



HAL
open science

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

Rafael Marquina-Blasco, Ana Fagoaga, Vicente Crespo Roures, Salvador Bailon, Carolina Mallol, Cristo M. Hernandez, Bertila Galván, Hugues-Alexandre Blain, Francisco Javier Ruiz-Sánchez

► To cite this version:

Rafael Marquina-Blasco, Ana Fagoaga, Vicente Crespo Roures, Salvador Bailon, Carolina Mallol, et al.. Applying the UDA-ODA discrimination technique to a herpetological association: the case of the Middle Palaeolithic site of El Salt (Alcoi, Spain). *Journal of Anthropological and Archaeological Sciences*, 2022, 14 (139), <10.1007/s12520-022-01604-4>. <hal-03952510>

HAL Id: hal-03952510

<https://hal.science/hal-03952510v1>

Submitted on 23 Jan 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

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

3
4 Rafael MARQUINA-BLASCO^{1,2}, Ana FAGOAGA^{1,2,3}, Vicente D. CRESPO^{2,4,5}, Salvador BAILON⁶, Carolina
5 MALLOL^{7,8}, Cristo M. HERNÁNDEZ⁹, Bertila GALVÁN⁹, Hugues-Alexandre BLAIN^{3, 10}, Francisco Javier RUIZ-
6 SÁNCHEZ^{1,2}.

7
8 1 Palaeontology of Cenozoic Vertebrates Research Group, Universitat de València, Burjassot, Spain.

9 <https://orcid.org/0000-0002-1923-7601> rafael.marquina@uv.es

10 2 Museu Valencià d'Història Natural, Alginet, Valencia, Spain.

11 3 Institut Català de Paleoecologia Humana i Evolució Social, Universitat Rovira i Virgili, Tarragona, Spain.

12 4 División de Paleontología de Vertebrados, Universidad Nacional de la Plata. Facultad de Ciencias Naturales y Museo
13 (CONICET). Paseo del Bosque, s7n, B1900FWA. La Plata, Argentina.

14 5 Museo Paleontológico de Alpuente. Avenida de San Blas 17, 46178, Alpuente, Spain.

15 6 Histoire naturelle de l'Homme préhistorique, UMR 7194 and Archeozoologie, Archeobotanique: sociétés, pratiques,
16 environnements, UMR 7209, MNHN, CNRS, 55, rue Buffon, CP 55, 75005 Paris, France.

17 7 Instituto Universitario de Bio-Organica Antonio González (IUBO), Universidad de La Laguna, Santa Cruz de
18 Tenerife, Spain.

19 8 Departamento de Geografía e Historia, Universidad de La Laguna, Campus de Guajara, 38071, La Laguna, Santa
20 Cruz de Tenerife, Spain..

21 9 Grupo de Investigación: "Sociedades cazadoras-recolectoras paleolíticas" UDI de Prehistoria, Arqueología e Historia
22 Antigua, Facultad de Geografía e Historia, Universidad de La Laguna, Campus de Guajara, 38071, La Laguna, Santa
23 Cruz de Tenerife.

24 10 Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002, Tarragona, Spain.

25 **Abstract**

26 El Salt (Middle Palaeolithic; Alcoi, Spain) is a key site for understanding the extirpation of Neanderthals in the eastern
27 Iberian Peninsula. To improve our understanding of the palaeoclimatic context in which this process took place, we
28 applied the UDA-ODA discrimination technique to a fossil herpetological assemblage, which provide from
29 Stratigraphical Units (SU) Xb (52.3 ± 4.6 ka) and V ($45.2 \pm 3.4/44.7 \pm 3.4$ ka) at the site. This method is based in the
30 application of an ecological criterion, the maximum altitude of each species on each Iberian range, to discern and

31 remove those areas that do not meet their ecological requirements (UDA) from those that do (ODA) but despite of this,
32 are included in its distribution from Atlases from which the common distribution species is going to be extracted.
33 Results indicate the existence of an alternation between colder and wetter moments and warmer and drier ones; all of
34 them in a more humid context than nowadays. Climate was slightly warmer than nowadays in SU Xb, whereas was
35 cooler in SU V. However, previous palaeoclimatic reconstruction methods applied to the same association shows less
36 precipitation variation between SUs. These results do not fully agree with those provided by small mammals from the
37 same SUs, which indicate an increase of the temperatures whereas rainfall experienced the contrary. These differences
38 could be related with the wider distribution of the Iberian herpetofauna, and some differences in the applied ecological
39 criterion. Furthermore, herpetofaunal palaeoclimatic reconstruction shows that the abandonment of the site by
40 Neanderthals seems to have occurred in a progressive aridification context.

41

42

43 **Key words**

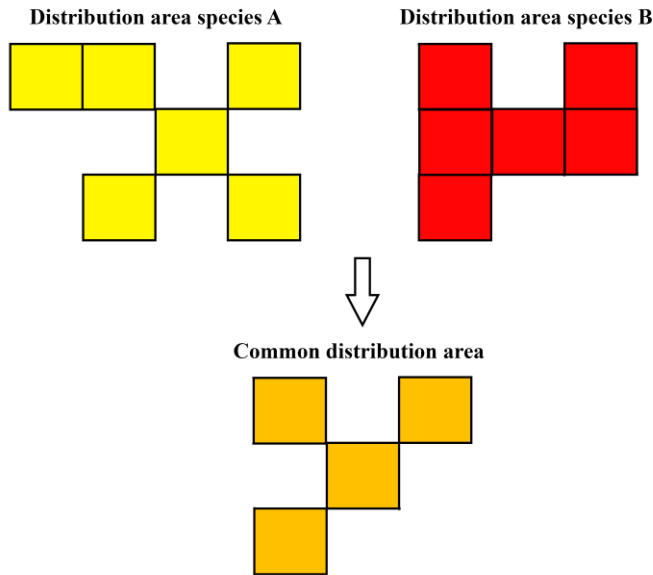
44 Palaeoclimate; Late Pleistocene; Iberian Peninsula; Neanderthal disappearance; GIS; MER method.

46 **1. INTRODUCTION**

47 The use of fossil assemblages to propose palaeoclimatic reconstruction has been a constant since the very beginning of
48 palaeontological studies (Blain et al. 2018). As currently occurs, biological communities are not independent of the
49 abiotic components (Birks et al. 2010). As a consequence of the changes and variations of these components, the
50 composition and structure of the biological communities changes along the time (Grayson 1981). In this sense, several
51 works have demonstrated the effects of the present impact that the current global climatic change is leading in many
52 biological communities (i.e. Araújo et al. 2006). Of course, these changes are observable on the fossil record too (Willis
53 et al. 2010). This “climatic response” and the current existence of modern relatives for calibration purposes, allow the
54 use of fossil remains as palaeoclimatic proxies in accordance to the requirements proposed by Bradley (1999).

55 Two main groups can be distinguished in the palaeoclimate reconstruction methods based on biological samples: (i)
56 qualitative methods and (ii) quantitative methods (Birks et al. 2010). In the first group, the palaeoclimatic
57 reconstructions are presented in descriptive terms like warm, polar, wetter, cold or dry; without providing a numerical
58 valuation to eliminate the ambiguity inherent in these descriptions (Porch 2010). The second group includes those that
59 provide direct values to infer past environments (Birks et al. 2010). Different quantitative methods have been developed
60 for the reconstruction of past Quaternary climate using fossil faunal assemblages (Birks et al. 2010). One of them, the
61 Mutual Climatic Range (MCR) was outlined by Atkinson et al. (1986, 1987). It is based in the assumption that a
62 particular species has a known climatic tolerance range, thus if this species was present at a site in the past then the
63 climate was included within its tolerance limits. Likewise, a group of species that cohabited at the same site and time is
64 supposed that the palaeoclimate conditions must have situated in the combined climatic tolerance range of all the
65 assemblage. MCR has been applied to a wide range of organisms, such insects (Atkinson et al., 1986, 1987; Coope,
66 1994; Elias, 1994, 1997, 2001; Coope et al., 1998; Elias et al., 1999; Miller and Elias, 2000; Alfimov and Berman,
67 2009), plants (Sinka and Atkinson, 1999; Pross et al., 2000; Thompson et al., 2012), terrestrial mollusc (Moine et al.,
68 2002) and ostracods (Horne, 2007; Horne et al., 2012). Blain (2009) proposed a modification of the MER methodology
69 by using the current geographical distribution of the fossil assemblage to extrapolate the palaeoclimatic conditions to
70 the palaeontological/archaeological site studied (Figure 1). Because MCR methodology is based in the climatic co-
71 occurrence of species assemblages, and not with the geographic sympatry area, Lyman (2016) proposed renaming the
72 technique outlined by Blain (2009) such as UTM-MCR. In this way, Blain et al. (2016) proposed the new name of
73 Mutual Ecogeographic Range (MER) method. We prefer the second name by two reasons. Firstly, MER is a more
74 intuitive name for a technique based on current geographical area occupied for a determined species. Secondly, the term
75 MER has been used yet in various works (i. e. Blain et al. 2018 and references therein). Regarding to small vertebrates,

76 MER method has been used with birds (Núñez-Lahuerta et al. 2016), herpetofauna (Blain, 2009; Blain et al. 2009,
77 2013; Marquina-Blasco et al. 2017, 2021), small mammals (López-García et al. 2010, 2011; Fagoaga et al. 2018,
78 2019b), and a combination of the two latter (López-García et al. 2014, 2021; Rey-Rodríguez et al. 2016; Connolly et al.
79 2019).

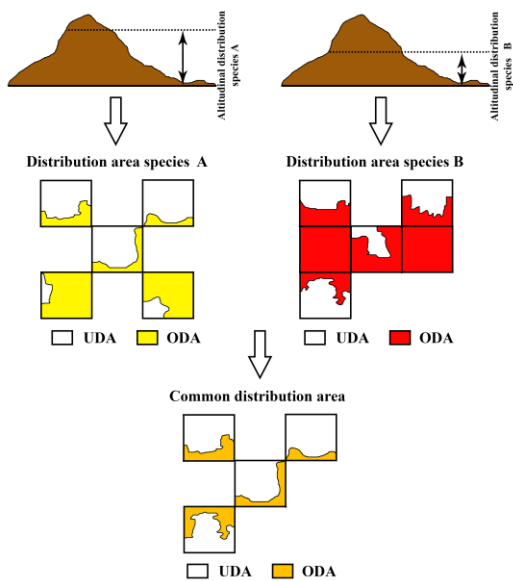


80

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

83 Several authors have already enumerated the weaknesses (and strengths) of the major approaches used to reconstruct
84 past climate from biological proxies (e.g. Birks et al., 2010). As advantages, the MCR and, by extension, MER
85 methodology do not need sophisticated mathematical apparatus and the availability of an important database on the
86 current distribution area of species (at least in the case of vertebrates) neither a significant amount of climatic data
87 (Alfimov and Berman, 2009). As many other methods, the MER method follows actualism, because it relies on the
88 current distribution of the species, assuming that the fossil representatives of the extant species have the same climatic
89 tolerances and preferences as their living counterparts. However, there are known examples of species that have
90 experienced a disruption of their ecological niche during their natural history, i. e. *Microtus cabreræ* (Castellanos-Frías
91 et al. 2018). However, this trouble is easily solved by considering in the study a suite of taxa with similar habitat
92 preferences (Grayson 1981). In the case of taxa with a distribution area strongly modified by human activity (i. e.,
93 *Microtus cabreræ* and *Testudo (Chersine) hermanni*), they are not considered in the analysis (Fernández-García et al.,
94 2018). Another problem related to this method is the possible absence of current biological communities analogous to
95 the fossil one (Birks et al. 2010). Guiot and Vernal (2007) proposed the use of the most similar assemblage as a possible
96 solution to this trouble. Another assumption when applying this method is that the current distribution of species are
97 exclusively determined by climatic parameters, omitting other factors as interspecific interactions (MacArthur, 1984;

98 Chesson, 2000; Chave et al., 2002) and historical factors, i. e. geographical barriers (Morales Martín and Lizana Aria,
99 2011). Thus, the current distribution area of the species rarely coincides with its potential distribution area (Morales
100 Martín and Lizana Aria, 2011). One of the requirements for the application of MER method is that the current
101 distribution of the defined species may be well known. In general, it can be considered that the degree of knowledge of
102 present distribution area of vertebrates in Spain is high, due to the existence of numerous atlases of different
103 geographical levels and several citizen science projects, focused mainly in herpetofauna (AHE, 2021) and birds
104 (SEO/Birdlife, 2021). Unfortunately, the databases of distribution area of species (i. e. national atlases of herpetofauna)
105 are based on unnatural units, 10 × 10 km UTM square grids (Pleguezuelos et al. 2002; Loureiro et al. 2018; AHE,
106 2021). This artefact strongly affects the validity of the palaeoclimatic reconstruction (Martínez-Solano and Sanchiz,
107 2005; Fagoaga et al. 2019a). The surface occupied by each unit (100 km²), could include areas with a strongly
108 topographical heterogeneity (Martínez-Solano and Sanchiz, 2005; Fagoaga et al. 2019a). In topographically diverse
109 regions such as Iberian Peninsula (Font Tullot 2000), climatic conditions vary significantly between geographically
110 proximate locations. Moreover, species are not present anywhere within the 100 km² of the UTM square because not all
111 of the territory responds to the ecological needs of these (Fagoaga et al. 2019a). In this sense, the use of the territory by
112 a species depends on the environmental context and by the interactions established among co-occurring taxa. As a result,
113 we could be introducing bias into our palaeoclimatic reconstruction by including areas (and its climatic values) where
114 some species could not be present (Fagoaga et al. 2019a). To improve the accuracy of the palaeoclimatic reconstruction
115 derived from MER method, Fagoaga et al. (2019a) define the UDA-ODA discrimination technique. Basically, this new
116 method is based in the application of an ecological criterion for the discrimination of Occupation Distribution Areas
117 (ODA), where in theory the species is present, from those where its presence is highly doubtful, the Uncertain
118 Distribution Area (UDA) (Figure 2). Although Fagoaga et al. (2019a) consider it a method totally distinct to MER
119 method, actually both are a different approach of the same strategy: the search of the common distribution area of a
120 given fossil biological assemblage. As Kothari (2004) denotes methods are more general, given the theoretical framework
121 (search of common distribution area, that is MER) for the development of different behaviours and instruments to
122 perform research (application of a ecological criterion to record the climatic data). Despite the fact that this discussion
123 may seem trivial, in reality the definition and distinction of the methods and techniques developed is a key tool for the
124 correct development of scientific knowledge. Failure to do this step correctly could lead to robust methods and
125 techniques being discarded due to confusion generated by the incorrect use of terminology (Lyman, 2016).



