Macaluso, Loredana; Bertini, Adele; Carnevale, Giorgio; [et al.]. «A combined palaeomodelling approach reveals the role as selective refugia of the Mediterranean peninsulas». Palaeogeography, Palaeoclimatology, Palaeoecology, Vol. 625 (September 2023), art. 111699. DOI 10.1016/j.palaeo.2023.111699

A combined palaeomodelling approach reveals the role as selective refugia of the Mediterranean peninsulas

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Declaration of interests. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data supporting statement: Data supporting the results are available in the Supplementary Material of this study.

Running title: Climate and extirpation of herpetofauna

Keywords: Ecological Niche Modelling, fossils, herpetofauna, palaeobotany, hypsodonty of mammals, conservation palaeobiology

Author contributions. LM, MD, AV and GC conceived the study and collected data. LM and FC performed the ENM analyses, AB and EM provided palaeobotanical data, JE and JS performed the hypsodonty analyses. LM, MD and AB wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Abstract

The northern Mediterranean reptiles and amphibians show contrasting biogeographic histories during the Plio-Pleistocene. The influence of European climate changes on the evolution of the biogeographic ranges of taxa with a rich fossil record is determined herein combining different proxies to obtain well-supported palaeoclimatic scenarios. Ecological Niche Modelling through the ensemble modelling approach was used to reconstruct the climatic niche of selected reptile and amphibian genera, combining modern occurrences with seven independent bioclimatic variables. The obtained model was then projected on past scenarios using fossil data to crosscheck the validity of the climatic explanation for the selective extirpations. Palaeobotanical proxies and the hypsodonty of mammals were used to reconstruct the humidity pattern of the last million years in the studied area. The climate of the Italian Peninsula during the Last Glacial Maximum was proved herein to be unsuitable for many reptile taxa, which persisted in this area until the Early or Late Pleistocene, whereas they survived till the present day in the Iberian and/or Balkans peninsulas. On the contrary, all the proxies agree that Italy was comparably more humid than the other peninsulas during the Pliocene and Pleistocene, therefore allowing the prolonged survival of amphibian taxa (including the still living *Salamandrina* and *Speleomantes*), which became extinct or extirpated elsewhere in Europe. An intensification of the conservation efforts concerning amphibians, particularly sensitive to the global climate change, is recommended in the Italian Peninsula, which acted as an amphibian refugium for Europe due to its peculiar climatic history.

1. Introduction

The latitudinal patterns of biodiversity of European organisms are currently well known, whereas the longitudinal patterns have only been marginally explored (Atkinson et al., 2007).

In the southern part of Europe, this is mainly reflected in a generally similar role as Quaternary biodiversity refugia attributed to the three major Mediterranean peninsulas (from West to East: the Iberian, the Italian, and the Balkan peninsulas). It is generally assumed that these three peninsulas, together with the adjoining Anatolian one, acted as refugia during the Pleistocene global cooling (see Schmitt et al., 2021 for a recent biogeographic analysis of the Italian Peninsula). However, comparative analyses investigating how this happened in the different European peninsulas are far from being exhaustive (see different contributions and literature cited in Weiss & Ferrand, 2007).

The Italian geographic province (sensu Lanza & Corti, 1996, which includes not only the political region of Italy but also part of southeastern France, Corsica, and the Istria region) currently has the most diversified amphibian fauna of the Mediterranean Region and comprises the highest number of endemic species of Europe: about 50% of the amphibian species of this province is endemic (Sindaco et al., 2006; Speybroeck et al., 2020). Furthermore, the presence of three endemic genera of urodeles (*Euproctus*, *Salamandrina* and *Speleomantes*) is of exceptional relevance. Such high rate of endemism contrasts with the particularly low rate of endemic reptiles (17%; see fig. 5 in Sillero et al., 2014), with only one endemic genus and comparatively few endemic species, mainly restricted to islands (Bologna & Mazzotti, 2006; Sindaco et al., 2006; Speybroeck et al., 2020).

Why does the Italian geographic province comprise so many amphibian endemisms and such a low number of endemic reptiles? And did other European Mediterranean peninsulas undergo different dynamics that ultimately led to different patterns of diversity? Did climate have a major role in shaping these diverging patterns? Answering to such questions is important not only to understand the geographic distribution and the evolutionary history of these taxa but also for conservation purposes, as time is running out and conservation efforts are limited and often need to be prioritised. A first attempt to answer such questions has been done by the recent work of Macaluso et al. (2021a), in which the multivariate approach of Ecological Niche Modelling (ENM) was used to evaluate the possible climatic influence on the extirpation of the Italian endemic genus *Salamandrina*. Climate changes during the last 3.3 million years were possibly responsible for its extirpation from most of Europe, whereas it still survives in Italy, during all the chosen time bins. The present work is conceived as a prosecution and strengthening of the conclusions of Macaluso et al. (2021a), applying a similar approach to European taxa of amphibians and reptiles that showed significant reductions or shifts of their geographic ranges during the Neogene and Quaternary to better answer the questions presented at the beginning of this paragraph and further understand the possible different roles of the three southern European peninsulas. After a synthesis of the distribution of fossil remains from Miocene to Late Pleistocene, climate is evaluated as possible driver for the selective extirpations of different herp taxa through ENM. Given the uncertainty of palaeoclimatic reconstructions, two different palaeontological approaches are used in tandem with ENM to support or contradict the results of the models. First, the palaeobotanical record of Europe is used to qualitatively find possible analogies between floral composition, vegetation structure, and herpetological distributional patterns, as fossil plants are largely considered good indicators of the climatic conditions of the past (see e.g. Combourieu Nebout et al., 2015; Martinetto et al., 2017 and references therein). Second, we use mean ordinated hypsodonty of large herbivorous mammals from Pliocene to Pleistocene European fossil localities as a proxy of precipitation in the corresponding terrestrial environments (Fortelius et al., 2002, 2003, 2006; 2016; Eronen et al., 2010; Žliobaitė et al., 2016, 2018; Oksanen et al., 2019; Saarinen et al., 2021). Mean ordinated hypsodonty of large herbivorous mammal communities correlates with annual precipitation, even in extant terrestrial environments (Eronen et al., 2010; Žliobaitė et al., 2016, 2018), because of factors that favour hypsodonty in dry environments where the combined effect of air-transported mineral dust and phytolith-rich vegetation causes increased wear on the teeth of herbivorous mammals (Fortelius et al., 2002; Damuth & Janis, 2011; Kaiser et al., 2013; Madden, 2015; Sanson et al., 2017).

2. Material and Methods

2.1 Selection of taxa

In this study, we selected taxa for ENM analyses that are characterized by selective extirpations in Europe, testified by a well-documented fossil record. The fossil remains of the selected taxa should be easily identifiable at least at genus level, so that their past distribution deduced from the fossil record is not affected by misinterpretations and erroneous identifications. Due to scarce or uncertain fossil record, the following taxa were excluded: the anuran *Discoglossus* (whose fossils, if fragmentary, are easily misinterpreted as *Latonia* or viceversa due to the uniformity of their skeletal morphology; see Biton at al., 2013, 2016); the large 'Oriental vipers' possibly related to *Macrovipera* and *Montivipera*; the soft-shelled turtles (*Tryonyx*); the monitor lizards (*Varanus*); the gecko *Euleptes* (that not only has a very poor fossil record, but whose only extant species *E. europea* is considered to have originated in Central Mediterranean islands and to be currently in expansion; Delaugerre et al., 2011; Daza et al., 2014; Villa & Delfino, 2019a; Villa et al., 2022).

