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Applying the UDA-ODA discrimination technique to a herpetological association: the case of the Middle Palaeolithic site of El Salt (Alcoi, Spain)

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Abstract

El Salt (Middle Palaeolithic; Alcoi, Spain) is a key site for understanding the disappearance of Neanderthals in the eastern Iberian Peninsula, a process that is observed along its stratigraphic sequence. To improve our understanding of the palaeoclimatic context in which this process took place, we applied the UDA-ODA discrimination technique to the fossil herpetological assemblages from Stratigraphic Units (SU) Xb (52.3 ± 4.6 ka) and V ($45.2 \pm 3.4/44.7 \pm 3.4$ ka). This method is based in the application of an ecological criterion, the maximum altitude of each species on each Iberian range, to discern and remove those areas that do not meet their ecological requirements (UDA) from those that do (ODA), which are included in its distribution from Atlases from which the common distribution species is going to be extracted. Results indicate the existence of an alternation between "cold and wet" moments with "warm and dry" ones, all of them in a more humid context than nowadays. Climate was slightly warmer than nowadays in SU Xb, whereas was cooler in SU V. Regarding MAP, our results show less variation between SUs than it has been provided by previous studies. These results do not fully agree with those provided by small mammals from the same SUs, which indicate an increase of the temperatures whereas rainfall experienced the contrary. These differences could be related with the wider distribution of the Iberian herpetofauna, and some differences in the applied ecological criterion. Furthermore, herpetofaunal palaeoclimatic reconstruction shows that the abandonment of the site by Neanderthals seems to have occurred during an arid phase.

Keywords Palaeoclimate · Late Pleistocene · Iberian Peninsula · Neanderthal disappearance · GIS · MER method

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Introduction

The use of fossil assemblages to propose palaeoclimatic reconstruction has been a constant since the very beginning of palaeontological studies (Blain et al. 2018). Biological communities are not independent of the abiotic components (Birks et al. 2010). As a consequence of the changes and variations of these components, the composition and structure of the biological communities change along the time (Grayson 1981). In this sense, several works have demonstrated the effects of the present impact that the current global climatic change is leading in many biological communities (i.e. Araújo et al. 2006; Feehan et al. 2009; Moreno-Rueda et al. 2012; Sherwin et al. 2013; Enriquez-Urzelai et al. 2019). Of course, these changes are observable on the fossil record too (Willis et al. 2010). This "climatic response" and the current existence of modern relatives for calibration purposes allow the use of fossil remains as palaeoclimatic proxies in accordance to the requirements proposed by Bradley (1999).

Two main groups can be distinguished in the palaeoclimate reconstruction methods based on biological samples: (i) qualitative methods and (ii) quantitative methods (Birks et al. 2010). In the first group, the palaeoclimatic reconstructions are presented in descriptive concerning temperature (warm, cold, polar) and precipitation regimes (wet or dry), without providing a numerical valuation to eliminate the ambiguity inherent in these descriptions (Porch 2010). The second group includes those that provide direct values to infer past environments. Different quantitative methods have been developed for the reconstruction of past Quaternary climate using fossil faunal assemblages (Hernández Fernández and Peláez-Campomanes 2003; Royer et al. 2020). One of them, the Mutual Climatic Range (MCR), was outlined by Atkinson et al. (1986, 1987). It is based in the assumption that a particular species has a known climatic tolerance range, thus if this species was present at a site in the past because the climatic conditions were included within its tolerance limits. Likewise, it is supposed that for a determinate biological assemblage, the palaeoclimate conditions must have situated in the combined climatic tolerance range of all the assemblage. MCR has been applied to a wide range of organisms, such as insects (Atkinson et al., 1986, 1987; Coope, 1994; Elias, 1994, 1997, 2001; Coope et al., 1998; Elias et al., 1999; Miller and Elias, 2000; Alfimov and Berman, 2009), plants (Sinka and Atkinson, 1999; Pross et al., 2000; Thompson et al., 2012), terrestrial mollusc (Moine et al., 2002) and ostracods (Horne, 2007; Horne et al., 2012). Blain (2009) proposed a modification of the MCR methodology by using the current geographical distribution of the fossil assemblage to extrapolate the palaeoclimatic conditions to the palaeontological/archaeological site studied (Fig. 1). Because MCR methodology is based in the climatic co-ocurrence of species assemblages, and not with the geographic sympatry area, Lyman (2016) proposed renaming the technique outlined by Blain (2009) such as UTM-MCR. In this way, Blain et al. (2016) proposed the new name of Mutual Ecogeographic Range (MER) method. We prefer the second name by two reasons. Firstly, MER is a more intuitive name for a technique based on current geographical area occupied for a determined species. Secondly, the term MER has been used yet in various works (i.e. Blain et al. 2018 and references therein). Regarding small vertebrates, MER method has been used with birds (Núñez-Lahuerta et al. 2016), herpetofauna (Blain, 2009; Blain et al. 2009, 2013, in which the authors named the method as MCR; Marquina-Blasco et al. 2017, 2021a), small mammals (López-García et al. 2014, 2011; Fagoaga et al. 2018; Fernández-García et al., 2020; Álvarez-Vena et al., 2020) and a combination of the two latter (López-García et al. 2014, 2021; Rey-Rodríguez et al. 2016; Connolly et al. 2019).

Several authors have already enumerated the weaknesses (and strengths) of the major approaches used to reconstruct past climate from biological proxies (e.g. Birks et al. 2010; Lobo et al. 2016; Lyman 2017). As advantages, the MCR and, by extension, MER methodology do not need sophisticated mathematical apparatus and the availability of an important database on the current distribution area of species (at least in the case of vertebrates) neither a significant amount of climatic data (Alfimov and Berman 2009). Moreover, MER method, rather than other methods, is an easier tool for calculating climate parameters because it allows to do so only with superimposition of distribution maps in a GIS environment (Fagoaga et al. 2019a). As many other methods, the MER method follows actualism, because it relies on the current distribution of the species, assuming that the fossil representatives of the extant species have the same climatic tolerances and preferences as their living counterparts. However, there are known examples of species that have experienced a disruption of their ecological niche during their natural history, i.e. *Microtus cabrerae* (Castellanos-Frías et al. 2018). It supposes a potential losing of climatic conditions historically favourable for the studied taxon due to probable extirpation of specialized lineages (Stewart 2009). Unfortunately, it is a limit inhered to the palaeoclimatic reconstructions that must be assumed. In the case of taxa with a distribution area strongly modified by human activity (i.e. *Microtus cabrerae* and *Testudo* (*Chersine*) *hermanni*), they are not considered in the analysis (Fagoaga et al., 2018). Another problem related to this method is the possible absence of current biological communities analogous to the fossil

Fig. 1 Schematic explanation of the Mutual Ecogeographic Range (MER) method, which is based in the detection of the current common distribution area of a determined fossil assemblage

Distribution area species A

Distribution area species B

Common distribution area
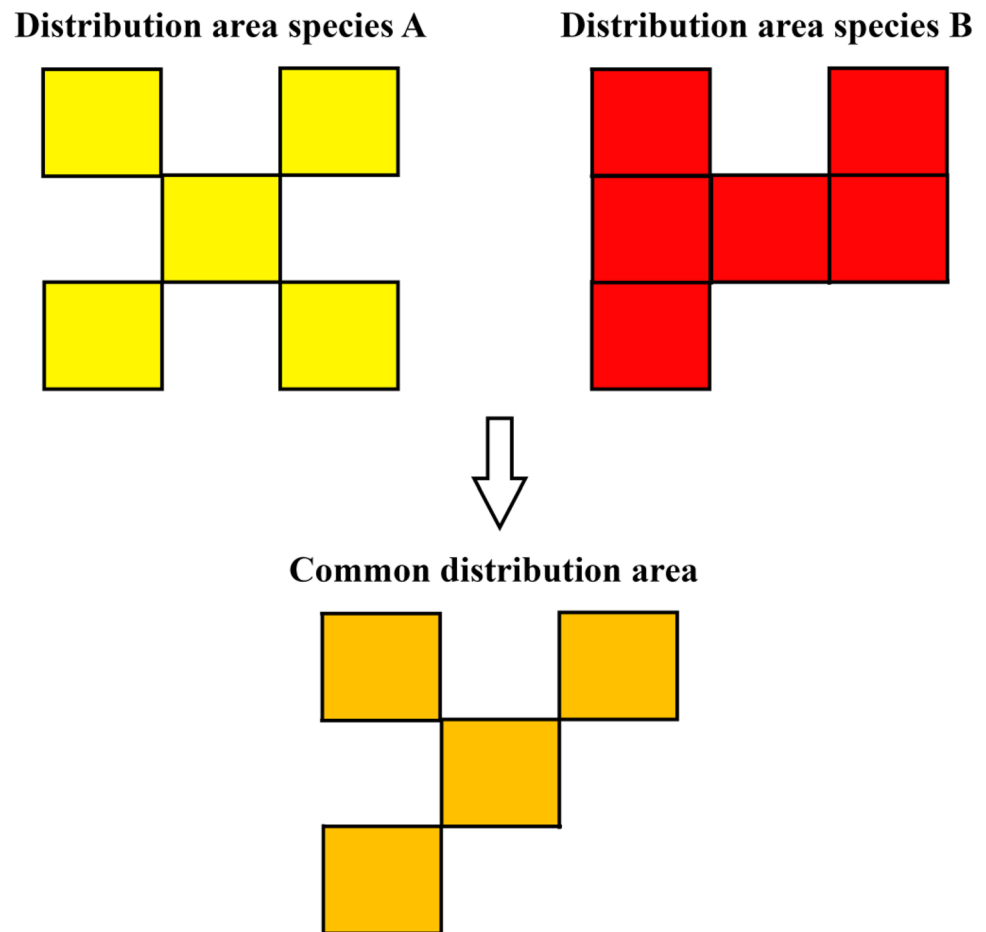
one (Birks et al. 2010). These non-analogue communities represent biological assemblages that were sympatric or coexisted in the past but today are allopatric or do not co-occur in an area or habitat (Lyman, 2017). These are the result of the individualistic response of species populations to environmental change, and the degree of its record increase with greater time depth (Stewart 2009). Guiot and Vernal (2007) proposed the use of the most similar assemblage as a possible solution to this trouble. Another assumption when applying this method is that the current distribution of species is exclusively determined by climatic parameters, omitting other factors as interspecific interactions (MacArthur, 1984; Chesson, 2000; Chave et al., 2002) and historical factors, i.e. geographical barriers (Morales Martín and Lizana Aria, 2011). Thus, the current distribution area of the species rarely coincides with its potential distribution area (Morales Martín and Lizana Aria, 2011). One of the requirements for the application of MER method is that the current distribution of the defined species may be well known. In general, it can be considered that the degree of knowledge of present distribution area of vertebrates in Spain is high, due to the existence of numerous atlases of different geographical

levels and several citizen science projects, focused mainly in herpetofauna (AHE, 2021) and birds (SEO/Birdlife, 2018). Unfortunately, the databases of distribution area of species (i.e. national atlases of herpetofauna) are based on unnatural units, 10×10 km UTM square grids (Pleguezuelos et al. 2002; Loureiro et al. 2018; AHE, 2021). This artefact strongly affects the validity of the palaeoclimatic reconstruction (Martínez-Solano and Sanchiz, 2005; Fagoaga et al. 2019a). The surface occupied by each unit (100 km^2) could include areas with a strong topographical heterogeneity (Martínez-Solano and Sanchiz, 2005; Fagoaga et al. 2019a). In topographically diverse regions such as Iberian Peninsula (Font Tullot 2000), climatic conditions vary significantly between geographically proximate locations. Moreover, species are not present everywhere within the 100 km^2 of the UTM square because not all of the territory respond to the ecological needs of these (Fagoaga et al. 2019a). In this sense, the use of the territory by a species depends on the environmental context and by the interactions established among co-occurring taxa. As a result, we could be introducing bias into our palaeoclimatic reconstruction by including areas (and its climatic values) where some species could not be present

(Fagoaga et al. 2019a). To improve the accuracy of the palaeoclimatic reconstruction derived from MER method, Fagoaga et al. (2019a) define the UDA-ODA discrimination technique. Basically, this new method is based in the application of an ecological criterion for the discrimination of Occupation Distribution Areas (ODA), where in theory the species is present, from those where its presence is highly doubtful, the Uncertain Distribution Area (UDA) (Fig. 2). Although Fagoaga et al. (2019a) consider it a method totally distinct to MER method, actually both are a different approach of the same strategy: the search of the common distribution area of a given fossil biological assemblage. As Kothari (2004) denotes, methods are more general, given the theorical framework (search of common distribution area, that is MER) for the development of different behaviours and instruments to perform research (application of an ecological criterion to record the climatic data). Despite the fact that this discussion may seem trivial, in reality the definition and distinction

of the methods and techniques developed are key tools for the correct development of scientific knowledge. Failure to do this step correctly could lead to robust methods and techniques being discarded due to confusion generated by the incorrect use of terminology (Lyman, 2016).