126

127 **Figure 2. Schematic explanation of the UDA-ODA discrimination technique, which is based in the application of**
 128 **an ecological criterion for the discrimination of the occupied areas (ODA) by a determined species from those of**
 129 **uncertain distribution (UDA), which does not accomplish with the ecological requisites of this species. After this**
 130 **discrimination, the method detect the current common ODA of a fossil assemblage.**

131 It has long recognised that the evolution of the climate has a crucial impact in the natural history of humans and, for that
 132 reason, palaeoclimatic reconstructions feature prominently in palaeoanthropological debates (Haywood et al. 2019). In
 133 this sense, the disappearance process of the Neanderthals has been focused from this topic. This event took place during
 134 Marine Isotope Stage (MIS) 3 (ca. 30–60 ka in accordance with Railsback et al. (2015)) (e.g. Mallol et al., 2012). This
 135 was an unstable climatic period in the Late Pleistocene that was characterised by alternating warm phases with
 136 expanding forests and cold phases when semi-arid areas developed (e.g. Fletcher and Sánchez-Goñi 2008). The reason/s
 137 behind the demise of the Neanderthals is an unresolved debate in the scientific community. Although numerous
 138 hypotheses that have been proposed to explain this event, these can be grouped in three categories (Vaesen et al. 2021).
 139 The first one is related with the migration of anatomically modern humans (AMH) in Europe, which competed with the
 140 Neanderthals for the resources and, finally, the last were replaced by the first (Mellars 2004). However, due to the
 141 scarcity of human remains in Late Pleistocene sites of the Iberian Peninsula (Strauss 2018), direct contact between both
 142 humans groups is hard to demonstrate (Vaquero et al. 2006; Mallol et al. 2012). Thus, this contact has been mainly
 143 based only on lithic tools. Nevertheless, whereas the Mousterian is well assumed that have been manufactured by
 144 Neanderthals (Vaquero et al. 2006), the attribution of Aurignacian tools to Homo sapiens? is highly controversial
 145 (Strauss 2018). Moreover, there are several problems related to the proposed dates for the contact between both human
 146 groups in several Iberian sites. As Wood et al. (2013) pointed out, the studied period is close to the practical limit for
 147 radiocarbon dating; postdepositional disturbance processes on dated elements and archaeological evidences cannot be

148 discarded; diagnostic elements in the lithic assemblage are lacking; and finally, some proposed radiocarbon dates are
149 inaccurate due to the use of inadequate pretreatment protocols. The second group of hypotheses are related to the
150 apparent small size of Neanderthal populations and the limited interconnectedness between them (Vaesen et al. 2021).
151 These particularities would have made them highly susceptible to inbreeding, allee effects and stochastic fluctuations
152 (Finlayson 2004; Vaesen et al. 2019). Finally, the third group points out that the demise of Neanderthals was related
153 with environmental factors, i. e. climate change (Bradtmöller et al. 2012). During its existence, Neanderthals were
154 highly influenced by climate, reaching its northernmost limit during warm episodes (Stewart 2005). Although at the
155 beginning of the MIS 3 Neanderthals were widespread around Europe, their distribution range was gradually shrinking
156 towards the south (Stewart 2009). The present consensus establishes that the final demise of Neanderthals took place at
157 Iberian Peninsula probably during Heinrich Event (HE) 4 (*ca.* 40.2-38.3 ka) (Bradtmöller et al. 2012) or just before its
158 onset (*ca.* 40.2 ka) (Wood et al. 2013; Galván et al. 2014; Wolf et al. 2018). In Mediterranean coastal areas severe
159 aridity episodes has been detected during this HE (Sepulchre et al. 2007); however, at least for the interior area of the
160 Iberian Peninsula, the mentioned climate deterioration does not seem to have coincided with HE 4 (Wolf et al. 2018).

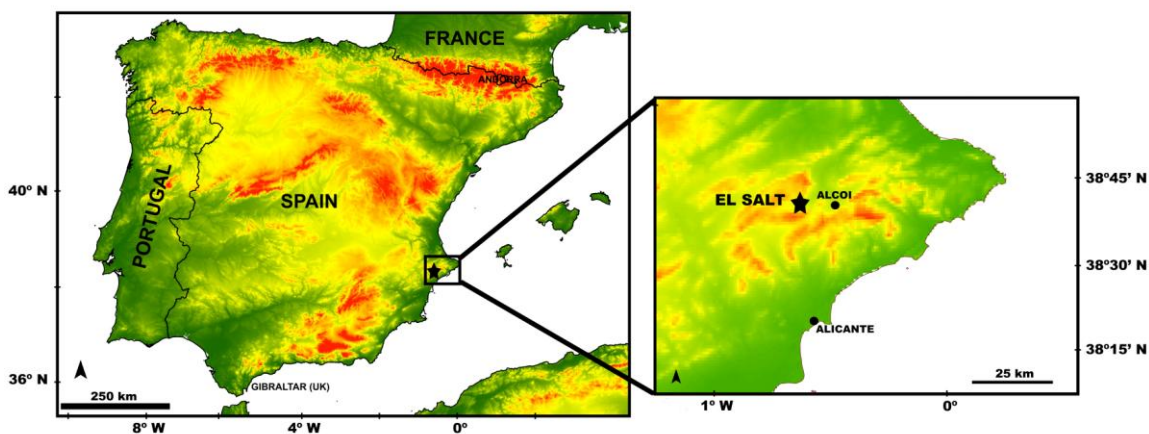
161
162 The Central coastal region of the Spanish Mediterranean coast has yielded numerous Middle Palaeolithic sites (Eixea et
163 al. 2020). Among them, El Salt site (Alcoi, Spain) is a key locality for studying the disappearance of Neanderthals in
164 the region. Its high value lies in the fact that the archaeological sequence of El Salt records different occupation phases,
165 in which a transition from recurrent to sporadic human occupation (and finally, an abandonment of the site) have been
166 identified (Galván et al. 2014). Moreover, El Salt yielded six Neanderthal teeth, possibly belonging to an individual
167 from one of the last groups in the region (Garralda et al. 2014). The vertebrate faunal assemblage recovered from the
168 site allows studying and interpreting the climatic evolution at local level in the south-eastern Iberian Peninsula during
169 the Middle Palaeolithic and the possible impact on the local palaeoecology and, therefore, on the human populations
170 inhabiting the area. In this sense, the study of the small vertebrates assemblages from El Salt has been focused on this
171 topic (Marquina-Blasco et al. 2017, 2021; Fagoaga et al. 2018, 2019a, b). Until now the majority of these works has
172 been based on the application of MER method (Marquina-Blasco et al. 2017, 2021; Fagoaga et al. 2018, 2019b), with
173 its inherent limitations already discussed above. Later, Fagoaga et al. (2019a) developed and applied the UDA-ODA
174 discrimination technique to the small mammal assemblages provided by Stratigraphical Unit (SU) Xb and V from El
175 Salt site. Thus, the aim of this study is to reconstruct the environmental conditions prevailing in SU Xb and V from El
176 Salt site, based on the application of this technique **UDA-ODA discrimination technique** on the amphibian and reptiles
177 assemblages recovered from both SUs for the first time to this kind of fauna. Our results are discussed with previous
178 works of palaeoclimatic reconstruction based on small vertebrates and other proxies from El Salt. In addition, we

179 contextualize our results with the debate about the disappearance of Neanderthals, focusing on the ecological context in
180 which these events occurred.

181

182 2. GEOLOGICAL SETTING

183 The Middle Palaeolithic site of El Salt (Alcoi, Alicante) (716,673; 4,284,952; 30S) (Figure 3) rests against a 38 m-high
184 Paleocene limestone wall at 680 m above sea level. The wall is the result of a trust fault of Eocene limestone over
185 Paleocene conglomerates. At the upper part of the wall the course of the Barxell River was stopped by the presence of
186 the limestone, creating a palaeolake that outflowed over the fault. As a result, a large travertine building was created
187 along more than 2.5 km in the foothills of the Serra de Mariola (Galván et al. 2014).



188

189 **Figure 3. Geographic location of the El Salt site (black star) in the Iberian Peninsula.**

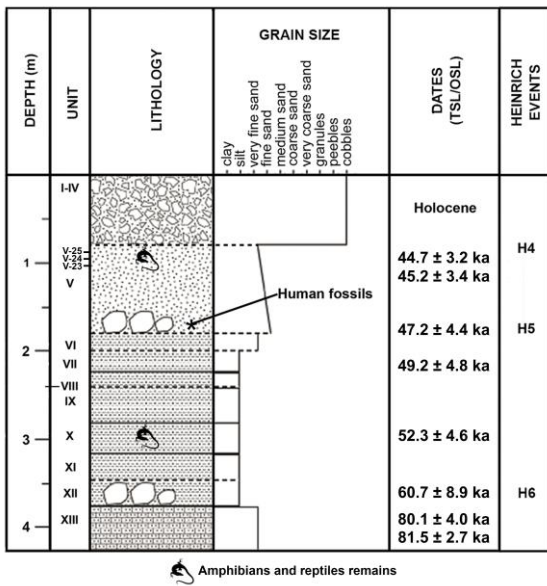
190 The sedimentary sequence of the site consists of thirteen lithostratigraphic units (Fumanal 1994) grouped into five
191 segments, in basis of its macroscopic textural appearance and archaeological context (Galván et al 2014) (Figure 4).

192 From base to top:

- 193 • SU XIII: subtravertine platform of unknown thickness. Its top has been dated by U/Th as 81.5 ± 2.7 ka and
194 80.1 ± 4 ka (MIS 5a- ca. 82–71 ka) (Galván et al. 2014). This SU is archaeological sterile.
- 195 • SU XII to IX: these units consist of 1.5 m of horizontally bedded fine sand, with several large blocks at their
196 base and related to a first episode of roof collapse (Galván et al. 2014). This part of the sequence has been
197 dated, using thermoluminescence (TL), as 60.7 ± 8.9 ka (SU XII) and 52.3 ± 4.6 ka (SU X) (Galván et al.
198 2014), placing the sequence at the beginning of MIS 3, before event HE 5 (Galván et al. 2014). These SUs
199 contain the highest concentration of archaeological remains and combustion features within the entire
200 sequence.
- 201 • SU VIII to V: in this sequence a gradually decrease of human occupation evidences is recorded that ends quite
202 spatially reduced. SU VI is covered by a significant accumulation of large blocks, produced by the collapse of
203 the roof of the travertine structure. Six Neanderthal teeth attributed to a juvenile or young adult were recovered
204 from the base of SU V (Garralda et al. 2014). These remains may represent one of the last occurrences of

205 Neanderthals in the region (Garralda et al. 2014). The top of SU VI has been dated by TL as between $52.3 \pm$
 206 4.6 and 47.2 ± 4.4 ka, whereas the base of SU V has been dated by optically stimulated luminescence (OSL) as
 207 45.2 ± 3.4 ka (Galván et al. 2014). The middle part of SU V has been dated by OSL as 44.7 ± 3.2 ka, before
 208 HE 4 ($40.2\text{--}38.3$ ka) (Galván et al. 2014). The upper part of SU V consists of a 50 cm-thick layer, truncated by
 209 a Holocene erosive episode. It is constituted by massive sandy silt with heterogeneous gravel in the top 20 cm,
 210 from which two small flint blades, a few undifferentiated flakes, and a small combustion structure have been
 211 recovered (Garralda et al. 2014).

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



218
 219 **Figure 4. Lithostratigraphic column of El Salt showing the different Stratigraphic Units (SU) described by**
 220 **Fumanal (1994), lithology of each SU and its proposed datation (Galván et al., 2014). Modified from Garralda et**
 221 **al. (2014).**

223

224 **3. MATERIAL, METHODS, AND ABBREVIATIONS**

225 To conduct the palaeoclimatic reconstruction, we apply the UDA-ODA discrimination technique (Fagoaga et al. 2019a)
 226 on the amphibians and reptiles assemblage from SU Xb (Xb-11 S3) and two different segments of the SU V: V-24
 227 (surfaces (S) 7, 8, and 9), and V-25 (Table 1). The faunal list of the analyzed assemblages has been taken from
 228 Marquina-Blasco et al. (2017, 2021). This method is based on the application of an ecological criterion to distinguish
 229 those areas that are ecologically habitable for each species (ODA) from those that, in principle, lack the necessary
 230 requirements for use by the taxon (UDA). After this, the method searches the modern biogeographic co-occurrence of
 231 the ODAs of species described in a palaeontological or archaeological site. As discrimination factor we have use
 232 elevation for each species. The choice of this criterion was based on several points: (i) ease of implementing this
 233 information in Geographic Information Systems (GIS); (ii) existence at Spanish level, and to a lesser extent in Portugal,
 234 of distribution atlases with altitudinal distribution information on herpetofauna at various administrative levels: national
 235 (i.e., Pleguezuelos et al. 2002; Loureiro et al. 2008), regional (i.e., Bea 1985; Llorente et al. 1995), provincial (i.e.,
 236 Pérez-Mellado 1983; Barberá et al. 1999), protected areas (i.e., Santos et al. 2005; Domínguez et al. 2012), and even
 237 particular mountainous systems (Martínez-Rica 1983; Lizana et al. 1988); (iii) altitudinal distribution of Iberian reptile
 238 and amphibian species is relatively well known; (iv) in the case of Iberian reptiles, the maximum altitude reached by
 239 species is a better discriminant than mean altitude when performing a biogeographical analysis (Saint Girons 1982); and
 240 (v) altitude is a very important factor in explaining the distribution of amphibians and, especially, reptiles due to its
 241 clear effect on temperature and precipitation (Soares and Brito 2007).

242 **Table 1. Faunal list from Stratigraphic Unit Xb (Marquina-Blasco et al. 2017) and V (Marquina-Blasco et al.**
 243 **2021) from El Salt. 1: presence; 0: absence.**

	Xb		V		
	11		24	S7	25
	S3		S9	S8	--
Anura indet.	0		0	0	0
<i>Pelodytes</i> sp.	0		1	0	0
<i>Alytes obstetricans</i>	1		1	1	1
<i>Epidalea calamita</i>	1		1	1	1
<i>Bufo bufo</i> s.l.	1		0	0	0
<i>Blanus cinereus</i> s.l.	1		0	0	0
Lacertilia indet.	0		1	1	1

<i>Chalcides bedriagai</i>	1	1	1	1	1
Lacertidae indet.	0	1	1	1	1
cf. <i>Acanthodactylus erythrurus</i>	1	0	0	0	0
Serpentes indet.	0	1	1	1	1
Colubridae indet.	0	1	1	1	0
<i>Coronella</i> sp.	0	1	0	1	0
<i>Coronella</i> sp./ <i>Zamenis</i> sp.	0	1	0	0	0
cf. <i>Zamenis scalaris</i>	1	0	0	0	0
<i>Natrix maura</i>	0	0	1	0	0
<i>Vipera latastei</i>	0	1	0	1	0

244 We have considered here the entire Iberian Peninsula, an area with natural geographical limits. The choice of this
245 analytical unit is also supported by the fact that some species that could potentially appear in the site are Iberian
246 endemisms (e.g. *Chalcides bedriagai*). The biogeographic cartography of amphibians and reptiles for Spain is provided
247 by the Servidor de Información de Anfibios y Reptiles de España (SIARE) (AHE 2021); for Portugal, it is provided by
248 Loureiro et al. (2008). Using ArcGis 9.1®, the climatic parameters are estimated by overlapping the co-occurrence
249 areas and the current climate layers with a 30-arcseconds resolution grid from WorldClim 1.4 (Hijmans et al. 2005).
250 Both sets of data (co-occurrence areas and climate layers) are represented in the same spatial reference system (EPSG
251 4326, WGS 84 UTM datum coordinate projection system). The bioclimatic parameters extracted from the cartography
252 supplied by Hijmans et al. (2005) are: BIO 1 (mean annual temperature, MAT), BIO 5 (maximum temperature of the
253 warmest month, MaxTW), BIO 6 (minimum temperature of the coldest month, MinTC), and BIO 12 (annual
254 precipitation, MAP).

