Topography explains the distribution of genetic diversity in one of the most fragile European hotspots

Article *in* Diversity and Distributions · January 2019

DOI: 10.1111/ddi.12836

CITATIONS
5

READS
299

5 authors, including:

Mario Fernández-Mazuecos
Complutense University of Madrid
79 PUBLICATIONS **910** CITATIONS
SEE PROFILE

Alberto José Coello
Spanish National Research Council
12 PUBLICATIONS **36** CITATIONS
SEE PROFILE

Pablo Vargas
Spanish National Research Council
540 PUBLICATIONS **7,123** CITATIONS
SEE PROFILE

Received: 13 November 2017 | Revised: 17 July 2018 | Accepted: 28 July 2018

DOI: 10.1111/ddi.12836

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Topography explains the distribution of genetic diversity in one of the most fragile European hotspots

José Luis Blanco-Pastor[1,2] | Mario Fernández-Mazuecos[1] | Alberto J. Coello[1,3] | Julia Pastor[1] | Pablo Vargas[1]

[1]Real Jardín Botánico de Madrid (RJB-CSIC), Madrid, Spain

[2]INRA, Centre Nouvelle-Aquitaine-Poitiers, UR4 (URP3F), Lusignan, France

[3]Universidad Rey Juan Carlos, Madrid, Spain

Correspondence
José Luis Blanco-Pastor, INRA, Centre Nouvelle-Aquitaine-Poitiers, UR4 (URP3F), Lusignan, France.
Email: jose-luis.blanco-pastor@inra.fr

Funding information
The Spanish Ministry for Environment, and Rural and Marine Affairs, Grant/Award Number: 005/2008; Spanish National Research Council, CSIC; Spanish Ministry of Education, Grant/Award Number: AP2007-01841 and FPU16/05681; Spanish Ministry of Economy and Competitivity, Grant/Award Number: IJCI-2015-23459

Editor: Aibin Zhan

Abstract

Aim: To investigate factors that explain the spatial pattern of genetic diversity in three closely related species (*Linaria glacialis*, *Linaria nevadensis* and *Chaenorhinum glareosum*) endemic to a fragile high mountain ecosystem.

Location: The alpine belt of Sierra Nevada, Spain.

Methods: We analysed the spatial pattern of cpDNA diversity of the three species. To explain the distribution of genetic diversity, we investigated the effect of topographic features and the evolutionary history of the species (demography, habitat availability and colonization dynamics).

Results: Genetic diversity was heterogeneous across the landscape. We found moderate positive correlation values between genetic diversity indices of the two *Linaria* species. We also observed moderate negative correlation values between genetic diversity indices of *C. glareosum* and those of *L. glacialis* and *L. nevadensis*. Topographic variables correlated positively with genetic diversity of the *Linaria* species and negatively with genetic diversity of *C. glareosum*. Bayesian skyline plots (BSPs) displayed a shared demographic pattern with a population size stabilization/increase since the LGM (the last 21 kyr) in all three species. Discrete phylogeographical analyses showed similar patterns of westward diffusion for *L. nevadensis* and *C. glareosum*. Species distribution models pointed to similar range dynamics in all three species, with a reduction in range size since the LGM.

Main conclusions: Different dispersal abilities, demographic trends and colonization patterns can hardly explain the differences in spatial patterns of genetic diversity between the *Linaria* species and *C. glareosum*. In contrast, topographic features seem to be an important factor to explain the distribution of genetic diversity in the alpine belt of Sierra Nevada. We point to a relevant role of microniche partitioning in determining patterns of genetic diversity distribution in alpine Mediterranean ecosystems. Furthermore, we highlight the role of microhabitat heterogeneity in the maintenance of distinct lineages, species and genetic diversity in high mountain biodiversity hotspots.

