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RESEARCH ARTICLE

From the mountains to the sea: Rethinking Mediterranean glacial refugia as dynamic entities

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Abstract

Aim: Glacial refugia are areas of primary importance for the evolution and conservation of biodiversity. Yet, their geographic location remains loosely defined even in intensively studied areas, preventing a thorough understanding of their role in the spatiotemporal biodiversity dynamics. With this study, we aim to locate the major glacial refugia within the biodiversity hotspot of the Italian peninsula, to understand the processes that warranted the long-term persistence of biodiversity in the face of climate changes.

Location: Italian peninsula.

Taxon: Terrestrial vertebrates.

Methods: We calibrated species distribution models (SDM) for 22 lineages of terrestrial vertebrates endemic to the Italian peninsula and projected the SDMs to the last-glacial maximum conditions. Then, we combined single-lineage projections to investigate the location and spatiotemporal dynamics of multi-species glacial refugia.

Results: Multi-species refugia were mostly found in coastal areas that have been flooded by the post-glacial marine transgressions, and that are currently below the sea level. Indeed, we identified six major areas acting as glacial refugia, mainly located outside the current coastline in the southern part of the peninsula and along the western coast. These areas were close to previously inferred locations of glacial refugia and genetic diversity hotspots, but none coincided with them.

Conclusions: Results from this study outline glacial refugia as highly dynamic units. Most of the identified refugial areas have been lost by post-glacial sea-level rise. Accordingly, species persistence through the Late Pleistocene was not granted by long-term environmental stability, but by the opportunity to shift species' distributions along altitudinal gradients, following changes in climate and habitat suitability. Notably, our results decouple glacial refugia from hotspots of genetic diversity. Thus, the current location of a hotspot should not be taken as evidence for the occurrence of a glacial refugium in that location—even though a refugium is likely to be located somewhere nearby.

KEYWORDS
biodiversity hotspots, Mediterranean peninsulas, Pleistocene glacial cycles, species distribution modelling, vertebrates

1 | INTRODUCTION

Understanding how species change their distribution in response to climate changes is a long-standing topic for ecology, biogeography and conservation biology. Compelling evidence has shown that most species changed their distribution in response to the Pleistocene climate changes, contracting their distribution to refugial areas during periods of unfavourable climate and spreading during favourable climatic phases (Bennett & Provan, 2008; Hewitt, 1996, 2000, 2004). Even now, we are observing changes in species distributions associated with the human-induced climate changes (Lenoir & Svenning, 2015; Svenning et al., 2008), with major implications for species persistence, community structure and ecosystem functioning (Espíndola et al., 2012; Thomas et al., 2004; Urban, 2015). Because of the dynamic nature of species distribution, integrating dynamic processes into conservation policies is mandatory to preserve biodiversity in the face of the ongoing climate changes (Adam et al., 2022; Román-Palacios & Wiens, 2020).

Glacial refugia guaranteed species survival during past unfavourable climate changes and are commonly considered biodiversity hotspots at both species and intraspecific levels (Hewitt, 1996, 2011; Petit et al., 2003; Taberlet et al., 1998). In fact, fine-scale genetic investigations revealed the occurrence of multiple, distinct evolutionary lineages within single refugial areas (e.g. Canestrelli, Cimmaruta, et al., 2006; Canestrelli & Nascetti, 2008; Canestrelli, Zangari, & Nascetti, 2006; Miraldo et al., 2011; Querejeta & Castresana, 2018; Schultze et al., 2020), often coupled with remarkable variation in the levels of genetic diversity among populations. Such a marked intraspecific genetic structure within refugial areas has been linked to the effects of repeated cycles of population fragmentations within distinct sub-refugia, followed by secondary contacts and genetic admixture (Canestrelli et al., 2010, 2014; Dufresnes et al., 2016; Gómez & Lunt, 2007). Due to the link between glacial refugia and biodiversity hotspots, glacial refugia are increasingly acknowledged as areas of primary importance for the evolution and conservation of biodiversity, at all levels of organization (Cheng et al., 2014; Hampe & Petit, 2005; Hu et al., 2019; Keppel et al., 2012; Zampiglia et al., 2019).