It has long recognized that the evolution of the climate has a crucial impact in the natural history of humans and, for that reason, palaeoclimatic reconstructions feature prominently in palaeoanthropological debates (Haywood et al. 2019). In this sense, the disappearance process of the Neanderthals has been focused from this topic. This event took place during Marine Isotope Stage (MIS) 3 (ca. 30–60 ka in accordance with Railsback et al. (2015)) (e.g. Mellars 2004; Sepulchre et al. 2007; Jennings et al. 2011; Mallol et al. 2012). This was an unstable climatic period in the Late Pleistocene that was characterized by alternating warm phases with expanding forests and cold phases when semi-arid areas developed (e.g. Moreno et al., 2002; Sánchez-Goñi and Fletcher 2005; Fletcher and Sánchez-Goñi 2008). The reason/s behind the

Fig. 2 Schematic explanation of the UDA-ODA discrimination technique, which is based in the application of an ecological criterion for the discrimination of the occupied areas (ODA) by a determined species from those of uncertain distribution (UDA), which does not accomplish with the ecological requisites of this species. After this discrimination, the method detects the current common ODA of a fossil assemblage
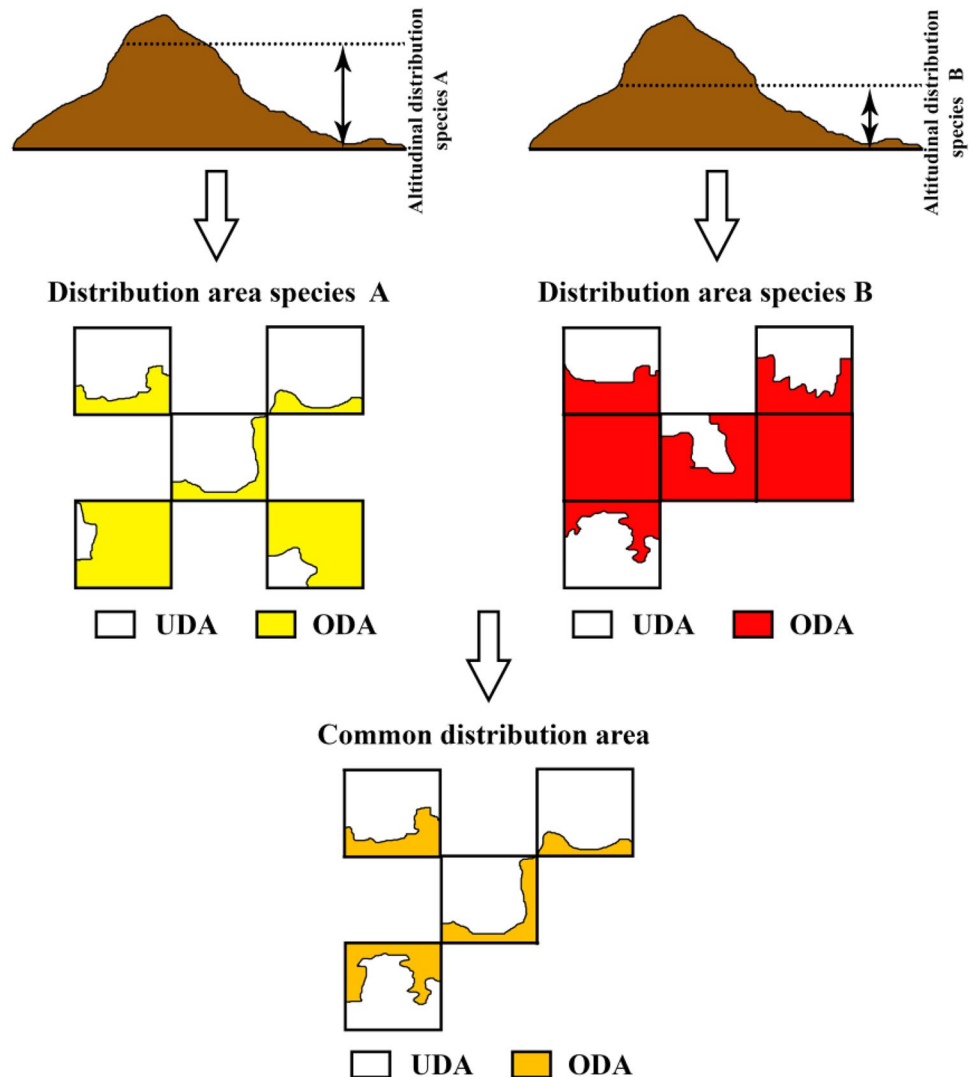
demise of the Neanderthals is an unresolved debate in the scientific community. Although numerous hypotheses have been proposed to explain this event, these can be grouped in three categories (Vaesen et al. 2021). The first one is related with the migration of anatomically modern humans (AMH) in Europe, which competed with the Neanderthals for the resources and, finally, the last was replaced by the first (Mellars 2004). However, due to the scarcity of human remains in Late Pleistocene sites of the Iberian Peninsula (Strauss 2018), direct contact between both human groups is hard to demonstrate (Vaquero et al. 2006; Mallol et al. 2012). Thus, this contact has been mainly based only on lithic tools. However, the lithic assemblages corresponding to this complex phase are scarce and, on many occasions, not very diagnostic. On the other hand, they are not associated with human remains that allow us to recognize their authorship with precision. Moreover, there are several problems related to the proposed dates for the contact between both human groups in several Iberian sites. As Wood et al. (2013) pointed out, the studied period is close to the practical limit for radiocarbon dating; postdepositional disturbance processes on dated elements and archaeological evidences cannot be discarded; diagnostic elements in the lithic assemblage are lacking; and finally, some proposed radiocarbon dates are inaccurate due to the use of inadequate pretreatment protocols. The second group of hypotheses are related to the apparent small size of Neanderthal populations and the limited interconnectedness between them (Vaesen et al. 2021). These particularities would have made them highly susceptible to inbreeding, Allee effects and stochastic fluctuations (Finlayson 2004; Vaesen et al. 2019). Finally, the third group points out that the demise of Neanderthals was related with environmental factors, i.e. climate change (Bradtmöller et al. 2012). During its existence, Neanderthals were highly influenced by climate, reaching its northernmost limit during warm episodes (Stewart 2005). Although at the beginning of the MIS 3, Neanderthals were widespread around Europe, and their distribution range was gradually shrinking towards the south (Stewart 2009). The present consensus establishes that the final demise of Neanderthals took place at Iberian Peninsula probably during Heinrich Event (HE) 4 (*ca.* 40.2–38.3 ka) (Bradtmöller et al. 2012) or just before its onset (*ca.* 40.2 ka) (Wood et al. 2013; Galván et al. 2014; Wolf et al. 2018). In Mediterranean coastal areas, severe aridity episodes have been detected during this HE (Sepulchre et al. 2007); however, at least for the interior area of the Iberian Peninsula, the mentioned climate deterioration does not seem to have coincided with HE 4, 42 ka (Wolf et al. 2018). In any case, the process of disappearance of the Neanderthals seems to have initially taken place in the interior of the peninsula and later in coastal areas (Finlayson, 2004).

The Central Spanish Mediterranean coastal region has yielded numerous Middle Palaeolithic sites (Eixea et al. 2020). Among them, El Salt site (Alcoi, Spain) is a key locality for studying the disappearance of Neanderthals in the region. Its high value lies in the fact that the archaeological sequence of El Salt records different occupation phases, in which a transition from recurrent to sporadic human occupation (and finally, an abandonment of the site) has been identified (Galván et al. 2014). Moreover, El Salt yielded six Neanderthal teeth, possibly belonging to an individual from one of the last groups in the region (Garralda et al. 2014). Multidisciplinary studies of the site allowed to establish and interpret the climatic evolution at local level in the southeastern Iberian Peninsula during the Middle Palaeolithic and the possible impact on the local palaeoecology and, therefore, on the human populations inhabiting the area. In this sense, the study of the small vertebrates assemblages from El Salt has been focused on this topic (Marquina-Blasco et al. 2017, 2021a; Fagoaga et al. 2018, 2019a, b). Until now, the majority of these works has been based on the application of MER method (Marquina-Blasco et al. 2017, 2021a; Fagoaga et al. 2018, 2019b), with its inherent limitations already discussed above. Later, Fagoaga et al. (2019a) developed and applied the UDA-ODA discrimination technique to the small mammal assemblages provided by Stratigraphical Unit (SU) Xb and V from El Salt site. Thus, the aim of this study is to reconstruct the environmental conditions prevailing in SU Xb and V from El Salt site, based on the application of this technique on the amphibian and reptiles assemblages recovered from both SUs for the first time to this kind of fauna. Our results are discussed with previous works of palaeoclimatic reconstruction based on small vertebrates and other proxies from El Salt (Gómez de la Rúa et al. 2010; Vidal-Matutano 2016; Marquina-Blasco et al. 2017, 2021a; Fagoaga et al. 2018, 2019a, b; Vidal-Matutano et al. 2018; Leierer et al. 2019). In addition, we contextualize our results with the debate about the disappearance of Neanderthals, focusing on the ecological context in which these events occurred.

Geological setting

The Middle Palaeolithic site of El Salt (Alcoi, Alicante) (38°41′12.57″N; 0°30′33.16″W) (Fig. 3) rests against a 38-m-high Paleocene limestone wall at 680 m above sea level. The wall is the result of a trust fault of Eocene limestone over Paleocene conglomerates. At the upper part of the wall, the course of the Barxell River was stopped by the presence of the limestone, creating a palaeolake that outflowed over the fault. As a result, a large travertinic building was created along more than 2.5 km in the foothills of the Serra de Mariola (Galván et al. 2014).