KEYWORDS
comparative phylogeography, genetic diversity, high mountain, niche partitioning, Quaternary, topography

1 | INTRODUCTION

High mountains provide key ecosystem services that are particularly sensitive to anthropogenic global warming. These habitats are likely to undergo abrupt changes in the next decades. In high mountain species, numerous studies have evidenced a general pattern of range contraction as species move upward in elevation because of climate change (Engler et al., 2011; Gottfried et al., 2012; Pauli, Gottfried, & Grabherr, 1996; Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005; Walther, Beißner, & Burga, 2005). Under this trend, the habitats of alpine flora are expected to be drastically reduced in the next few years, which may result in rapid extinctions (Parmesan, 2006; Pauli et al., 2012). Alpine plants have already become rarer in the period 2001–2008 on the European continent, whereas plants from lower elevations have become more common at high altitudes as a response to global warming (Pauli et al., 2012; Steinbauer et al., 2018). Given this evidence for a rapid and profound effect of global climate change on alpine biodiversity, attention has been focused on the consequences for ecosystems and species. Effects on genetic diversity have largely been neglected to date, presumably due to evaluation difficulties (Schwartz, Luikart, & Waples, 2007; but see, Gugerli et al., 2008; Miraldo et al., 2016). Despite the sparseness of available evidence, genetic diversity is particularly relevant for species persistence, as it provides the raw material for evolution by natural selection (Fisher, 1930) and is pivotal for future adaptation in the face of climate change (Hughes, Inouye, Johnson, Underwood, & Vellend, 2008).

Many factors can be responsible for the distribution of genetic diversity in high mountain ecosystems. In the European continent, population size contractions and expansions have been common during Quaternary glacial cycles, when latitudinal and altitudinal range shifts caused demographic changes and bottlenecks (Hewitt, 2004). European plant species with large distribution ranges harbour a higher genetic diversity in glacial refugia (Gugerli & Holderegger, 2001; Hewitt, 2000; Magri et al., 2006; Taberlet, 1998) and in suture zones where distinct evolutionary lineages met after the last glaciation (Petit et al., 2003; Taberlet, 1998). While there is ample literature on spatial patterns of genetic diversity in European high mountain plants, particularly from the Alps and central European mountains (Mráz et al., 2007; Pachschwöll et al., 2015; Paun, SchÖnswetter, Winkler, & Tribsch, 2008; Ronikier, Cieślak, & Korbecka, 2008; Schönswetter, Stehlik, Holderegger, & Tribsch, 2005), much less is known about patterns of southern European alpine plants (but see Vargas, 2003; García-Fernández, Iriondo, Escudero, Aguilar, & Feliner, 2013; Surina, Schneeweiss, Glasnovič, & Schönswetter, 2014). This is particularly concerning as the extinction risk of species is even higher on Mediterranean summits, where distribution ranges are much smaller and higher levels of biodiversity and endemism are found compared with other European mountains (Pauli et al., 2012). Indeed, genetic diversity, genetic structure and colonization routes have not been studied in depth in alpine species from south-western Europe (but see Kropf, Comes, & Kadereit, 2006; Blanco-Pastor, Fernández-Mazuecos, & Vargas, 2013). It is known that past climate changes had a lower impact on these areas than on northern latitudes, and the risk of population bottlenecks was presumably reduced by limited altitudinal migration in response to climatic warming and cooling (Hewitt, 1996). Also, in species with small range sizes, recurrent gene flow among populations may have buffered genetic diversity loss resulting from past environmental constraints (Blanco-Pastor et al., 2013).