255 The abbreviations used in this text are as follows: AHE (Asociación Herpetológica Española); AMH (anatomically
256 modern humans); CV (Coefficient of Variation); HE (Heinrich Event); MAT (mean annual temperature); MAP (mean
257 annual precipitation); MER (Mutual Ecogeographic Range method); MIS (marine isotope stage); MinTC (minimum
258 temperature of the coldest month); MaxTW (maximum temperature of the warmest month); ODA (Occupied
259 Distribution Area); S (excavation surface); SIARE 5Servidor de Información de Anfibios y Reptiles de España°; SU
260 (Stratigraphic Unit); TL (thermoluminescence dating method); UDA (Uncertain Distribution Area), σ (Standard
261 Deviation).

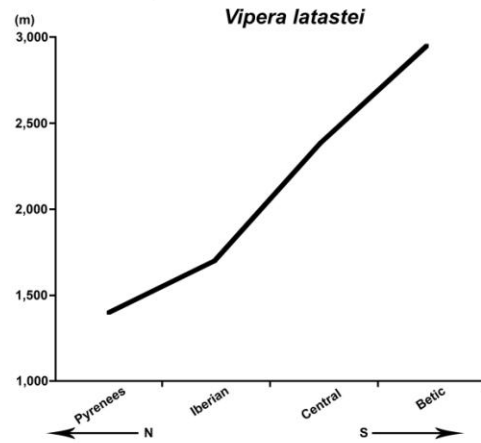
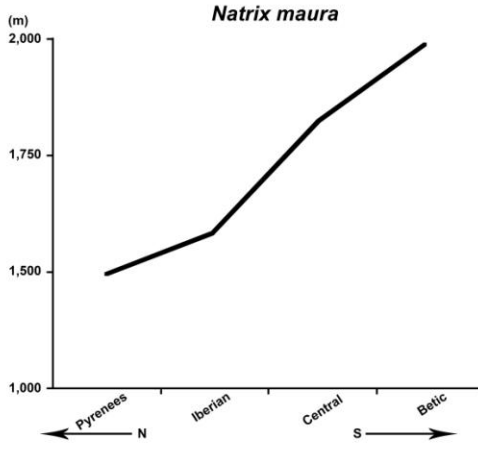
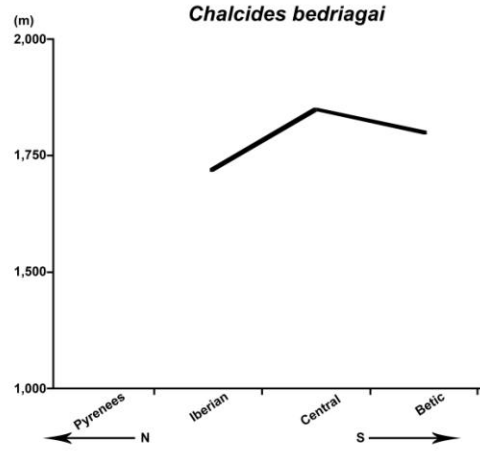
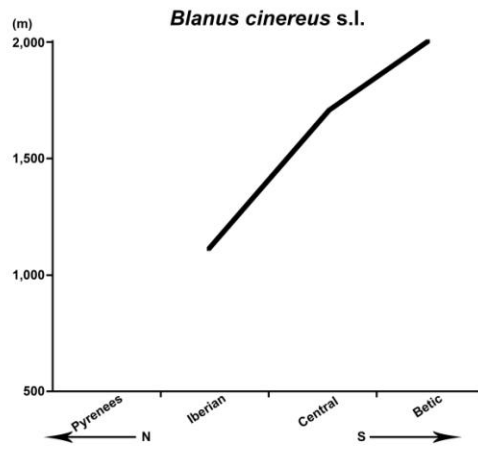
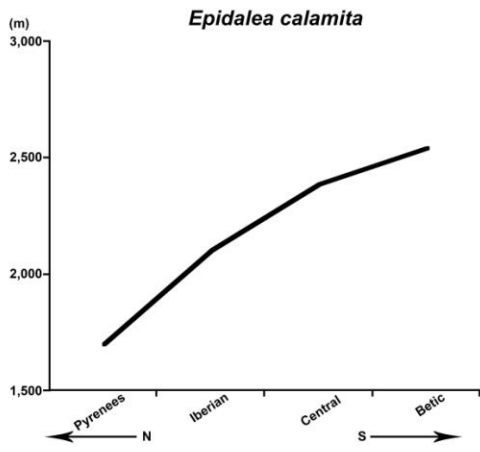
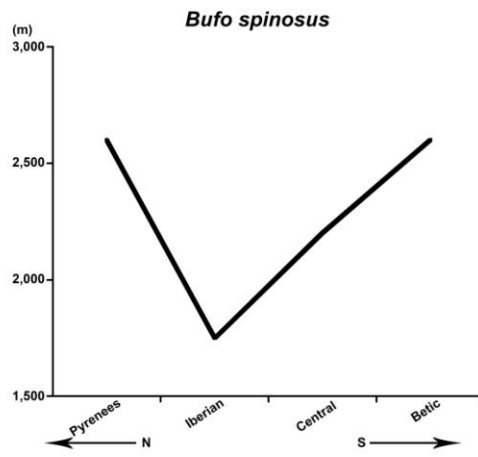
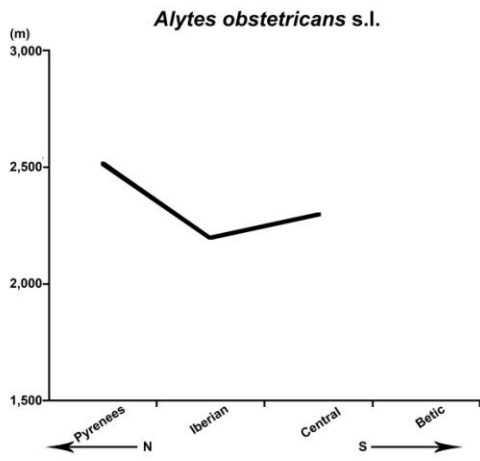
263 **4. RESULTS**264 *4.1. Altitudinal range of the target species*

265 A total of 89 works have been evaluated for the determination of the altitudinal range in the mountain range of the
 266 herpetological species included in the assemblage of SU Xb and V from El Salt site. The detailed list of these
 267 references, which include papers, books, atlases, field guides, and technical reports, are included in the Supplementary
 268 Material 1. The obtained results show an increase in the maximum height from North to the South (Table 2), except for
 269 *Alytes obstetricans*, which reaches higher altitude in the Pyrenees than other southern ranges, i.e. Iberian and Central
 270 Range (Figure 5). Table 2 summarizes the maximum altitude reached by each species in every mountain system in the
 271 Iberian Peninsula, the detailed information about it is included in the Supplementary Material 2.

272 **Table 2. Maximum altitude reached by each species in the different mountain systems of the Iberian Peninsula**
 273 **for ODA (based on specialized literature) and for UTM grid (based on the calculated maximum value from 10 ×**
 274 **10 km UTM square grids distribution area), which are obtained from the elevation model provided by Hijmans**
 275 **et al. (2005). Δ: Differences between the altitudes used for the determination of ODA and those provided by**
 276 **atlases. Sources: Duguy et al. (1979); Falcón Martín (1982); Martínez Rica (1983); Pérez Mellado (1983); Bas**
 277 **López (1984); Bea (1985); Lizana et al. (1988); Galán and Fernández (1993); Mejjide et al. (1994); Llorente et al.**
 278 **(1995); Pleguezuelos and Villafranca (1997); Barberá et al. (1999); Fernández-Cardenete et al. (2000); Serrano**
 279 **Ezaguerrri et al. (2001); Bosch (2002); Morales et al. (2002); Ayllón et al. (2003); Vences et al. (2003); Malkmus**
 280 **(2004); Soares et al. (2005); Hernández-Sastre and Ayllón, 2007; García-Cardenete (2008); González-Fernández**
 281 **(2011); Domínguez et al. (2012); Puente Montiel (2013); Ferrer et al. (2018).**

		Pyrenees	Cantabrian	Galician	Iberian	Central	Montes de Toledo	Sierra Morena	Betic
<i>Alytes obstetricans</i> s.l.	ODA	2516	1670	1500	2200	2300	--	--	--
	UTM grid	3154	2414	2051	2205	2358	--	--	--
	Δ	-638	-744	-551	-5	-58	--	--	--
<i>Bufo spinosus</i>	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
<i>Epidalea calamita</i>	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
<i>Blanus cinereus s.l.</i>	ODA	--	--	--	1100	1700	1200	1200	2000
	UTM grid	--	--	--	1348	2386	1579	1230	3322
	Δ	--	--	--	-248	-686	-379	-30	-1322
<i>Chalcides bedriagai</i>	ODA	--	--	1103	1720	1850	1200	1200	1800
	UTM grid	--	--	1823	1937	2386	1579	1223	3322
	Δ	--	--	-720	-217	-536	-379	-23	-1522
<i>Natrix maura</i>	ODA	1500	1270	1210	1580	1800	1100	1100	1950
	Atlases	3016	2414	2051	2205	2386	1579	1230	3322
	Δ	-1516	-1144	-841	-625	-586	-479	-130	-1372
<i>Vipera latastei</i>	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



284 **Figure 5. Evolution of the maximum altitude of the herpetofauna species studied with respect to the latitudinal**
 285 **gradient of four Iberian mountain systems (from north to south: Pyrenees, Iberian System, Central System and**
 286 **Betic System).**

287 *4.2. Method comparison per variable and species*

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

292 **Table 3. Mean values and Standard Deviation (σ), and Coefficient of Variation (CV) of MAT (Mean Annual**
 293 **Temperature), MaxTW (maximum Temperature of the Warmest Month), MinTC (Minimum Temperature of**
 294 **the Coldest Month), and MAP (Mean Annual Precipitation), for each species of amphibians and reptiles**
 295 **identified in El Salt site according to the Portuguese Atlas (Loureiro et al. 2018) and in herpetofauna distribution**
 296 **server for Spain, SIARE (AHE 2021), ODA, and UDA. T-test significance level is calculated between values of**
 297 **ODA and UDA. Δ : Differences between the obtained results based on MER and ODA.**

	MER			ODA			UDA			T-test	Δ
	MEAN	σ	CV	MEAN	σ	CV	MEAN	σ	CV		
<i>Alytes obstetricians</i> s.l.											
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
<i>Bufo spinosus</i>											
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
<i>Epidalea calamita</i>											
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
<i>Blanus cinereus</i> 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
<i>Chalcides bedriagai</i>											
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

298

299 *4.3. Method comparison per variable and species*

300 As the above case, the T-test for independent samples for all assemblages and bioclimatic parameters analysed shows
 301 significant differences within ODA and UDA ($p < 0.01$) (Tabla 4; Figure 6). The first shows higher values for MAT,
 302 MaxTW, and MinTC than the second. For its part, UDA shows higher values for MAP than ODA (Tabla 4). The
 303 biggest differences between ODA and UDA have been recorded in Xb-11 S3 for MAT, MaxTW, and MinTC (+6.85 °C,
 304 +6.64 °C, and +6.47 °C, respectively) and in V-25 for MAP (-269.85 mm). In contrast, the smallest differences are
 305 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,
 306 and, MAP: -180.92 mm).

307 **Tabla 4. Mean values, Standard Deviation (σ), and Coefficient of Variation (CV) of MAT (Mean Annual**
 308 **Temperature), MaxTW (maximum Temperature of the Warmest Month), MinTC (Minimum Temperature of**
 309 **the Coldest Month), and MAP (Mean Annual Precipitation), for each studied assemblage using MER, ODA, and**
 310 **UDA methods. T-test significance level is calculated between values of ODA and UDA. Δ : Differences between**
 311 **the obtained results based on MER and ODA.**

	MER			ODA			UDA			T-test	Δ
	MEAN	σ	CV	MEAN	σ	CV	MEAN	σ	CV		
Xb-11 S3											
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

312

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

317 *4.4. MER vs ODA*

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

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

324

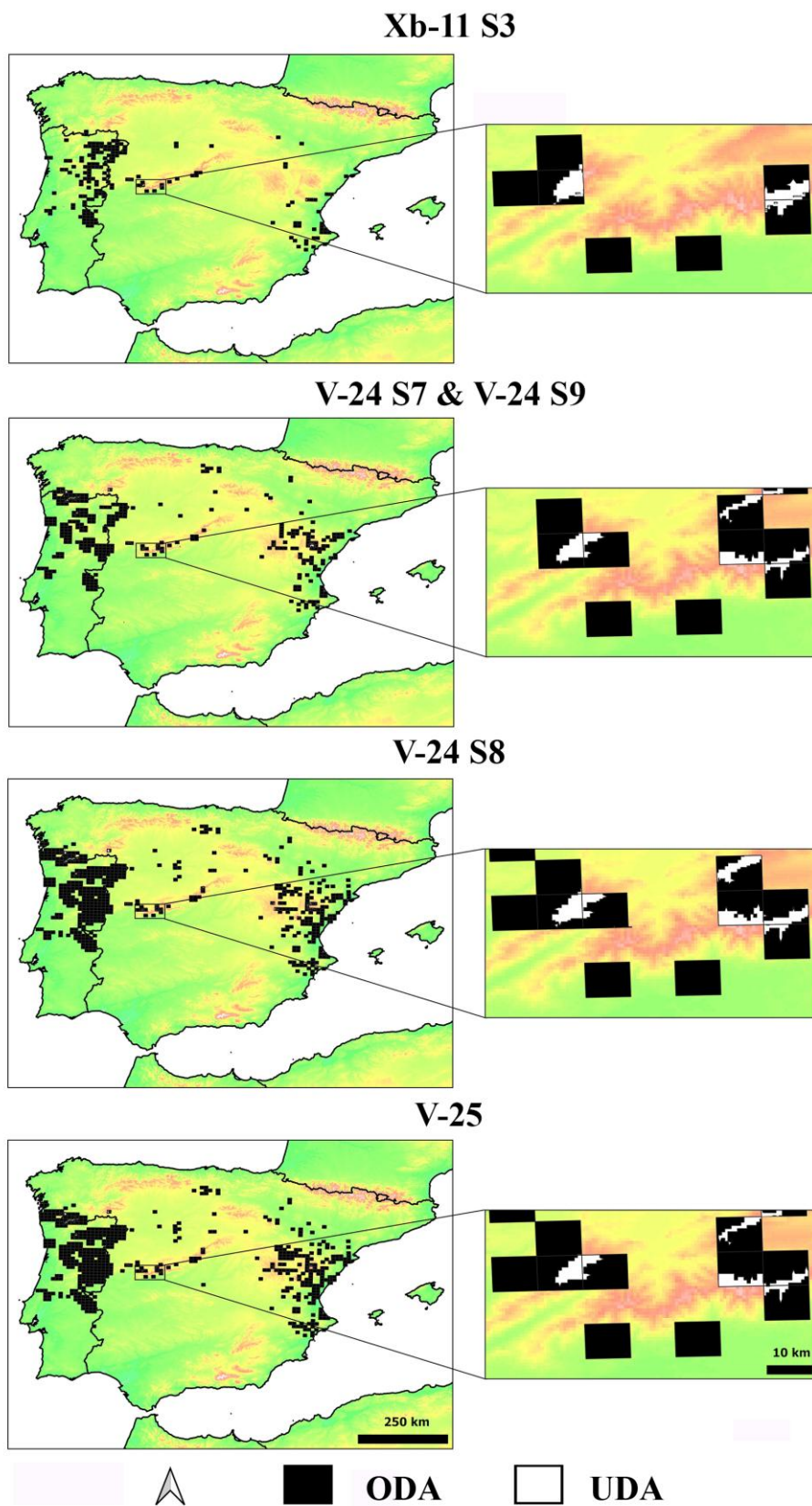


Figure 6. ODA (black areas) and UDA (white areas) of the common distribution areas for the different assemblages of fossil herpetofauna from El Salt site.