The sedimentary sequence of the site consists of thirteen lithostratigraphic units (Fumanal 1994) grouped into five
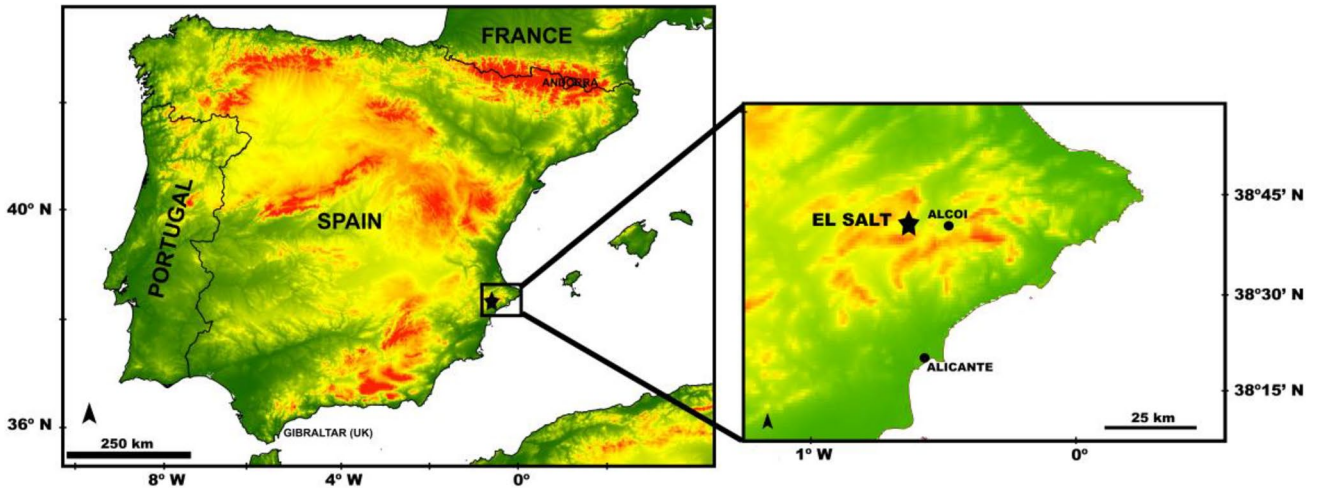
Fig. 3 Geographic location of the El Salt site (black star) in the Iberian Peninsula

segments, in basis of its macroscopic textural appearance and archaeological context (Galván et al. 2014) (Fig. 4). From base to top:

- SU XIII: subtravertine platform of unknown thickness. Its top has been dated by U/Th as 81.5 ± 2.7 ka

Fig. 4 Lithostratigraphic column of El Salt showing the different Stratigraphic Units (SU) described by Fumanal (1994), lithology of each SU and its proposed datation (Galván et al., 2014). Modified from Garralda et al. (2014)
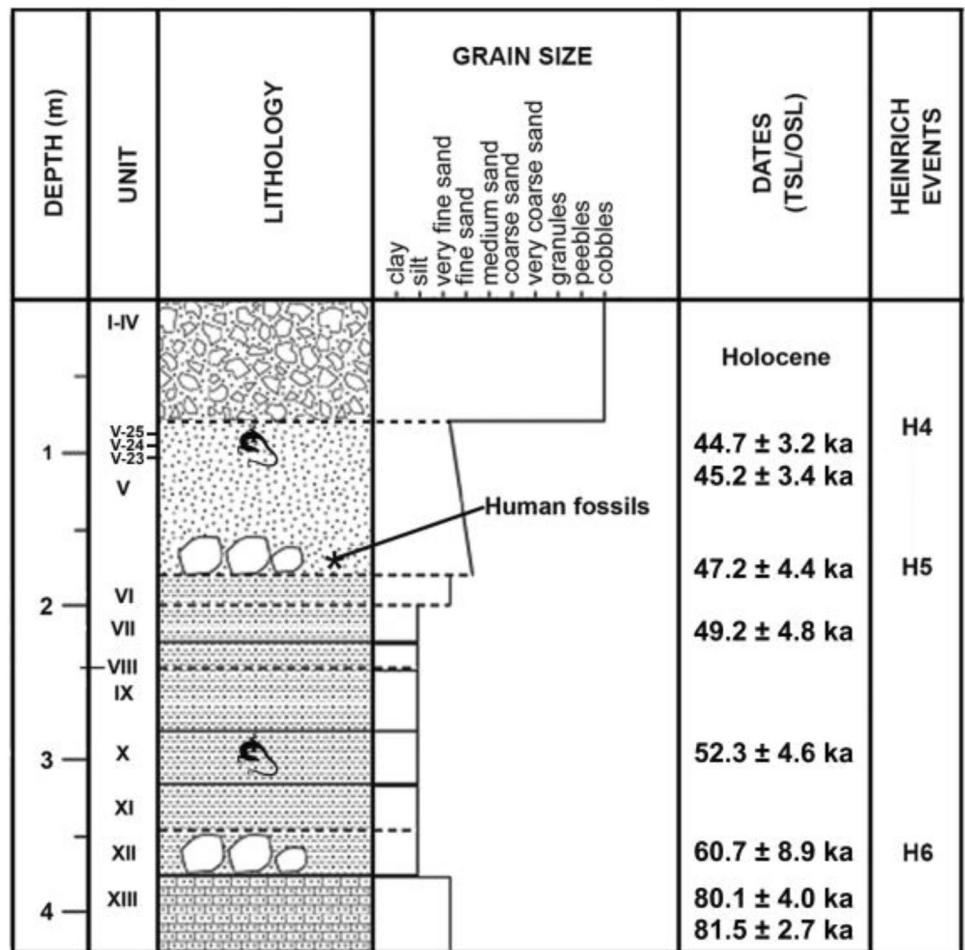
Amphibians and reptiles remains

and 80.1 $\pm$ 4 ka (MIS 5a- ca. 82–71 ka) (Galván et al. 2014). This SU is sterile from an archaeological point of view.

- SU XII to IX: these units consist of 1.5 m of horizontally bedded fine sand, with several large blocks at their base and related to a first episode of roof collapse (Galván et al. 2014). This part of the sequence has been dated, using thermoluminescence (TL), as 60.7 $\pm$ 8.9 ka (SU XII) and 52.3 $\pm$ 4.6 ka (SU X) (Galván et al. 2014), placing the sequence at the beginning of MIS 3, before event HE 5 (Galván et al. 2014). These SUs contain the highest concentration of archaeological remains and combustion features within the entire sequence.

- SU VIII to V: in this sequence, a gradual decrease of human occupation evidences is recorded that ends quite spatially reduced. SU VI is covered by a significant accumulation of large blocks, produced by the collapse of the roof of the travertine structure. Six Neanderthal teeth attributed to a juvenile or young adult were recovered from the base of SU V (Garralda et al. 2014). These remains may represent one of the last occurrences of Neanderthals in the region (Garralda et al. 2014). The top of SU VI has been dated by TL as 47.2 $\pm$ 4.4 ka. SU V shows two parts distinguishable on the basis of their macroscopic textural features (Galván et al., 2014). Thus, the lower SU V is formed by the horizontal accumulation of a predominantly geogenic sandy sediment. It has been dated by optically stimulated luminescence (OSL) as 45.2 $\pm$ 3.4 ka (Galván et al. 2014). The upper part of SU V consists of a 50-cm-thick layer, truncated by a Holocene erosive episode. It is constituted by massive sandy silt with heterogeneous gravel in the top 20 cm, from which two small flint blades, a few undifferentiated flakes, and a small combustion structure have been recovered (Garralda et al. 2014). The top of the SU V has been dated by OSL as 44.7 $\pm$ 3.2 ka, before HE 4 (40.2–38.3 ka) (Galván et al. 2014).

- SU IV to I: gravelly deposit with a 1.3-m-thick stratigraphic segment constituted by a stratified succession of channels filled with different beds of gravelly sands with cobbles, separated by sharp erosional contacts. Neolithic pottery mixed with late Upper Palaeolithic, Epipalaeolithic and Mesolithic lithic remains indicates that this deposit is of Holocene age (Galván et al. 2014). This together with the biochronological contradiction of the recovered small vertebrate fauna (presence of *Microtus arvalis*, extirpated in the region at the end of the Late Pleistocene) denotes reworked episode/s of this deposit (Fagoaga et al. 2021).

Table 1 Faunal list from Stratigraphic Unit Xb (Marquina-Blasco et al. 2017) and V (Marquina-Blasco et al. 2021) from El Salt. 1: presence; 0: absence

	Xb	V		
	11		24	25
	S3	S9	S8	S7	–
Pelodytes sp.	0	1	0	0	0
Alytes obstetricans	1	1	1	1	1
Epidalea calamita	1	1	1	1	1
Bufo bufo s. l.	1	0	0	0	0
Blanus cinereus s. l.	1	0	0	0	0
Chalcides bedriagai	1	1	1	1	1
Lacertidae indet	0	1	1	1	1
cf. *Acanthodactylus erythrurus*	1	0	0	0	0
Colubridae indet	0	1	1	1	0
Coronella sp.	0	1	0	1	0
Coronella sp./*Zamenis* sp.	0	1	0	0	0
cf. *Zamenis scalaris*	1	0	0	0	0
Natrix maura	0	0	1	0	0
Vipera latastei	0	1	0	1	0

Material, methods and abbreviations

To conduct the palaeoclimatic reconstruction, we apply the UDA-ODA discrimination technique (Fagoaga et al. 2019a) on the amphibians and reptiles assemblage from SU Xb (Xb-11 S3) and two different segments of the SU V: V-24 (surfaces (S) 7, 8 and 9) and V-25 (Table 1). The study of these samples allows us to compare a moment of recurrent anthropological occupation of the site (SU Xb) with the context of human disappearance recorded in SU V. The faunal list of the analyzed assemblages has been taken from Marquina-Blasco et al. (2017, 2021a). This method is based on the application of an ecological criterion to distinguish those areas that are ecologically habitable for each species (ODA) from those that, in principle, lack the necessary requirements for use by the taxon (UDA). After this, the method searches the modern biogeographic co-occurrence of the ODAs of species described in a palaeontological or archaeological site. As discrimination factor, we have used elevation for each species. The choice of this criterion was based on several points: (i) ease of implementing this information in Geographic Information Systems (GIS); (ii) existence at Spanish level, and to a lesser extent in Portugal, of distribution atlases with altitudinal distribution information on herpetofauna at various administrative levels: national (i.e. Pleguezuelos et al. 2002;

Loureiro et al. 2008), regional (i.e. Bea 1985; Llorente et al. 1995), provincial (i.e. Pérez-Mellado 1983; Barberá et al. 1999), protected areas (i.e. Santos et al. 2005; Domínguez et al. 2012) and even particular mountainous systems (Martínez-Rica 1983; Lizana et al. 1988); (iii) altitudinal distribution of Iberian reptile and amphibian species is relatively well known; (iv) in the case of Iberian reptiles, the maximum altitude reached by species is a better discriminant than mean altitude when performing a biogeographical analysis (Saint Girons 1982); and (v) altitude is a very important factor in explaining the distribution of amphibians and, especially, reptiles due to its clear effect on temperature and precipitation (Soares and Brito 2007).

We have considered here the entire Iberian Peninsula, an area with natural geographical limits. The choice of this analytical unit is also supported by the fact that some species that could potentially appear in the site are Iberian endemisms (e.g. *Chalcides bedriagai*). The biogeographic cartography of amphibians and reptiles for Spain is provided by the Servidor de Información de Anfibios y Reptiles de España (SIARE) (AHE 2021); for Portugal, it is provided by Loureiro et al. (2008). Both sources show the distribution of each species in UTM grids of 10×10 km. The discriminatory criterion described above is applied to these to differentiate between ODA and UDA. Using ArcGis 9.1®, the climatic parameters are estimated by overlapping the co-occurrence areas and the current climate layers with a 30-arcsecond resolution grid from WorldClim 1.4 (Hijmans et al. 2005). Both sets of data (co-occurrence areas and climate layers) are represented in the same spatial reference system (EPSG 4326, WGS 84 UTM datum coordinate projection system). The bioclimatic parameters extracted from the cartography supplied by Hijmans et al. (2005) are BIO 1 (mean annual temperature, MAT), BIO 5 (maximum temperature of the warmest month, MaxTW), BIO 6 (minimum temperature of the coldest month, MinTC) and BIO 12 (annual precipitation, MAP).