To determine conservation priorities for particular communities (e.g., reserve design), it is important to evaluate extinction risk in multiple species (Moritz & Faith, 1998), including assessments of the spatial distribution of genetic diversity (Jay et al., 2012). Phylogeography, originally defined as the historical reconstruction of intraspecific lineages in a spatial framework (Avise, 1987), has been extensively used as a tool for conservation purposes (e.g., Bos & Sites, 2001; Holland & Hadfield, 2002; Karl, Castro, Lopez, Charvet, & Burgess, 2011; Nersting & Arctander, 2001; Shaffer, Fellers, Randal, Oliver, & Pauly, 2004). Phylogeographical analyses and associated tools allow estimation of the geographical origin, colonization routes, demographic events, age of lineage divergences and population structure of species. All this information can be used to infer past and present factors that account for the current distribution of genetic diversity. Most phylogeographical studies focus on a single species (or a complex of closely related species) and thus provide limited insights into common patterns. In contrast, comparative phylogeography aims to compare the spatial distribution of intraspecific lineages of multiple species resulting from a common geographical setting and associated environmental factors. These factors may account for shared patterns of colonization or population size variation (Bermingham & Moritz, 1998). In the European region, plant species with similar distributions, habitats and life histories have been used to look into common colonization routes and patterns of genetic diversity distribution at the continental scale. However, phylogeographical patterns do not seem to be largely shared across species (Nieto Feliner, 2014; Vargas, 2003), which can be explained by environmental heterogeneity across the European continent. In contrast, at the regional level, common patterns of genetic structure have been described for plants from the Alps, and these patterns have been associated with ecological factors influencing dispersal (Alvarez et al., 2009). As a foundation for informed conservation planning, it is important to investigate if common patterns of genetic structure and diversity can also be found at the smaller spatial scales of Mediterranean mountains, where dispersal and gene flow may play a significant role.

Here, we use topographic data and comparative phylogeography to analyse factors responsible for the distribution of genetic diversity in related species inhabiting the summits of Sierra Nevada National Park (Spain). Conservation planning in Mediterranean mountain biodiversity hotspots, such as Sierra Nevada, needs immediate attention. This mountain range is located in south-eastern Spain nearby the Mediterranean Sea, and it includes the highest peak in the Iberian Peninsula (Mulhacén, 3,479 m a.s.l.). It served as a refugium for many European species during glacial ages (Blanca et al., 1998; González-Sampériz et al., 2010). The highest vegetation belt in Sierra Nevada (cryoromediterranean or alpine belt) is considered

one of the most fragile European ecosystems (Blanca et al., 1998; Cañadas et al., 2014).

Our study system comprises three endemic species from the tribe Antirrhineae (Plantaginaceae). This tribe includes, among others, *Chaenorhinum* and *Linaria*, two genera that shared a most recent common ancestor around the Oligocene–Miocene boundary (Vargas et al., 2014). Although major evolutionary changes have occurred in the last 25 million years, certain traits related to life cycle (herbaceous habit), habitat preferences (rocky soils) and biotic interactions (bee pollinators) are phylogenetically conserved (Benedí & Güemes, 2009; Guzmán, Gómez, & Vargas, 2015; Sáez & Bernal, 2009). In particular, three species of Antirrhineae (*Linaria glacialis* Boiss., *Linaria nevadensis* (Boiss.) Boiss. & Reut. and *Chaenorhinum glareosum* (Boiss.) Willk.) are distributed on the same highest peaks across a small area of Sierra Nevada (2,500–3,479 m), and they all occur on rocky and humid metamorphic soils close to melting snowfields. One of these species (*L. glacialis*) is vulnerable to extinction (UICN category VU B2ab (ii,iii,iv,v); C2a(i); D2; Moreno, 2010) and has been studied in detail to assess the consequences of past and future climate variation on genetic diversity (Blanco-Pastor et al., 2013). The latter study revealed the following: (a) The potential habitat of this species in Sierra Nevada underwent little change during glacial and interglacial stages of the late Quaternary; (b) climatic oscillations in the last millennia moderately affected its demographic trend; and (c) high gene flow may prevent drastic genetic diversity loss during future range contraction. The question remains as to whether related species endemic to the alpine Sierra Nevada share similar phylogeographical histories and spatial patterns of genetic diversity.

The comparative approach using related species with similar ecological requirements is useful to better understand the effect of historical factors, such as demography and colonization routes, on the current distribution of genetic diversity within biodiversity hotspots. Our hypothesis is that similar dispersal capacities and a weak effect of historical events such as the Quaternary climatic cycles (as already observed for *L. glacialis*) have favoured the occurrence of the highest genetic diversity in the same areas for the three species. Alternatively, distinct demographic/phylogeographical histories or niche partitioning may have led to contrasting patterns of genetic diversity distribution. To evaluate these hypotheses, we first analysed the spatial distribution of plastid DNA (cpDNA) diversity. We then performed correlation analyses between genetic diversity and topographic variables. To interpret the observed genetic diversity patterns, we also performed evolutionary reconstructions: (a) demographic reconstructions from genetic data; (b) species distribution modelling; and (c) Bayesian phylogeographical analyses.