The fossil record of the European herpetofauna was assessed by the analysis of the fosFARbase (Böhme & Ilg, 2003), the Paleobiology Database (McClennen et al., 2017), and the Italian Palaeoherpetofaunas Database (Delfino, 2002 [updated to 2022]), combined with literature (e.g. Delfino, 2003, 2004; Delfino et al., 2005; Venczel & Sanchiz, 2005; Chesi et al., 2007, 2009; Blain et al., 2009; Georgalis et al., 2018a, b, 2019; Villa et al., 2018a, b; Villa & Delfino, 2019a; Collareta et al., 2020; Syromyatnikova et al., 2021; Loréal et al., 2023).

Modern occurrences of extant taxa were obtained from the Global Biodiversity Information Facility (www.GBIF.org), including in the query all "human observations" of the European species of the selected genera (see below), with coordinates uncertainty equal or less than 5000 meters, to match with the spatial resolution of the current bioclimatic variables (2.5 arc/min) as suggested by Sillero & Barbosa (2021). Data point occurrences downloaded from GBIF included all the available occurrences of the following taxa: *Pseudopus apodus* (https://doi.org/10.15468/dl.m8au23), *Mauremys leprosa*, *M. caspica*, and *M. rivulata* (https://doi.org/10.15468/dl.zjesfb), *Blanus* spp. (https://doi.org/10.15468/dl.nndkny), *Chioglossa lusitanica* (https://doi.org/10.15468/dl.nn9pmz), *Speleomantes* spp. (https://doi.org/10.15468/dl.u4w87f), *Hierophis cypriensis*, *H. gemonensis*, and *H. viridiflavus* (https://doi.org/10.15468/dl.fzefep). Data about the species of *Blanus* from the Anatolian region were obtained also from the recently published paper by Şahin et al. (2021), whereas data about *Speleomantes* were added using all records of the extant species of this genus available in the atlas database of the *Societas Herpetologica Italica* (SHI). The sand boa *Eryx* was excluded from the analysis because public data concerning its current distribution are evidently incomplete.

The data points were subsequently projected using QGIS 3.28 (QGIS, 2022) and compared with the current distribution reported by Sindaco and Jeremčenko (2008) and Sindaco et al. (2013); occurrences outside the current distribution of the taxa were excluded from the dataset. Furthermore, duplicates were removed, and spatial thinning was used to space occurrence records a defined distance from each other to avoid spatial autocorrelation (Aiello-Lammens et al., 2015). The total of kept occurrences per each genus after the cleaning procedure reported above is as follows: *Pseudopus*, 509 occurrences; *Mauremys*, 1737 occurrences; *Blanus*, 854 occurrences; *Chioglossa*, 284 occurrences; *Speleomantes*, 526 occurrences; *Hierophis*, 7800 occurrences.

2.2 Ecological Niche Modelling

Nineteen bioclimatic variables (see Appendix S1 for a complete list) for the current (1979–2013) climate scenario were downloaded from PaleoClim (Brown et al., 2018) at a resolution of 2.5 arc-minutes. Bioclimatic variables were clipped at the European scale. Pearson's pairwise correlation coefficients were calculated with R (R Core Team, 2013) to measure the autocorrelation between the variables. To reduce co-correlation between variables and prevent overfitting, we retained the combinations of climate variables with a Pearson's coefficient of less than 0.75 (see Appendix S2 and S3). Seven independent variables were selected: temperature seasonality, mean temperature of the wettest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, precipitation seasonality, precipitation of the wettest quarter, and precipitation of the warmest quarter. The same independent bioclimatic variables were downloaded for different time bins, chosen as representatives of different climatic phases during the Plio-Pleistocene:

- Last Glacial Maximum (LGM; ca. 21,000 years BP; Karger et al., 2021);
- Last Interglacial (LIG; ca. 130,000 years BP; Otto-Bliesner et al., 2006);
- MIS 19, Pleistocene (Brown et al., 2018);
- mid-Piacenzian warm period (3.205 Ma; Dowsett et al., 2013; Hill, 2015);
- Marine Isotope Stage M2, Pliocene (ca. 3.3 Ma; Dolan et al., 2015).

Climatic niches and projections on past climatic scenarios were estimated using the Ensemble Modelling approach through the 'biomod2' package of R v. 4.2-2 (Thuiller et al., 2014). As all the geographic range of the genera is covered, 1000 pseudo-absences were randomly chosen within the background pixels for a total of five replications. We implemented five ENM methods, including regression (MARS, multivariate adaptive regression splines; Friedman, 1991), classification (GBM, generalized boosting models; Friedman et al., 2000) and complex models (ANN, artificial neural networks; Thuiller et al., 2009; Random Forest; Liaw & Wiener, 2002; MaxEnt v. 3.4.1; Phillips et al., 2017). Model tuning was performed using the following R packages: 'SDMtune' v. 1.3.0 (Vignali et al., 2020) for GBM, ANN, and RF; 'ENMeval' v. 2.0.4 (Kass et al., 2021) for MaxEnt; 'caret' v. 6.0.94 (Kuhn, 2008) for MARS. Tuning results and settings and the selected hyperparameters (based on higher testing Area Under the ROC Curve) are reported in Appendix S4. Cross-validation was done based on 10 repetitions of data splitting (70% of data used for training and 30% used for testing). Model performance was assessed using: the true skill statistic (TSS), the receiver characteristic operator (ROC), and the continuous Boyce index. In all these cases, evaluation scores span from -1 to +1: positive values indicate a model presenting predictions that are consistent with the presence distribution in the evaluation dataset, whereas values lower than 0 are considered worse than a random model (Allouche et al. 2006). For the ensemble forecasting maps, the selection criteria are TSS values, with a proportional weights method (i.e. best-performing models weighting more in the construction of the ensemble forecasting maps). The maps obtained as output from the software show the potential climatic niche and were modified using QGIS 3.28 (QGIS, 2022). To allow the discussion of the influence of certain bioclimatic variables, the Multivariate Environmental Similarity surface method, or MESS (Elith et al. 2010), was also used in selected time bins (see below).

2.3 Hypsodonty of large mammals

The humidity patterns for Pliocene to Pleistocene in Europe and the Mediterranean realm were evaluated analysing the hypsodonty of large mammals for 5.3 – 3.5 Ma (Early Pliocene), 3.5 – 2.6 Ma (Late Pliocene), 2.6 – 1.8 Ma (early Early Pleistocene, 1.8 – 0.781 Ma (late Early Pleistocene), 0.781 – 0.425 Ma (early Middle Pleistocene), and 0.425 – 0.13 Ma (late Middle Pleistocene). Following the methodology introduced by Fortelius et al. (2002), we use ordinated hypsodonty values for large herbivorous mammal species: 1 (brachydont = low-crowned), 2 (mesodont = medium-crowned), and 3 (hypsodont = high-crowned). We present the locality mean ordinated hypsodonty-based humidity estimates as colour-interpolated hypsodonty maps following the methodology of Fortelius et al. (2002) and Eronen et al. (2010). For interpolations, we used MapInfo 12.5 for thematic mapping and grid interpolation, with the following settings: 30 km grid size; 600 km search radius; 600 grid border. For the interpolation method, we used an inverse distance weighted algorithm (IDW). The colour codes in the hypsodonty maps range from blue to red, with blue indicating humid conditions (very low mean ordinated hypsodonty close to 1), green indicating sub-humid conditions (mean ordinated hypsodonty around 1.4), yellow indicating intermediate humidity (mean ordinated hypsodonty around 1.8), orange indicating relatively dry conditions (mean ordinated hypsodonty around 2.2), and red indicating arid conditions (mean ordinated hypsodonty around 2.6 and higher). For the hypsodonty maps, we used data from the NOW database (www.now.org, data downloaded 17.06.2022) for the Early and Late Pliocene, with and addition of Red Crag Nodule Bed from UK for the Late Pliocene based on published faunal lists and taxonomic revisions (Lister, 1999; Rivals & Lister, 2016). For the Early and Middle Pleistocene, we used mean ordinated hypsodonty data mainly from Saarinen et al. (2021), with the following additions:

