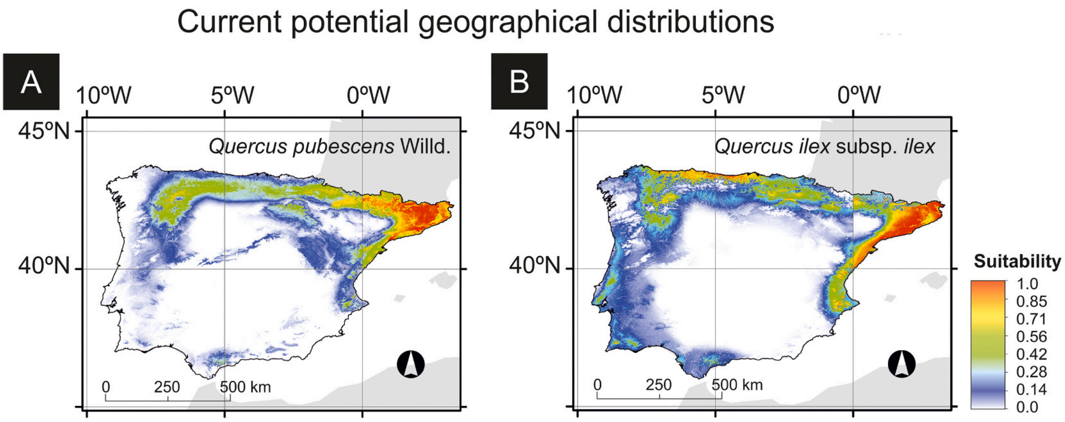

Fig. 4. Distribution maps of current suitable habitats of A) *Quercus pubescens* Willd. and B) *Quercus ilex* subsp. *ilex*.

Table 3

The values show averages of 10 replicate runs, estimating the relative contributions of the environmental and territorial variables to the MaxEnt model. The percentage contribution determines the jackknife; in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable. Permutation importance shows the values of that variable on training presence, and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown, normalized to percentages.

		Quercus pubescens Willd.		*Quercus ilex* subsp. *ilex*	
Variable	Description	Percent contribution	Permutation importance	Percent contribution	Permutation importance
Temperature factors					
bio4	Temperature seasonality	30.4	13.8	41.9	39.5
bio8	Mean temperature of wettest quarter	9.5	12.2	24.8	13.8
bio9	Mean temperature of driest quarter	33.8	22.1	4.7	10.4
Precipitation factors					
bio13	Precipitation of wettest month	18.3	45.6	14.1	21.1
bio19	Precipitation of coldest quarter	3.4	5.8	13.2	13.7
Geographical factors					
Slope	In degrees	4.6	0.4	1.3	1.5

layers of La Serreta (Allué, 2010) and Barranc d'en Fabra (Ros, 1996), and the Late Neolithic layer of Cova Gran de Santa Linya (Allué, unpublished) (Fig. 6 in turquoise). The anthracological assemblage for the Early-Middle Neolithic points to a less mixed oak forest formation (deciduous and evergreen oaks), and an increased presence of shrubby vegetation. Thus, thermophilous shrubby taxa such as lentisk (*Pistacia lentiscus*) olive (*Olea europea*) and evergreen oaks are more abundant than mesophilous taxa. The Late Neolithic layer of Cova Gran de Santa Linya has many similarities with group 1, even though boxwood is less present. It has therefore been separated from the cluster.

The fourth and fifth groups from the Early-Middle Neolithic (see Fig. 6 in blue and purple, respectively) include Camp del Colomer (Piqué et al., 2015) and Cova del Vidre (Alcolea, 2017) (group 4), and Coves del Fem (Alcolea, 2017) and Balma Margineda (Heinz and Vernet, 1995) (group 5). Likewise, the Late Neolithic site of Roques del Sarró (Vila and Piqué, 2012) appears as an outlier, with high frequencies of maquis formations, with species such as *Pistacia lentiscus* (67.6%). The anthracological data of the fourth group indicate high frequencies of conifers, mainly montane pines (*Pinus sylvestris*-type), the most representative taxon in the assemblage. In addition, values for deciduous oaks and yew (*Taxus baccata*) are higher than for evergreen oaks. The other woody taxa are present in low relative frequencies. The anthracological assemblage for the fifth group shows high values for montane pines and low values for deciduous oaks.