2 | METHODS

2.1 | Sampling strategy and DNA sequencing

We collected 254 individual plants from three species of the tribe Antirrhineae: *Linaria glacialis* (13 populations, 100 individuals), *Linaria nevadensis* (≡ *L. aeruginea* subsp. *nevadensis* (Boiss.) D.A. Sutton; 14 populations, 60 individuals) and *Chaenorhinum glareosum* (11 populations, 94 individuals; Figure 1). Sampling and DNA sequencing strategies are detailed in Blanco-Pastor, Vargas, and Pfeil (2012) and Blanco-Pastor et al. (2013). The area covered by population sampling was representative of the entire distribution ranges of the three species. The number of individuals sampled per population was proportional to population density at each sampling site. These species inhabit schistose screes in the alpine vegetation belt of Sierra Nevada. Specifically, *L. glacialis* is usually more abundant on rocky soils at 2,700–3,400 m; *L. nevadensis* prefers rocky soils at 2,300–3,300 m (Sáez & Bernal, 2009); and *C. glareosum* is commonly found in rock fissures and less developed soils at 1,800–3,400 m (Benedí & Güemes, 2009). The two *Linaria* species have winged seeds (2.4–3.1 × 2.4–2.6 mm in *L. glacialis*; 1.2–2 × 1.1–1.5 mm in *L. nevadensis*), while *C. glareosum* displays small nonwinged seeds (0.7–0.9 × 0.4–0.5 mm). Seed dispersal seems to be mediated by wind in all three species. Establishment and survival across heterogeneous landscapes requires seed dispersal as a primary factor. Plastid DNA (cpDNA) is maternally inherited in Antirrhineae (Corriveau & Coleman, 1988) and has been widely used in plant phylogeography to make inferences on past colonization by seed and on current distribution patterns of genetic diversity linked to colonization dynamics (Avise, 2009). Therefore, our comparative study was focused on cpDNA sequence data. The *L. glacialis* data set was taken from Blanco-Pastor et al. (2013) and contains genetic information from the plastid regions rpl32-trnL^{UAG} and rps162F2-trnK^{UUU}. The *L. nevadensis* and *C. glareosum* data sets were newly generated for this study. The latter two data sets contain the two plastid regions rpl32-trnL^{UAG} and trnQ-rps16. These DNA regions were selected after a pilot study in which 10-20 DNA regions (Shaw, Lickey, Schilling, & Small, 2007) where tested for variability across four geographically representative individuals of each species.

2.2 | Haplotype networks

The geographical representation of haplotypes and haplotype lineages is a useful analysis for a visual inspection of the spatial distribution of genetic diversity. After alignment with MAFFT v.1.3.3 (Katoh, Misawa, Kuma, & Miyata, 2002; Katoh & Standley, 2013) and further manual adjustments, we reconstructed haplotype networks using the haploNet function of the R package "pegas" (Paradis, 2010). Haplotype networks were built using an infinite sites model (i.e., uncorrected or Hamming distance, Hamming, 1950) of DNA sequences and pairwise deletion of missing data, as implemented in "pegas." The haploNet function returned the most probable links among haplotypes, and the number of mutational steps for each link. Insertions/deletions were not considered for the inference of haplotypes.

2.3 | Population genetic diversity analyses

To further characterize the spatial distribution of genetic diversity in the three species, we grouped individual genotypes in populations of each species and calculated three genetic diversity indices with the R package "PopGenome" (Pfeifer, Wittelsbürger, Ramos-Onsins, & Lercher, 2014): within population nucleotide diversity (Hudson, Slatkin, & Maddison, 1992; Wakeley, 1996), within population haplotype diversity (Hudson et al., 1992) and number of segregating sites. To infer the value of the genetic diversity estimators across the approximate distribution area of the species, we performed spatial interpolations using the obtained population-specific values and the inverse distance weighting (IDW) method implemented in QGIS 2.16.3 (QGIS Development Team 2016). Then, we clipped interpolated layers to an area representative of the current range size of the study species, the Sierra Nevada National Park. To account for the potential influence of unequal sample sizes across populations, we performed individual resampling with replacement with a threshold of five individuals per population. For each diversity index, mean values across 1,000 replicates were used in correlation analyses (see below).