- Red Crag and Norwich Crag (UK), Ahl Al Oughlam (Morocco), and Ain Boucherit, Ain Jourdel, and Saint Arnaud (Algeria) for the early Early Pleistocene (2.6 – 1.8 Ma);
- East Runton Early Pleistocene assemblage (UK), Tighenif (Morocco) and Ain Hanech (Algeria) for the late Early Pleistocene (1.8 – 0.781 Ma);
- Kolkotova Balka / Tiraspol (Moldova), Petralona Cave (Greece), and Trlica levels TRL 5-7 (Bosnia-Herzegovina) for the early Middle Pleistocene (0.781 – 0.425 Ma);
- Marathousa 1 (Greece) and Treugol´naya Cave (Russia) for the late Middle Pleistocene (0.425 – 0.13 Ma).

The references for these additions can be found in Appendix S5. In addition to these, the following updates to stratigraphic ages of fossil large mammal localities were made compared to information in the NOW-database:

- early Early Pleistocene: Blassac la Girondie, France (Paquette et al., 2021), Villaroya, Spain (Saarinen et al., 2021; Cirilli et al., 2023), Tsalka, Georgia (Kahlke et al., 2011), and Gulyazi, Turkey (Kostopoulos and Sen, 1999)
- late Early Pleistocene: Peyrolles (Valli et al., 2006; Nomade et al., 2014)

2.4 Palaeobotanical data

The qualitative analyses of the floral composition of Europe and the consequent climatic deductions from pollen data discussed in the present paper refer to the results of published palynological studies (see in 3.3.) sometimes including multi-method approaches too (e.g. Climatic Amplitude Method, Modern Analog Technique, and Weighted Averaging Partial Least-Squares Regression). The latter have been especially applied to several pollen sequences of the Mediterranean area to provide quantitative estimates of climate and bioclimate parameters (e.g. Fauquette et al., 1998, 1999, 2006; Fauquette & Bertini, 2003; Combourieu Nebout et al., 2009, 2015; Bertini et al., 2010; Sinopoli et al., 2019).

3. Results

3.1 Fossil record of the herpetofauna

Under a literal reading of the fossil record of extant taxa, a strong disparity between the amphibians and reptiles that inhabit the Mediterranean peninsulas is clearly rooted in the past (Table 1). Few taxa display a reduction of the geographic range at northern latitudes, but they survived in all the peninsulas where they were already present in origin (i.e. they were not extirpated from any peninsula where they were living). Among these taxa, the urodeles *Speleomantes* and *Chioglossa* were distributed up to central Europe during Miocene and they currently survive only in the Italian and Iberian peninsulas respectively, being extirpated from northern latitudes (Fig. 1A-B, 2; Venczel & Sanchiz, 2005; Blain et al., 2009; Villa et al., 2018a). The snake *Hierophis* was present in northern areas of Europe during the Pliocene (Szyndlar, 2012), but currently shows a more southern distribution throughout northwestern Europe and the Apennine and Balkan Peninsulas (Appendix S6); concerning the Iberian Peninsula, this genus is now present only at its northeastern edge (Sillero et al., 2014) and it apparently never had a broader Iberian range (Böhme and Ilg, 2003).

The fossil record of other taxa, on the other hand, testifies for an uneven survival at southern latitudes as well. Some taxa were present in two or three of the Mediterranean peninsulas and currently only survive in one of them, whereas some others were previously present in all of the three peninsulas and currently persist in two of them (Table 1). More in detail, according to the fossil record, there is no evidence for range shrinkage of reptile taxa that were once widespread in Europe and now exclusively survive in the Italian province (except for the above-discussed case of *Euleptes*; see Villa et al., 2022, for a discussion of the fossil record and biogeographic patterns of the gekkotan lineage leading to the European leaf-toad gecko). Indeed, the latter geographic unit lost in the last one or two million years at least three genera that still inhabit other northern Mediterranean peninsulas (Delfino, 2002, 2003, 2006; Chesi et al., 2007; Delfino et al., 2008): that is, the legless lizard *Pseudopus* (Fig. 3A, still present in a very restricted area of the North-East of the Italian geographic province, an area somehow overlapping with the geographic definition of the Balkan Peninsula), the terrapin *Mauremys* (Fig. 3B), the amphisbaenian *Blanus* (Fig. 3C). The large ‘Oriental vipers’ possibly related to *Macrovipera* and *Montivipera*, soft-shelled turtles (*Tryonyx*), and monitor lizards (*Varanus*) may be further included in this context of losses for the Italian province. However, their poor (or poorly recognizable) fossil record makes them unsuitable for the analyses presented herein.

On the contrary, two of the three Italian endemic urodeles, *Salamandrina* and *Speleomantes,* had a larger spatial range in the past that, at least for the former, extended from Iberia to the Balkans during the Miocene (Böhme, 2003; Venczel & Sanchiz, 2005; Delfino, 2006; Delfino & Sala, 2007; see also Vieites et al., 2007; Macaluso et al., 2021b). Italy also hosted one of the last European occurrences of the giant alytid frog *Latonia*, which went extirpated before the end of the Pliocene in the rest Europe but survived until the Early Pleistocene in central Italy (Rage & Rocek, 2003; Sorbelli et al., 2021) and until the Middle Pleistocene in North Hungary (Szentesi, 2019). *Latonia* only survives in a very restricted, humid area in the Middle East today (Biton et al., 2013; Perl et al., 2017). The allocaudate *Albanerpeton* also represents a clade of amphibians that was thought to go extinct in the Early Pliocene, but was found still thriving in an Early Pleistocene locality in northern Italy (Venczel & Gardner, 2005; Delfino & Sala, 2007; Villa et al., 2018a; Gardner et al., 2021).

3.2 Ecological Niche Modelling and hypsodonty of mammals

The ENM run using 'biomod2' resulted in the ensemble models reported in Figures 1H, 2D, 4A-C.5, and Appendix S6. The average values of the evaluation scores for each algorithm are reported in Appendix S7. Based on average TSS (ranging from 0.86 and 0.986), ROC (ranging from 0.966 and 0.992), and Boyce index (ranging from 0.61 and 0.964) values for testing data (Appendix S8), the models are well-supported. Projections on past climate scenarios are reported in Figure 1C-G, 2A-C, 5A-C.1-5, and Appendix S6. The three Mediterranean peninsulas clearly show different suitability levels during the different time bins, depending on the taxon. This difference in suitability is widely commented in the Discussion section.