5. DISCUSSION

5.1. Altitudinal range of the target species

All the species studied show euryhypsas behavior, being 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 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 Figure 5), 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, it can be seen that the difference between the altitude used for the identification of ODAs, based on the consultation of the available scientific literature, and that obtained without these discrimination criterion (i.e., UTM grid of 10 × 10 km) is, in general, greater in reptiles than in amphibians (Table 2). In this sense, *Natrix maura* shows the major difference in the northernmost mountain ranges (Galician Massif, -841 m; Cantabrian Range, -1,144 m; Pyrenees, -1,516 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 trends 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 rufus* 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 2007), and for climatic parameters (Martínez-Freiría et al. 2008). Regarding to *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 both *C. bedriagai* and both species of the genus *Blanus* (*Blanus rufus* and *Blanus cinereus*) the range of these species is far from be 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. Again, reptile species present a greater reduction area than the amphibians, especially on ophidians (Table 5; Figure 7).

Table 5. Surface (ha) occupied by the different distribution units of each evaluated species. Reduction refers to the percentage by which the area occupied by the ecologically based distribution (ODA) has been reduced compared to that from UTM 10 × 10 km grids (UTM grid).

	UTM grid	ODA	UDA	Reduction
<i>Alytes obstetricans</i> s.l.	24,602,329.00	24,433,100.00	169,229.00	0.69
<i>Bufo spinosus</i>	43,633,218.00	43,416,964.00	216,254.00	0.50
<i>Epidalea calamita</i>	41,824,117.00	41,556,874.00	267,243.00	0.64
<i>Blanus cinereus</i> s.l.	18,113,151.00	17,986,829.00	126,322.00	0.70
<i>Chalcides bedriagai</i>	14,232,348.00	14,088,468.00	143,880.00	1.01
<i>Natrix maura</i>	42,531,852.00	41,632,317.00	899,535.00	2.11
<i>Vipera latastei</i>	14,615,103.00	14,387,799.00	227,304.00	1.56

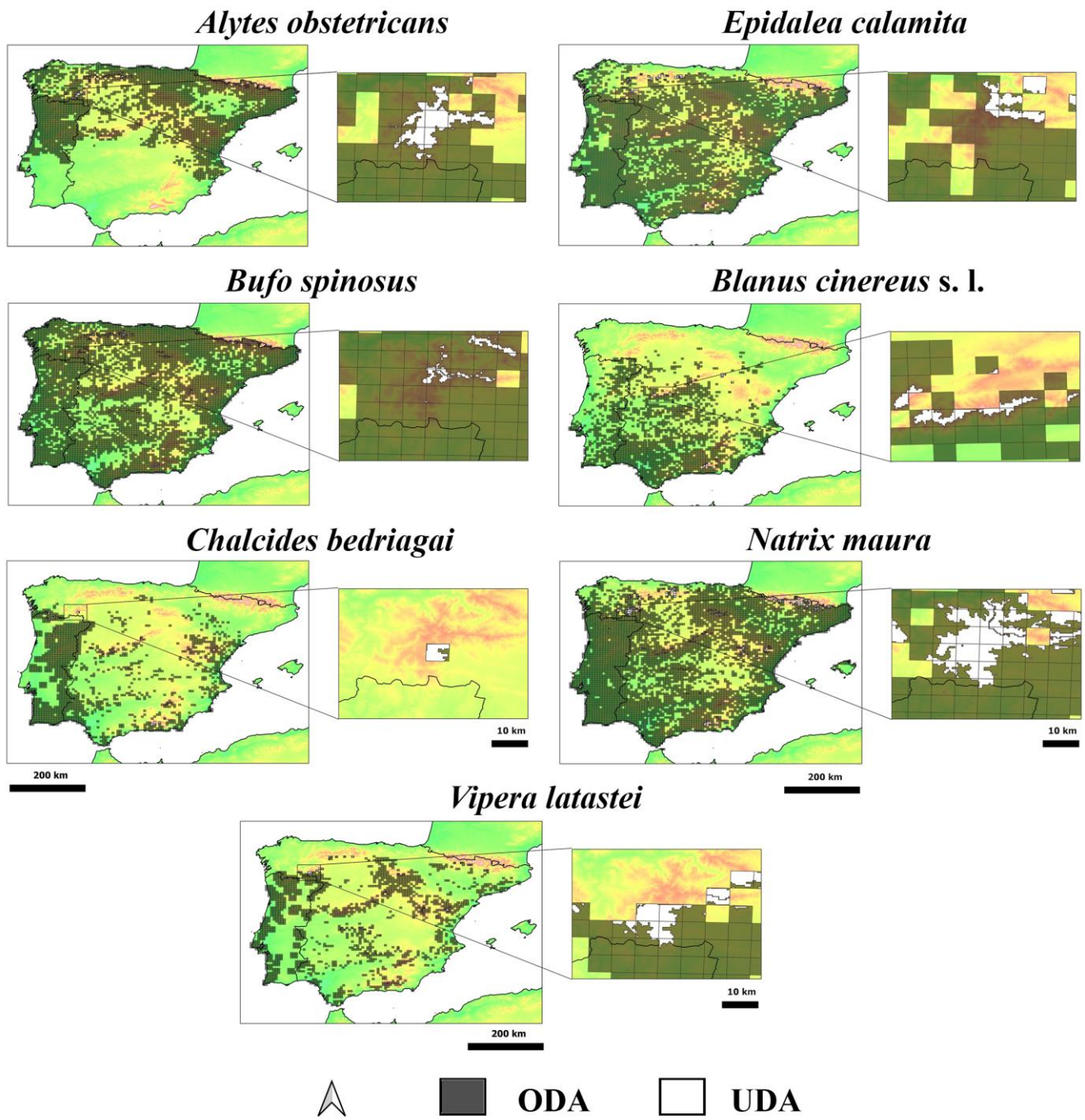


Figure 7. ODA (grey area) and UDA (white area) of each species of the studied assemblages.

5.2. 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 to 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 roughly 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 criteria based, in this case, on the maximum altitude of each species. The implemented discrimination criteria, the maximum altitude per Iberian range, resulted in the elimination of the higher cotes of the respective mountains. As the temperatures decreases 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 of *Blanus cinereus* s.l. in the case of MaxTW and *Epidalea calamita* for MinTC. These three taxa are considered as 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 to 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 (Tabla 4). In general, precipitation increases with elevation (Daly et al. 1993 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).

As well as herperofauna, small mammals from the same SUs of El Salt site, shows lower mean temperatures and higher rainfall in UDA results than ODA ones, except *Microtus arvalis* which behaves in the opposite way (Fagoaga et al. 2019a).

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

5.3. 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 (Tabla 4). Again, these differences seem to be related with the delete 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). Thus, 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, except for the case of MaxTW from V-24 S8. Regarding to MAP, the σ is smaller for ODA in the samples of Xb-11 S3 and V-24 S8 (Tabla 4). On the other hand, the σ in the means obtained by ODA is higher than in MER for the rest of the associations studied. 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 (Tabla 4). Thus, on this basis, the results obtained using MER show a higher relative variability than ODA.

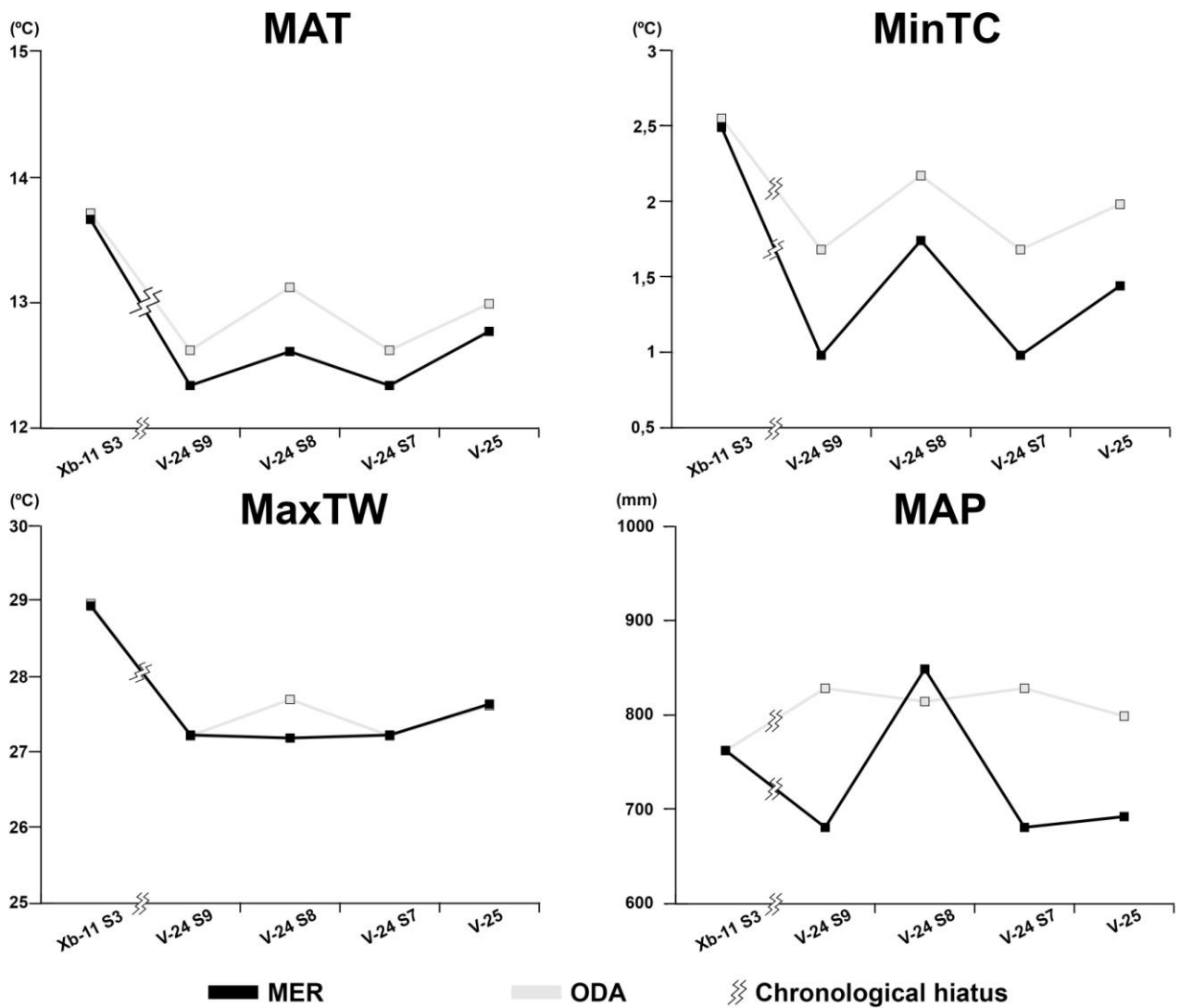


Figure 8. Comparison between the paleoclimatic reconstruction from Stratigraphic Units Xb and V of El Salt obtained by MER (black line) and ODA/UDA discrimination methodology (grey line). MAT (mean annual temperature, °C); MaxTW (maximum temperature of the warmest month, °C); MinTC (minimum temperature of the coldest month, °C); MAP (mean annual precipitation, mm).

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

(

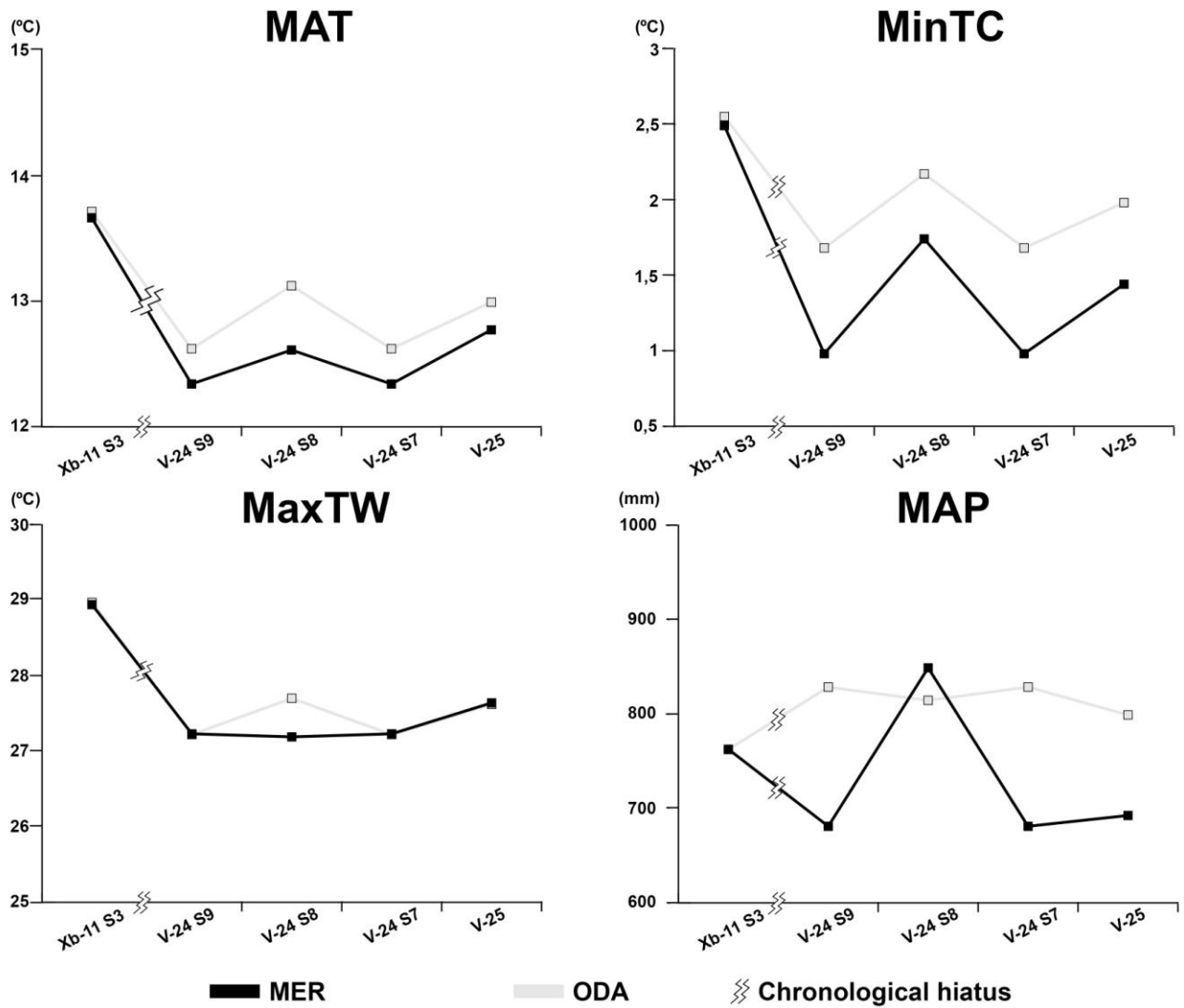


Figure 8). It is explained by the elimination of higher altitudes, in which are recorded the lower values of that parameters. Unlike with climatic results derived from each of the species, those obtained from association are disparate, as they do not behave equally between associations and parameters. 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