Nonetheless, identifying the exact location of glacial refugia remains a challenging task. Traditionally, past species distributions were inferred from paleo-pollen and fossil records (Bennett et al., 1991; Huntley & Birks, 1983). However, fossil and pollen information are scanty and taxonomically, temporally and spatially biased, not allowing a complete reconstruction of the entire species range. Moreover, inferences based on fossil and pollen information are affected by the uncertainty surrounding the fossil age estimates and the exact taxonomic assignment (Bennett & Provan, 2008). A possible workaround is offered by species distribution models (SDMs). SDMs are correlative models in which current or past species distribution is coupled with environmental variables (Guisan & Zimmermann, 2000). SDMs can be projected back and forth in time, obtaining a probabilistic picture of species distribution in the past or in the future, and they can offer a good geographical and temporal accuracy (Maiorano et al., 2013). However, SDMs have limitations as well (Araújo et al., 2019; Peterson, 2011; Waltari et al., 2007). The standard approach to SDM, using occurrence data for the whole species to model a unique species' ecological niche, overlooks the role of intraspecific diversity and local adaptations in the niche evolution (Zimmermann et al., 2010). Some authors have shown that SDMs calibrated using subspecies as the unit of analysis do not match with SDMs calibrated considering the species as a whole (D'Amen et al., 2013; Pearman et al., 2010). Not surprisingly, studies on glacial refugia based on SDMs accounting for intraspecific diversity estimated refuge locations with higher resolution and in areas that were unexpected basing on previous knowledge (Chiocchio et al., 2021; Espíndola et al., 2012; Wielstra et al., 2018). This evidence casts doubts on the current knowledge on glacial refugia location as identified with traditional SDMs, even in intensively studied areas—such as the Italian peninsula.

The Italian Peninsula has been an iconic region for studies on the impact of Pleistocene climate changes on biodiversity (Hewitt, 2000, 2004; Taberlet et al., 1998). The high species and genetic richness of the Italian and the other Mediterranean peninsulas, if compared with the rest of Europe, has been considered linked to the presence of Pleistocene glacial refugia (Hewitt, 2011). In principle, the location of these glacial refugia were approximated to the areas holding the current hotspots of species/genetic diversity, corresponding for the Italian peninsula to the southern portion of the Apennine chain (Petit et al., 2003). Yet, evidence from genetic studies suggested the presence of more refugial areas within the Italian peninsula (Canestrelli et al., 2010; Canestrelli, Cimmaruta, et al., 2006; Canestrelli & Nascetti, 2008; Canestrelli, Zangari, & Nascetti, 2006), not necessarily coinciding with the genetic diversity hotspots (e.g. Chiocchio et al., 2021). Therefore, to date, the actual locations of glacial refugia within the Italian peninsula have still to be properly clarified.

With this study, we aim at identifying the geographic location of the major glacial refugia within the Italian peninsula, in order to shed light on the processes ensuring the long-term conservation of biodiversity in the face of climate changes. To do so, we (i) collected the available information on distribution and intraspecific genetic structure for 22 endemic lineages of terrestrial vertebrates inhabiting the peninsula, (ii) developed a specific SDM for each distinct intraspecific lineage, (iii) projected the SDMs to the last-glacial maximum conditions, (iv) combined single-lineage projections into multi-species models to estimate fine-scale locations of the major glacial refugia within the Italian peninsula.

2 | MATERIALS AND METHODS

2.1 | Dataset collection

We focused on the intraspecific lineages of terrestrial vertebrates endemic to the Italian peninsula (islands excluded; see Figure S1 for a map including the main toponyms used in this study). We excluded

the cold-adapted species *Icthyosaura alpestris* and *Rana temporaria* because they did not retract their distribution in refugia during the glacial phases (Chiocchio et al., 2017; Vences et al., 2013). To account on intraspecific diversity and local adaptations in the niche evolution (Zimmermann et al., 2010), we followed the approach delineated in Pearman et al. (2010), by calibrating the SDMs on single independent evolutionary lineages rather than on the whole species range. To do so, we inspected the available literature on each species genetic structure and identified the lineage boundaries based on genetic information—if any. Then, we selected the taxa for which we could identify a unique and distinct evolutionary lineage which distribution was entirely included within the Italian peninsula. Finally, we selected only occurrences that could be referred to these lineages, so that each model was fully representative of the niche of the evolutionary lineage evolved within the Italian peninsula. The final dataset included 22 lineages, of which 16 were amphibians, three reptiles and three mammals (Table 1).