The series of hypsodonty maps indicates that dry climatic conditions were present in the Iberian and Balkan peninsulas already during the Pliocene, and that they became even drier during the Pleistocene, with the exception of the northeast of the Iberian peninsula (Fig. 5). In contrast, Italy remained relatively more humid throughout the Early Pliocene to late Middle Pleistocene period, with mean hypsodonty values being mostly closer to those of central and northwestern Europe, compared to the relatively more arid Iberian and Balkan peninsulas. In general, the mean ordinated hypsodonty values mostly indicate a latitudinal aridity pattern, with relatively more humid conditions north of the Alps and drier conditions in the Mediterranean realm from the Pliocene to the Pleistocene (see also Fortelius et al., 2002, 2003, 2006). Italy stands out as markedly more humid than the rest of the Mediterranean realm throughout the Pliocene to late Middle Pleistocene interval.

3.3 Clues from palaeobotany

Palaeobotanical data from peri-Mediterranean sedimentary successions point out the key role of southern European latitudes as vegetation refugia under the effects of palaeoenvironmental and palaeoclimatic changes during the late Neogene and Quaternary (e.g. Tzedakis, 2007; Svennings et al., 2008; Tzedakis et al., 2009; Médail & Diadema, 2009; Donders et al., 2021; Bertini & Combourieu-Nebout, 2023). The Mediterranean flora and vegetation suffered their major changes (e.g. prominent development of steppe) only after the Messinian Salinity Crisis, in coincidence with the phase of maximal expansion of the Arctic glaciation and the start of glacial/interglacial (G/I) cycles (duration 40 ky) at about 2.6 Ma. The longitudinal temperature gradient was specifically attested by the preservation of thermophilous elements in the eastern Mediterranean areas under the effects of the Asiatic monsoon (e.g. Suc & Popescu, 2005). In southeastern Spain, aridity is documented, in the Middle Miocene and from the Zanclean to the Gelasian (e.g. Carrión et al., 2010, Jimenez-Moreno et al., 2010, and references therein), by the high percentage of herbs in pollen spectra (e.g. Poaceae, Asteraceae with *Artemisia*, Amaranthaceae), which also include some subdesertic taxa such as *Nitraria*, *Neurada, Prosopis, Lygeum, Ephedra,* Caesalpiniaceae, *Acacia*, and *Calligonum*. A thermal threshold, according to palynological evidence and climatic quantifications on Messinian and Zanclean sites, was traced between Barcelona and Tarragona. A similar threshold also occurs today, separating thermo-Mediterranean from meso-Mediterranean formations (Fauquette et al., 1999). In North Africa and in southern European sites (Sicily), similar conditions were detected (Suc & Bessais, 1990; Bertini et al., 1998; Fauquette et al., 2006), with assemblages dominated by herbs (e.g. Poaceae, Asteraceae, *Plantago*, *Erodium*) including sub-desertic plants (e.g. *Lygeum, Nitraria*, *Calligonum*, and *Neurada*), nowadays typical of the southern Mediterranean region. On the contrary, in sites with latitude higher than 42°, prevalent warm and humid conditions were palynologically attested by wet, subtropical to temperate (sensu

Trewartha-Köppen; see Belda et al., 2014) forest taxa as well as by the paucity of herbs during the Messinian, including the MSC (e.g. Bertini, 2006; Bertini & Martinetto, 2011, 2014), and the Pliocene (in particular from the mid-Piacenzian warm period; Bertini & Roiron, 1997; Bertini, 2010, 2013; Martinetto et al., 2017, Vieira & Zetter, 2020). At a European scale, a major plant extirpation corresponding to the Piacenzian-Gelasian transition (Martinetto, 1999; Martinetto et al., 2017; Suc et al., 2018) was probably caused by the absence of sufficiently humid refugia in southern areas. However, unlike the rest of Europe, a few thermophilous plants requiring wet summers (*Cephalotaxus*, *Toddalia*, *Sequoia*, *Symplocos* subgen. *Hopea*) managed to survive in some areas such as central Italy, at least, until the Gelasian (Martinetto, 2001; Martinetto et al., 2017). In central Europe, on the other hand, the foregoing taxa are documented by macrofossils just up to the Piacenzian. During the Quaternary, in central and southern Europe, alternations of *Artemisia* steppe and thermophilous forest marked the overall glacial-interglacial vegetation changes, especially along the Mediterranean littoral. The subtropical forest disappeared from the Mediterranean area at ca 1.2 Ma, together with a reduction of other forests and a spreading of a steppe ecosystem. However, in peculiar areas (e.g. northern Italy), the alternations are rather expressed by a spread of altitudinal coniferous forest (mainly *Picea*), without significant expansion of steppe vegetation, followed by the typical reestablishment of thermophilous forest (Bertini, 2001, 2010, and references therein). The *Picea*-dominated forests during Early Pleistocene glacial phases are documented in northern Italy at the foothills of both Apennines (Emilia-Romagna region) and Alps (Lombardia and Piemonte regions), where also the macroflora testifies for the persistence, even during cooler vegetational phases, of forest types dominated by *Picea* and some deciduous angiosperms still with distinct exotic affinity (*Carya, Magnolia, Phellodendron, Symplocos* sect. *Palura*; Cavallo & Martinetto, 2002). These plants evidently found wet and rather ‘warm’ (Mean Coldest Month T > 0°C) refugial conditions in southern Europe until the Early-Middle Pleistocene transition (Martinetto & Sami, 2001; Denk et al., 2022). In both southern Italy and the eastern Mediterranean, some pollen records indicate the spread of alpine vegetation during glacial phases (e.g. in southern Italy) and the settlement of wooded steppes in earlier phases of interglacials (see references in Bertini, 2010). The Early-Middle Pleistocene climate transition (Head & Gibbard, 2015) and the instauration of G/I cycles of 100 kyrs gave rise to new major changes in the floristic and vegetational assemblages, which progressively attained a modern aspect. A general decline in winter temperature and annual precipitation from the Early Pleistocene to the Holocene, with main changes around 2.0 Ma, 1.4-1.3 Ma, and 0.5 Ma, was detected for the Italian Peninsula (Combourieu-Nebout et al., 2015). During the last 0.3 Ma, the reduction in moisture availability and/or the increase in seasonal drought intensity promoted a further general reduction of those habitats that had been previously more largely distributed in the Mediterranean (Combourieu-Nebout et al., 2015; Magri et al., 2017).

4. Discussion

The fossil record indicates that several taxa composing the extant southern European herpetofauna had a much wider distribution during the Miocene and Pliocene. The geographic ranges of three genera have been identified herein as having been affected by a southern contraction, without an extirpation from the peninsulas where they were already present: these taxa are the two urodeles *Speleomantes* (Fig. 1) and *Chioglossa* (Fig. 2), and the snake *Hierophis* (Appendix S6). The former two taxa are currently endemic respectively of the Italian geographic province (as defined by Lanza & Corti, 1996) and of the Iberian Peninsula, but during the Miocene they were present in central Europe as well (Macaluso et al., 2022). The third genus, *Hierophis*, shows a somehow similar southern contraction of the range (Appendix S6). Climate seems to be an important driver of these geographic shifts. The persistence of *Hierophis* in central-eastern Europe during the Late Pliocene is supported by the high climatic suitability during the mid-Piacenzian Warm Period (mPWP, Appendix S6). ENM analyses highlight that the climatic suitability of central Europe is low or zero from the Late Pliocene onward for the two urodele genera (Fig. 1-2). Similarly to what was concluded for *Salamandrina* by Macaluso et al. (2021a), the lack of a Pliocene fossil record out from their current geographic range prevents the detection of a direct connection between the Late Pliocene/Pleistocene climate and the extirpation of these urodeles, as it is possible that their geographic range was already reduced at that time. The increasing aridity during the Early Pliocene (as well as during the Messinian; Fig. 5) calculated through the hypsodonty analyses suggests that the eradication probably started during this time interval. The same hypothesis is also supported for southeastern Spain by the presence of abundant herbs (including subdesertic taxa documenting aridity) from the Zanclean to the Gelasian.