4.4. Suitable distribution maps of the two oak species based on the Middle Holocene climatic scenario (8.200 to 4.2 ka BP) and site location

The two distribution maps of suitable habitats for the two species studied are attached in ASCCI format (Supplementary Material 3). Fig. 7 shows the locations of Early-Middle Neolithic archaeological sites and suitable distributions for both oaks. The sites located in the north-eastern inland area, including La Draga, Cova d'en Pau, Bauma del Serrat Pont, Plansallosa and Cova de l'Avellaner (group 1), and Cova 120 (group 2) are within habitats poorly-moderately suited to *Quercus pubescens* and unsuitable for *Quercus ilex* subsp. *ilex* (Table 4). Nevertheless, La Draga and Cova d'en Pau are located near a moderately suitable habitat for *Quercus pubescens*, as well as near a poorly suitable habitat for *Quercus ilex* subsp. *ilex*.

The sites located in coastal and pre-coastal areas, including Cova del Frare, Can Sadurní and Cova de la Guineu (group 1), Cova Bonica (group 2), and La Serreta and Barranc d'en Fabra (group 3) are in areas with a moderate to high suitability for *Quercus pubescens*, and near areas with a low to moderate suitability for *Quercus ilex* subsp. *ilex* (see Table 4). Near these sites, Cova del Toll (group 1) is in an area moderately suitable for *Quercus pubescens* but unsuitable for *Quercus ilex* subsp. *ilex*. Moreover, the inland locations of Cova Colomera (group 1), Camp del Colomer and Cova del Vidre (group 4), and Coves del Fem and Balma Margineda (group 5) are in an unsuitable area for *Quercus ilex* subsp. *ilex*. Nevertheless, Cova Colomera, Coves del Fem and Cova del Vidre are within habitats poorly-moderately suited to *Quercus pubescens*, although Camp del Colomer and Balma Margineda are in an area where the species does not occur.

The Late Neolithic sites are shown in Fig. 8, along with the habitat suitability distributions for *Quercus pubescens* and *Quercus ilex* subsp. *ilex*. Group 1, including Cova 120, Bauma del Serrat Pont, La Prunera and Cova Colomera, and group 3, including Cova Gran de Santa Linya are in the least-moderately suitable habitat for *Quercus pubescens* and in an unsuitable habitat for *Quercus ilex* subsp. *ilex*. Moreover, different trends can be observed in group 2. Auvelles is in unsuitable areas for both species, unlike the sites located in the coastal and pre-coastal areas, such as Cova de la Guineu and Santa Maria dels Horts, which are located within de moderately suitable habitats for both oak species (see Table 4). Finally, Roques del Sarró (group 4) are in unsuitable habitats.

5. Discussion

5.1. Physical-environmental factors and current suitable habitats for oak woodlands in the NE Iberian Peninsula

MaxEnt models have emerged as a promising tool for predicting suitable habitats and estimating the ecological niches of the species in a given geographical area (Dudík et al., 2007; Elith et al., 2011; Merow et al., 2013; Peterson et al., 2015). We applied this approach to gain an understanding of how forest oak ecosystems respond to climatic factors and geographical features in the Iberian Peninsula. As important components of forests distributed in the western Mediterranean region, the two oak species analysed are of special interest in evaluating plant-environment interactions (Moreno-Fernández et al., 2021). Our results demonstrate a significant contribution of temperature and precipitation seasonality factors in both MaxEnt models. Thus, our results suggest that the temperature factor ‘Temperature seasonality’ (bio4) and the factor ‘Precipitation of the wettest month’ (bio13) are more influential to the occurrence of both oak species in the Iberian Peninsula. The marginal response curves in bio4 seem to be different for both oak species, as *Quercus pubescens* responds to highest values of temperature seasonality than *Quercus ilex* subsp. *ilex*. However, the responses of both species seem to be similar in bio13, although *Quercus pubescens* responds to highest values than *Quercus ilex* subsp. *ilex*. ‘Mean temperature of driest quarter’ (bio9) also contributed significantly to the ENM of *Quercus pubescens*, whereas ‘Mean temperature of wettest quarter’ (bio8) and ‘Precipitation of coldest quarter’ (bio19) contributed significantly to the ENM of *Quercus ilex* subsp. *ilex*.

The Mediterranean climate regime is notably characterised by a water deficit during the summer drought season. Interactions between drought and plant communities have been intensively debated (e.g., Carrión et al., 2010b; Maestre et al., 2005). Several studies on drought stress response patterns suggest a higher drought tolerance in evergreen