(

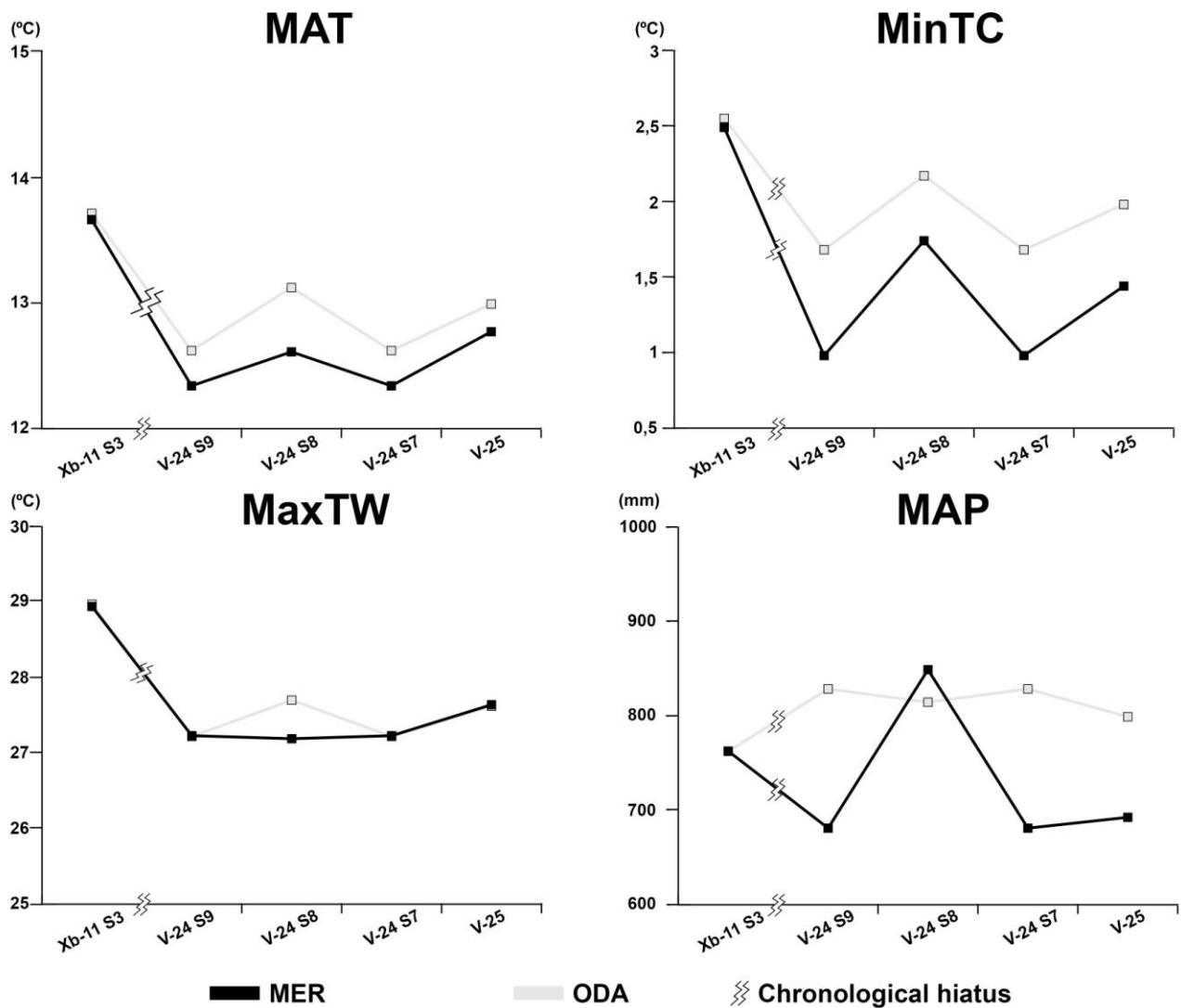


Figure 8). These results are difficult to interpret and may be due to the effect of the influence of orography on small/medium scale conditions. In the Iberian Peninsula most of the ranges are distributed from west to east (i. e., Pyrenees, Cantabrian Range, and Central Range) (Font Tullot 2000; Pascual and Sanz 2017); as a consequence 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. 1998; Gong et al. 2008; Shepard and Burbrink 2008; Foord et al. 2014). 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 inhabits 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) 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 Marmol 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 were the values of MaxTW and MAP are higher based on UDA-ODA discrimination technique than MER method there are a major reduction of the area occupied by southern slopes than northern ones (Table 6). 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 (Table 6). Consequently, it is reduced the theoretically highest values of rainfall and the lowest values of MaxTW.

Table 6. Surface occupied by Northern (N) and Southern (S) slopes in the occupied distribution area (ha) of mutual distribution of the different studied assemblages of fossil herpetofauna from SU Xb and V of El Salt site, based on MER and ODA. ODA-MER reflects the differences between the occupied area of ODA minus MER.

		N	S
V-24 S3	MER	112,736,424.93	134,344,164.13
	ODA	110,820,493.10	133,128,296.75
	ODA-MER	-1,915,931.83	-1,215,867.37
V-24 S7	MER	214,766,446.38	234,324,327.89
	ODA	207,491,992.16	226,359,031.47
	ODA-MER	-7,274,454.22	-7,965,296.42
V-24 S8	MER	329,978,118.96	374,108,287.66
	ODA	318,873,133.48	363,163,069.33

	ODA-MER	-11,104,985.47	-10,945,218.33
V-24 S9	MER	214,766,446.38	234,324,327.89
	ODA	207,491,992.16	226,359,031.47
	ODA-MER	-7,274,454.22	-7,965,296.42
V-25	MER	353,922,203.69	390,898,288.45
	ODA	346,753,196.74	383,123,585.46
	ODA-MER	-7,169,006.94	-7,774,702.99

Comparing with current values at the site and regarding to temperatures, the palaeoclimatic reconstruction based on UDA-ODA discrimination technique show a context with higher temperatures in older SU (Xb) than today (+0.07 °C), that is MAT, MaxTW, and MinTC. In SU V, these temperature parameters are lower than the present one (Table 7). In the case of MAP, in all samples from both units values are higher than the rainfall recorded nowadays at Alcoi (Table 7). The same pattern has been reported for the same assemblages using the MER method (Marquina-Blasco et al. 2017, 2021a). 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 7). The other two parameters, MaxTW and MAP, do not show any common pattern (Table 7). Thus, MaxTW shows lower values than the current ones in all samples of the SU V. Regarding to MAP, Xb-11 S3 and V-24 S8 show lower differences respect to current values in ODA-UDA discrimination methodology than in MER method.

Table 7. 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
-----------------	--------	--------	--------	--------	--------

Comparing values obtained for the units analysed, 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 palaeoclimatic reconstruction seems to draw a scenario of an alternation of moments with higher temperature (Su Xb-11 S3, V-24 S8, and V-25) with others of lower temperatures (V-24 S9 and V-24 S8). The main differences between methods are related with the parameters MaxTW and, especially, MAP. Regarding to 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 is 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 S8, and V-25) with others of lower temperatures (V-24 S9 and V-24 S7). As show in the

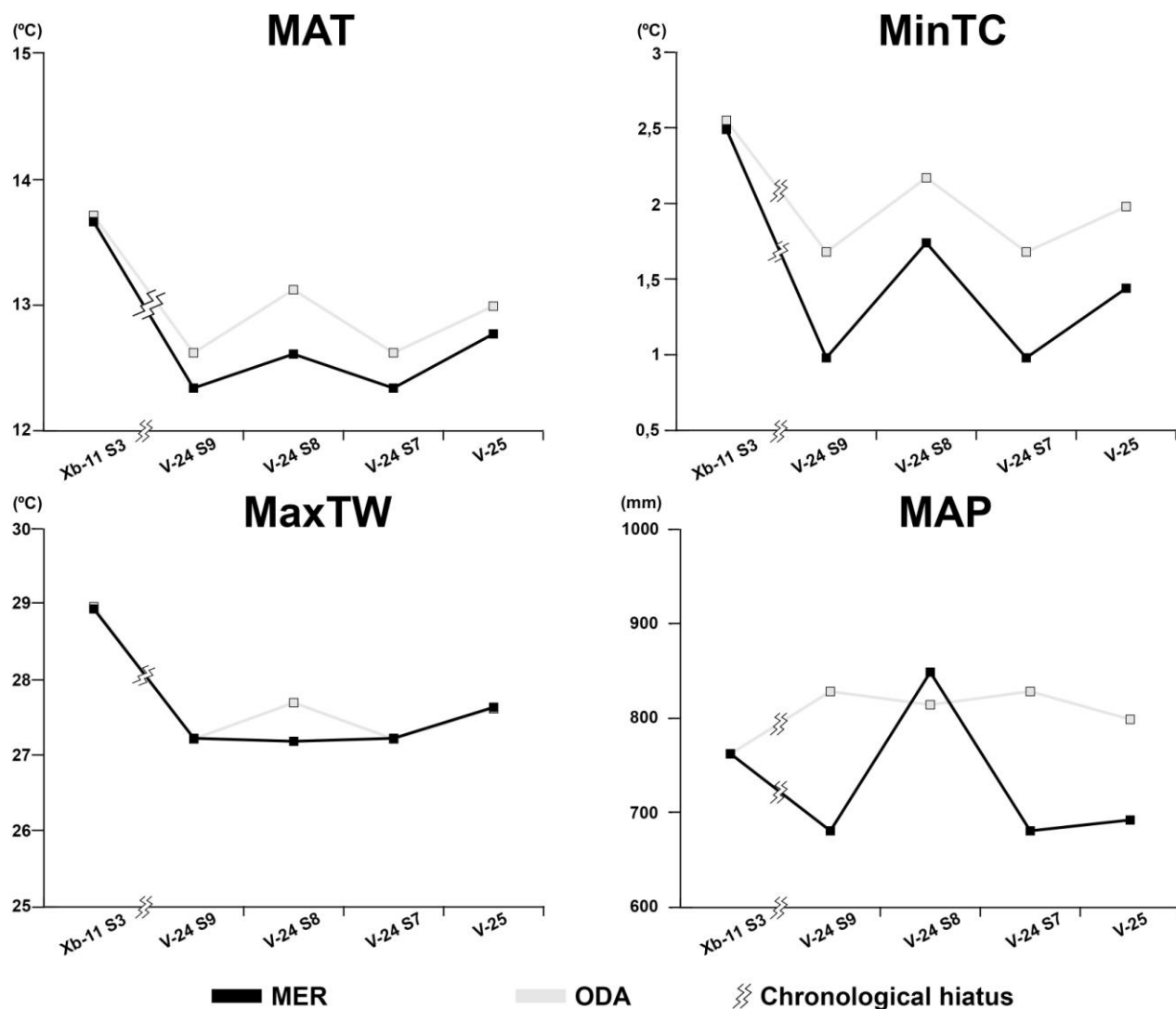


Figure 8, the palaeoclimatic reconstruction based on MER method the samples with higher MAT values are coincident with the higher ones of MAP (Xb-11 S3, V-24 S8, and V-25) (Marquina-Blasco et al. 2021a). Roughly, there seems to be an alternation between “warm and wet” and “cooler and drier” moments. 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.

5.4. Herpetofauna vs small mammals and other proxies

The small mammal associations of the same SUs studied yielded the same pattern as herpetofauna based on UDA-ODA discrimination technique compared with MER method. In all the assemblages 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) (Figure 9). As Marquina-Blasco et al. (2021)

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 both groups. The covered area of these distributions in the case of small mammals is more geographical located to the north and northwest of the Iberian Peninsula, whereas in the case of 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 distribution of Iberian reptiles and amphibians is a more studied issue than the regarded to 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 presented 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 dependent of the degree of refinement of the established ecological criteria for the definition of UDAs and ODAs. Considering 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 herpetofauna, 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).

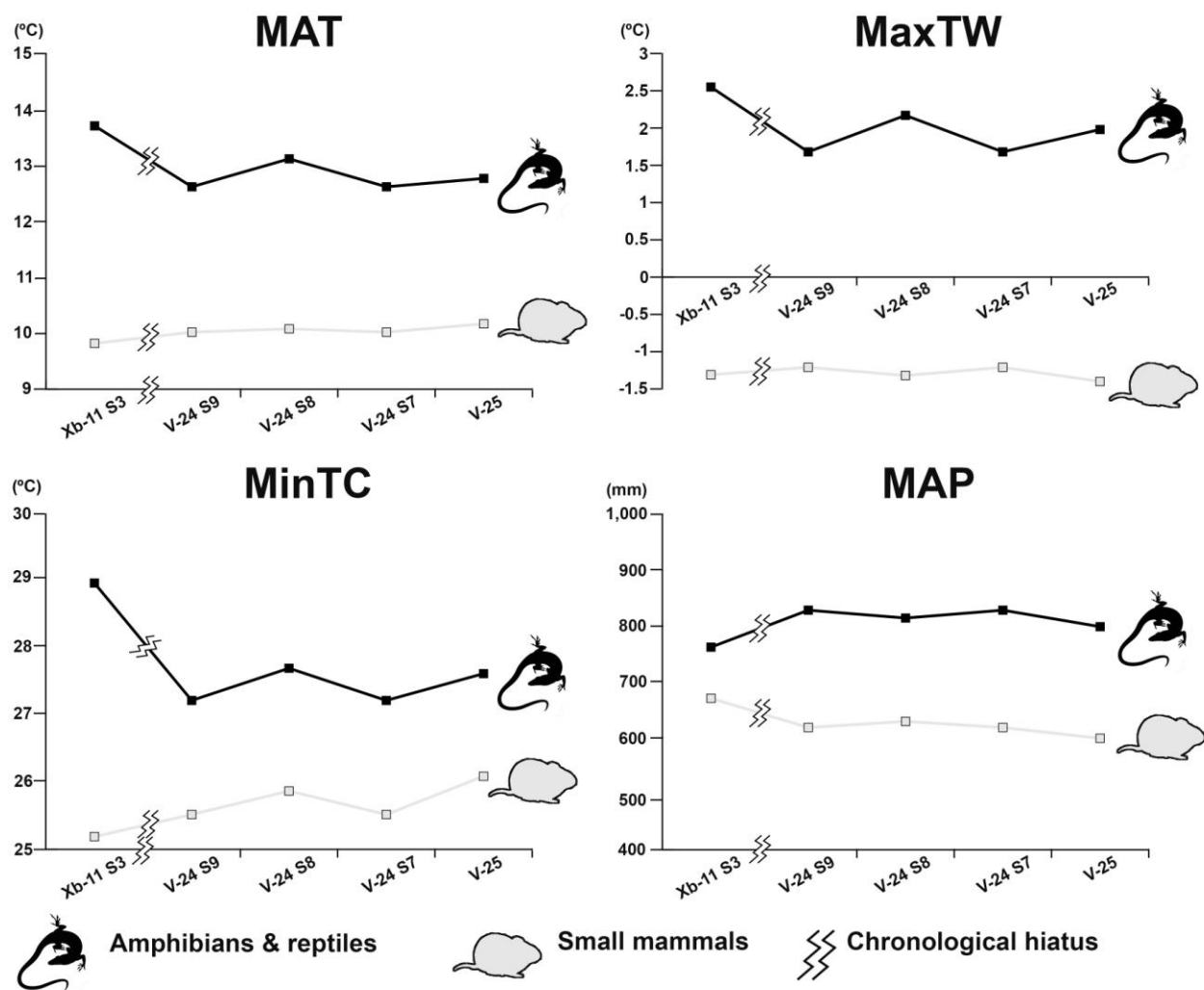


Figure 9. Evolution of the bioclimatic parameters after the application of the UDA-ODA discrimination technique to the fossil assemblages of herpetofauna and small mammals from Stratigraphic Units Xb and V of El Salt. MAT (mean annual temperature, °C); MaxTW (maximum temperature of the warmest month, °C); MinTC (minimum temperature of the coldest month, °C); MAP (mean annual precipitation, mm). Black line, herpetofauna; grey line, small mammals.