The analysis of the European fossil record of the herpetofauna in the interval Miocene-Recent clearly indicates a prolonged survival in the Italian Peninsula of amphibians that went extirpated or extinct elsewhere: not only *Speleomantes* and *Salamandrina*, but also the frog *Latonia* (Sorbelli et al., 2021) and the enigmatic amphibian *Albanerpeton* (Gardner et al., 2021). At the same time, this geographic region shows a progressive impoverishment in reptiles that in many cases still inhabit the other northern Mediterranean peninsulas. This is the case of *Pseudopus*, currently only present in the Balkans and in Anatolia but occupying in the past also the Italian Peninsula (Fig. 3), and of *Mauremys* and *Blanus*, that went extirpated from Italy but survived in Iberia and in the Balkans.

The reason of this asymmetry can be found in the climatic evolution of Europe during the Plio-Pleistocene. In fact, the climate of the Italian Peninsula was already proved to be particularly suitable for *Salamandrina*, especially when compared with the lower suitability shown by the other two peninsulas (Macaluso et al., 2021a). The present work provides similar data concerning *Speleomantes* (Fig. 1). Noteworthy is the fact that both cited urodeles are characterized by the absence or the reduction of lungs and are therefore invariably tied to cool and humid environments (Lanza, 1983; Lanza et al., 1995) to maintain the gas exchange rate within a physiologically acceptable range (Spotila, 1972). It could be deduced that the Italian geographic province provided at least locally and seasonally a high level of moisture allowing the survival of these amphibians during the late Cenozoic. The evaluation of humidity patterns in Europe and the Mediterranean area from the Early Pliocene to the Middle Pleistocene based on mean ordinated hypsodonty of large herbivorous mammal communities indicates that Italy remained consistently less dry than the Iberian and Balkan peninsulas throughout this period (Fig. 5). The *Picea*-dominated forests during Early Pleistocene glacial phases in northern Italy further support this hypothesis: as a matter of fact, they indicate the presence of wet conditions in contrast to what is seen in the rest of Europe, where habitats were dominated by steppe. Interestingly, plant remains testifying these climatic conditions were found at the foothills of the Apennines (Emilia-Romagna region; Fauquette & Bertini, 2003), not far from the area currently showing the highest endemism rate for the amphibians (the contact zone between Alps and Apennines; fig. 5 of Sillero et al., 2014). A refugium with similar condition was present in the northwestern coast of Iberia for the salamander *Chioglossa*, also characterized by lung reduction (Lanza, 1983; García-París et al., 2004; Fig. 2). Wet climate is documented by the presence of Ericaceae along the Atlantic coast of the Iberian Peninsula and by the persistence of plants requiring wet and humid summers in the Italian Peninsula until the Gelasian. The rather humid conditions of Italy are also confirmed by high-resolution palynological data from 6 to 21 ka (Bartlein et al., 2011). Higher humidity during the Pliocene and Quaternary in the Italian Peninsula compared to Iberia and Balkans are confirmed by all the proxies used in this work. Despite being more humid than the other peninsulas, it is essential to underline that during the Pleistocene Italy is still to be considered dry on average (Fig. 5), explaining the fact that some of the amphibian genera still went extinct (in the case of *Albanerpeton*) or extirpated (in the case of *Latonia*) during this time bin, probably due to more strict physiological requirements related to humidity or other environmental factors.

Conversely, the Italian Peninsula was climatically unsuitable for the reptile taxa studied herein, especially during the Last Interglacial and the Last Glacial Maximum (Fig. 4). More in detail, the suitability of the legless lizard *Pseudopus* through time is highly compatible with its fossil record, as the distribution of this genus is strongly reduced in the Italian Peninsula during the LGM and the last fossil occurrences are Late Pleistocene in age (Fig. 4A), supporting the hypothesis of a climatic explanation for its extirpation. The suitability in certain areas of the Balkans and in Anatolia is high in all the examined time bins. Interestingly, Iberia seems suitable as well (Fig. 4A), but fossil record suggests that *Pseudopus* did not reach the southern part of the peninsula during Plio-Pleistocene (Fig. 4), for some unrelated reason.

The turtle *Mauremys* was present in all the three Mediterranean peninsulas from Miocene to Late Pleistocene and now only survives in the Balkans and Iberian ones (Fig. 4B). The persistence of suitable climatic conditions for this taxon in Italy until the Late Pleistocene is demonstrated by the ENM analyses. During the LIG a good suitability is present in restricted areas, including the one where the last Italian fossil occurrence was found (in Latium; Chesi et al. 2007). Subsequently, during the LGM, the Italian suitability drops (with this peninsula being almost entirely white in the map; Fig. 4B.5), whereas suitable areas persist in the southern part of the other two peninsulas. Interestingly, there is no time bin where the suitability of Sardinia is low to the point of explaining the extirpation of *Mauremys* from this island, suggesting that other factors may have acted on this (like interspecific competitions or predations). Climate had also a limited impact on the persistence of *Speleomantes* in Sardinia, as it seems that its climate was unsuitable for this genus during the LGM (when this genus was already present on the island). In fact, these salamanders are highly resistant to external unfavourable climatic conditions because of their lifestyle, as they inhabit subterranean systems (Vignoli et al., 2008).

As far as the amphisbaenian *Blanus* (Fig. 4C) is concerned, the suitability in southern Italy drops earlier than for the other two reptile genera *Pseudopus* and *Mauremys*, being already low during the MIS19 (Fig. 4C.3) and becoming especially low during the Late Pleistocene (Fig. 4C.4-C.5). Once again, this supports a climatic explanation for the extirpation of this genus from the area, considering that the last Italian fossil occurrence is from the Early Pleistocene of southeastern Italy. Concerning this genus, it is important to underline that due to the problematic identification at genus level of fossils of amphisbaenians represented exclusively by vertebrae (Villa & Delfino, 2019b; Villa et al., 2019), the rarity of fossils in western Europe (where fossil amphisbaenians are known and somehow abundant but not identified at the genus level) should not be considered as evidence of absence of *Blanus*.

The data presented herein therefore suggest that the absence of suitable climate during the Last Glacial Maximum (or other rather recent glacial phases) caused the extirpation of reptilian taxa from Italy, whereas the relatively warmer climate of the southern parts of Iberia and Balkans and western part of Anatolia allowed the persistence of reptiles in these latter peninsulas. These results are consistent with the high genetic diversity of *Mauremys leprosa* in southern Iberia (Fritz et al., 2006) and of *Pseudopus apodus* in western Anatolia (Jandzik et al., 2021). In particular, an important role might have been played by the colder summer temperature in the Italian province during the LGM. In fact, based on the MESS, the temperature of the warmest quarter of the year of the Italian province during the LGM is the most different variable compared to the extant variables in the areas associated with the occurrence points (Appendix S9). This parameter might have been important for reptiles as the temperature during development is specifically important for the physiologic equilibrium of the embryos (Singh et al., 2020), especially for genera with Temperature-Dependent Sex Determination such as *Mauremys* (Okada et al., 2010) and for generally thermophilus taxa such as *Blanus* and *Pseudopus*.