For each lineage, we generated a set of occurrence points by pooling data from different sources: published literature (Table 1), scientific databases (CKmap 5.3.8; Stoch, 2000–2005), citizen science databases (Observado; www.observation.org) and the Global Biodiversity Information Facility (which combines citizen science and museum databases; www.gbif.org). Citizen science databases were filtered by removing occurrences not associated with accurate photograph, date and coordinates, and keeping only 'research grade' data (i.e. species occurrences confirmed by at least three different users). We also removed all duplicated occurrences (both within and across datasets), and all the occurrences with a spatial accuracy >1 km. To limit data clustering (measured by Moran's I) and sampling bias, which are common when data come from different sources and/or different sampling scheme (De Oliveira et al., 2014; Rangel et al., 2006; Varela et al., 2014), we applied the spatial thinning procedure implemented in the *spThin* R library (Aiello-Lammens et al., 2015). The thinning procedure requires a minimum distance below which all occurrences are discarded except one, chosen randomly. To define a lineage-specific thinning distance, (1) we generated 10,000 sets of *n* random points covering the same area sampled by the real occurrences and with *n* equal to the number of available occurrences; (2) for each set of *n* random points, we calculated the mean nearest neighbour distance; (3) considering all 10,000 sets of random points, we calculated the average nearest neighbour distance. Using this overall average distance as threshold, we obtained five alternative sets of occurrences in which clustering is minimized (Table S2). These five sets were used for alternative model calibration. For each of these five sets, all occurrences not considered in calibration were used for model evaluation.

2.2 | Species distribution modelling approach

For each lineage, we generated a distinct SDM using an ensemble forecasting approach (Thuiller et al., 2009) trying to adhere to the best practices in the field (Araújo et al., 2019). We included in the analyses five SDM algorithms: generalized linear models (GLMs); generalized additive models (GAM's); generalized boosted models (GBM's); multivariate adaptive regression spline (MARS); and maximum entropy (Maxent). All algorithms were calibrated for each taxon with exactly the same study area, the same occurrences and the same background points.

Considering the geographic distribution of each lineage, we designed four different calibration areas: for most of the lineages, the SDMs were calibrated considering the entire Italian peninsula, island excluded; for lineages occurring over Italy and Sicily (*Hyla intermedia* southern lineage and *Podarcis siculus* southern lineage), the island of Sicily was added to the calibration area; for lineages with a distribution limited to the southern portion of the peninsula and Sicily (*Bufo bufo* southern lineage), we considered a calibration area limited to the southern Apennine (defined using the Sangro and Volturno river watershed as the northern border) and included Sicily; for the three lineages with a distribution limited to the southernmost portion of the peninsula (*Lissotriton italicus* southern lineage; *Sciurus meridionalis*; and *Myodes glareolus*), the calibration area was limited to the Italian peninsula south to the Sangro and Volturno rivers (see Figure S2).

To limit the impact of sampling biases, we used a target-group approach to generate background points for SDM calibration (Ranc et al., 2017). We extracted from Maiorano et al. (2013) all the presence data available in Italy for all amphibians, reptiles and mammals focusing on the same families of our target lineages (see Table 1). We pooled amphibian and reptile occurrences, because they are commonly observed by the same experts (i.e. herpetologists) and thus are expected to share the same sampling bias. The spatial distribution of both background datasets is available in Figure S3 while the full list of the target-group species included is available in Table S1. Because the data from southern Italy were too scanty to provide a reliable set of background points, for the three lineages with a distribution limited to the southernmost portion of peninsula (*L. italicus* southern lineage; *S. meridionalis*; and *M. glareolus*), we generated 4000 random background points from the calibration area.

Bioclimatic data for current and past (last glacial maximum, 21,000 years before present, therein LGM) climatic conditions were obtained from WorldClim (1.4, Hijmans et al., 2005; 30 arc-second resolution for current climate, 2.5 arcminute resolution for the past climate). To limit multicollinearity, we calculated the variance inflation factors (VIF) among all the 19 variables available for current conditions and retained only variables with VIF <5 (Zuur et al., 2010).