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). In our case, 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, also in the both evaluated methods, MER (Marquina-Blasco et al. 2017, 2021a) and UDA-ODA (this work). However, in the case of small mammals this parameter descends continuously from Xb-11 S3 to V-25 (Fagoaga et al. 2019a, b), whereas our results show a more erratic evolution, with an apparent decline in the MAP value between V-24 S7 to V-25. 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 than 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 eolian 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). 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 (Galván et al. 2014).

5.5. 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 has 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 a depositional processes dominated by gravitational component to another dominated by aeolian component and increase in the episodes 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 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 although it is slightly higher in the more modern SU than in the older one, the value obtained seems to indicate an evolution towards drier conditions. Thus the MAP value obtained in V-24 S7 is higher than in V-25.

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, behavior and networks after the occurrence of cold phases (Delagnes and Rendu 2011). In the case of Eastern Iberia, Neanderthals occupations are related always with highly structures 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 that rainfall, rather than temperatures, was a crucial parameter for Neanderthals 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, on the disappearance of Neanderthals in the region is a plausible explanation. However, more research is needed for clarify this question. In any case, as our results point out, 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.

6. 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 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 σ 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 CV in the mean of each bioclimatic parameter. Thus, this method of palaeontological reconstruction is more accurate, not only on a theoretical level in the sense of applying an ecological criterion that makes more sense of the distributions used, but also appears to be statistically more robust.

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 widely distribution range of the Iberian species of amphibians and reptiles. Regarding to small mammals, the species presents, in general, 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 for definition of ODA of these species had not defined for each Iberian mountain system. Thus, our results and those provided by small mammals' distribution 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 drier and an apparent colder conditions from older SU (Xb) to modern ones (V), some differences are observed. In this sense, our results draw a more erratic evolution.

Regarding to the anthropic use of El Salt site, our results demonstrate that the abandonment process of the site took place in a context of a progressive aridification, as other proxies also point out. Whether there is a causal relationship between the two processes is a matter for future multidisciplinary work to discern.

7. REFERENCES

- AHE (2021) SIARE (Servidor de Información de Anfibios y Reptiles de España). Asociación Herpetológica Española. <http://siare.herpetologica.es/bdh>. Accessed January 2020.
- Alfimov AV, Berman DI (2009) Possible errors of the mutual climatic range (MCR) method in reconstructing the Pleistocene climate of Beringia. *Entomol. Rev.* 89:487-499. <https://doi.org/10.1134/S0013873809040137>
- Araújo MB, Thuiller W, Pearson R G (2006) Climate warming and the decline of amphibians and reptiles in Europe. *J. Biogeogr.* 33:1712-1728. <https://doi.org/10.1111/j.1365-2699.2006.01482.x>
- Atkinson TC, Briffa KR, Coope GR, Joachim MJ, Perry DW (1986) Climatic calibration of coleopteran data. In: Bergland BE (Ed.) *Handbook of Holocene Palaeoecology and Palaeohydrology*. John Wiley and Sons, Chichester, pp 851-858.

- Atkinson TC, Briffa KR, Coope GR (1987) Seasonal temperatures in Britain during the past 22,000 years, reconstructed from beetle remains. *Nature* 325:587-592. <https://doi.org/10.1038/325587a0>
- Ayllón E, Bustamante P, Cabrera F, Flox AJ, Galindo AJ, Gosálvez RU, Hernández JM, Morales M, Torralvo C, Zamora, F (2003) Atlas provisional de distribución de los anfibios y reptiles de la provincia de Ciudad Real (Castilla-La Mancha, España). *Zool. baetica* 13/14:155-203.
- Barberá JC, Ayllón E, Trillo S, Astudillo G, (1999) Atlas provisional de distribución de los anfibios y reptiles de la provincia de Cuenca (Castilla-La Mancha, España). *Zool. baetica* 10:123-148.
- Barbosa AM, Real R, Muñoz AR, Brown JA, (2013) New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Divers. Distrib* 19:1333-1338. <https://doi.org/10.1111/ddi.12100>.
- Bas López S (1984) Biogeografía de los Anfibios y Reptiles de Galicia, un Ensayo de Síntesis. *Amphib-reptil.* 5:289-310. <https://doi.org/10.1163/156853884X-005-03-10>
- Bas López S (1986) Los anfibios y reptiles de Ancares (Lugo, N. O. España). *Munibe* 38:89-98.
- Bea A (1981) Herpetofauna de Guipúzcoa: Estudio Faunístico y Relaciones con la Climatología. *Munibe* 33:115-154.
- Bea A (1985) Atlas de los anfibios y reptiles de Álava, Vizcaya y Guipúzcoa. In: Álvarez J, Bea A, Faus JM, Castián E, Mendiola I (eds.) Atlas de Los Vertebrados Continentales de Álava, Vizcaya y Guipúzcoa. Gobierno Vasco. Departamento de Política Territorial y Transportes. Viceconsejería del Medio Ambiente, Bilbao, pp. 57-99.
- Begum F, Bajracharya R M, Sharma S, Sitaula BK (2010) Influence of slope aspect on soil physico-chemical and biological properties in the mid hills of central Nepal. *Int. J. Sustain. Dev. World Ecol.* 17:438-443. <http://doi.org/10.1080/13504509.2010.499034>
- Birks HJB, Heiri O, Seppa H, Bjune AE (2010) Strengths and weaknesses of quantitative climate reconstructions based on Late-Quaternary. *Open Ecol. J.* 3:68-110. <https://doi.org/10.2174/1874213001003020068>
- Blain H-A (2009) Contribution de la paléoherpétofaune (Amphibia & Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne. *Treballs Mus. Geol. Barcelona* 16, 39-170.
- Blain H-A, Bailon S, Cuenca-Bescós G, Arsuaga JL, Bermúdez de Castro JM, Carbonell E (2009) Long-term climate record inferred from Early-Middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina cave, Atapuerca, Spain. *J. Hum. Evol.* 56: 55-65. <https://doi.org/10.1016/j.jhevol.2008.08.020>
- Blain H-A, Gleed-Owen CP, López-García JM, Carrión JS, Jennings R, Finlayson G, Finlayson C, Giles-Pacheco F (2013) Climatic conditions for the last Neanderthals: Herpetofaunal record of Gorham's Cave, Gibraltar. *J. Hum. Evol.* 64: 289-299. <https://doi.org/10.1016/j.jhevol.2012.11.003>
- Blain H-A, Lozano-Fernández I, Agustí J, Bailon S, Menéndez LG, Espígares PO, Ros-Montoya S, Jimenez JMA, Toro-Moyano I, Martínez- Navarro B, Sala R (2016) Redefining upon the climatic background of the early Pleistocene

hominid settlement in western Europe: Barranco Leon and Fuente Nueva-3 (Guadix-Baza basin, SE Spain). *Quat. Sci. Rev.* 144:132-144. <https://doi.org/10.1016/j.quascirev.2016.05.02>.

Blain H-A, Silva JAC, Arenas JMJ, Margari V, Roucoux K, (2018) Towards a Middle Pleistocene terrestrial climate reconstruction based on herpetofaunal assemblages from the Iberian Peninsula: state of the art and perspectives. *Quat. Sci. Rev.* 191:167-188. <https://doi.org/10.1016/j.quascirev.2018.04.019>.

Bosch J (2002) *Alytes obstetricans* (Laurenti, 1768). Sapo partero común. In: Pleguezuelos JM, Márquez R, Lizana M (eds.) Atlas y Libro Rojo de los Anfibios y Reptiles de España. Segunda impresión. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid, 82-84.

Bradley RS (1999) Paleoclimatology. Reconstructing Climates of the Quaternary. International Geophysics Series, 64. Academic Press, Burlington.

Bradt Möller M, Pastoors A, Weniger B, Weniger GC (2012) The repeated replacement model-Rapid climate change and population dynamics in late Pleistocene Europe. *Quat. Int.* 247: 38-49. <https://doi.org/10.1016/j.quaint.2010.10.015>

Brito JC, Crespo EG (2002) Distributional analysis of two vipers (*Vipera latastei* and *V. seoanei*) in a potential area of sympatry in the Northwestern Iberian Peninsula. In: Schuett GW, Hoggren M, Douglas ME, Greene HW (eds) *Biology of the Vipers*. Eagle Mountain Publishing Eagle Mountain, UT, 230-257.

Castellanos-Frías E, García N, Virgós E (2018) Assessment of the effect of climate changes in the Late Pleistocene and Holocene on niche conservatism of an arvicolid specialist. *Sci. Rep.* 8:9780. <https://doi.org/10.1038/s41598-018-28000-0>

Chave J, Muller-Landau HC, Levin SA (2002) Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.* 62:153-168. <https://doi.org/10.1086/324112>

Chesson P (2000) General theory of competitive coexistence in spatially-varying environments. *Theor. Popul. Biol.* 58:211-237.

Connolly R, Jambriña-Enríquez M, Herrera-Herrera AV, Vidal-Matutano P, Fagoaga A, Marquina-Blasco R, Marin-Monfort M D, Ruiz-Sánchez FJ, Laplana C, Bailon S, Pérez L, Leierer L, Hernández CM, Galván B, Mallol C (2019) A multiproxy record of palaeoenvironmental conditions at the Middle Palaeolithic site of Abric del Pastor (Eastern Iberia). *Quat. Sci. Rev.* 225:106023. <https://doi.org/10.1016/j.quascirev.2019.106023>

Coope GR (1994) The response of insect faunas to glacial-interglacial climatic fluctuations. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 344:19-26. <https://doi.org/10.1098/rstb.1994.0046>.

Coope GR, Lemdahl G, Lowe JJ, Walkling A, (1998) Temperature gradients in northern Europe during the last glacial-Holocene transition (14-9 ¹⁴C kyr BP) interpreted from coleopteran assemblages. *J. Quat. Sci.* 13:419-433. [https://doi.org/10.1002/\(SICI\)1099-1417\(199809\)13:5<419::AID-JQS410>3.0.CO;2-D](https://doi.org/10.1002/(SICI)1099-1417(199809)13:5<419::AID-JQS410>3.0.CO;2-D).

- Daly C, Neilson RP, Phillips DL (1994) A Statistical-Topographic Model for Mapping Climatological Precipitation Over Mountain Terrain. *J. Appl. Meteorol.* 33:140-158. [https://doi.org/10.1175/1520-0450\(1994\)033<0140:ASTMFM>2.0.CO;2](https://doi.org/10.1175/1520-0450(1994)033<0140:ASTMFM>2.0.CO;2).
- Delagne A, Rendus W (2011) Shifts in Neandertal mobility, technology and subsistence strategies in western France. *J. Archaeol. Sci.* 38: 1771-1783. <http://doi.org/10.1016/j.jas.2011.04.007>.
- Domínguez J, Lamosa A, Pardavila X, Martínez-Freiría F, Regos A, Gil A, Vidal M (2012) Atlas de los vertebrados terrestres reproductores en el Parque Natural Baixa Limia-Serra do Xurés y ZEPVN-LIC Baixa Limia. Xunta de Galicia, A Coruña.
- Dubayah RC (1994) Modeling a solar radiation topoclimatology for the Rio Grande River Basin. *J. Veg. Sci.* 5:627-640. <https://doi.org/10.2307/3235879>
- Duguy R, Martínez Rica JP, Saint-Girons H (1979) La répartition des vipères dans les Pyrénées et les régions voisines du nord de l'Espagne. *Ext. Bull. Soc. Hist. nat. Toulouse* 115:359-377.
- Elias SA (1994) *Quaternary Insects and Their Environments*. Smithsonian Institution, Washington, DC.
- Elias SA (1997) The mutual climatic range method of palaeoclimatic reconstruction based on insect fossils: new applications and interhemispheric comparisons. *Quat. Sci. Rev.* 16:1217-1225. [https://doi.org/10.1016/S0277-3791\(97\)00029-2](https://doi.org/10.1016/S0277-3791(97)00029-2)
- Elias SA (2001) Mutual climatic range reconstructions of seasonal temperatures based on Late Pleistocene fossil beetle assemblages in Eastern Beringia. *Quat. Sci. Rev.* 20:77-91. [https://doi.org/10.1016/S0277-3791\(00\)00130-X](https://doi.org/10.1016/S0277-3791(00)00130-X).
- Elias SA, Andrews JT, Anderson KH (1999) Insights on the climatic constraints on the beetle fauna of coastal Alaska, USA, derived from the Mutual Climatic Range method of paleoclimate reconstruction. *Arct Antarct Alp Res* 31:94-98. <https://doi.org/10.1080/15230430.1999.12003284>.
- Eixea A, Chacón MG, Bargalló A, Sanchis A, Romagnoli F, Vaquero M, Villaverde V (2020) Neanderthal Spatial Patterns and Occupation Dynamics: A Focus on the Central Region in Mediterranean Iberia. *J. World Prehistory* 33:267-324. <https://doi.org/10.1007/s10963-020-09143-3>
- Fagoaga A, Ruiz-Sánchez FJ, Laplana C, Blain H-A, Marquina R, Marin- Monfort MD, Galván B (2018) Palaeoecological implications of Neanderthal occupation at Unit Xb of El Salt (Alcoi, eastern Spain) during MIS 3 using small mammals proxy. *Quat. Int.* 481:101-112. <https://doi.org/10.1016/j.quaint.2017.10.024>
- Fagoaga A, Blain H-A, Marquina-Blasco R, Laplana C, Sillero N, Hernández CM, Mallol C, Galván B, Ruiz-Sánchez FJ (2019a) Improving the accuracy of small vertebrate-based palaeoclimatic reconstructions derived from the Mutual Ecogeographic Range. A case study using geographic information systems and UDA-ODA discrimination technique. *Quat. Sci. Rev.* 223:105969. <https://doi.org/10.1016/j.quascirev.2019.105969>