Interestingly, a distribution similar to the one of *Blanus* and *Mauremys* is shown by the cyprinid freshwater genus *Messinobarbus* (Bianco, 1998), suggesting that the patterns highlighted herein might be valid for other groups of ectothermic vertebrates as well.

5. Conclusions

Despite them being generally grouped together as southern refugia during the Plio-Pleistocene climatic oscillations, this work, focused on longitudinal differences, demonstrates that the Iberian, Italian, and Balkan peninsulas acted as selective refugia for different taxa of the herpetofauna. Climate was herein proved as an important driver that led to such biogeographic pattern (with the exception of the island of Sardinia). The Italian geographic province was unsuitable during the LGM for some reptile genera (*Blanus*, *Mauremys*, and *Pseudopus*), that persisted in the Italian Peninsula until the Early or Late Pleistocene, without surviving up to the current day. The Balkan (and the adjacent Anatolian) and the Iberian peninsulas, especially when it comes respectively to their eastern and southern portions, had a better role as refugia for the considered reptiles, which is consistent with both fossil record and genetic analyses. Conversely, the Italian geographic province acted as selective refugium for amphibians (*Albanerpeton*, *Latonia*, *Salamandrina*, *Speleomantes*) thanks to its higher humidity during the Pliocene and Pleistocene, as highlighted by ENM and hypsodonty analyses, as well as by the prolonged survival of plants requiring wet summers. Half of these genera are now either extirpated (*Latonia*) or extinct (*Albanerpeton*) from the peninsula, possibly due to their stricter physiological requirements in terms of humidity that did not allow their survival during the comparatively drier Pleistocene. However, the persistence in the Italian geographic province of two endemic genera, *Salamandrina* and *Speleomantes*, is of exceptional relevance. The future persistence of *Salamandrina* was already reported to be in danger (Macaluso et al., 2021a) due to the human-induced climate change, and the European cave salamander (*Speleomantes*) might have to face a similar fate. In an ideal world, no prioritisation would be needed for conservation practices, but, as we are running out of time and the conservation efforts are still too limited, setting conservation priorities is becoming more and more relevant. We suggest that combining ENM and palaeoclimatic approaches with fossil record should help determining priority areas for conservation. In this case study, we demonstrate that, given the unique role Italy played as an amphibian European refugium during Pliocene and Pleistocene times, the conservation efforts concerning this group of ectothermic tetrapods should be necessarily intensified in this area.

Acknowledgements

This work was supported by Grants (ex-60% 2018-2020) from the Università degli Studi di Torino. AV is funded by the Agencia Estatal de Investigación through a Juan de la Cierva-Formación grant (FCI2019-039443-I/AEI/10.13039/501100011033). MD acknowledges the Generalitat de Catalunya (CERCA Program), and the Spanish Agencia Estatal de Investigación (CGL2016-76431-P, AEI/FEDER, EU). JS wishes to acknowledge Academy of Finland (project nr. 340775). LM thanks P. Mannion, L. Jones, and A. A. Chiarenza (University College London) for providing practical and theoretical help concerning the methodology and S. Salvidio for critical comments on the literature. The authors also thank three anonymous reviewers for the constructive comments on a previous draft. The "Commissione Atlante" (Atlas Commission) of the *Societas Herpetologica Italica* provided the distribution data of extant *Speleomantes* spp. on the UTM grid.

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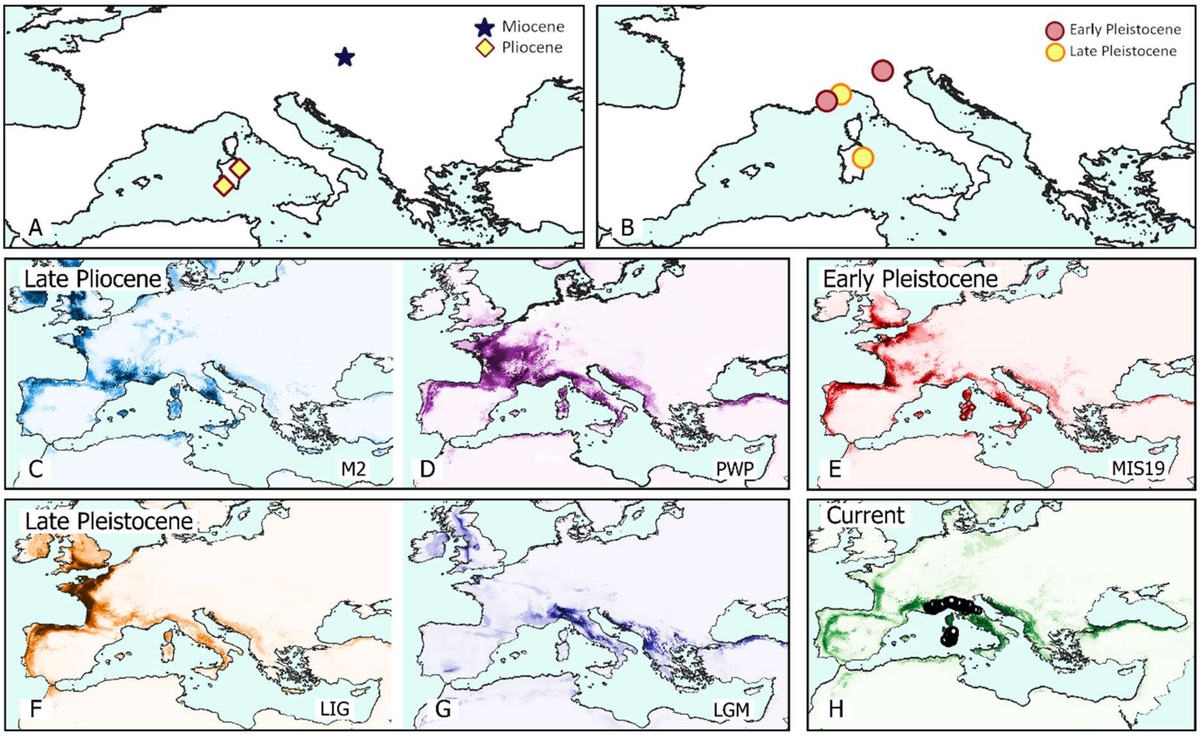
Captions

Figure 1. Distribution of the fossil record of *Speleomantes* sp. (spanning from Miocene and Pliocene, in A, to Pleistocene, in B) and climatic suitability for the genus during different time bins (from Late Pliocene to present), based on modern occurrences of *Speleomantes* spp. (reported in H). Abbreviations: LGM = Last Glacial Maximum; LIG = Last Interglacial; M2 = Marine Isotope Stage M2; PWP = Pliocene Warm Period. Darker colours show areas with better-predicted conditions. To notice that the Italian Peninsula is consistently suitable for this genus in all the time bins.

963 
Miocene
Pliocene
A
Early Pleistocene
Late Pleistocene
B
Late Pliocene
C
M2
D
PWP
Early Pleistocene
E
MIS19
Late Pleistocene
F
LIG
G
LGM
Current
H

964

Figure 2. Ensemble model projections on different time bins (from Late Pliocene to present) for *Chioglossa* spp. and distribution of Miocene fossil record. Current distribution in D. Abbreviations: LIG = Last Interglacial; M2 = Marine Isotope Stage M2.