2.4 | Spatial distribution of genetic diversity

To evaluate whether the spatial distribution of genetic diversity was similar in the three species, we performed correlation tests. To achieve this, the interpolated raster layers were loaded in R (R Development Core Team 2014) with the package "raster" (Hijmans & van Etten, 2014). Then, a total of 1,642 spatial samples were taken systematically from raster layers using the sampleRegular function (see Supporting Information Figure S1). We used sampled values from each species and each genetic diversity index to compute pairwise Pearson's correlation analyses. Additionally, to assess the association between genetic diversity and topographic complexity in the region, we also computed correlation tests between the genetic diversity layers and three raster layers with information on topography in the alpine belt of Sierra Nevada. Specifically, we used layers representing aspect (values between 0° and 360° representing the azimuth that slopes are facing), roughness (largest intercell difference of a central pixel and its surrounding cell, as defined in Wilson, O'Connell, Brown, Guinan, and Grehan (2007)) and slope (in degrees). Topographic variables were computed with QGIS 2.16.3 (QGIS

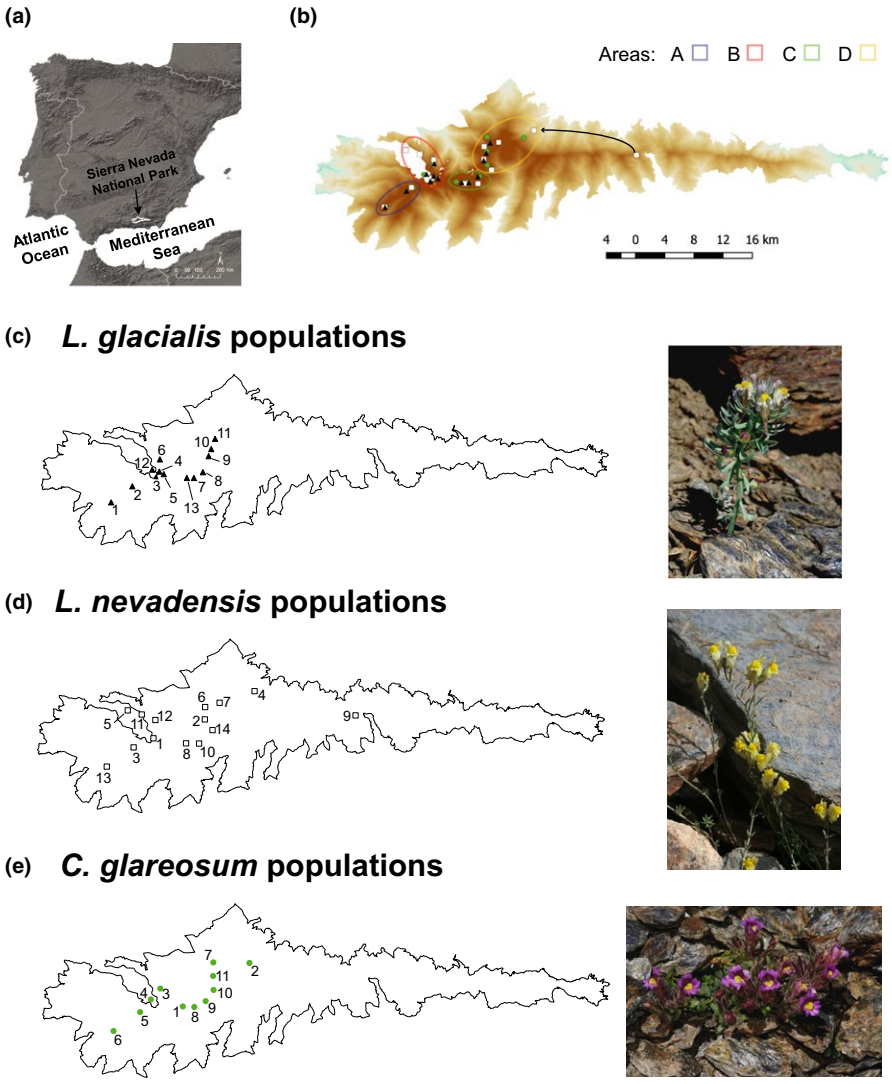

FIGURE 1 (a) Location of the study area. (b) The SRTM3 digital elevation model (DEM) of Sierra Nevada National Park and delimitation of four areas based on the geography and topography of Sierra Nevada. Areas were used in the Bayesian discrete phylogeographical analyses of Figure 5. (c–e) Population sampling sites and pictures of the three study species. Photographs by J.L. Blanco-Pastor (d) and J. Ramírez (c, e) [Colour figure can be viewed at wileyonlinelibrary.com]

Development Team 2016) from a digital elevation model at 25-m grid resolution available from the National Centre of Geographical information (CNIG) of the Spanish National Geographical Institute (http://centrodedescargas.cnig.es). All correlation values were plotted in a correlation matrix using the R package "corrplot" (Wei & Simko, 2013).

2.5 | Neutrality/demography analyses

To compare demographic events in the three species that might have affected their levels of genetic diversity, neutrality tests were performed on cpDNA matrices. We calculated Tajima's *D* (Tajima, 1989), which is expected to be close to zero under neutrality. Positive values represent a lack of rare alleles and may be due to balancing selection or population contraction, while negative values indicate an excess of low-frequency alleles and can represent a recent selective sweep or population expansion. We also calculated the Fu and Li's *D* and *F* tests (Fu & Li, 1993) including outgroup samples (see below). The *F* statistic is the normalized version of the *D* statistic. Fu and Li's statistics are based on the number of mutations in external branches of a gene genealogy. The mutations in external branches of a genealogy represent recent mutations. Positive values of the statistic may indicate recent negative selection (low frequency of novel deleterious alleles), old positive selection (high frequency of an old advantageous allele) or a recent population contraction. Negative values may indicate long-term balancing selection or recent population expansion. Significance of Tajima's and Fu and Li's statistics was evaluated