The abbreviations used in this text are as follows: AHE (Asociación Herpetológica Española); AMH (anatomically modern humans); CV (Coefficient of Variation); HE (Heinrich Event); MAT (mean annual temperature); MAP (mean annual precipitation); MCR (Mutual Climatic Range); MER (Mutual Ecogeographic Range method); MIS (marine isotope stage); MinTC (minimum temperature of the coldest month); MaxTW (maximum temperature of the warmest month); ODA (Occupied Distribution Area); S (excavation surface); SIARE (Servidor de Información de Anfibios y Reptiles de España); SU (Stratigraphic Unit); TL (thermoluminescence dating method); UDA (Uncertain Distribution Area), σ (Standard Deviation).

Results

Altitudinal range of the target species

A total of 89 works have been evaluated for the determination of the altitudinal range in the mountain range of the herpetological species included in the assemblage of SU Xb and V from El Salt site. The detailed list of these references, which include papers, books, atlases, field guides and technical reports, is included in Supplementary Material 1. The obtained results show an increase in the maximum height from North to the South (Table 2), except for *Alytes obstetricans* s. l., which reaches higher altitude in the Pyrenees than other southern ranges, i.e. Iberian and Central Range. Table 2 summarizes the maximum altitude reached by each species in every mountain system in the Iberian Peninsula. The detailed information about it is included in Supplementary Material 2.

Method comparison per variable and species

The application of the *T*-test for independent samples of each climatic parameter (MAT, MinTC, MaxTW and MAP) in each species determined in the herpetofaunal assemblage from El Salt shows significant differences between ODA and UDA ($p < 0.01$) (Table 3). ODA shows higher mean values for those climatic parameters related with temperatures (MAT, MinTC and MaxTW) than UDA; regarding MAP, UDA had higher mean values than ODA (Table 3).

Method comparison per variable and assemblage

As the above case, the *T*-test for independent samples for all assemblages and bioclimatic parameters analyzed shows significant differences within ODA and UDA ($p < 0.01$) (Table 4). The first shows higher values for MAT, MaxTW and MinTC than the second. For its part, UDA shows higher values for MAP than ODA (Table 4). The biggest differences between ODA and UDA have been recorded in Xb-11 S3 for MAT, MaxTW and MinTC ($+6.85$ °C, $+6.64$ °C and $+6.47$ °C, respectively) and in V-25 for MAP (-269.85 mm). In contrast, the smallest differences are obtained in V-24 S9 and V-24 S7 for all bioclimatic parameters (MAT: $+5.55$ °C; MaxTW: $+4.75$ °C; MinTC: $+5.37$ °C, and MAP: -180.92 mm).

In general, the Standard Deviation (σ) is smaller in the results obtained using UDA distribution than those obtained by ODA. However, there are some cases where the opposite situation is observed (MAT in Xb-11 S3 and all values for MAP from SU V). As the above case, Coefficient of Variation (CV) is also higher in ODA than UDA, except for the results obtained for MAT in Xb-S3 11 and V-25 (Table 4).

Table 2 Maximum altitude reached by each species in the different mountain systems of the Iberian Peninsula for ODA (based on specialized literature) and for UTM grid (based on the calculated maximum value from 10×10 km UTM square grids distribution area), which are obtained from the elevation model provided by Hijmans et al. (2005). Δ: Differences between the altitudes used for the determination of ODA and those provided by atlases. Sources: Duguy et al. (1979); Falcón Martín (1982); Martínez Rica (1983); Pérez Mellado (1983); Bas López (1984); Bea (1985); Lizana et al. (1988); Galán and Fernández (1993); Meijide et al. (1994); Llorente et al. (1995); Pleguezuelos and Villafranca (1997); Barberá et al. (1999); Fernández-Cardenete et al. (2000); Serrano Ezaguerri et al. (2001); Bosch (2002); Morales et al. (2002); Ayllón et al. (2003); Vences et al. (2003); Malkmus (2004); Soares et al. (2005); Hernández-Sastre and Ayllón, 2007; García-Cardenete (2008); González-Fernández (2011); Domínguez et al. (2012); Puente Montiel (2013); Ferrer et al. (2018)

		Pyrenees	Cantabrian	Galician	Iberian	Central	Montes de Toledo	Sierra Morena	Betic
Alytes obstetricans s. l.	ODA	2516	1670	1500	2200	2300	–	–	–
	UTM grid	3154	2414	2051	2205	2358	–	–	–
	Δ	− 638	− 744	− 551	− 5	− 58	–	–	–
Bufo spinosus	ODA	2600	1670	1800	1750	2200	1120	1120	2600
	UTM grid	3154	2414	2051	2205	2386	1579	1230	3322
	Δ	− 554	− 744	− 251	− 455	− 186	− 459	− 110	− 722
Epidalea calamita	ODA	1700	1220	2000	2100	2386	1200	1200	2540
	UTM grid	2724	2157	2051	2205	2386	1579	1230	3201
	Δ	− 1024	− 937	− 51	− 105	0	− 379	− 30	− 661
Blanus cinereus s. l.	ODA	–	–	–	1100	1700	1200	1200	2000
	UTM grid	–	–	–	1348	2386	1579	1230	3322
	Δ	–	–	–	− 248	− 686	− 379	− 30	− 1322
Chalcides bedriagai	ODA	–	–	1103	1720	1850	1200	1200	1800
	UTM grid	–	–	1823	1937	2386	1579	1223	3322
	Δ	–	–	− 720	− 217	− 536	− 379	− 23	− 1522
Natrix maura	ODA	1500	1270	1210	1580	1800	1100	1100	1950
	UTM grid	3016	2414	2051	2205	2386	1579	1230	3322
	Δ	− 1516	− 1144	− 841	− 625	− 586	− 479	− 130	− 1372
Vipera latastei	ODA	1400	1200	1250	1700	2386	1000	1000	2950
	UTM grid	2545	2051	2051	2205	2386	1579	1230	3322
	Δ	− 1145	− 851	− 801	− 505	0	− 579	− 230	− 372

MER vs ODA

In general, the results obtained between two common distribution areas, those provided by atlases, MER and ODA, are similar. For these parameters related with temperature, MAT, MaxTW and MinTC, are higher in ODA than in MER (Table 4). However, the studied assemblage from V-24 S7, V-24 S9 and V-25 has provided higher values for MaxTW in MER than ODA.

Regarding MAP, the results based in MER are higher than ODA in Xb-11 S3 and V-24 S8. The opposite is true for the other samples, i.e. MAP values are higher in ODA than in MER (Table 4).

MER results of MAT, MaxTW and MinTC show a slightly higher σ in all samples that those obtained with ODA. This pattern is not observed in the case of MAP. In this case, the differences between MER and ODA are dependent of the sample. Thus, σ_{ODA} is higher in Xb-11 S3, V-24 S7, V-24 S9 and V-25, showing the rest of assemblages the opposite situation. Regarding CV, in general this statistical parameter is lower in the ODA results than the MER ones for all the studied bioclimatic parameters, except in the case of MAP in the assemblages recovered from Xb-11 S3 and V-24 S9.

Discussion

Altitudinal range of the target species

All the species studied show euryhypsas behaviour, which means all of them are distributed from sea level to high altitudes in most of the Iberian mountain systems, in agreement with previous studies on this subject (i.e. Pleguezuelos and Villafranca 1997). In this sense, Iberian species of herpetofauna with a narrow altitudinal distribution range are scarce (Pleguezuelos and Villafranca 1997), which is related with the wide distribution

Table 3 Mean values and Standard Deviation (σ), and Coefficient of Variation (CV) of MAT (mean annual temperature), MaxTW (maximum temperature of the warmest month), MinTC (minimum temperature of the coldest month) and MAP (mean annual precipitation), for each species of amphibians and reptiles identified in El Salt site according to the Portuguese Atlas (Loureiro et al. 2018) and in herpetofauna distribution server for Spain, SIARE (AHE 2021), ODA and UDA. *T*-test significance level is calculated between values of ODA and UDA. Δ: Differences between the obtained results based on MER and ODA

	MER			ODA			UDA				
Alytes obstetricians s. l.	**MEAN**	σ	**CV**	**MEAN**	σ	**CV**	**MEAN**	σ	**CV**	***T*-test**	Δ
MAT (°C)	11.95	2.69	22.51	12	2.63	21.92	5.01	2.27	45.31	0	0.05
MaxTW (°C)	26.22	3.05	11.63	26.27	2.99	11.38	19.52	3.17	16.24	0	0.05
MinTC (°C)	1.05	3.08	293.33	1.09	3.04	278.90	−5.11	2.04	−39.92	0	0.04
MAP (mm)	777.63	294.71	37.90	774.54	293.32	37.87	1183.14	161.04	13.61	0	−3.09
Bufo spinosus											
MAT (°C)	13.11	2.89	22.04	13.14	2.84	21.61	5.7	2.52	44.21	0	0.03
MTW (°C)	28.17	3.82	13.56	28.21	3.78	13.40	21.33	3.99	18.71	0	0.04
MTC (°C)	1.84	3.18	172.83	1.87	3.14	167.91	−5.1	2.06	−40.39	0	0.03
MAP (mm)	685.3	267.72	39.07	683.51	266.72	39.02	1023.48	237.67	23.22	0	−1.79
Epidalea calamita											
MAT (°C)	13.6	2.61	19.19	13.64	2.56	18.77	6.86	1.76	25.66	0	0.04
MTW (°C)	29.16	3.39	11.63	29.21	3.34	11.43	21.62	2.65	12.26	0	0.05
MTC (°C)	2.04	2.97	145.59	2.07	2.94	142.03	−3.6	1.59	−44.17	0	0.03
MAP (mm)	622.74	236.63	38.00	620.05	234.83	37.87	1012.54	159.13	15.72	0	−2.69
Blanus cinereus s. l.											
MAT (°C)	14.98	2.12	14.15	15.03	2.03	13.51	8.22	2.2	26.76	0	0.05
MTW (°C)	31.29	2.54	8.12	31.33	2.5	7.98	26.07	1.84	7.06	0	0.04
MTC (°C)	3.12	2.69	86.22	3.18	2.62	82.39	−3.97	2.14	−53.90	0	0.06
MAP (mm)	572.19	173.24	30.28	571.06	172.55	30.22	715.63	198.63	27.76	0	−1.13
Chalcides bedriagai											
MAT (°C)	14.28	2.52	17.65	14.35	2.44	17.00	7.81	1.79	22.92	0	0.07
MTW (°C)	29.29	2.88	9.83	29.34	2.84	9.68	24.46	2.49	10.18	0	0.05
MTC (°C)	3.16	3.06	96.84	3.23	2.99	92.57	−3.36	2.68	−79.76	0	0.07
MAP (mm)	684.71	274.34	40.07	680.91	271.19	39.83	1042.09	332.36	31.89	0	−3.80
Natrix maura											
MAT (°C)	13.57	2.77	20.41	13.74	2.56	18.63	6.5	2.05	31.54	0	0.17
MTW (°C)	28.84	3.57	12.38	29.01	3.39	11.69	21.33	3.46	16.22	0	0.17
MTC (°C)	2.19	3.1	141.55	2.34	2.96	126.50	−4.28	1.81	−42.29	0	0.15
MAP (mm)	658.58	252.94	38.41	650.34	247.31	38.03	1020.71	228.32	22.37	0	−8.24
Vipera latastei											
MAT (°C)	12.99	2.78	21.40	13.07	2.73	20.89	8.33	2.57	30.85	0	0.08
MTW (°C)	28.28	3.13	11.07	28.34	3.08	10.87	24.49	4.3	17.56	0	0.06
MTC (°C)	1.7	3.38	198.82	1.77	3.35	189.27	−2.99	1.98	−66.22	0	0.07
MAP (mm)	685.43	255.9	37.33	682.54	254.75	37.32	869.13	267.89	30.82	0	−2.89

and a high ecological tolerance of these species in the region (Sillero et al. 2009). In general, amphibians reach higher maximum altitudes than reptile species (see Fig. 1 in Supplementary Material 2), which is mainly related with the different evolution of temperatures and moisture against the elevation (Heatwole 1982). Thus, temperature decreases linearly with the altitude (approximately 0.50 °C/100 m), whereas the rainfall is positively related with the altitude (Font Tullot 2000). Nevertheless, this explanation is simplistic since there are other factors that also influence this distribution, such as the decrease of the environmental heterogeneity and vegetation cover (Heatwole 1982), and lower presence of potential preys (Lizana et al. 1990), among others. Thus, as Table 2 denotes the differences between the maximum altitude reached in ODA for each species, based on the consultation of the available scientific literature, and the present in the whole UTM grid of 10 × 10 km is, in general, greater in reptiles than in amphibians. In this sense, *Natrix maura* shows the major difference in the northernmost mountain ranges