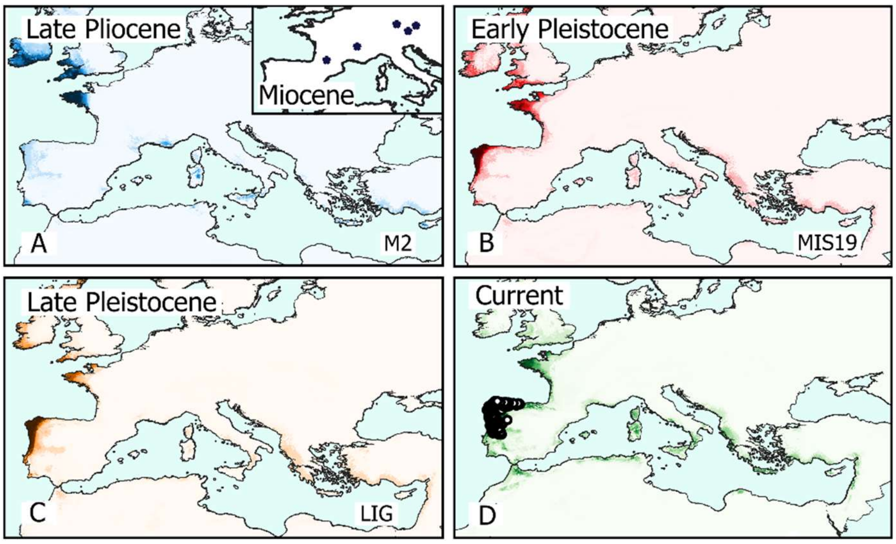


Figure 3. Fossil record of reptile taxa that were extirpated from the Italian geographic province (*Pseudopus* in A, *Mauremys* in B, and *Blanus* in C) compared with their current distribution (A-C.2; based on the occurrences used to train the models in this study). Fossil record from Late Pliocene onward is reported in Figure 4.

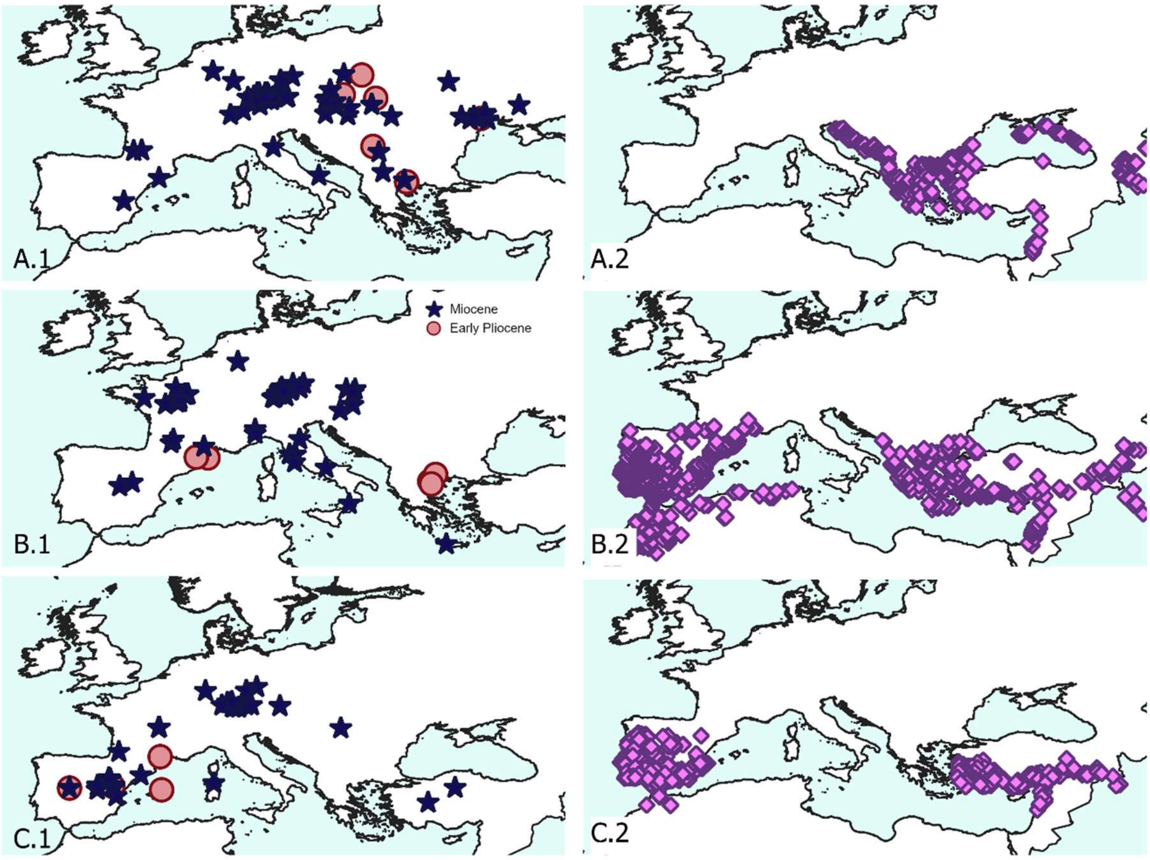


Figure 4. Climatic suitability of *Pseudopus* (A), *Mauremys* (B), and *Blanus* (C) during different time bins (from Late Pliocene to present). Fossil record from of each genus from Late Pliocene on is reported in the small squares within the corresponding time bins. Abbreviations: LGM = Last Glacial Maximum; LIG = Last Interglacial; M2 = Marine Isotope Stage M2; PWP = Pliocene Warm Period. Darker colours show areas with better-predicted conditions. To notice that suitability in the Italian Peninsula drops during the LGM for both *Pseudopus* and *Mauremys* (A.5, B.5) and during Early Pleistocene for *Blanus* (C.3), matching the fossil record and therefore supporting a climatic explanation for their extirpation.