Bioclimatic variables for the LGM were extracted from the three available global circulation models (GCMs): the Community Climate System Model (CCSM4), the Model for Interdisciplinary Research on Climate (MIROC-ESM) and the Max-Planck-Institute Earth System Model (MPI-ESM-P). All these layers implemented the reconstruction of past climate conditions according to the LGM coastline, therefore including the coastal areas that have now been submerged by the post-glacial sea-level rise. For each GCM, we considered the same set of bioclimatic variables retained for the current climate after VIF analysis.

TABLE 1 List of the 22 lineages of terrestrial vertebrates endemic of the Italian Peninsula considered in this study, literature on the intraspecific genetic structure for each species and dataset summary: total occurrences refers to all the data considered for each lineage after applying the thinning distance (details in the Section 2); calibration and evaluation occurrences represents the subsets of the total occurrences used for model calibration and model evaluation, respectively.

Intraspecific lineages		Reference	Total occurrences	Calibration occurrences	Evaluation occurrences	Background points
Amphibia						
1	*Salamandra salamandra gigliolii*	Bisconti, Porretta, et al. (2018)	258	111	147	7759
2	*Salamandrina perspicillata*	Canestrelli, Zangari, and Nascetti (2006)	222	132	90	7760
3	*Salamandrina terdigitata*	Canestrelli, Zangari, and Nascetti (2006)	89	42	47	7877
4	*Lissotriton italicus*—northern lineage	Canestrelli, Sacco, and Nascetti (2012)	83	49	34	7883
5	*Lissotriton italicus*—southern lineage	Canestrelli, Sacco, and Nascetti (2012)	36	21	15	4000
6	*Lissotriton vulgaris meridionalis*	Maura et al. (2014)	374	250	124	15,184
7	*Triturus carnifex*—northern lineage	Canestrelli, Salvi, et al. (2012)	245	166	79	15,743
8	*Triturus carnifex*—southern lineage	Canestrelli, Salvi, et al. (2012)	299	184	115	7667
9	*Bombina pachypus*	Canestrelli, Cimmaruta, et al. (2006)	352	182	170	7614
10	*Bufo bufo*—northern lineage	Chiocchio et al. (2021)	540	369	171	6655
11	*Bufo bufo*—southern lineage	Chiocchio et al. (2021)	245	154	91	4715
12	*Hyla intermedia*—northern lineage	Canestrelli et al. (2007)	364	250	114	7603
13	*Hyla intermedia*—southern lineage	Canestrelli et al. (2007)	331	221	110	7891
14	*Pelophylax lessonae*	Canestrelli et al. (2008)	576	407	169	7564
15	*Rana dalmatina*	Canestrelli et al. (2014)	146	71	75	7820
16	*Rana italica*	Canestrelli and Nascetti (2008)	442	257	185	7563
Reptilia						
17	*Testudo hermanni hermanni*	Chiocchio et al. (2022)	173	91	82	7793
18	*Podarcis muralis*—northern lineage	Salvi et al. (2013)	64	34	30	7902
19	*Podarcis siculus*—southern lineage	Senczuk et al. (2017)	686	432	254	7606
Mammalia						
20	*Talpa romana*	Canestrelli et al. (2010)	116	53	63	1881
21	*Sciurus meridionalis*	Wauters et al. (2017)	154	43	111	4000
22	*Myodes glareolus*	Chiocchio et al. (2019)	61	24	37	4000

2.3 | Model evaluation, projections and glacial refugia

For each lineage, and for each SDM algorithm, we generated five distinct models using different calibration datasets, generating a total of 25 models for each lineage. Each model was evaluated by measuring the area under the curve (AUC) of the receiver operating characteristic curve (Swets, 1988). Models with AUC values ≥0.7 were then projected under the current climate. The final ensemble SDM for each lineage was calculated as the weighted average of all available models (weights for each model based on the respective AUC value; Marmion et al., 2009), and then projected over the Italian peninsula. We also transformed the continuous ensemble model into binary presence/absence map, considering the threshold that maximizes the true skill statistics (maxTSS; Freeman & Moisen, 2008).