- Fagoaga A, Laplana C, Marquina-Blasco R, Machado J, Marin-Monfort MD, Crespo VD, Hernández CM, Mallol C, Galván B, Ruiz-Sánchez FJ (2019b) Palaeoecological context for the extinction of the Neanderthals: a small mammal study of stratigraphic Unit V of the El Salt site, Alcoi, eastern Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 530:163-175. <https://doi.org/10.1016/j.palaeo.2019.05.007>
- Fagoaga A, Marquina-Blasco R, Gracia-Monferrer D, Martínez-Ortí A, Vidal-Matutano P, Sánchez-López L, Mallol C, Hernández CM, Galván B, Bailon S, Ruiz-Sánchez FJ, Laplana C (2021). Small vertebrates from a Holocene gravelly deposit at El Salt (Alcoi, Alicante). *Spanish J. Palaeontol.* 36. <https://doi.org/10.7203/sjp.36.1.20307>
- Falcón Martín JM (1982) Los anfibios y reptiles de Aragón. Librería General, Zaragoza.
- Fernández-Cardenete JR, Luzón-Ortega JM, Pérez-Contreras J, Tierno de Figueroa JM (2000) Revisión de la distribución y conservación de los anfibios y reptiles en la provincia de Granada (España). *Zool. baetica* 11:77-104.
- Fernández-García M, López-García JM, Bennàsar M, Gabucio MJ, Bargalló A, Gema Chacón M, Saladié P, Vallverdú J, Vaquero M, Carbonell E (2018) Paleoenvironmental context of Neanderthal occupations in northeastern Iberia: The small-mammal assemblage from Abric Romaní (Capellades, Barcelona, Spain). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 506:154-167. <https://doi.org/https://doi.org/10.1016/j.palaeo.2018.06.031>.
- Ferrer J, Fontelles F, Sort F, Guixé D, Vidal-Coll Y (2018) Confirmació de la presència de l'escurçó ibèric *Vipera latastei* al Solsonès i al sud est de l'Alt Urgell i descripció d'una nova zona de simpatria amb escurçó pirinenc *Vipera aspis*. *But. Soc. Cat. Herpetol.* 25:88-101.
- Finlayson C (2004) Neanderthals and Modern Humans: An Ecological and Evolutionary Perspective. Cambridge University Press, Cambridge.
- Fletcher W, Sánchez-Goñi MA (2008) Orbital and sub-orbital scale climate impacts on vegetation of the Western Mediterranean basin over the last 48 000 years. *Quat. Res.* 70:451-464. <https://doi.org/10.1016/j.yqres.2008.07.002>
- Font Tullot I (2000) Climatología de España y Portugal. Ediciones Universidad de Salamanca, Salamanca.
- Foord SH, Gelebe V, Prendini L (2015) Effects of aspect and altitude on scorpion diversity along an environmental gradient in the Soutpansberg, South Africa. *J. Arid Environ.* 113:114-120. <http://doi.org/10.1016/j.jaridenv.2014.10.006>
- Galán P (1988) Segregación ecológica en una comunidad de ofidios. Doñana, *Acta Vertebrata* 15:59-78.
- Galván B, Hernández CM, Mallol C, Mercier N, Sistiaga A, Soler V (2014) New evidence of early Neanderthal disappearance in the Iberian Peninsula. *J. Hum. Evol.* 75:16-27. <https://doi.org/10.1016/j.jhevol.2014.06.002>.
- García-Cardenete L (2008) Nuevos datos de distribución de anfibios y reptiles en los Picos de Europa y su entorno. *Bol. Asoc. Herpetol. Esp.* 19:73-75.

- Garralda MD, Galván B, Hernández CM, Mallol C, Gómez JA, Maureille B (2014) Neanderthals from El Salt (Alcoy, Spain) in the context of the latest Middle Palaeolithic populations from the southeast of the Iberian Peninsula. *J. Hum. Evol.* 75:1-15. <https://doi.org/10.1016/j.jhevol.2014.02.019>.
- Gómez de la Rúa D, Mallol Duque C, Galván Santos B, Hernández Gómez CM (2010) Una visión geoarqueológica general del yacimiento musteriense de El Salt (Alcoy, Alicante) a partir de la micromorfología. *Recerques del Mus. d'Alcoi* 19:19-32.
- Gong X, Brueck H, Giese KM, Zhang L, Sattelmacher B, Lin S (2008) Slope aspect has effects on productivity and species composition of hilly grassland in the Xilin River Basin, Inner Mongolia, China. *J. Arid Environ.* 72:483-493. <https://doi.org/10.1016/j.jaridenv.2007.07.001>
- González Hidalgo JC, Bonet A, Echeverría MT (1996) Efecto de la orientación de la ladera sobre algunas comunidades arbustivas del semiárido central de la depresión del Ebro. *Mediterránea* 15: 21-31.
- González Fernández JE (2011) Anfibios ibéricos conservados en las colecciones zoológicas: catálogo, evaluación y museología científica. Ph. D. Thesis, Universidad Complutense de Madrid.
- Grayson DK (1981) A critical view of the use of archaeological vertebrates in paleoenvironmental reconstruction. *J. Ethnobiol.* 1:28-38.
- Guiot J, de Vernal A (2007) Transfer functions: methods for quantitative paleoceanography based on microfossils. In: Hillaire-Marcel C, de Vernal A (Eds.) *Proxies in Late Cenozoic Paleoclimatology*. Elsevier, Amsterdam, pp. 523-63.
- Haywood AM, Valdes PJ, Aze T, Barlow N, Burke A, Dolan AM, von der Heydt, AS, Hill DJ, Jamieson SSR, Otto-Bliesner BL, Salzmann U, Saupe E, Voss J (2019). What can Palaeoclimate Modelling do for you? *Earth Syst. Environ.* 3:1-18. <https://doi.org/10.1007/s41748-019-00093-1>.
- Heatwole H, (1982) A review of structuring in herpetofaunal assemblages. *US Fish and Wildl. Res. Rep.* 13:1-19.
- Hernández-Sastre PL, Ayllón E (2007) Situación de La Herpetofauna En La Provincia de Toledo. Diputación de Toledo, Toledo.
- Higham T, Douka K, Wood R, Ramsey CB, Brock F, Basell L, Camps M, Arrizabalaga A, Baena J, Barroso-Ruiz C, Bergman C, Boitard C, Boscato P, Caparrós M, Conard NJ, Draily C, Froment A, Galván B, Gambassini P, García-Moreno A, Grimaldi S, Haesaerts P, Holt B, Iriarte-Chiapusso M-J, Jelinek A, Jordá Pardo JF, Maíllo-Fernández J-M, Marom A, Maroto J, Menéndez M, Metz L, Morin E, Moroni A, Negrino F, Panagopoulou E, Peresani M, Pirson S, de la Rasilla M, Riel-Salvatore J, Ronchitelli A, Santamaria S, Semal P, Slimak L, Soler J, Soler N, Villaluenga A, Pinhasi R, Jacobi R (2014) The timing and spatiotemporal patterning of Neanderthal disappearance. *Nature* 512: 306-309. <https://doi.org/10.1038/nature13621>

- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25:1965-1978. <https://doi.org/10.1002/joc.1276>
- Horne DJ (2007) A mutual temperature range method for Quaternary palaeoclimatic analysis using European non-marine Ostracoda. *Quat. Sci. Rev.* 26:1398-1415. <https://doi.org/10.1016/j.quascirev.2007.03.006>
- Horne DJ, Curry BB, Mesquita-Joanes F (2012) Mutual Climatic Range Methods for Quaternary Ostracods. *Developments in Quaternary Sciences* 17, Elsevier, pp 65-84. <https://doi.org/10.1016/B978-0-444-53636-5.00005-6>.
- Jennings R, Finlayson C, Fa D, Finlayson G (2011) Southern Iberia as a refuge for the last Neanderthal populations. *J. Biogeogr.* 38: 1873-1885. <https://doi.org/10.1111/j.1365-2699.2011.02536.x>.
- Kothari C (2004) *Research methodology: methods and techniques*. 2nd edition. New Age International, New Delhi.
- Kutiel P, Lavee H, Ackermann O (1998) Spatial distribution of soil surface coverage on north and south facing hill slopes along a Mediterranean to extreme arid climatic gradient. *Geomorphology* 23:245–256. [https://doi.org/10.1016/S0169-555X\(98\)00007-5](https://doi.org/10.1016/S0169-555X(98)00007-5).
- Leierer L, Jambrina-Enríquez M, Herrera-Herrera AV, Connolly R, Hernandez CM, Galván B, Mallol C, (2019) Insights into the timing, intensity and natural setting of Neanderthal occupation from the geoarchaeological study of combustion structures: a micromorphological and biomarker investigation of El Salt, unit Xb, Alcoy, Spain. *PLoS One* 14:e0214955. <https://doi.org/10.1371/journal.pone.0214955>.
- Lizana M (2002) *Bufo bufo* (Laurenti, 1768). Sapo común, Escuerzo. In: Pleguezuelos JM, Márquez R, Lizana M (Eds.) *Atlas y Libro Rojo de Los Anfibios y Reptiles de España*, 2a impresión. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid, pp. 103-106.
- Lizana M, Ciudad MJ, Pérez-Mellado V (1988) Distribución altitudinal de la Herpetofauna en el Macizo Central de la Sierra de Gredos. *Rev. Esp. Herp.* 3:55-67.
- Lizana M, Pérez-Mellado V, Ciudad MJ, (1990) Analysis of the structure of an amphibian community in the Central System of Spain. *Herpetol. J.* 1: 435-446.
- Llorente GA, Montori A, Santos X, Carretero MA (1995) *Atlas dels amfibis i rèptils de Catalunya i Andorra*, 1a Edició. ed. Edicions El Brau, Figueres.
- López P (2002) *Blanus cinereus* (Vandelli, 1797). Culebrilla ciega. In: Pleguezuelos JM, Márquez R, Lizana M. (eds.) *Atlas y Libro Rojo de los Anfibios y Reptiles Españoles*. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid, pp. 154-156.
- López-García JM, Cuenca-Bescós G (2010) Évolution climatique durant le Pléistocène Supérieur en Catalogne (nord-est de l'Espagne) d'après l'étude des micromammifères. *Quaternaire* 21: 249-257. <https://doi.org/10.4000/quaternaire.5597>

- López-García JM, Cuenca-Bescós G, Finlayson C, Brown K, Pacheco FG (2011) Palaeoenvironmental and palaeoclimatic proxies of the Gorham's cave small mammal sequence, Gibraltar, southern Iberia. *Quat. Int.* 243:137-142. <https://doi.org/10.1016/j.quaint.2010.12.032>
- López-García JM, Blain H-A, Bennàsar M, Fernández-García M (2014) Environmental and climatic context of Neanderthal occupation in southwestern Europe during MIS3 inferred from the small-vertebrate assemblages. *Quat. Int.* 326:319-328. <https://doi.org/dx.doi.org/10.1016/j.quaint.2013.09.010>
- López-García JM, Blain H-A, Sánchez-Bandera C, Cohen J, Lebreton L, Montuire S, Stewart JR, Desclaux E (2021) Multi-method approach using small vertebrate assemblages to reconstruct the Marine Isotope Stage 6 climate and environment of the Lazaret cave sequence (Maritime Alps, Nice, France). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 577:110529. <https://doi.org/10.1016/j.palaeo.2021.110529>
- Loureiro A, de Almeida NF, Carretero MA, Paulo OS (2008) Atlas Dos Anfíbios e Répteis de Portugal, 1st Editio. Instituto da Conservação da Natureza e da Biodiversidade, Lisboa.
- Lyman RL (2016) The mutual climatic range technique is (usually) not the area of sympatry technique when reconstructing paleoenvironments based on faunal remains. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 454:75-81. <https://doi.org/10.1016/j.palaeo.2016.04.035>
- MacArthur RH (1984) *Geographical Ecology e Patterns in the Distribution of Species*. Princeton University Press, Princeton.
- Machado J, Perez L (2016) Temporal frameworks to approach human behaviour concealed in Middle Palaeolithic palimpsests: a high-resolution example from El Salt Stratigraphic Unit X (Alicante, Spain). *Quat. Int.* 417:66-81. <https://doi.org/10.1016/j.quaint.2015.11.050>.
- Malkmus R (2004) *Amphibians and Reptiles of Portugal, Madeira and the Azores-Archipelago*. A.R.G. Gantner Verlag K.G., Ruggell.
- Mallol C, Hernández CM, Machado J, (2012) The significance of stratigraphic discontinuities in Iberian Middle-to-Upper Palaeolithic transitional sites. *Quat. Int.* 275:4-13. <https://doi.org/10.1016/j.quaint.2011.07.026>.
- Maluquer-Margalef J, Escoriza D, Lozano A (2009) Aportacions sobre la distribució altitudinal de *Chalcides bedriagai* (Boscá, 1880) al massís de Penyagolosa (Castelló) i el poblament herpetològic del vessant nord del massís. *But. Soc. Cat. Herpetol.*, 18:44-50.
- Marquina R, Fagoaga A, Crespo VD, Ruiz-Sánchez FJ, Bailon S, Hernández CM, Galván B (2017) Amphibians and squamate reptiles from the stratigraphic unit Xb of El Salt (Middle Palaeolithic; Alcoy, Spain): palaeoenvironmental and palaeoclimatic implications. *Spanish J. Palaeontol.* 32:219-312. <https://doi.org/10.7203/sjp.32.2.17045>