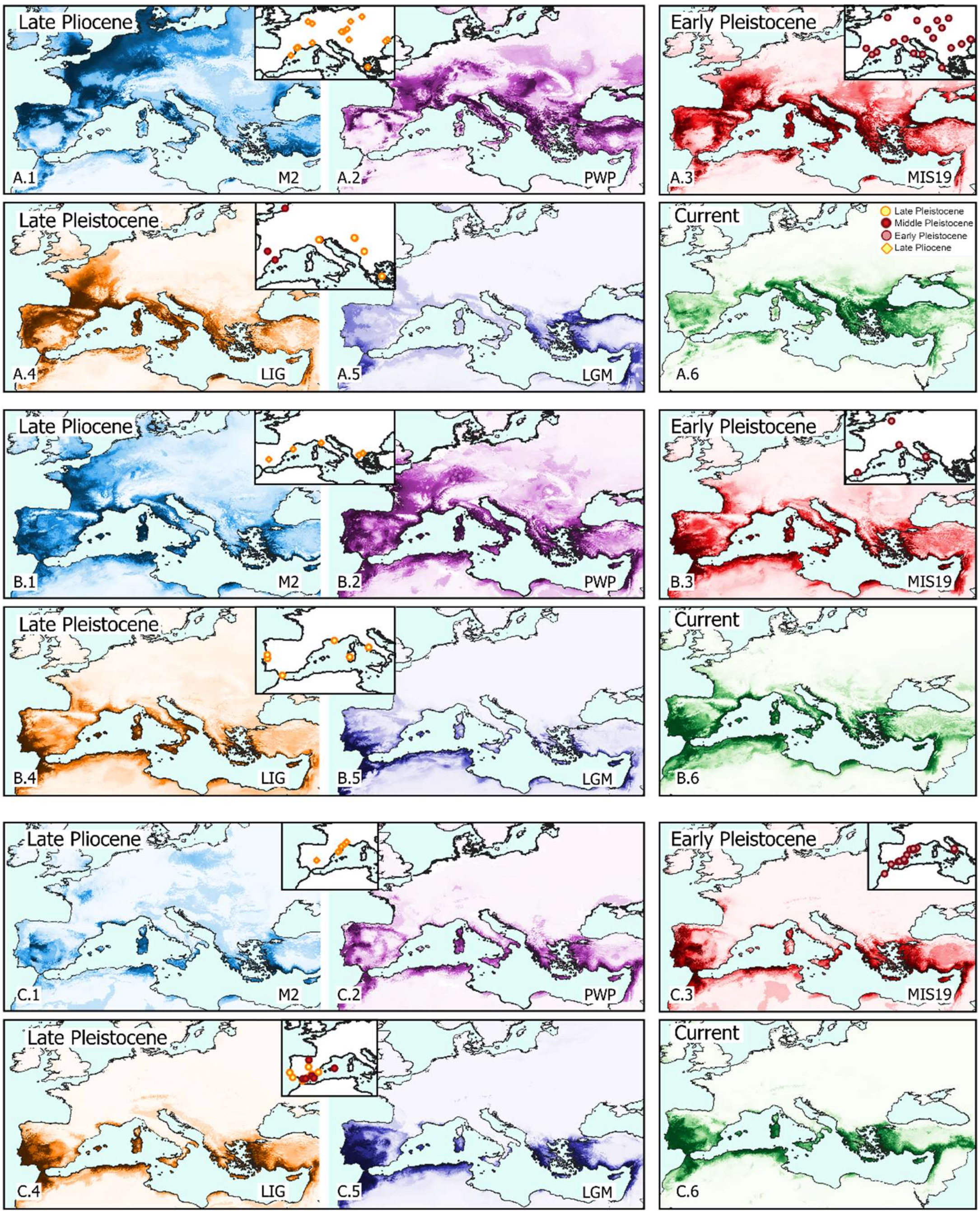


Figure 5. Colour-interpolated maps showing mean ordinated hypsodonty in fossil large herbivorous mammal communities from the Early Pliocene to the late Middle Pleistocene. Blue indicates humid conditions (low mean ordinated hypsodonty, close to 1), red indicates arid conditions (high mean ordinated hypsodonty, close to 2.6 and above). The spectrum in between from green to yellow and orange indicates progressively dryer intermediate climatic conditions.

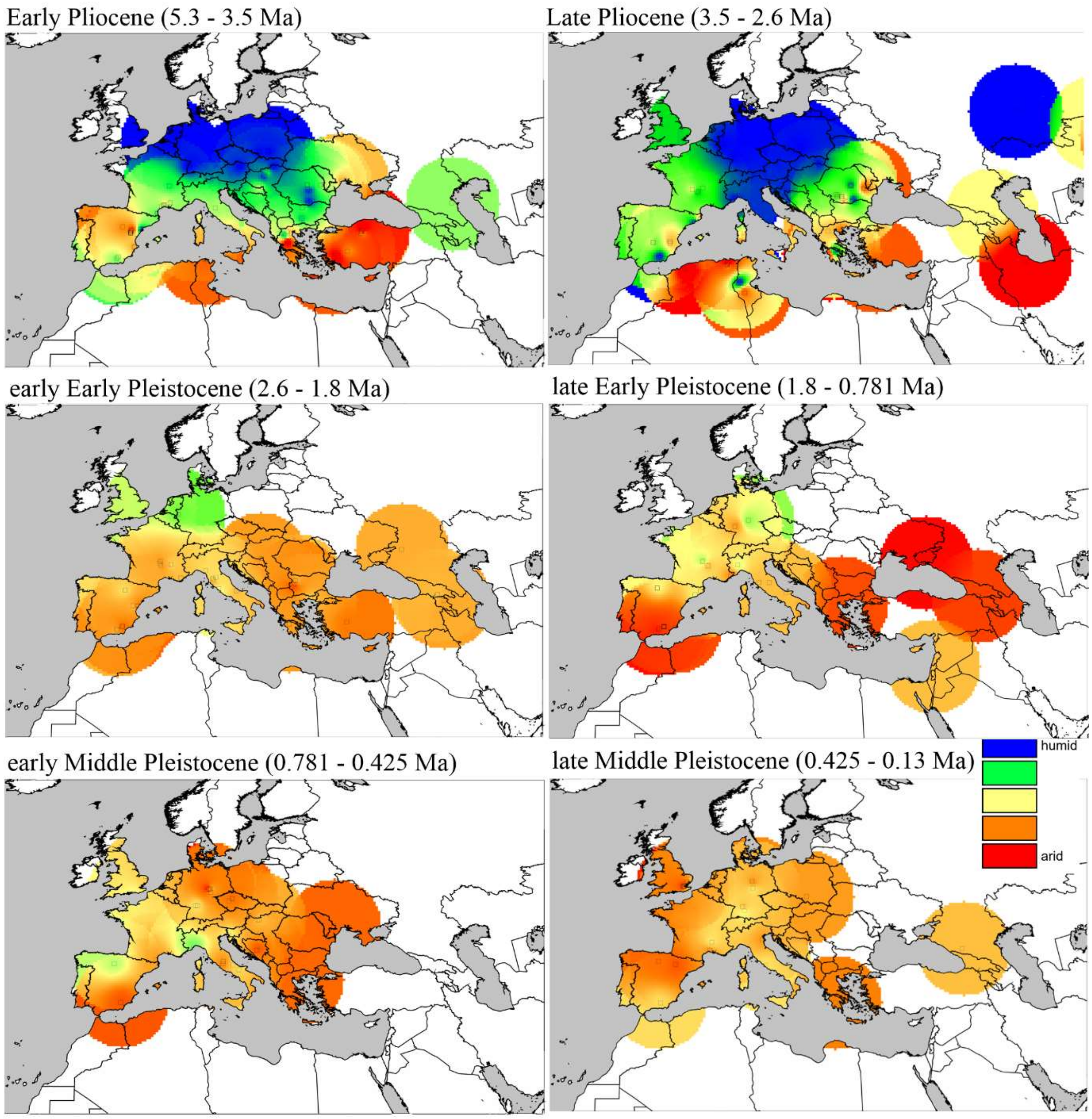


Table 1. Presence data of selected components of the European herpetofauna, showing extirpation patterns testified by the fossil record.

Genus	Central Europe		Iberian Peninsula		Italian Peninsula		Balkans Peninsula		Climatic analyses
	Past	Present	Past	Present	Past	Present	Past	Present	
Chioglossa	X		X	X					This work
Speleomantes	X				X	X			This work
Euleptes	X				X	X			No
Hierophis	X			Limited to part close to Pyrenees	X	X	X	X	This work
Salamandrina	X		X		X	X	X		Macaluso et al. 2021a
Pseudopus	X		Limited to part close to Pyrenees		X		X	X	This work
Mauremys	X		X	X	X		X	X	This work
Blanus	X		X	X	X			X	This work