For each lineage, the ensemble model was projected over the Italian peninsula considering the LGM climate under each GCM and binarized using the same maxTSS threshold described above. SDM projected over past climates could include areas whose climate fall outside the range of values considered in calibration, and where projections are therefore unreliable. To evaluate the reliability of our results, we applied a multivariate environmental similarity surface (MESS) analysis as implemented in the *dismo* R package (Elith et al., 2010) to all LGM projections.

For each lineage, considering the binary projections, we defined as glacial refugia all areas with the maximum concordance possible among the three GCM. Glacial refugia for all lineages were overlapped in a single map of multi-species glacial refugia for terrestrial vertebrates.

3 | RESULTS

3.1 | Species distribution data and climatic predictors

We collected at least 30 occurrences for each lineage (mean 266.18; SD 179.15). After the thinning procedure was applied, the occurrences spanned from a minimum of 21 (*L. italicus* southern lineage) to a maximum of 407 (*Pelophylax lessonae*) (see Table 1). Overall, the thinning procedure retained 56% of the original occurrences, which were used as calibration datasets; the other 44% of occurrences were used for model evaluation. The dataset of occurrences for each species is available on Dryad (https://doi.org/10.5061/dryad.r2280gbjr). The dataset of background points extracted from Maiorano et al. (2013) consisted in 8214 points for amphibians and reptiles, and 2005 points for mammals. The datasets of background points are provided as Data S1 on Dryad (to be populated after acceptance).

After the VIF analysis, we retained from a minimum of six to a maximum of seven bioclimatic variables for each lineage, according to the different calibration area and the different set of background point used (Table S3). Temperature seasonality and mean temperature of the wettest quarter were considered for all lineages; mean diurnal temperature range and precipitation of the wettest month were selected for most lineages.

3.2 | Model evaluation

Overall, model performance was good, with all models but one showing AUC ≥0.7 (Table S4). Mean AUC values ranged from 0.96 (SD ±0.01) for *Salamandrina terdigitata* to 0.73 (SD ±0.05) for *Lissotriton vulgaris meridionalis*.

The SDM projections on current climatic conditions for each lineage are shown in Figures S4 and S5. For all the analysed taxa, our SDMs provide a reliable picture of the current species distribution, matching well with the most updated map of species distribution (Lanza, 2007; Sindaco, 2006).

3.3 | Past distribution and identification of glacial refugia

The MESS analysis identified the north-east of the study area as outside of the climate range used in model calibration in all the GCMs. CCSM4 had areas as outside climate range also in the west coast of the Italian peninsula (Figure S6).

The SDM projections on past climatic conditions for each lineage are shown in Figures S7–S9. For most of the lineages, we found a substantial overlap among the three GCMs: for 14 lineages we found areas classified as suitable for all GCMs; for six lineages, we found areas of overlap for at least two GCMs; only two lineages (*Salamandra salamandra gigliolii* and *S. meridionalis*) showed complete discordance among the three GCMs.

While five lineages showed wider glacial refugia (*B. bufo* southern lineage, *H. intermedia* northern lineage, *L. italicus* northern lineage, *S. salamandra gigliolii* and *Talpa romana*), most of the estimated refugia were small and fragmented, and were located mainly in the southern portion of the peninsula, as well as along the western coasts. All lineages showed refugia located along the coasts, with the exception of *H. intermedia* northern lineage, *Triturus carnifex* northern lineage, *M. glareolus* and *S. meridionalis*, whose refugia were limited to the internal mountain regions (see Figure S10).

By overlapping the estimated refugia for all lineages, we found that most of the multi-species refugia have now been submerged by the post-glacial sea-level rise (Figure 1). The map of multi-species refugia, obtained by overlapping the area of maximum concordance among the different GCMs for each lineage, showed that multi-species refugia were mainly located outside of the current coastline, in the southern part of the peninsula and along the western coast. Overall, multi-species refugia covered 10.4% of the study area, subdivided into six main areas: the Calabrian region, the southern Apulia, the coastline of Cilento, the coastline of Tuscany, the coastline of southern Latium and the Ligurian Alps (in the north-west of the peninsula). The Calabrian region, the south of Apulia and the