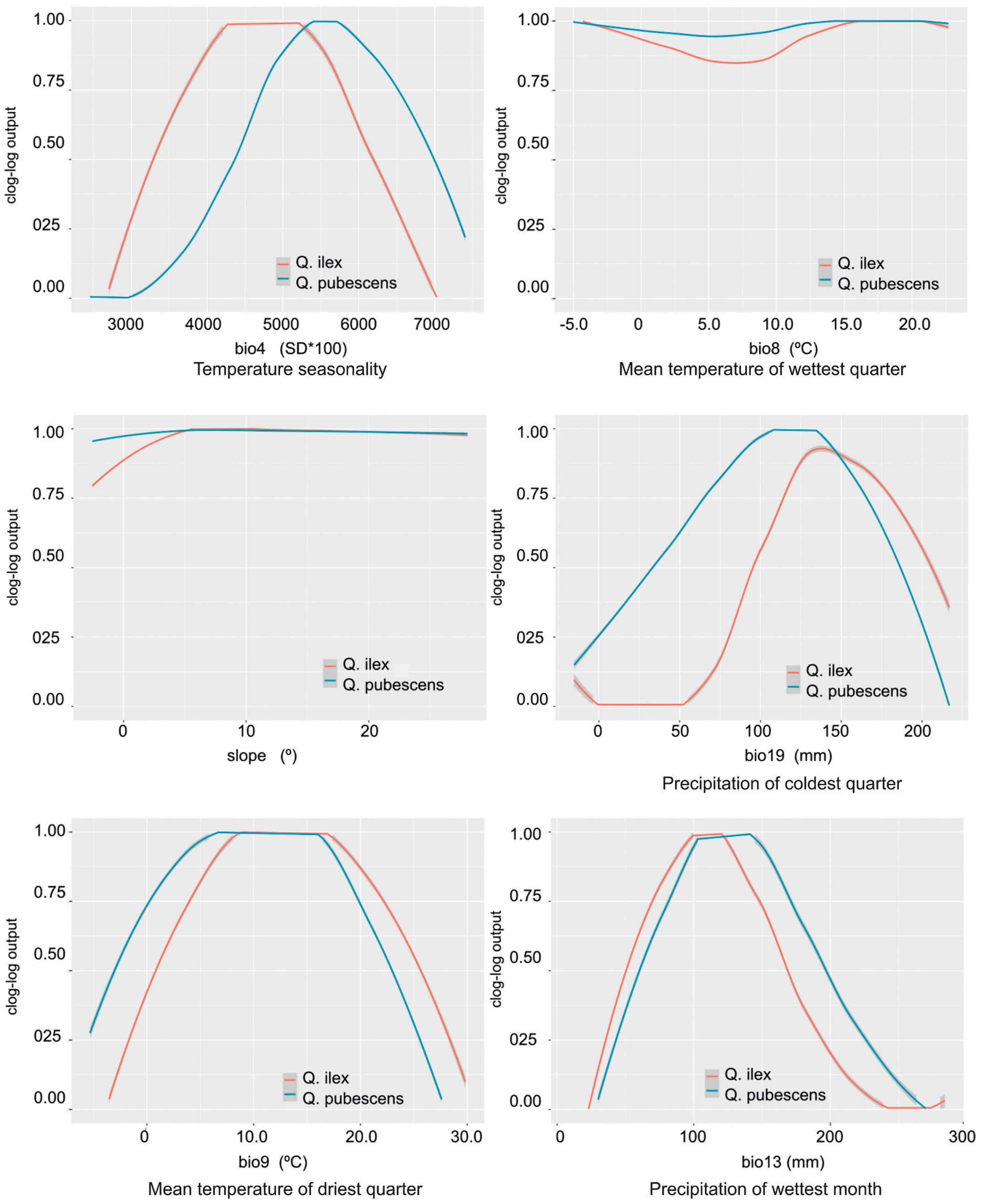

Fig. 5. Marginal response curve plots of the environmental variables used in MaxEnt related to *Quercus pubescens* and *Quercus ilex* subsp. *ilex*. The x-axis reflects the variation in value of the variable, and the y-axis reflects the probability of the species occurring in the study area.

than in deciduous oak species (e.g., Damesin et al., 1998; Mediavilla and Escudero, 2004; Vaz et al., 2010). Früchtenicht et al. (2018) suggested that the good performance of the two Mediterranean oak species during drought seasons could be a consequence of a better water supply achieved through a deeper root system. Furthermore, Madritsch et al. (2019) pointed out that there are individual-specific mechanisms that explain the differences in drought tolerance between evergreen and deciduous oak species, such as differences in specialized genes and proteins.

Quercus ilex has thin, deep, vertical roots, and water absorption depends mainly on the local precipitation regime (Baquedano and Castillo, 2007) as the species requires well-drained soils. This root mechanism, which reflects the probability of undergoing greater water stress in wet or rainy areas (Gea-Izquierdo et al., 2009), could explain the result obtained for the variable 'Precipitation during the wettest month' (bio13) (see Table 3). Thus, the high-water flow in the roots of *Quercus ilex*, especially in the dry season, may be one of the reasons for the high water requirements of the species. This may explain why the species does not occur in areas where water availability is low in the dry season. *Quercus pubescens* has a different strategy for its root system, which is mainly used for shallow water uptake and is relatively active in shallow soil layers, so it primarily depends on the kind of soil and slope conditions (Di Iorio et al., 2005) and is more efficient in water absorption at higher elevations. Furthermore, higher elevations could be related to cold conditions, as can be demonstrated by the high contribution for cold conditions (bio9). The slope variable does not contribute much to the ENM of *Quercus pubescens* and holds little importance, though elevation range was the most influential geographical variable for explaining the occurrence of the species.