using neutral coalescent simulations with 10,000 replicates. Simulations were based on the observed number of segregating sites, assuming no recombination and with a significance level fixed to 0.05. Historical demography was further analysed using the mismatch distribution (Rogers & Harpending, 1992). The observed distribution of the frequency of pairs of individuals who differ by a certain number of nucleotide differences was tested against the expected distribution under constant population size and expansion or decline models. All calculations were made with the program DnaSP v5 (Librado & Rozas, 2009).

The Bayesian skyline plot (BSP) implemented in the software package BEAST v1.8.0 (Drummond & Rambaut, 2007) is a method for estimating past population dynamics through time from a sample of molecular sequences without dependence on a prespecified parametric model of demographic history (Drummond, Rambaut, Shapiro, & Pybus, 2005). BSP analyses for the three species were set as follows. Plastid DNA regions of each species were concatenated and analysed with BEAST. Given the low information content of each DNA region separately, a single partition with a single substitution model estimated by AIC values in jModeltest 2 v0.1.10 (Darriba, Taboada, Doallo, & Posada, 2012) was defined for each DNA sequence dataset. Based on previous estimates of cpDNA mutation rates for herbaceous plants (Wolfe, Li, & Sharp, 1987), uniform prior distributions for substitution rates were set in a strict clock model, with a range of 1×10^{-10} to 1×10^{-8} s/s/year. A coalescent Bayesian skyline prior was set as tree model with five groups of coalescent intervals and a piecewise-constant skyline model. A uniform prior was set for the base frequencies with 0 and 1 as lower and upper limits. For the HKY and TrN substitution models, the prior distribution for the transition-transversion parameter (kappa) was set as a log-normal distribution with Mean = 1 and *SD* = 1.5 (Drummond & Bouckaert, 2015). The prior for the Bayesian skyline population size parameter was set to a uniform distribution with a conservative upper limit of 100 million individuals. For the analysis of *L. glacialis* data, we included a prior for the root height of the tree with a truncated normal distribution (mean 96,000 years, standard deviation 96,000, lower limit = 0, upper limit = 1.0 E7 years), derived from the divergence time between *L. glacialis* and its sister species *L. verticillata* (Blanco-Pastor et al., 2013). A similar root height prior was set for *L. nevadensis*: a truncated normal distribution (mean 95,000 years, standard deviation 94,000, lower limit = 0, upper limit = 1.0 E7 years) derived from the divergence time between *L. nevadensis* and its sister species *L. amoi* (Blanco-Pastor et al., 2013). For *C. glareosum*, we used a truncated normal distribution (mean 75,000 years, standard deviation 77,000, lower limit = 0, upper limit = 1.0 E7 years), a conservative prior derived from the approximate divergence time between *C. glareosum* and its sister species *C. villosum* (Guzmán et al., 2015). Analyses were run for 100 million generations, with a sample frequency of 10,000. The Tracer 1.6 software (Rambaut & Drummond, 2016) confirmed that effective sample sizes (ESS) were adequate, with values above 400 and plots showing equilibrium after discarding the burn-in.