Table 4 Mean values, Standard Deviation (σ) and Coefficient of Variation (CV) of MAT (mean annual temperature), MaxTW (maximum temperature of the warmest month), MinTC (minimum temperature of the coldest month) and MAP (mean annual precipitation), for each studied assemblage using MER, ODA and UDA methods. *T*-test significance level is calculated between values of ODA and UDA. Δ: Differences between the obtained mean values based on MER and ODA

Xb-11 S3	MER			ODA			UDA			*T*-test	Δ
	MEAN	σ	CV	MEAN	σ	CV	MEAN	σ	CV		
MAT (°C)	13.66	2.11	15.45	13.71	2.03	14.81	8.56	2.09	24.42	0.00	0.05
MaxTW (°C)	28.94	2.03	7.01	28.97	2	6.90	25	1.49	5.96	0.00	0.03
MinTC (°C)	2.49	2.36	94.78	2.55	2.29	89.80	−2.76	2.1	−76.09	0.00	0.06
MAP (mm)	762.68	263.06	34.49	762.38	263.1	34.51	788.72	258.12	32.73	0.08	−0.3
V-24 S9											
MAT (°C)	12.34	2.62	21.23	12.62	2.35	18.62	8.11	1.43	17.63	0.00	0.28
MaxTW (°C)	27.23	2.49	9.14	27.22	2.48	9.11	22.79	1.3	5.70	0.00	−0.01
MinTC (°C)	0.98	2.91	296.94	1.68	2.75	163.69	−2.05	2.33	−113.66	0.00	0.7
MAP (mm)	681.08	292.31	42.92	828.49	324.84	39.21	1175.65	361.41	30.74	0.00	147.41
V-24 S8											
MAT (°C)	12.61	2.38	18.87	13.12	2.21	16.84	8.06	1.41	17.49	0.00	0.51
MaxTW (°C)	27.19	2.53	9.30	27.7	2.43	8.77	23.17	1.52	6.56	0.00	0.51
MinTC (°C)	1.74	2.70	155.17	2.17	2.61	120.28	−2.57	2.21	−85.99	0.00	0.43
MAP (mm)	848.89	331.03	39.00	814.46	321.16	39.43	1017.35	380.16	37.37	0.00	−34.43
V-24 S7											
MAT (°C)	12.34	2.62	21.23	12.62	2.35	18.62	8.11	1.43	17.63	0.00	0.28
MaxTW (°C)	27.23	2.49	9.14	27.22	2.48	9.11	22.79	1.3	5.70	0.00	−0.01
MinTC (°C)	0.98	2.91	296.94	1.68	2.75	163.69	−2.05	2.33	−113.66	0.00	0.7
MAP (mm)	681.08	292.31	42.92	828.49	324.84	39.21	1175.65	361.41	30.74	0.00	147.41
V-25											
MAT (°C)	12.77	2.47	19.34	12.99	2.31	17.78	8.14	1.57	19.29	0.00	0.22
MaxTW (°C)	27.64	2.51	9.08	27.62	2.47	8.94	22.9	1.44	6.29	0.00	−0.02
MinTC (°C)	1.44	2.84	197.22	1.98	2.74	138.38	−1.99	2.37	−119.10	0.00	0.54
MAP (mm)	692.53	303.89	43.88	799	318.79	39.90	1179.7	364.65	30.91	0.00	106.47

(Galician Massif, −841 m; Cantabrian Range, −1144 m; Pyrenees, −1516 m; and Iberian Range, −625 m). The altitudinal distribution of *N. maura* seems to be limited by the presence of water bodies in the environment and for the low temperatures reached in the higher elevations (Santos 2015). Moreover, in the areas where *N. maura* cohabited with the congeneric *Natrix astreptophora*, as in the north of Spain, the former tends to inhabit lower altitudes than the second (Malkmus 2004); however, both species avoid direct competition by different use of trophic resources and ecological segregation (Galán 1988). In the rest of the systems, the species showing the greatest difference are also reptiles: *Vipera latastei* in Montes de Toledo and Sierra Morena ranges from −579 and −230 m, respectively, *Blanus cinereus* s. l. in Central Range −686 m and *Chalcides bedriagai* in the Betic Range −1,522 m. As the case of *N. maura*, the distribution of *V. latastei* in the Northern Iberian Peninsula is limited by the presence of parapatric viper species, *Vipera seoanei* and *Vipera aspis*, which reached higher altitudes than the former (Duguy et al. 1979; Saint Girons 1980; Brito and Crespo 2002), and for climatic parameters (Martínez-Freiría et al. 2008). Regarding *C. bedriagai*, the species does not seem to be limited in its altitudinal distribution by winter temperatures, contrary to strictly thermophilic species. On the other hand, it seems to select positively those points with low precipitation during the hottest periods of the year and with abundant sun exposure (Maluquer-Margalef et al. 2009). However, given the cryptic ecology of *C. bedriagai* and both species of the genus *Blanus* (*Blanus rufus* and *Blanus cinereus*), the range of these species is far from being well known in many areas of the Iberian Peninsula (Pollo 2002; López 2002).

Due to this reduction in the altitudinal limit applied to all species, there is also a reduction in the total occupied area of the ODAs of each species compared to the distribution provided by the atlases (Fig. 5). Again, reptile species present a greater reduction area than the amphibians, especially on ophidians (see Supplementary Material 3).
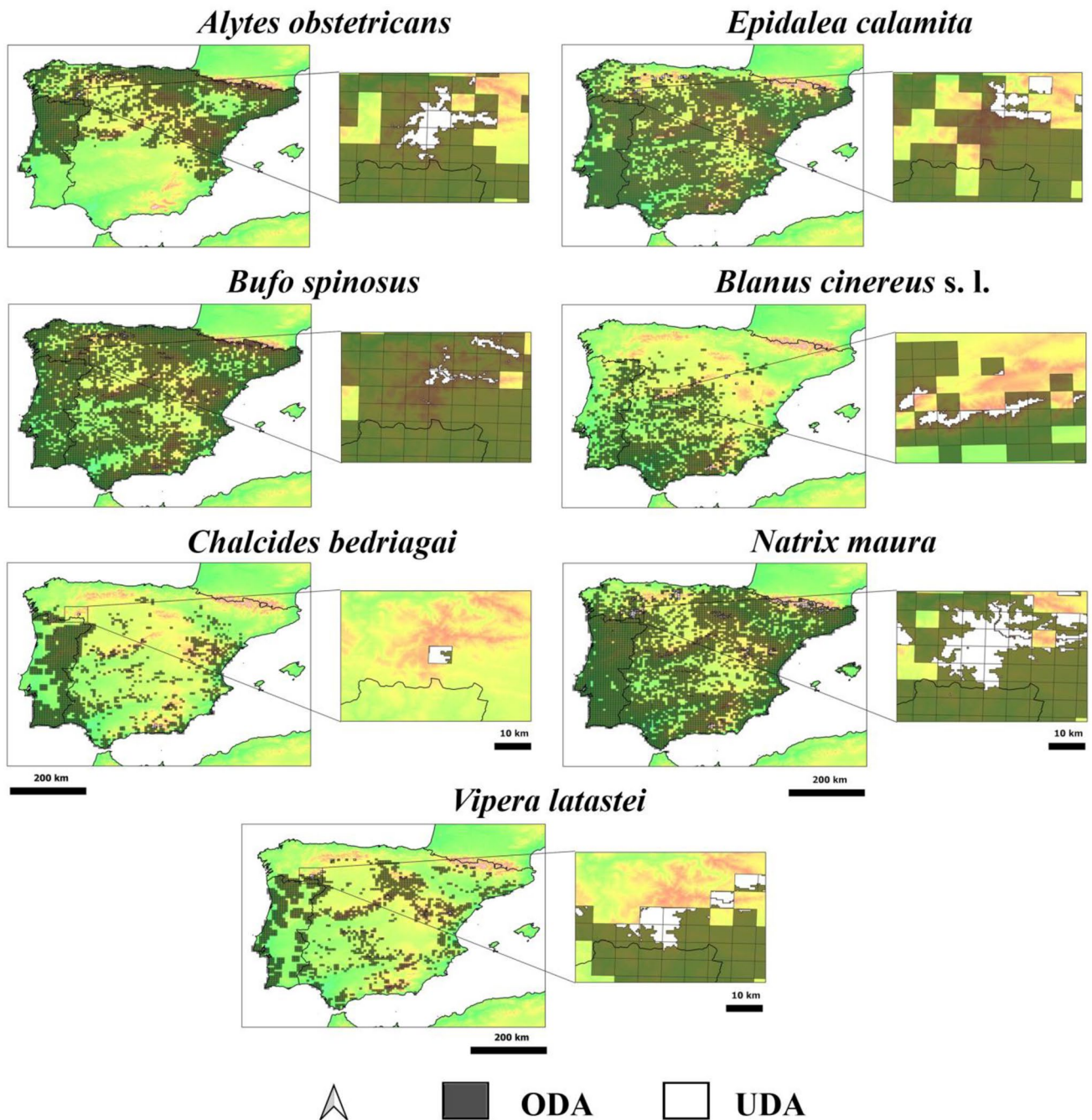
Fig. 5 Distribution areas for each species of the studied assemblages recovered from El Salt site denoted as 10×10 km UTM square grids. The ODA (black area) and UDA (white area) are indicated in each square

Discussion of the methods per variable and species

The reduction in the area occupied by each species is reflected in a modification in the evaluated bioclimatic parameters. Regarding temperatures, ODA yielded higher mean values for temperatures and lower ones for rainfall than UDA for all species (Table 3). As Fagoaga et al. (2019a) pointed out, ODA which is actually more linked to the species provide a more accurate distribution than atlases, which are based on a rough estimation of the distribution area of the species (Barbosa et al. 2013). As a result, UDA-ODA discrimination method provides more accurate bioclimatic values due to the implementation of an ecological discrimination criterion based, in this case, on the maximum altitude of each species. The implemented discrimination criterion, the maximum altitude per Iberian range, resulted

in the elimination of the higher heights of the respective mountains. As the temperatures decrease with the altitude, it is expected that the lower values were deleted in our estimations. Thus, an increase in these values is recorded (MAT, MaxTW and MinTC). The obtained values with this methodology are incremented between $+0.17$ and $+0.03$ for MAT, $+0.17$ and $+0.04$ for MaxTW and $+0.15$ and $+0.03$ for MinTC. In all these cases, *Natrix maura* shows the major reduction. This taxon shows the major differences between the maximum altitude recorded in the literature and the altitude provided in the atlases (Table 2). On this part, *Bufo spinosus* presents the minor difference in the three bioclimatic parameters, together with *Blanus cinereus* s. l. in the case of MaxTW and *Epidalea calamita* for MinTC. These three taxa are considered the species with fewer differences in the recorded maximum altitude (Table 2), at least for Pyrenees and Cantabrian Range for *Bufo spinosus* (-554 and -744, respectively); Galician Massif, Central Range and Montes de Toledo for *Epidalea calamita* (-51, 0 and -379 m, respectively); and Montes de Toledo for *Blanus cinereus* s. l. (-379 m).