The Iberian Peninsula is a region that has a wide range of climatic

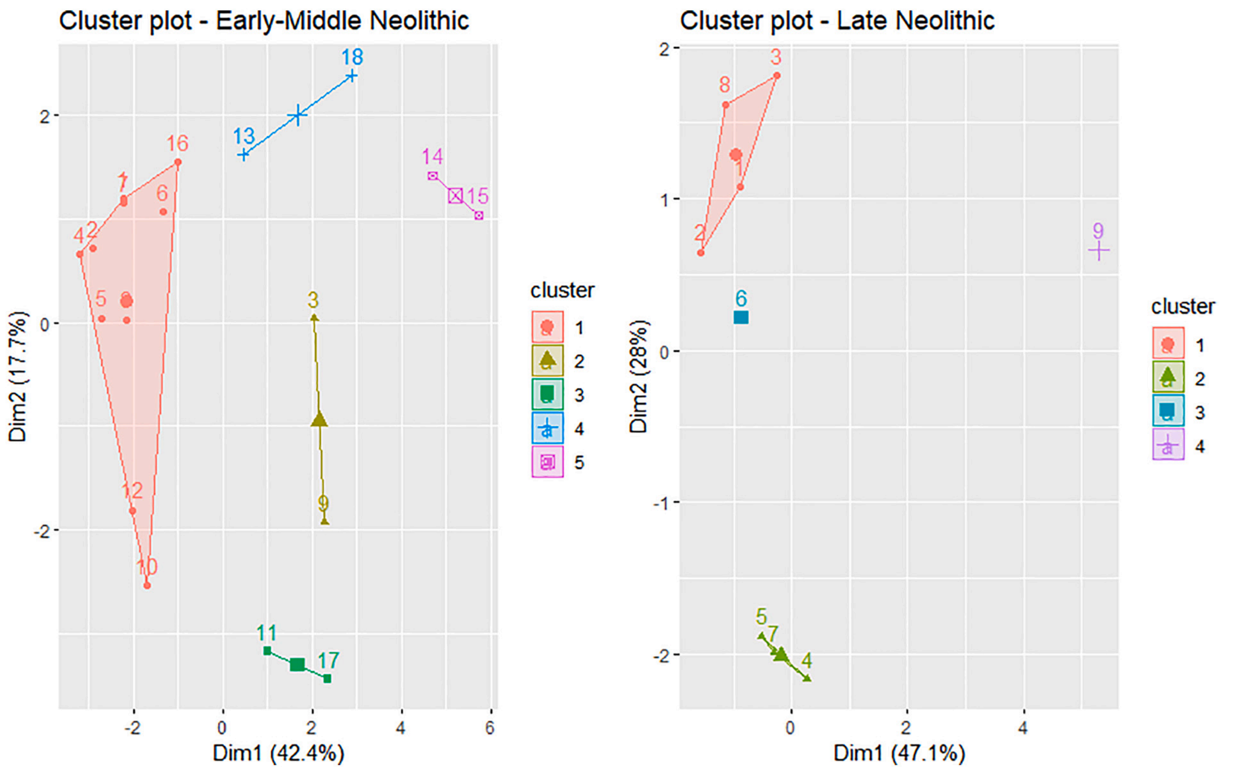

Fig. 6. Cluster plots according to anthracological data during the Middle Holocene. Early-Middle Neolithic: 1. La Draga; 2. Cova d'en Pau (III); 3. Cova 120 (III); 4. Bauma del Serrat Pont (III.4); 5. Plansallosa; 6. Cova de l'Avellaner; 7. Cova del Toll; 8. Cova del Frare; 9. Cova Bonica; 10. Can Sadurní; 11. La Serreta; 12. Cova de la Guineu (Id); 13. Camp del Colomer; 14. Balma Margineda; 15. Coves del Fem; 16. Cova Colomera; 17. Barranc d'en Fabra and 18. Cova del Vidre; Late Neolithic: 1. Cova 120 (II); 2. Bauma del Serrat Pont (III.3); 3. La Prunera; 4. Santa Maria dels Horts; 5. Cova de la Guineu (Ic); 6. Cova Gran de Santa Linya; 7. Auvelles; 8. Cova Colomera and 9. Roques del Sarró.