2.6 | Bayesian phylogeographical analyses

Similar migration routes may lead to similar spatial distribution of genetic diversity in different species. To reconstruct and compare the historical migration routes of the three study species, cpDNA sequence data sets were examined using a Bayesian discrete phylogeographical analysis (DPA; Lemey, Rambaut, Drummond, & Suchard, 2009). This procedure was preferred over the recently proposed structured coalescent method BASTA (De Maio, Wu, O'Reilly, & Wilson, 2015). Unlike BASTA, DPA does not require prior knowledge of population sizes and migration rates and allows the inclusion of outgroup species to ensure the accurate rooting of genealogies. Although DPA has the drawback of being sensitive to biased sampling (unlike BASTA; De Maio et al., 2015), our sampling can be considered essentially unbiased, as the three species were collected from the same areas roughly in proportion to their prevalence.

Analyses were conducted in BEAST v1.8.0. (Drummond & Rambaut, 2007). For each study species, an outgroup sequence was included (*L. verticillata* for *L. glacialis*, *L. amoi* for *L. nevadensis* and *C. villosum* for *C. glareosum*) and all ingroup sequences were constrained as a monophyletic group. We defined four areas (A–D) based on the geography and topography of Sierra Nevada (Figure 1b) and assigned each ingroup sample to one of them. Distribution ranges of outgroup species, outside the study area, were not considered informative and were therefore set as undetermined. Prior substitution models were chosen with jModeltest 2 v0.1.10 (Darriba et al., 2012) as performed

in the previous section (BSP). Areas were mapped under an asymmetric substitution model, and we implemented a Bayesian stochastic search variable selection (BSSVS) procedure to invoke a limited number of rates (diffusion routes) that explain the diffusion process. To simplify the analysis and facilitate convergence, a strict molecular clock was implemented, with a constant size coalescent tree prior. Root height calibrations and substitution rate priors were included as in Bayesian skyline plot analyses (see above). For each species, three MCMC analyses were run for 10 million generations, sampling every 1,000 generations. Analysis with TRACER confirmed adequate sample sizes. The three chains were combined using LOGCOMBINER after discarding the first 10% of sampled generations as burn-in, and trees were summarized in a MCC tree using TREEANNOTATOR. Finally, a Bayes factor (BF) test was performed in SPREAD3 v0.9.6 (Bielejec et al., 2016) to identify rates that were frequently invoked to explain the diffusion process. Rates yielding a BF > 3 were plotted (Lemey et al., 2009).

2.7 | Species distribution modelling

The current spatial distribution of genetic diversity can be the outcome of historical constraints on available habitat. Specifically, past climatic events may have limited colonization in climatically heterogeneous environments. To investigate this, we performed species distribution modelling (SDM). We evaluated the potential range of the three study species under present conditions and projected it to last interglacial (LIG, c. 120–140 kya), last glacial maximum (LGM, c. 22 kya) and mid-Holocene (MH, c. 6 kya) conditions. We employed the maximum entropy algorithm, as implemented in MAXENT v3.4 (Phillips, Anderson, & Schapire, 2006). The methods described in Blanco-Pastor et al. (2013) were used, with some modifications. The study area encompassed Sierra Nevada and surrounding regions (latitude 36.5 to 37.5°N, longitude 2 to 4°W).