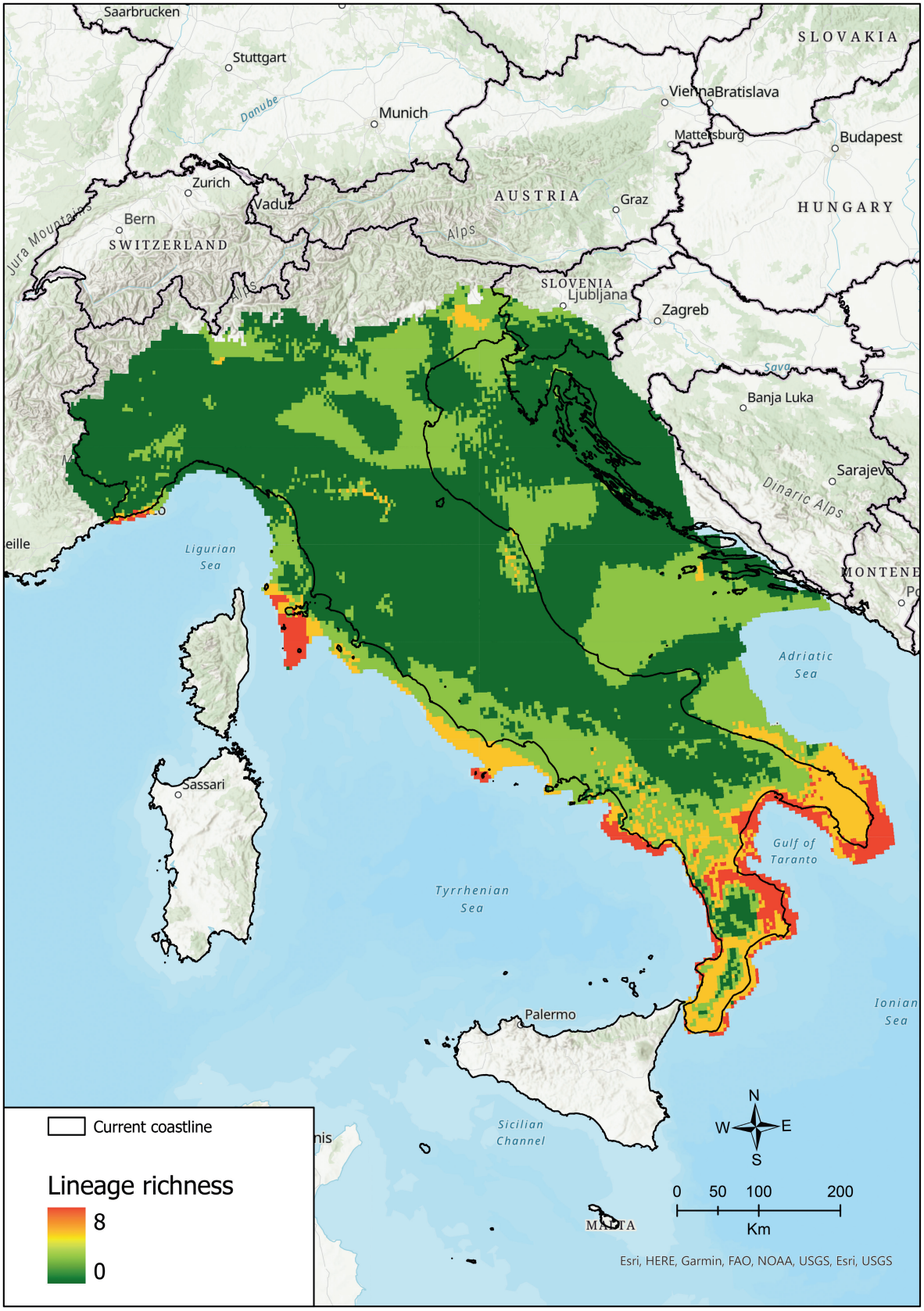

FIGURE 1 Distribution of the major glacial refugia for terrestrial vertebrates within the Italian peninsula during the last glacial maximum, obtained by overlapping the area of maximum concordance among the different global circulation models for each lineage; areas with higher lineage richness (red colours) define multi-species glacial refugia.

coastline of Cilento were the refugial areas with the highest species richness.