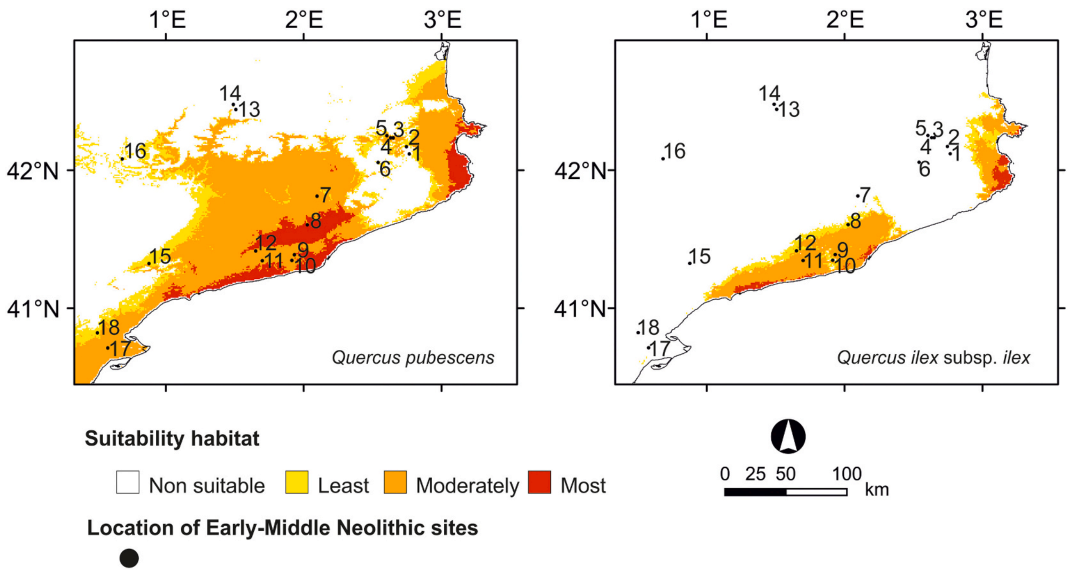

Fig. 7. Habitat suitability maps of A) *Quercus pubescens* and B) *Quercus ilex* subsp. *ilex* under a Middle Holocene climatic scenario of the NE Iberian Peninsula, and the locations of Early-Middle Neolithic sites with anthracological data. 1. La Draga; 2. Cova d'en Pau; 3. Cova 120; 4. Bauma del Serrat Pont; 5. Plansallosa; 6. Cova de l'Avellaner; 7. Cova del Toll; 8. Cova del Frare; 9. Cova Bonica; 10. Can Sadurní; 11. La Serreta; 12. Cova de la Guineu; 13. Camp del Colomer; 14. Balma Margineda; 15. Coves del Fem; 16. Cova Colomera; 17. Barranc d'en Fabra and 18. Cova del Vidre.

regionalisation due to its heterogeneous orography and geographical particularities (Rivas-Martínez, 1987). This complexity makes it necessary to be caution in assessing the importance of the environmental variables used in the two MaxEnt models, which respond mainly to bioclimatic factors. Presence-background methods compare the environmental conditions and geographical features of the study area with the conditions used by the species in order to distinguish between suitable and unsuitable habitats (Phillips et al., 2006). However, it is important to note that just because a habitat could be suitable, does not mean that the species would be present. And, conversely, just because a

Table 4
Results of predicted suitability values according to the coordinates (pixel) of the Neolithic sites that are included in this study. Period: Archaeological period; Group: Anthracological groups; Id: the site number as shown in Fig. 7 and Fig. 8.

Period	Group	Id	Site	*Q. pubescens* (value)	Suitability habitat	*Q. ilex* (value)	Suitability habitat
Early Neolithic	1	1	La Draga	0.21	Least	0	Non suitable
	1	2	Cova d'en Pau	0.22	Least	0	Non suitable
	2	3	Cova 120	0.39	Moderately	0	Non suitable
	1	4	Bauma del Serrat Pont	0.37	Moderately	0	Non suitable
	1	5	Plansallosa	0.36	Moderately	0	Non suitable
	1	6	Cova de l'Avellaner	0.22	Least	0	Non suitable
	1	7	Cova del Toll	0.56	Moderately	0	Non suitable
	1	8	Cova del Frare	0.77	Most	0.26	Least
	2	9	Cova Bonica	0.71	Most	0.45	Moderately
	1	10	Can Sadurní	0.29	Moderately	0.58	Moderately
	2	11	La Serreta	0.61	Moderately	0.42	Moderately
	1	12	Cova de la Guineu	0.54	Moderately	0.3	Moderately
	4	13	Camp del Colomer	0	Non suitable	0	Non suitable
	5	14	Balma Margineda	0	Non suitable	0	Non suitable
	5	15	Coves del Fem	0.25	Least	0	Non suitable
	1	16	Cova Colomera	0.22	Least	0	Non suitable
	3	17	Barranc d'en Fabra	0.36	Moderately	0	Non suitable
	4	18	Cova del Vidre	0.29	Moderately	0	Non suitable
Late Neolithic	1	1	Cova 120	0.39	Moderately	0	Non suitable
	1	2	Bauma del Serrat Pont	0.37	Moderately	0	Non suitable
	1	3	La Prunera	0.24	Least	0	Non suitable
	2	4	Santa Maria dels Horts	0.61	Moderately	0.46	Moderately
	2	5	Cova de la Guineu	0.54	Moderately	0.3	Moderately
	3	6	Cova Gran de Santa Linya	0.2	Least	0	Non suitable
	2	7	Auvelles	0	Non suitable	0	Non suitable
	1	8	Cova Colomera	0.22	Least	0	Non suitable
	4	9	Roques del Sarró	0	Non suitable	0	Non suitable