Regarding rainfall, the results show a decrease in the obtained values by UDA-ODA discrimination method in all species compared to those provided by the application of MER method (Table 3). In general, precipitation increases with elevation (Daly et al. 1994 and reference therein). For this reason, the elimination of higher altitudes results in lower values for this parameter compared with the values obtained with the complete range in a determined grid. Thus, the range of values varies between -8.24 and -1.13 mm between MER and UDA techniques (Table 2). As the above cases, *Natrix maura* shows the highest reduction in MAP (-8.24 mm), followed by *Chalcides bedriagai* (-3.80 mm), and *Alytes obstetricans* (-3.09 mm).

Similar to the results obtained for the herpetofauna, UDAs calculated for small mammals from the same SUs of El Salt site show lower mean temperatures and higher rainfall than in ODAs, except *Microtus arvalis*, which behaves in the opposite way (Fagoaga et al. 2019a).

Additionally, as σ is lower in the obtained values in ecological criterion distribution area than those obtained by the distribution based on UTM 10×10 km grid, the first technique provides results statistically more robust.

## Discussion of the methods per variable and assemblage

In all associations, ODA yielded higher mean values for temperatures and lower ones for rainfall than UDA (Table 4). Again, these differences seem to be related with the deletion of the highest altitudes in the delimitation of ODAs against UDAs. As mentioned above, ODA provides more accurate climatic and distributional information than those

provided by the intersection of the distribution area provided by atlases (Fagoaga et al. 2019a). With the use of the latter, it is assumed that a determinate species has the same possibilities to inhabit anywhere within the UTM 10×10 km square grid (100 km^2). As mentioned in the "Results" section, the σ is, in general, higher in ODA than UDA except for MAT in Xb-11 S3 and MAP in all assemblages of the SU V. In the case of the bioclimatic parameters related with temperatures (MAT, MinTC and MaxTW), UDA seems to be constituted by homogeneous environments. Regarding MAP, all associations from SU V occupy a larger area than in the case of Xb-11 S3 (Fig. 6). Since precipitation is highly influenced by local orographic features, the MAP values obtained by UDA are disparate. The surface (ha) occupied by the different distribution units of each assemblage is included in Supplementary Material 4.

After applying an ecological discrimination criterion, as highest range reached by each species in the different Iberian ranges, we have introduced results theoretically more representative of the evaluated assemblage than the use of the whole area of the grid. As a result, the palaeoclimatic reconstructions are more accurate than those obtained in similar methodologies as MER (Fagoaga et al. 2019a). Furthermore, statistically the ODA values appear more reliable than those obtained by MER. In this sense, the σ is smaller in all cases for the bioclimatic parameters related with temperature. About MAP, the σ is smaller for ODA in the sample of V-24 S8 (Table 4). In the rest of the studied assemblages, the σ in the means obtained by ODA is higher than in MER for the rest of the associations studied (Table 4). In regard to CV, which relate the extent of variability in relation to the mean, its values are lower in ODA than in MER, except for MAP in Xb-11 S3 and V-24 S8 (Table 4). Thus, on this basis, the results obtained using MER show in general a higher relative variability than ODA.

The obtained results for each MAT and MinTC absolute values based on UDA-ODA discrimination technique are slightly higher than those obtained with the MER method (Fig. 7). It is explained by the elimination of higher altitudes, in which are recorded the lower values of that parameters. Unlike with climatic results derived from each of the species, those obtained from association are disparate, as they do not behave equally between associations and parameters. The new palaeoclimatic reconstruction yields higher values of MaxTW in Xb-11 S3 and V-24 S8 than the calculated by MER, whereas this parameter is slightly lower in V-24 S9, V-24 S7 and V-25. As in the latter case, MAP values also present disparate results, while V-24 S7, V-24 S9 and V-25 values are higher using ODA than those based on atlas distribution, in Xb-11 S3 and V-24 S8 they are lower (Fig. 7). These results are difficult to interpret and may be due to the effect of the influence of orography on small/medium scale conditions. In the Iberian Peninsula, most of the ranges

Fig. 6 Common distribution areas for the different assemblages of fossil herpetofauna from El Salt site denoted as 10×10 km UTM square grids. The ODA (black area) and UDA (white area) is indicated in each square
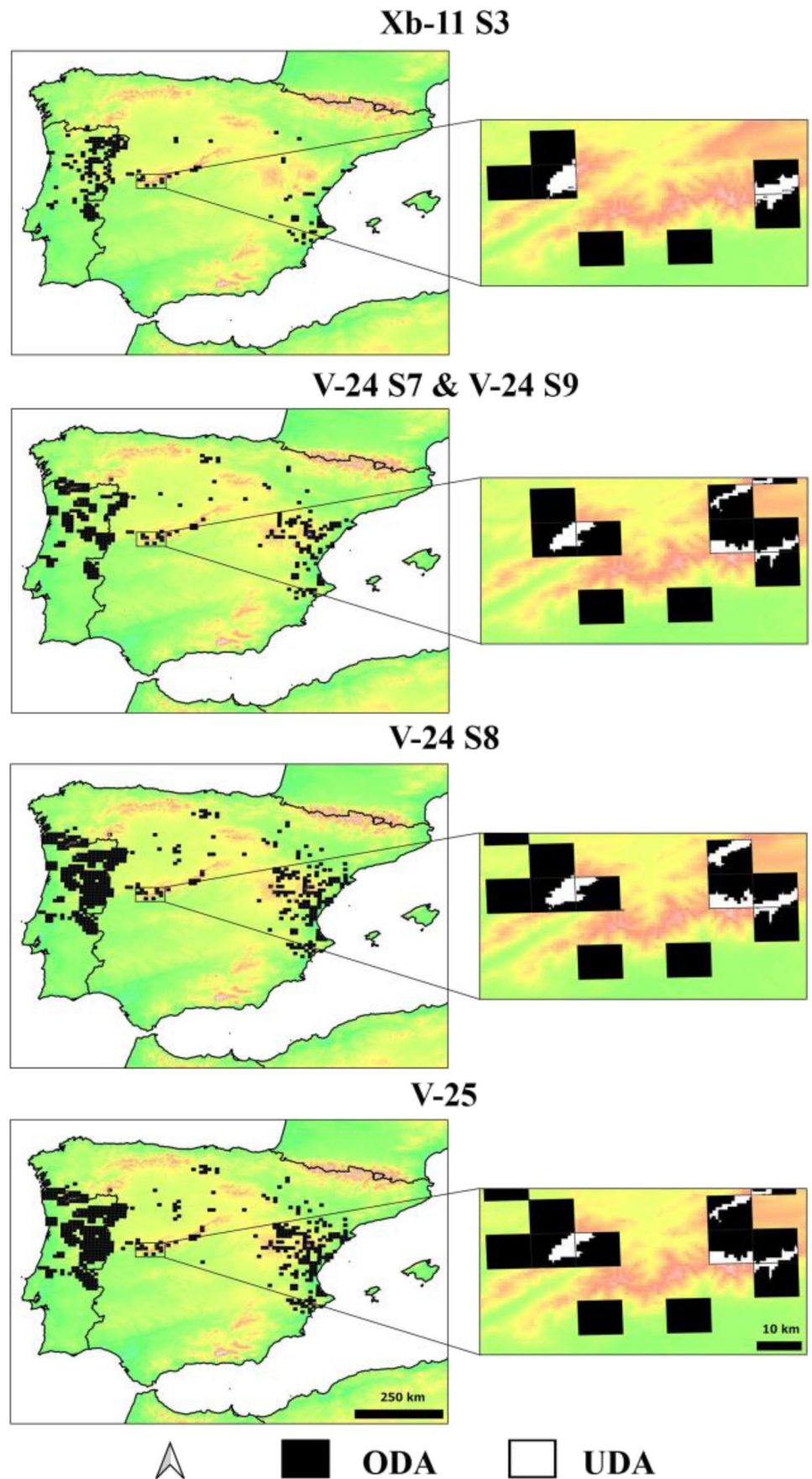
Fig. 7 Comparison between the palaeoclimatic reconstruction from Stratigraphic Units Xb and V of El Salt obtained by MER (black line) and ODA/UDA discrimination methodology (grey line). MAT (mean annual temperature, °C); MaxTW (maximum temperature of the warmest month, °C); MinTC (minimum temperature of the coldest month, °C); MAP (mean annual precipitation, mm). Values obtained for small mammal associations come from Fagoaga et al. (2019b)
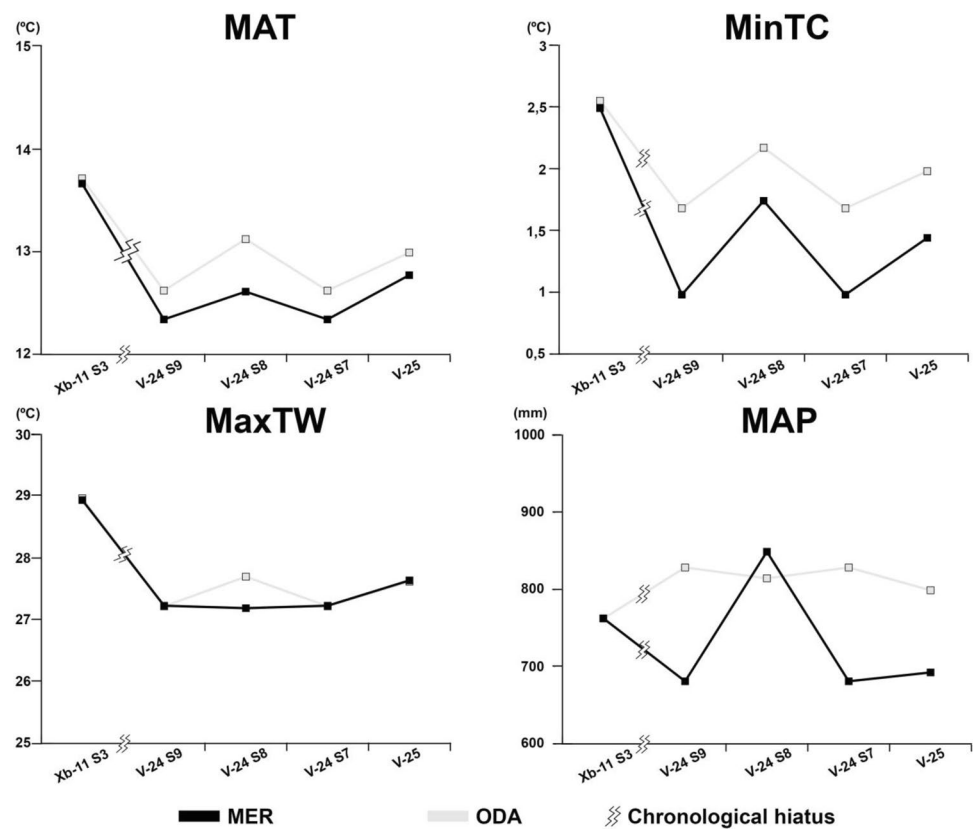
are distributed from west to east (i.e. Pyrenees, Cantabrian Range and Central Range) (Font Tullot 2000; Pascual and Sanz 2017); because of this general orientation, there is a particularly strong interaction with the atmospheric flows with northern and southern components (Pascual and Sanz 2017). Moreover, the orientation of the Earth relative to the sun causes a latitudinal gradient in solar radiation (Dubayah 1994). In the case of the Northern Hemisphere, the sun is slightly oriented to the south. As a result, there are strong local gradients in solar radiation, which is not only influenced by the slope orientation, but also on elevation, slope angle and shadowing (Dubayah 1994). As a result, the southern slope tends to be drier and hotter than the northern slope (Dubayah 1994; Kutiel et al. 1998; Begum et al. 2010). In Mediterranean areas, the southern slopes are dominated by stones and bare soil patches. In contrast, the slopes oriented to the north show dominance by biological components (Kutiel et al. 1998). This influences both directly and indirectly the distribution of plant and animal species, composition of biological communities, biological productivity, species richness, structures and densities of plant communities (Dubayah 1994; González Hidalgo et al. 1996; Gong et al. 2008; Shepard and Burbrink 2008; Foord et al. 2015). In this sense, the climatic gradient between both slopes plays a crucial role in the distribution of the amphibians and reptiles, especially in the areas bordering the species' distribution areas. For example, some amphibian species in arid areas preferably inhabit northern slopes, as the salamander *Plethodon auachitae* in the Ouachita Mountains, western Arkansas and southeastern Oklahoma (USA) (Shepard and Burbrink 2008). In Galicia (northwestern Spain; Atlantic Bioregion), Mediterranean species of lacertids, i.e. *Podarcis bocagei* and *Podarcis guadarramae*, seems to positively select southern-oriented slopes, whereas lizards with Atlantic ecological preferences, as *Zootoca vivipara* or *Iberolacerta monticola*, use all slopes indifferently (Bas López 1986). A similar case is the southern populations of *Coronella austriaca* in the Iberian Peninsula, which seem to select positively northern slopes (but not exclusively), where conditions are cooler and more humid than in other parts of the mountain range (Martínez del Mármol et al. 2020). Considering these differences in temperatures and humidity, the probabilities of founding amphibians in northern slopes are higher than on southern ones, whereas the opposite trend is observed on reptiles, at least for northern Spain (Bea 1981). This gradient is also recorded in our results. In fact, in those assemblages where the values of MaxTW and MAP are higher based on UDA-ODA discrimination technique than MER method, there is a major reduction of the area occupied by southern slopes than northern ones (Supplementary Material 5). On the contrary, the reduction area on Xb-11 S3 and V-24 S8, in which both MaxTW and MAP are lower in MER than in ODA, has been