4 | DISCUSSION

4.1 | Rethinking glacial refugia as dynamic entities

The Italian peninsula has been recognized as a major climatic refugium for temperate species during Pleistocene glacial epochs (Hewitt, 2011). Several studies indicated the southern mountain regions as the most important refugia, as they harbour relict populations showing genetic legacies of long-term survival throughout the Pleistocene (Canestrelli et al., 2010, 2014; Canestrelli & Nascetti, 2008; Chiocchio et al., 2019). Our results support southern Italy as the main refugial area for terrestrial vertebrates. However, we found that most of the refugia were located along Pleistocene coastal plains that are currently below the sea level. Together with the occurrence of genetic diversity hotspots in mountain regions close to these refugial areas, our results suggest that the Pleistocene history of refugial populations might have been much more dynamic than previously thought. Hence, environmental stability of refugial areas and demographic stability of refugial populations might not be universal 'trademarks' of glacial refugia (Brown et al., 2020; Carnaval et al., 2009).

Results from this study emphasize the importance of areas that are currently covered by the sea as putative glacial refugia. In fact, 41% of the estimated multi-species refugial area is currently below the sea level, and four out of the six identified multi-species refugia are almost completely flooded. Glacial refugia in coastal areas have been already identified for North American flora and fauna (Shafer et al., 2010), as well as for Mediterranean plants (Médail & Diadema, 2009) and some vertebrates (Bisconti et al., 2011; Chiocchio et al., 2021; Martínez-Freiría et al., 2020). However, in most cases, these refugia were located within or close to large coastal plains, suggesting long-term persistence within these environments, which is not the case here. Indeed, most of the coastal areas identified as glacial refugia in this study are suddenly replaced by mountain areas. Therefore, our results imply that the imprints of glacial refugia have been retained in current populations through dynamic processes carrying refugial populations from (past) coastal plains to (current) mountain ranges. Interestingly, this scenario can be seen as a retelling, over much smaller spatial scales, of the classical scenario predicted by early theoretical works on glacial–interglacial range dynamics across continental regions (see figure 6 in Hewitt, 1996).

For a long time, long-term climatic stability has been considered the main driver for the rise of hotspots of intraspecific diversity within glacial refugia (Brown et al., 2020; Carnaval et al., 2009, and reference therein). Indeed, reduced climatic variability within refugial areas was thought to result in longer demographic stability of populations and, consequently, in the accumulation of genetic variation through time (Carnaval et al., 2009; Harrison & Noss, 2017; Jansson, 2003). Our results provide additional new insights in support of an alternative scenario, whereby glacial refugia are seen as dynamic and even transient entities, and the rising of hotspots of intraspecific diversity as the result of the underling dynamic processes (Canestrelli et al., 2010; Chiocchio et al., 2021). In fact, fine-scale phylogeographic studies have been revealing that hotspots of genetic diversity coincide with areas of secondary contact and genetic admixture among populations differentiated within distinct sub-refugia (Canestrelli et al., 2010, 2014; Chiocchio et al., 2017, 2021; Gutiérrez-Rodríguez et al., 2017a, 2017b; Hewitt, 2011). Our results are in line with this scenario, as we estimated highly fragmented refugia for all the investigated taxa. However, we also identified refugia in areas currently below sea level, thus not allowing for the long-term persistence of populations. Populations within these refugial areas were forced to move upwards in neighbouring mountain regions, or to go extinct. Thus, the mountain regions situated adjacent to glacial refugia are fundamental for the long-term species persistence as much as glacial refugia, as they represent the areas where the species first arrived after glaciations. That is, dynamic processes, including population fragmentation, short-range migration and gene exchange among refugial populations, rather than long-term demographic stability, fit better the data and better explain the rise of hotspots of intraspecific biodiversity, at least in the south of the Italian peninsula.