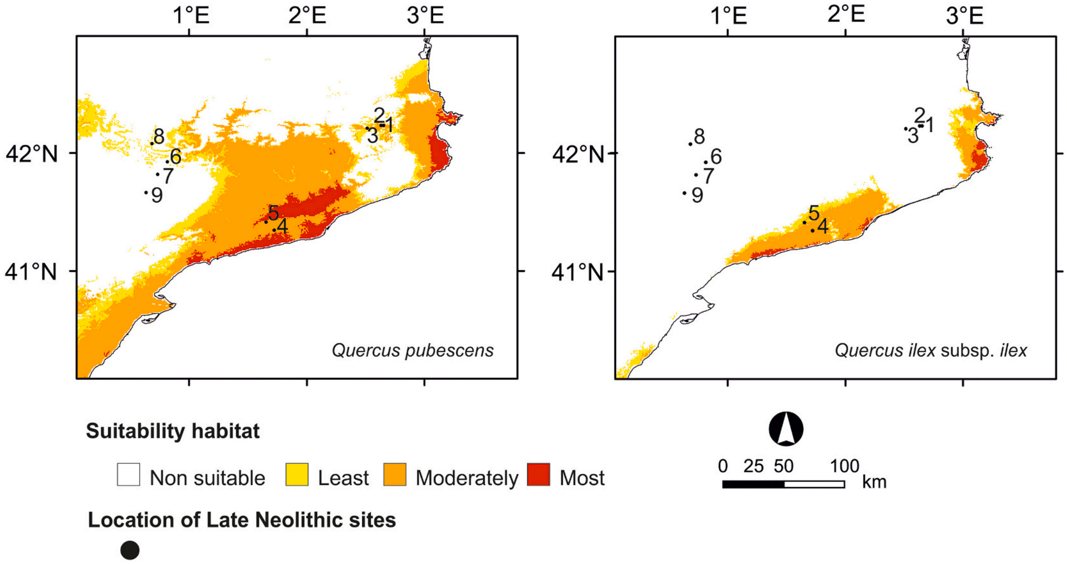

Fig. 8. Habitat suitability maps of A) *Quercus pubescens* and B) *Quercus ilex* subsp. *ilex* under a Middle Holocene climatic scenario in the NE Iberian Peninsula, and the locations of Late Neolithic sites with anthracological data. 1. Cova 120; 2. Bauma del Serrat Pont; 3. La Prunera; 4. Santa Maria dels Horts; 5. Cova de la Guineu; 6. Cova Gran de Santa Linya; 7. Auvelles; 8. Cova Colomera and 9. Roques del Sarró.

habitat could be unsuitable, does not mean that the species would be absent. Currently, many forested Mediterranean landscapes are in fact mosaics of habitats dominated by deciduous and evergreen oaks, with a mix of both species in many environments (e.g., Blondel et al., 1992; Dinerstein et al., 2017). Although it is certain that the dynamics of Mediterranean forests are complex and highly heterogeneous (e.g., Blondel et al., 2010; Burjachs et al., 2017; Carrión et al., 2010a; Di Rita et al., 2018; Médail and Diadema, 2009; Pausas and Keeley, 2009; Shachak et al., 2008), physical-environmental factors restrict their distribution and could limit the presence of certain dominant tree species (e.g., Newman et al., 2006; Pérez-Obiol et al., 2011; Warren and Seifert, 2011; Médail et al., 2019; Boonman et al., 2020;). Climatic changes have affected the precipitation regimes and drought conditions on different scales and under different conditions (e.g., Colville et al., 2020; González-Sampériz et al., 2017, 2020; Metzger et al., 2005; Uzquiano et al., 2016; Walker et al., 2018). Nevertheless, a local approach may be required to understand multifaceted vegetation histories.