focused on northern slopes than southern ones (Supplementary Material 5). Consequently, it is reduced the theorically highest values of rainfall and the lowest values of MaxTW.

Comparing with current values at the site and regarding temperatures, the palaeoclimatic reconstruction based on UDA-ODA discrimination technique shows a context with higher temperatures in older SU (Xb) than today (Table 5). In SU V, these temperature parameters are lower than the present one (Table 5). In the case of MAP, in all samples from both units, values are higher than the rainfall recorded nowadays at Alcoi (Table 5). The same pattern has been reported for the same assemblages using the MER method (Marquina-Blasco et al. 2017, 2021a) (Table 5). Due to the higher values of MAT and MinTC here obtained, the differences respect to the current temperatures recorded at Alcoi are higher than the observed with MER method (Table 5). The other two parameters, MaxTW and MAP, do not show any common pattern (Table 5). Thus, MaxTW shows lower values than the current ones in all samples of the SU V. Regarding MAP, Xb-11 S3 and V-24 S8 show lower differences respect to current values in ODA-UDA discrimination methodology than in MER method.

Comparing values obtained for the units analyzed in both methods, MAT and MinTC for the modern samples (SU V) are lower than the older ones (SU Xb). However, as mentioned above, the values obtained in ODA are higher than MER. The main differences between both methods are related with the parameters MaxTW and, especially, MAP. Regarding the first, the values are similar in all samples except for V-24 S8. In this latter, MaxTW is higher in ODA (27.70 °C) than in MER (27.19 °C). In this sense, the changes recorded by ODA for this bioclimatic parameter are more similar to the observed for MAT and MinTC. For MAP, the values are more constant between the different studied assemblages. That is in MER, the difference between the maximum and minimum values is 167.81 mm (maximum value in V-24 S8, 848.89 mm, and minimum value in

V-24 S9 and S7, 681.08 mm), whereas in ODA is 66.11 mm (V-24 S9 and S7, 828.49 mm, and Xb-11 S3, 762.38 mm).

The palaeoclimatic reconstruction seems to draw a scenario of an alternation of moments with higher temperature (Xb-11 S3, V-24 S7 and V-25) with others of lower temperatures (V-24 S9 and V-24 S8). As shown in Fig. 7, in the palaeoclimatic reconstruction based on MER method, the samples with higher MAT values are coincident with the higher ones of MAP (Xb-11 S3, V-24 S8 and V-25) (Marquina-Blasco et al. 2021a). Roughly, there seems to be an alternation between "warm and wet" and "cooler and drier" moments. However, palaeoclimatic reconstruction based on ODA draws a slightly different scenario. In this case, it seems to indicate that "warm and dry" phases alternated with "cold and wet" ones. Moreover, the variations of the values between samples are higher in MER than in ODA. This latter observation is related with the elimination of more extreme values provided in MER, but not in ODA.

## Herpetofauna vs small mammals and other proxies

The small mammal associations of the same SUs studied yielded the same pattern as the herpetofauna based on UDA-ODA discrimination technique compared with MER method. In all the assemblages of small mammals, MAT, MaxTW and MinTC are lower in ODA than MER, whereas MAP showed higher values in ODA than MER (Fagoaga et al. 2019a). However, our results show higher absolute values than those provided by Fagoaga et al. (2019a) (Fig. 8). As Marquina-Blasco et al. (2021a) pointed out, these differences are related to the resulted current mutual distribution obtained in both methods, MER (Fagoaga et al. 2018, 2019b) and UDA-ODA discrimination method (Fagoaga et al. 2019a) between the two groups. The latter used two types of discrimination criteria. As primary criterion, they used the altitudinal distribution range for each species for the entire Iberian Peninsula, except for the cases of *Sciurus vulgaris* and *Talpa occidentalis*, see Table 2 in Fagoaga et al. (2019a). Posteriorly, these authors applied for *Microtus arvalis* a correction on the distribution area of this species, due to the recent expansion of the vole from the 1970s related with the changes in the land use (irrigated crops and introduction of *Medicago sativa*) and agricultural intensification (Luque-Larena et al. 2013). The covered area of these distributions in the case of small mammals is located more to the north and northwest of the Iberian Peninsula, whereas in the case of the herpetofauna, this area is mainly formed by two distinct zones: one in the western Iberia and another in the east of Spain (Marquina-Blasco et al. 2017, 2021a). In general, Iberian species of reptiles and amphibians are well distributed along the peninsula, with few examples of taxa with limited distribution (Pleguezuelos et al. 2002; Sillero et al. 2009; AHE 2021). As far as we know, the altitudinal

Table 5 Difference between values obtained from the fossil assemblages of El Salt using the UDA-ODA discrimination technique (Δ_{ODA}) and MER method (Δ_{MER}) and current values in Alcoi (MAT: 13.64 °C; MaxTW: 28.49 °C; MinTC: 1.69 °C; MAP: 543.58 mm)

Δ_{ODA}	Xb-11 S3	V-24 S9	V-24 S8	V-24 S7	V-25
MAT (°C)	0.07	−1.02	−0.52	−1.02	−0.65
MaxTW (°C)	0.48	−1.27	−0.79	−1.27	−0.87
MinTC (°C)	0.86	−0.01	0.48	−0.01	0.29
MAP (mm)	218.80	284.91	270.88	284.91	255.42
Δ_{MER}	**Xb-11 S3**	**V-24 S9**	**V-24 S8**	**V-24 S7**	**V-25**
MAT (°C)	0.02	−1.30	−1.03	−1.30	−0.87
MaxTW (°C)	0.45	−1.26	−1.30	−1.26	−0.85
MinTC (°C)	0.80	−0.71	0.05	−0.71	−0.25
MAP (mm)	219.10	137.50	305.31	137.50	148.95

Fig. 8 Evolution of the bio-climatic parameters after the application of the UDA-ODA discrimination technique to the fossil assemblages of herpeto-fauna and small mammals from Stratigraphic Units Xb and V of El Salt. MAT (mean annual temperature, °C); MaxTW (maximum temperature of the warmest month, °C); MinTC (minimum temperature of the coldest month, °C); MAP (mean annual precipitation, mm). Black line, herpetofauna; grey line, small mammals. Values obtained for small mammal associations are from Fagoaga et al. (2019a)
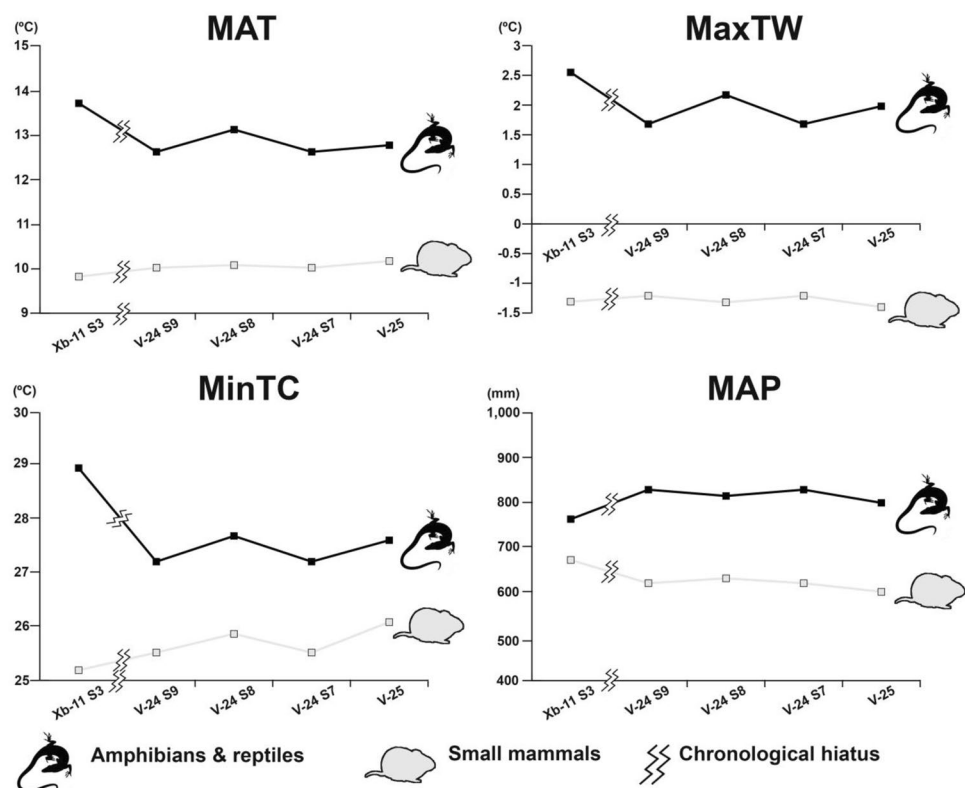
distribution of Iberian reptiles and amphibians is more stud-ied than that of small mammals. In fact, preliminary results of the present study, based only in the altitudinal limits for the whole Iberian Peninsula (Marquina-Blasco et al. 2021b), without taking into consideration the different mountain ranges, provided results highly different from those pre-sented in this work, at least for MAT and MAP from Xb-11 S3. In this case, MAT showed similar values (13.66 °C in MER; 13.67 °C in Marquina-Blasco et al. 2021b), whereas MAP was lower in Marquina-Blasco et al. (2021b) than in MER (756.27 mm and 762.68 mm, respectively). It denotes that UDA-ODA discrimination technique is highly depend-ent of the degree of refinement of the established ecological criteria for the definition of UDAs and ODAs. Consider-ing this, it is necessary the development of new studies that define the actual altitudinal distribution of small mammals on each Iberian mountain system to verify if, as herpeto-fauna, we could obtain more realistic and precise data for this group. Moreover, in the case of herpetofauna, almost all works about its altitudinal distribution only pointed out the maximum height reached by species; however, few of them are centred in the altitudinal distribution of determined taxa and/or its relation with the orientation of the mountains (i.e. Bea 1985).