- Marquina-Blasco R, Fagoaga A, Crespo VD, Bailon S, Mallol C, Hernández CM, Galván B, Ruiz-Sánchez FJ (2021a) Amphibians and reptiles as palaeoenvironmental proxies during the Late Pleistocene (MIS3): The case of Stratigraphic Unit V of El Salt, Alcoi, Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 571:110372. <https://doi.org/10.1016/j.palaeo.2021.110372>
- Marquina-Blasco R, Fagoaga A, Sánchez López L, Bailon S, Blain H-A, Mallol C, Hernández CM, Galván B, Ruiz-Sánchez FJ (2021b) Applying the UDA-ODA discrimination method to a herpetological assemblage from Subunit Xb of El Salt Middle Palaeolithic site (Alcoi, Spain): Preliminary results. In: López-García JM, Blain H-A, Blanco-Lapaz À, Rhodes SE (Eds.) Abstract Book of the 3rd Meeting of the ICAZ Microvertebrate Working Group. September 1st-2nd 2020. Tarragona (Spain). Institut Català de Paleoecologia Humana i Evolució Social, Tarragona, pp 53-54.
- Martínez del Mármol G, González de la Vega JP, López Herrera Ó, Smalbrugge S (2020) Récord altitudinal de *Coronella girondica* en Europa, y otro caso de posible sintopía con *Coronella austriaca* en Sierra Nevada (Granada, España). *Bol. Asoc. Herpetol. Esp.* 31: 101-104.
- Martínez-Freiría F, Sillero N, Lizana M, Brito JC (2008) GIS-based niche models identify environmental correlates sustaining a contact zone between three species of European vipers. *Divers Distrib.* 14:452-461. <http://doi.org/10.1111/j.1472-4642.2007.00446.x>.
- Martínez Rica JP (1983) Atlas Herpetológico Del Pirineo. *Munibe* 35:51-80. Martínez-Solano I, Sanchiz B (2005) Anfibios y Reptiles del Pleistoceno medio de Ambrona. *Zona Arqueológica* 5:232-239.
- Meijide M, Meijide F, Arribas O (1994) Atlas herpetológico de la provincia de Soria. *Bol. Asoc. Herpetol. Esp.* 8:45-58.
- Melchionna M, Di Febbraro M, Carotenuto F, Rook L, Mondanaro A, Castiglione S, Serio C, Veroa VA, Tesonea G, Piccoloa M, Felizola Diniz-Filho JA, Raia P (2018) Fragmentation of Neanderthals' pre-extinction distribution by climate change. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 496: 146–154. <https://doi.org/https://doi.org/10.1016/j.palaeo.2018.01.031>
- Mellars P (2004) Neanderthals and the modern human colonization of Europe. *Nature* 432:461-465. <https://doi.org/10.1038/nature03103>.
- Miller RF, Elias SA (2000) Late-glacial climate in Maritimes Region, Canada, reconstructed from mutual climate range analysis of fossil Coleoptera. *Boreas* 29:79-88. <https://doi.org/10.1111/j.1502-3885.200>
- Moine O, Rousseau DD, Antoine P (2002) Mise en évidence d'événements climatiques rapides par les faunes de mollusques terrestres des loess weichselien de Nussloch (Allemagne). *Quaternaire* 13:209-217. <https://doi.org/10.3406/quate.2002.1713.0.tb01202.x>

- Morales JJ, Lizana M, del Arco C (2002). Análisis de la distribución altitudinal de la herpetofauna en las sierras de Segovia. *Rev. Española Herpetol.* 16:20-42.
- Morales Martín J, Lizana Avia M (2011) El estado de la biodiversidad de los Vertebrados españoles. Causas de la riqueza de especies y actualización taxonómica. In: Viejo Montesinos JL (Ed.) Biodiversidad, aproximación a la diversidad botánica y zoológica de España. Memorias de la Real Sociedad Española de Historia Natural. Segunda época. Madrid, pp 285-342.
- Núñez-Lahuerta C, Cuenca-Bescós G, Sauqué V, Galán J (2016) Avian remains from the Upper Pleistocene (MIS3) site of Aguilón P-7, south of the Ebro River, Spain. *Hist. Biol.* 28:774-786. <http://doi.org/10.1080/08912963.2015.1028928>.
- Ochando J, Amorós G, Carrión JS, Fernández S, Munuera M, Camuera JON, Moreno GJ, Sampérez PG, Burjachs F (2021) Iberian Neanderthals in forests and savannahs. *J. Quat. Sci.* 1-28. <https://doi.org/10.1002/jqs.3339>
- Pascual R, Sanz G (2017) Aproximación a la Meteorología de Montaña. *Tiempo y Clima* 57:50-55.
- Pérez-Mellado V (1983) La herpetofauna de Salamanca: un análisis biogeográfico y ecológico. *Salamanca* 9:9-78.
- Pleguezuelos JM, Villafranca C (1997) Distribución altitudinal de la herpetofauna ibérica. In: Pleguezuelos JM (Ed.) Distribución y biogeografía de los anfibios y reptiles de España y Portugal. Asociación Herpetológica Española & Universidad de Granada, Granada, pp. 321-341.
- Pleguezuelos JM, Márquez R, Lizana M (2002) Atlas y Libro Rojo de Los Anfibios y Reptiles de España, 2a impresión. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid.
- Pollo C (2002). *Chalcides bedriagai* (Boscá, 1880. Eslizón ibérico. In: Pleguezuelos JM, Márquez R, Lizana M. (eds.) Atlas y Libro Rojo de los Anfibios y Reptiles Españoles. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid, pp. 163-165.
- Porch N (2010) Climate space, bioclimatic envelopes and coexistence methods for the reconstruction of past climates: a method using Australian beetles and significance for Quaternary reconstructions. *Quat. Sci. Rev.* 29:633-647. <https://doi.org/10.1016/j.quascirev.2009.10.014>.
- Pross J, Klotz S, Mosbrugger V (2000) Reconstructing palaeotemperatures for the Early and Middle Pleistocene using the mutual climatic range method based on plant fossils. *Quat. Sci. Rev.* 19:1785-1799. [https://doi.org/10.1016/S0277-3791\(00\)00089-5](https://doi.org/10.1016/S0277-3791(00)00089-5).
- Puente Montiel A (2013) Atlas de Anfibios de Asturias. Informe 1 (2013). Anfibios de Asturias. <http://www.anfibiosdeasturias.org/atlas-de-anfibios-de-asturias>. Accessed 01 July 2021.
- Railsback LB, Gibbard PL, Head MJ, Voarintsoa NRG, Toucanne S (2015). An optimized scheme of lettered marine isotope substages for the last 1.0 million years, and the climatostratigraphic nature of isotope stages and substages. *Quat. Sci. Rev.* 111:94-106. <https://doi.org/10.1016/j.quascirev.2015.01.012>.

- Reques R, Tejedo M (2002) *Bufo calamita* (Laurenti, 1768). Sapo corredor. In: Pleguezuelos JM, Márquez R, Lizana M (Eds.) Atlas y Libro Rojo de Los Anfibios y Reptiles de España, 2a impresión. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid, pp. 107-109.
- Rey-Rodríguez I, López-García JM, Bennasar M, Bañuls-Cardona S, Blain H-A, Blanco-Lapaz Á, Rodríguez-Álvarez X-P, de Lombera-Hermida A, Díaz-Rodríguez M, Ameijenda-Iglesias A (2016) Last Neanderthals and first Anatomically Modern Humans in the NW Iberian Peninsula: Climatic and environmental conditions inferred from the Cova Eirós small-vertebrate assemblage during MIS 3. *Quat. Sci. Rev.* 151:185-197. <https://doi.org/10.1016/j.quascirev.2016.08.030>
- Saint Girons H (1980) Biogéographie et évolution des vipères européennes. *C.r. séances. Soc. biogéogr.* 496:146-172.
- Saint Girons H (1982) Influence Des Climats de Type Méditerranéen Sur l'écophysologie et La Répartition Des Reptiles. *Ecol Mediterr.* 8:245-252. <https://doi.org/10.3406/ecmed.1982.1951>.
- Santos X (2008) *Natrix maura* (Linnaeus, 1758). Cobra-de-água-viperina. In: Loureiro A, Ferrand de Almeida N, Carretero MA, Paulo OS (eds.) Atlas dos Anfíbios e Répteis de Portugal. Instituto da Conservação da Natureza e da Biodiversidade, Lisboa, 176-177.
- Santos X (2015) Culebra viperina-*Natrix maura*. In: Salvador A, Marco A (Eds.) Enciclopedia Virtual de los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid. <http://www.vertebradosibericos.org/>. Accessed 24 May 2021.
- Santos X, Llorente GA, Montori A, Carretero MA (2002) *Natrix maura* (Linnaeus, 1758). Culebra viperina. In: Pleguezuelos JM, Márquez R, Lizana M (eds.) Atlas y Libro Rojo de los Anfibios y Reptiles de España. Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid, 290–292.
- SEO/BirdLife (2021) Programas de seguimiento y grupos de trabajo de SEO/BirdLife 2020. SEO/BirdLife, Madrid.
- Sepulchre P, Ramstein G, Kageyama M, Vanhaeren M, Krinner G, Sánchez Goñi M-F, d'Errico F (2007) H4 abrupt event and late Neanderthal presence in Iberia. *Earth Planet. Sci. Lett.* 258:283-292. <https://doi.org/10.1016/j.epsl.2007.03.041>.
- Sepulchre P, Ramstein G, Kageyama M, Vanhaeren M, Krinner G, Sánchez-Goñi, M-F, d'Errico F, (2007) H4 abrupt event and late Neanderthal presence in Iberia. *Earth Planet. Sci. Lett.* 258, 283–292. <https://doi.org/10.1016/j.epsl.2007.03.041>.
- Serrano Ezaguerrri FJ, Torrijo Pardos A, Cano Muñoz JL, Lagares Latorre JL, Liberos Saura C, Martín Arnau M.Á., Pueyo Soler JM, Rosado Romero F, Ruiz Alba J, Sánchez Sancho JA (2001) Atlas provisional de anfibios y reptiles de la provincia de Teruel. *Bol. Asoc. Herpetol. Esp.* 12:62-70.

- Shepard DB, Burbrink FT (2008) Lineage diversification and historical demography of a sky island salamander, *Plethodon auachitae*, from the Interior Highlands. *Mol. Ecol.* 17:5315-5335. <http://doi.org/j.1365-294X.2008.03998.x>
- Sillero N, Brito JC, Skidmore AK, Toxopeus AG (2009) Biogeographical patterns derived from remote sensing variables: the amphibians and reptiles of the Iberian Peninsula. *Amphib-reptil* 30:185-206. <https://doi.org/10.1163/156853809788201207>.
- Sinka KJ, Atkinson TC (1999) A mutual climatic range method for reconstructing palaeoclimate from plant remains. *J. Geol. Soc. Lond.* 156:381-396. <https://doi.org/10.1144/gsjgs.156.2.0381>.
- Soares C (2008) *Bufo calamita* Laurenti, 1768. Sapo-corredor. In: Loureiro A, Ferrand de Almeida N, Carretero MA, Paulo OS (eds.) Atlas dos Anfíbios e Répteis de Portugal. Instituto da Conservação da Natureza e da Biodiversidade, Lisboa, 118–119.
- Soares C, Brito JC (2007) Environmental correlates for species richness among amphibians and reptiles in a climate transition area. *Biodivers. Conserv.* 16:1087-1102. <https://doi.org/10.1007/s10531-006-9070-5>
- Soares C, Alvares F, Loureiro A, Sillero N, Arntzen JW, Brito JC (2005) Atlas of the amphibians and reptiles of Peneda-Gerês National Park, Portugal. *Herpetozoa* 18:155-170.
- Stewart JR (2005) The ecology and adaptation of Neanderthals during the nonanalogue environment of Oxygen Isotope Stage 3. *Quat.Int.* 137:35-46. <https://doi.org/10.1016/j.quaint.2004.11.018>
- Stewart JR (2009) The evolutionary consequence of the individualistic response to climate change. *J. Evol. Biol.* 22:2362-2375. <https://doi.org/10.1111/j.1420-9101.2009.01859.x>
- Strauss LG (2018) The upper paleolithic of Iberia. *Trab. Prehist.* 75:9-51. <https://doi.org/10.3989/tp.2018.12202>.
- Tattersall I (2006) Who were the Neanderthals?. In: Demarsin B, Otte M (Eds.) Neanderthals in Europe. Proceedings of the International Conference, held in the Gallo-Roman Museum in Tongeren (September 17-19th 2004). Musée gallo-romain de Tongres, Tongres, pp. 9-14.
- Thompson RS, Anderson KH, Pellier RT, Strickland LE, Bartlein PJ, Shafer SL, (2012) Quantitative estimation of climatic parameters from vegetation data in North America by the mutual climatic range technique. *Quat. Sci. Rev.* 51:18-39. <https://doi.org/10.1016/j.quascirev.2012.07.003>.
- Trinkaus E (1995) Neanderthal mortality patterns. *J. Archaeol. Sci.* 22: 121-142. [https://doi.org/10.1016/S0305-4403\(95\)80170-7](https://doi.org/10.1016/S0305-4403(95)80170-7).
- Vaesen K, Scherjon F, Hemerik L, Verpoorte A (2019). Inbreeding, Allee effects and stochasticity might be sufficient to account for Neanderthal extinction. *PloS one* 14: e0225117. <https://doi.org/10.1371/journal.pone.0225117>

- Vaesen K, Dusseldorp GL, Brandt MJ (2021) An emerging consensus in palaeoanthropology: demography was the main factor responsible for the disappearance of Neanderthals. *Sci. Rep.* 11:1-9. <https://doi.org/10.1038/s41598-021-84410-7>
- Vaquero M, Maroto J, Arrizabalaga A, Baena J, Baquedano E, Carrión E, Jordá JJ, Martín M, Menéndez M, Montes R, Rosell J (2006) The Neandertal-Modern Human meeting in Iberia: A critical view of the cultural, geographical and chronological data. In: Conard NJ (Ed.) *When Neanderthals and Moderns Met*. Kerns Verlag, Tübingen, pp. 419-439.
- Vences M, Grossenbacher K, Puente M, Palanca A, Vieites DR (2003) The Cambalès fairy tale: Elevational limits of *Rana temporaria* (Amphibia: Ranidae) and other European amphibians revisited. *Folia Zool.* 52:189-202.
- Vidal-Matutano P, (2016) *Alrededor del fuego: paisaje, clima y gestión de los recursos leñosos en grupos cazadores-recolectores durante el Paleolítico medio (Alicante, España)*. PhD Thesis, Universitat de València.
- Vidal-Matutano, P, Pérez-Jordà G, Hernández CM, Galván B, (2018) Macrobotanical evidence (wood charcoal and seeds) from the Middle Palaeolithic site of El Salt, Eastern Iberia: palaeoenvironmental data and plant resources catchment areas. *J. Archaeol. Sci. Rep.* 19:454-464. <https://doi.org/10.1016/j.jasrep.2018.03.032>.
- Willis KJ, Bailey RM, Bhagwat SA, Birks, HJB (2010) Biodiversity baselines, thresholds, and resilience: testing predictions and assumptions using palaeoecological data. *Trends Ecol. Evol.* 25:583-91. <https://doi.org/10.1016/j.tree.2010.07.006>.
- Wolf D, Kolb T, Alcaraz-Castaño M, Heinrich S, Baumgart P, Calvo R, Sánchez J, Ryborz K, Schäfer I, Bliedtner M, Zech R, Zöllner L, Faust D (2018) Climate deteriorations and Neanderthal demise in interior Iberia. *Sci. Rep.* 8:7048. <https://doi.org/10.1038/s41598-018-25343-6>.
- Wood RE, Barroso C, Caparrós M, Jordá JF, Galván B, Davidson I, Higham TFG (2013) Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. *Proc. Natl. Acad. Sci. U. S. A.* 110:2781-2786. <https://doi.org/10.1073/pnas.1207656110>.

ACKNOWLEDGEMENTS

Research at El Salt is funded by the Spanish Government project HAR2015-68321-P (MINECO FEDER/UE), UV-INV_AE17-708551 (Universitat de València) and Conselleria d'Educació, Investigació, Cultura i Esport from the Valencian government. This investigation was also carried out thanks to the Prometeo Project of the Secretariat for Higher Education, Science, Technology and Innovation from Ecuador and the University of La Laguna (Tenerife, Spain). The authors are grateful to the El Salt excavation team for their help with the excavation, sieving and washing of sediment each year. We thank the editor and two anonymous reviewers for their comments, which greatly improved this manuscript.