In summary, our results have proved that MaxEnt models can effectively improve the accuracy of assessments of the function of the bioclimatic and geographical factors that may or may not be suitable for two Mediterranean oak species. The results have allowed us to evaluate how the potential distributions of these two oak formations could have been affected under the Middle Holocene climatic scenario in the NE Iberian Peninsula, and what form the relationships between human-plant communities may have taken.

5.2. Oak formations under the middle Holocene climatic scenario: An anthracological perspective (8.2– 4.2 ka BP)

Using MaxEnt, this study has provided, for the first time, two potential distribution maps for two sub-Mediterranean forest types (deciduous and evergreen oak woodlands) during the Middle Holocene in the NE Iberian Peninsula, in accordance with the palaeoclimatic reconstruction available on Worldclim.org (Fick and Hijmans, 2017). Our results showed that *Quercus pubescens* and *Quercus ilex* subsp. *ilex* have changed their suitable habitat ranges, probably in response to environmental conditions. Thus, during the Middle Holocene, the suitable area for *Quercus pubescens* may have been larger than that for *Quercus ilex* subsp. *ilex*. Our results showed that the suitability ranges on the central coast and in some southern areas may have been favourable for both species, although the suitable habitat for *Quercus pubesens* extended to the pre-coastal (pre-littoral) and inland areas.

Both the projected MaxEnt maps have distributions that overlap well with the sites, and they are both consistent with the anthracological groups that were obtained. These anthracological sequences indicate that deciduous oak woodlands were well established during the Neolithic period and had a certain degree of continuity. Additionally, the presence of sclerophyllous taxa indicates a tendency towards mixed oak forests in some locations. Moreover, our results have characterised five distinct vegetation formations, two of which were most exploited by Neolithic populations (group 1 and group 2). The first group of sites evidenced a plant community dominated by deciduous oak together with high frequencies of mesophilous taxa, mainly *Buxus sempervirens* and *Acer* sp. This landscape predominated during the Early to the Late Neolithic periods. All the archaeological sites included in this group are located within the habitat suitability range of *Quercus pubescens*. The climate was likely temperate and relatively humid in the vicinity of the inland Neolithic sites (Mas et al., 2022). Nevertheless, some of the Neolithic sites included in this group, such as Cova de la Guineu, Cova del Frare and Can Sadurní, are located near the central coast, in the least-moderately suitable habitat for *Quercus ilex* subsp. *ilex*. The development of Mediterranean vegetation is likely due to reduced precipitation and increased environmental aridity (Allué et al., 2009, 2017b; Carrión et al., 2007, 2010b; Pérez-Obiol et al., 2011). Based on this, some authors found a considerable increase in evergreen oak pollen in the coastal region and suggest that the spread of these trees could correspond to the onset of the Mediterranean climate (Jalut et al., 1997; Burjachs et al., 1997).

All the archaeological sites included in the second group are in the coastal area. The results of our models (see Table 3) demonstrate that these areas would delimit zones with lower and more irregular precipitation values (bio19 and bio13), as well as brusquer seasonal temperatures (bio9, bio8). As described in Section 4.2., the occurrence of *Quercus ilex* is more likely than that of *Quercus pubescens* in locations where seasonal precipitation has lower values (see Fig. 5). Montane conifers (*Pinus sylvestris*-type and *Taxus baccata*) and deciduous oak assemblages are characteristic of the fourth and the fifth groups of Neolithic sites. It is important to note that the anthracological data from these sites shows that both oaks either appear with low frequencies or are non-existent, and these sites are located far from highly suitable habitats. The high representation of conifers could be due to the fact that deciduous oak forests probably do not grow at high elevations where mountain pines are more likely to persist.

The anthracological sequences of Cova Colomera and Bauma del Serrat Pont include different Neolithic periods. However, the anthracological data showed that Neolithic populations would have selected mesophilic vegetation throughout the Neolithic. Furthermore, MaxEnt's results showed that the area around these sites was more suitable for deciduous oak than evergreen oak. The diachronic continuity of the landscape around these two sites suggests that the Neolithic activities in the vicinity may not have markedly affected the surrounding forest structure during the Early to Late Neolithic (e.g., Alcalde et al., 2005; Mas et al., 2022). In relation to these considerations, Alcalde et al. (2005) found archaeological evidence of short occupations at Bauma del Serrat del Pont. Moreover, Martín and Oms (2021) have suggested that Cova Colomera also seems to have been used seasonally by Neolithic groups for livestock practices, mainly the stabling of small herds for short periods.