It is strongly difficult to evaluate a possible bias due to taphonomical origin of the small vertebrates remains. Marin-Monfort et al. (2021) carried out a detailed taphonomic

study with small mammals assemblages from SU Xb and SU V. The main conclusion of that study was that the main predator in the production of the small mammal assemblages was the European eagle owl (*Bubo bubo*). Regarding her-petofauna, the taphonomy of that group is still poorly stud-ied (see references in Marquina-Blasco et al. 2021a). The preliminary taphonomic approaches of amphibians and rep-tiles from SUs Xb and V suggested a mixed origin of preda-tory activity by medium-large nocturnal raptor (possibly *B. bubo* or *Strix aluco*) and in situ natural death. However, it is remarkable that the predation of herpetofauna by birds of prey is, in general, anecdotic, at least in southwestern Europe (Martín and López, 1990). Nevertheless, some individuals of *B. bubo* seem to present some degree of specialization on amphibians, preying on them during its massive reproduc-tive concentration of anuran species (Andrews 1990). Due to that, *B. bubo* has an opportunistic feeding behaviour; it is considered that the prey assemblage provided by that species is an accurate representation of the small vertebrate com-munity living in the local habitat (Andrews 1990).

The palaeoclimatic reconstruction based on small mammals points to an evolution towards aridification of the region after the application of both methods, MER and UDA-ODA (Fagoaga et al. 2019a, b). For its part, the results based on reptiles and amphibians assemblages are coincident in the sense of lower rainfall in the modern SU than in the older ones in MER method (Marquina-Blasco

et al. 2017, 2021a). In the present work, the obtained results show higher values in SU V than in SU Xb. Thus, whereas in the case of small mammals, this parameter (MAP) descends continuously from Xb-11 S3 to V-25 (Fagoaga et al. 2019a, b); our results show a more erratic evolution, with an apparent decline in the MAP value between V-24 S7 and V-25. Furthermore, the differences in MAP values between the different SU V associations are greater for herpetofauna than for mammals. Additionally, the chronological evolution of the parameter between the different samples (i.e. from the oldest, V-24 S9 to the most modern, V-25) is similar, but with higher absolute values, than that provided by Fagoaga et al. (2019a) for the small mammal associations. Based on this, an apparent trend towards a progressively drier context is intuited. In contrast, in the MAT and MaxTW parameters, the reconstruction based on small mammals shows a gradual increase in values from the oldest (Xb) and modern (V) SUs. Regarding MinTC, these results indicate certain stability in this parameter. Overall, our results show a more erratic evolution, showing some instability in the parameters, interspersing moments with higher values (Xb-11 S3, V-24 S8 and V-25), with lower ones (V-24 S9 and V-24 S8).

The above-mentioned progression from older SU (Xb) more humid to drier modern ones (V) is also denoted by numerous proxies from El Salt site. In this sense, the change in the dynamic of sedimentation, from one mainly based on anthropogenic and geogenic deposition to a sporadic aeolian sedimentation, is related with colder climatic conditions (Gómez de la Rúa et al. 2010; Mallol et al. 2012). Anthracological results also point to an aridification trend giving the increment of *Juniperus* sp. and *Buxus sempervirens*, as well as the reduction and/or absence of the hygrophilous, heliophilous taxa, and pine trees from SU VIII to V (Vidal-Matutano 2016). Although the study of the palinological samples from El Salt site is still preliminary due to the scarce remains recovered and the existence of important palinological hiatus (i.e. SUs IX, X and XI are sterile), certain observations can be made about possible trends that reveal gradual decrease in temperatures and humidity (Dupré 1992). The mentioned aridification is also recorded in the scarce Iberian long continental pollen record as Padul peat bog and Cariguela Cave (Carrión 2012; Camuera et al. 2019). Thus, the Pollen Zone 2C from Padul shows the existence of two sub-phases. Between 60 and 51 ka, the pollen sequence shows the existence of relative high Mediterranean forest values; however, Camuera et al. (2019) pointed out a considerable decrease of the arboreal pollen in the second half of the zone until 43 ka. Moreover, analyses of n-alkane chain show a dominance of herbaceous plants in a dry or semi-dry climatic context in the middle of the SU V of El Salt site (Galván et al. 2014).

Implications for the last Neanderthals from El Salt

The human use of El Salt site shows clearly two major phases. The first, defined by the interval represented by SU XII to IX, is characterized by the presence of high concentration of human activity (archaeological remains, combustion residues and abundant faunal remains associated with lithic tools) of recurrent short-term and seasonal human occupation events (Galván et al. 2014; Machado and Pérez 2016; Leierer et al. 2019). The studies of palaeoclimatic and palaeoenvironmental reconstruction focused on SU Xb (52.3 ± 4.6 ka) drawn humid conditions with dominant forest formations (Marquina et al. 2017; Fagoaga et al. 2018, 2019b) in a supramediterranean sub-humid context (Vidal-Matutano et al. 2018). However, at the second phase (SU VIII to V), and in contrast to the former SUs, the human presence decreased until its apparent final abandonment of the site (Mallol et al. 2012; Galván et al. 2014). After this archaeological hiatus, at the uppermost layer of SU V, two small flint blades, a few undifferentiated *débitage* flakes and a small combustion feature were recovered (Galván et al. 2014). A similar pattern has been observed in other Iberian sites (Mallol et al. 2012). This process is coincident with colder and drier conditions. In this sense, the changes recorded in atmospheric circulation over the North Atlantic region during D/O stadials and HE have been related with an increment of the wind intensity in the Mediterranean region and, thus, higher aeolian sedimentation rates (Moreno et al. 2002). Probably related with it, at SU V, it is recorded a depositional dynamic change, from depositional processes dominated by gravitational component to another dominated by aeolian component, since the second episode of roof collapse (Gómez de la Rúa et al. 2010). Two dates are available for SU V. TL dating of the roof collapse, located at the base of this SU, and OSL dating obtained for its middle part, 45.2 ± 3.4 ka and 44.7 ± 3.2 ka respectively, indicates that the last Neanderthal occupations at El Salt took place prior to HE 4 (Galván et al. 2014). A similar date for the abandonment of inner Iberian territories (42 ka) has been proposed by Wolf et al. (2018).

The new methodology applied to the herpetofauna assemblage from both SUs shows a similar evolution; that is, cooler conditions in SU V (44.7 ± 3.2 ka) than in SU Xb (52.3 ± 4.6 ka). The particular case of MAP deserves a special comment, since it is slightly higher in the more modern SU than in the older one. The values obtained in the different surfaces of SU V are similar between them. However, the value obtained in V-24 S7 is slightly higher than those from V-25 are; it could indicate an evolution towards drier conditions. This pattern is also observed in the results provided by small mammals assemblages from SU V of El Salt site, that is a stability in MAP values

between V-24 S9, V-24 S8 and V-24 S7 with a subsequent decrease in V-25 (Fagoaga et al., 2019a).

The expansions/contractions of Neanderthal distribution areas were a constant in its natural history, which is related with numerous extirpations events and abandonments of sites (Trinkaus 1995). In this way, the northernmost populations were reached during warm periods, whereas cold intervals supposed the retraction to southern localities (Stewart 2005). The survival of all of these climate changes denotes high ecological and behavioural plasticity for these humans (Tattersall 2006). In fact, in some sites, there is an apparent change in the technology, behaviour and networks after the occurrence of cold phases (Delagnes and Rendu 2011). In the case of Eastern Iberia, Neanderthal occupations are related always with highly structured forest ecosystem (Ochando et al. 2021), where they would deploy their ambush-based hunting tactics (Stewart et al. 2019). Probably, this type of forest habitat could be a limiting factor for its distribution. Ecological models point out that 40 ky ago the potential habitat for Neanderthals was strongly reduced (Melchionna et al. 2018). Although as other extinction process, the demise of Neanderthals occurred in different chronologies at different European regions (Higham et al. 2014). However, as Jennings et al. (2011) suggested, the rainfall, rather than temperatures, was a crucial parameter for Neanderthal populations. If the aridification trend observed by different climatic proxies at El Salt site was the main factor, or at least one with high influence, the disappearance of Neanderthals in the region is a plausible explanation. However, more research is needed to clarify this question. In any case, as our results seem to indicate, in accordance with other biological proxies (charcoal, small mammals and, apparently, pollen), the disappearance of these humans at El Salt site, and by extension in the rest of the region, took place in a dry context.

Justification of the use of the UDA-ODA discrimination technique

Although from a statistical point of view the differences between the MER method and the UDA-ODA discrimination technique are minimal, the application of the latter is basically justified for two reasons:

i.   to give the palaeoclimatic reconstruction a greater ecological sense by using only the theoretical distribution area of each taxon described in the fossil association. Thus, we are working with natural units and not artificial ones as it is recorded in Portuguese and Spanish national atlases.

ii. to reduce the noise in the results due to the elimination of extreme data. In our case, the main difference

between the two techniques has resulted in the definition of a new precipitation context (Fig. 8).

As we demonstrate in this work, the results obtained using the UDA-ODA discrimination technique are highly dependent on the fossil association studied and the ecological criterion applied. In our work, the criterion applied also presents an important deviation, since the Iberian mountain systems have been treated as a whole without taking into account the particularities of each particular sierra into which they are subdivided. Achieving such a degree of definition is really complicated, and, to our knowledge, the altitudinal distribution of the Iberian herpetofauna is not known in such detail. On the other hand, theoretically, more diverse fossil associations than those studied in the present work could mark greater differences between the MER method and the UDA-ODA discrimination technique and/or by the combined study of reptiles and amphibians with other faunal groups (i.e. small mammals). In short, more research is needed.

Conclusions

The use of GIS software applied to MER method has allowed the development of new methodologies that apply techniques to improve the accuracy of palaeoclimatic reconstructions, such as UDA-ODA discrimination technique. In addition, it allows reproducible results to be obtained. In this sense, the use of the distribution area of species according to their ecological preferences (such as altitude range) as a discrimination factor provides a more accurate palaeoclimatic reconstruction due to its new biological point of view. Our results demonstrate that the application of the altitude range for each Iberian range preferably removes low values for temperature and high ones for rainfall, due to the evolution of these parameters with altitude (decrease in temperature with altitude and increase in precipitation). Moreover, for a statistical point of view, the results from the application of this method show in general slightly lower Standard Deviation compared to those obtained by MER method (except for MAP, but not in V-24 S8). The UDA-ODA discrimination technique presents, in general, a lower Coefficient of Variation in the mean of each bioclimatic parameter. Thus, this method of palaeoclimatic reconstruction is more accurate, not only on a theoretical level in the sense of applying an ecological criterion that makes more logical the distributions used, but also appears to be statistically more robust. However, it should be noted that the results are highly dependent on both the ecological criterion applied and the faunal association studied.

According to the palaeoclimatic reconstruction, climate was slightly warmer and wetter than today in

the older SU Xb (52.3 ± 4.6 ka). In contrast, in SU V (44.7 ± 3.2 ka), the climate was cooler and more humid than the recorded currently at Alcoi. The absolute values of the different bioclimatic parameters are higher than those based on small mammals assemblages. These differences between the obtained values are related with the wide distribution range of the Iberian species of amphibians and reptiles. Regarding small mammals, the species described in the association show, in general, a more limited distribution range. Moreover, the altitudinal distribution of small mammals species seems to be less studied than in herpetofauna. For this reason, the ecological criteria in previous works for definition of ODA of these species were not defined for each Iberian mountain system (Fagoaga et al., 2019a, b). Thus, our results and those provided by the distribution of small mammals are not comparable at all.

Although our results are, in general, coincident with other proxies studied at El Salt site, that is, an evolution towards colder and an intuited tendency towards drier conditions from older SU (Xb) to modern ones (V), some differences are observed. In this sense, our results draw a more erratic evolution. Under these conditions, the anthropic abandonment process of El Salt site seems to have taken place in a context of a progressive aridification, as other proxies point out and our results also seem to indicate. Whether there is a causal relationship between the two processes is a matter for future multidisciplinary work to discern.

Declarations

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