4.2 | Multiple glacial refugia within the Italian peninsula

We identified six areas of the Italian peninsulas which acted as major glacial refugia for temperate species: the Calabrian region, the south of Apulia, the coastline of Cilento, the coastline of Tuscany, the coastline of southern Latium and the Ligurian Alps (Figure 1). The Calabrian region was already acknowledged as glacial refugium for many temperate species by both fossil (Marra, 2009; Sala & Masini, 2007) and genetic data (Bisconti, Aloise, et al., 2018; Canestrelli et al., 2010, 2014; Chiocchio et al., 2019; Vega et al., 2010). Furthermore, accurate phylogeographic reconstructions inferred ancestral areas of genetically differentiated lineages in areas largely coinciding with the putative Calabrian refugia estimated here (Chiocchio et al., 2021). The Cilento region and the Ligurian Alps have also been already identified as glacial refugia or ancestral areas for divergent lineages in a number of taxa (Canestrelli, Sacco, & Nascetti, 2012; Canestrelli, Salvi, et al., 2012; Chiocchio et al., 2017; Sala, 1996; Bertolini et al., 1996; Stefani et al., 2004). Conversely, the role of the Apulian region as a glacial refugium is supported only by fossil evidence (Bedetti & Pavia, 2007; Mecozzi et al., 2018; Salari et al., 2019). Populations from this area rarely bear traces of genetic structure that can be linked to ancient isolation (but see Schultze et al., 2020). This pattern can be explained by two, not mutually exclusive, scenarios: (i) the absence of geographic barriers able to maintain long-term genetic isolation with northern populations, even during glacial maxima; (ii) severe community extinctions after the last glacial epoch. However,

the Apulian region has been less investigated than other regions with the phylogeographic toolbox, and more data are needed to depict the Pleistocene history of its biota. Finally, palynological, microfossils and sedimentological data suggested ecological stability and reduced climate changes along the western coastal plains of the peninsula during the last glacial phase (Lucchi, 2008), supporting our inference about the occurrence of glacial refugia along the coastline of Tuscany and Latium.

By calibrating single, distinct SDMs for distinct evolutionary lineages, we estimated more but narrower refugial areas if compared with SDM studies employing the whole species as unit of analysis (see e.g. Vences et al., 2013 for a comparison of *R. dalmatina* refugia estimation in the Italian peninsula). It is worth noting that cumulating LGM projections obtained by calibrating distinct models for distinct lineages of the same species do not coincide with projections based on models calibrated on the whole species (see e.g. Iannella et al., 2017 for a comparison with results on *L. italicus*). The higher resolution of SDMs calibrated on distinct evolutionary lineages can be explained by the proper dissection of the species niches (Pearman et al., 2010), which allows accounting for local adaptation processes (Pearman et al., 2010; Zimmermann et al., 2010).

5 | MAIN CONCLUSIONS

Results from this study outline glacial refugia as highly dynamic units. Most of the refugial areas identified in the Italian peninsula for terrestrial vertebrates have been lost by post-glacial marine transgressions. Accordingly, species persistence through the Late Pleistocene was not granted by environmental stability, but by the opportunity to shift species' distributions, following changes in climate and habitat suitability, buffering demographic contraction/expansion cycles triggered by climatic fluctuations. Importantly, our results decouple glacial refugia from hotspots of genetic diversity. While glacial refugia have played an essential role in preserving these hotspots through time, the current location of a hotspot should not be taken as evidence for the occurrence of a glacial refugium in that location, even though a refugium is likely to be located from somewhere nearby.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The datasets generated and analysed in this study are available in the DRYAD repository at the following link https://doi.org/10.5061/dryad.r2280gbjr.

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BIOSKETCH

Andrea Chiocchio is an evolutionary ecologist and biogeographer, broadly interested in the evolutionary processes shaping the distribution of biodiversity, at all its level of organization. This work is part of a wider project focused on understanding the processes generating hotspot of biodiversity. He and the other Authors collaborate on many questions related to how past and future climate changes affect the spatial patterns of biodiversity.

Author contributions: Andrea Chiocchio: data curation (equal); investigation (lead); validation (equal); writing—original draft (lead); writing—review and editing (equal). Luigi Maiorano: formal analysis (lead); investigation (equal); methodology (lead); validation (equal); writing—original draft (equal); writing—review and editing (equal). Alice Pezzarossa: data curation (lead); formal analysis (equal); investigation (equal); writing—original draft (equal); writing—review and editing (equal). Roberta Bisconti: data curation (equal); investigation (equal); writing—original draft (supporting); writing—review

and editing (equal). Daniele Canestrelli: conceptualization (lead), funding acquisition (lead); investigation (equal); supervision (lead); writing—original draft (equal); writing—review and editing (lead).

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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