The anthracological sequences of Cova 120 and Cova de la Guineu showed differences in the plant community between the Early Neolithic and the Late Neolithic. Hence, anthracological data of Cova 120 showed an increase in mesophilic vegetation during the Late Neolithic (from group 2 to group 1). Likewise, Cova de la Guineu showed more evergreen oak and thermophilic vegetation during the Late Neolithic (from group 1 to group 2). Moreover, MaxEnt's results suggested that the optimal environmental conditions for thermophilous vegetation and evergreen oak would not have occurred around Cova 120, as the area was not suitable for *Quercus ilex* subsp. *ilex*. In contrast, the area around Cova de la Guineu would have been moderately suited to both oak species. This is probably due to the environmental differences related to seasonality in these two areas, especially the different precipitation (bio13 and bio19) and temperature (bio4, bio8, and bio9) regimes. Our results are consistent with the fact that the aridity episode of the 8.2 ka BP event gave rise to a variety of responses in the NE Iberian Peninsula, as suggested by Revelles et al. (2015). These authors argued that the effect of the 8.2 ka BP event was mild or non-existent in some sub-Mediterranean regions, although it may have led to a drier environment in Mediterranean coastal areas and in high mountain areas. A key feature of this period could thus be the local seasonality of rainfall distribution, an important parameter that might explain the instability of Mediterranean landscapes (Berger and Guilaine, 2009). Moreover, regional climatic conditions, mainly the increase in aridity starting 4.2 ka BP (e.g., Allué et al., 2009, 2017b; Araus et al., 1997; Carrión et al., 2010a, 2010b) and the impact of human activities, would explain these diachronic changes in landscapes around these sites. These processes would favour an increase in shrub vegetation around Cova 120 with species such as *Buxus sempervirens* (temperate, humid area) and an increase in evergreen oaks and thermophilous vegetation in Cova de la Guineu (area with more seasonal climate and precipitation). Further studies related to forest management would definitely shed light on the impact of human activities on these vegetal formations (Delhon et al., 2009; Dufraisse et al., 2022).

Both the presence and the absence of different arboreal and shrubby species in Neolithic sites could be explained by the variations in local landscape composition and, in fact, environmental differences due primarily to aridity (Allué et al., 2009, 2017b). Additionally, the different strategies of wood gathering could be an important factor in interpreting plant associations (Kabukcu and Chabal, 2021). Therefore, we suggest that these associations could correspond to a local catchment area. As detailed above, the first and the second groups show the two types of woodlands that Neolithic human groups would have recurrently exploited. Both sub-Mediterranean deciduous oak and sclerophyllous woodland with evergreen oak were the most exploited landscapes in the NE Iberian Peninsula during the Middle Holocene. Nevertheless, montane pine forest (*Pinus sylvestris*, *Pinus uncinata* and *Pinus nigra*) was also harvested, although at a relatively reduced scale compared to oak. Our results show a good overlap between the two oak ENMs and the Neolithic sites that provided the anthracological data. This could be evidence that forest resources were exploited in locations close to settlements during the Neolithic, as some authors have suggested (e.g., Piqué et al., 2021). Wood harvesting is an activity that depends on social and economic contexts, and activities related to wood exploitation and forest management were probably partly conditioned by the environment.

6. Conclusions

Using MaxEnt, this study provides ecological niche models (ENM) for two oak species, the pubescent oak (*Quercus pubescens* Willd.) and the holm oak (*Quercus ilex* subsp. *ilex*), at present in the Iberian Peninsula and under the Middle Holocene climatic scenario in the NE Iberian Peninsula. Differences between suitable habitats for the two oak species seem to be due to different environmental tolerances. Seasonal temperature factors and seasonal rainfall are influential bioclimatic variables for the occurrence of both species, whereas geographical factors are not highly significant. Based on anthracological data from the Neolithic, we have distinguished five main plant associations in which Neolithic populations recurrently exploited forest resources. This study suggests that the Neolithic populations in the study area were largely dependent on resources from the forest, mainly deciduous oak forest with mesophilous taxa, and from Mediterranean oak forest. Finally, the results obtained in the potential oak palaeo-vegetation maps demonstrate a good overlap with the locations of the Neolithic sites analysed. Thus, Neolithic human groups that settled in open air sites and took advantage of caves and rock shelters to pursue their specialized activities were well aware of the potential of forests and probably gathered woody resources in the surrounding area. We found that the use of MaxEnt models improved our understanding of how climate dynamics might affect local patterns of vegetation distribution. We also highlight the importance of modelling palaeolandscape maps in order to shed light into human-environment interactions.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Bàrbara Mas reports financial support was provided by University of Barcelona. Santiago Riera reports financial support was provided by University of Barcelona. Ethel Allué reports financial support was provided by Catalan Institute of Human Paleo-Ecology and Social Evolution.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

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