We conducted two sets of analyses. In the first set, we used bioclimatic variables obtained from the widely used WORLDCLIM 1.4 database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) for current and past conditions. This included LIG layers from Otto-Bliesner, Marshall, Overpeck, Miller, and Hu (2006) and the most recent versions of MH and LGM layers, based on the CMIP5 project (three global climate models (GCMs): CCSM4, MIROC-ESM and MPI-ESM-P; http://www.worldclim.org/paleo-climate1). For comparison, we also used a previous version of LGM layers based on the PMIP2 project (two GCMs: CCSM and MIROC) that was already employed by Blanco-Pastor et al. (2013) in their analysis of *L. glacialis* (http://worldclim.org/past). Resolution was 30″ for current, LIG and MH layers, and 2.5′ for LGM layers. To avoid collinearity among bioclimatic variables, we excluded those displaying a high correlation coefficient with other variables ($|r| > 0.75$) in the study area. In addition to bioclimatic variables, we included a categorical lithological variable (M. Fernández-Mazuecos and B.J. Glover, unpublished) derived from the Lithostratigraphic Map of Spain (IGME 2006) and assumed to be constant through time. As a result, we used a final set of six variables: bio3 (isothermality), bio5 (maximum temperature of warmest month), bio6 (minimum temperature of coldest month), bio12 (annual precipitation), bio15 (precipitation seasonality) and lithology. The species occurrence data set included 103 georeferenced individuals of *L. glacialis*, 60 of *L. nevadensis* and 11 of *C. glareosum* obtained during our fieldtrips in July 2009/2010 (Supporting Information Tables S1–S3). After excluding data points occurring within the same pixel of environmental layers, a total of 24 occurrences of *L. glacialis*, 25 of *L. nevadensis* and 11 of *C. glareosum* were analysed. Of these, 80% were used for model training and 20% for model evaluation. The "fade by clamping" option was activated to avoid overprediction of suitability under environmental conditions outside the training range. For each species, ten subsample replicates were run. When more than one GCM was available for a time period (LGM, MH), an average model was calculated. The logistic output was converted to presence–absence using the maximum training sensitivity plus specificity logistic threshold.

In the second set of analyses, we used bioclimatic variables obtained from the recently published CHELSA 1.2 database (Karger et al., 2017) for current (http://chelsa-climate.org/downloads/) and LGM (PMIP3; http://chelsa-climate.org/last-glacial-maximum-climate/) conditions at a resolution of 30″. A higher predictive power of CHELSA climate data compared to WORLDCLIM data, particularly in mountain regions, has been suggested (Bobrowski & Udo, 2017; Kalan, Ivovic, Glasnovic, & Buzan, 2017). The LGM layer available in CHELSA is based on the PMIP3 project under the CCSM4 global climate model. To avoid collinearity, the methods described above were applied, resulting in a set of seven variables that included the six variables used in WorldClim-based analyses plus bio17 (precipitation of driest quarter). All other methodological details for model building and projection to the LGM followed those described above for WorldClim-based analyses.

3 | RESULTS

3.1 | Haplotype networks

Plastid DNA haplotypes and haplotype lineages showed no strong geographical structure for any of the three species (Figure 2). In *L. glacialis* (Figure 2a), we detected 10 haplotypes (haplotypes 2–11). Haplotype 1, representing the outgroup species *L. verticillata*, was not present in *L. glacialis* populations. The internal haplotypes 2 and 4 were widely distributed across populations. Haplotypes 5, 6, 8, 9, 10 and 11 were exclusive to single populations. In *L. nevadensis* (Figure 2b), we detected six haplotypes. The internal haplotype 1 was widely distributed across populations and shared with the outgroup species (*L. amoi*). Haplotypes 3, 4, and 6 were exclusive to single populations. In *C. glareosum* (Figure 2c), we detected 11 haplotypes. Haplotype 1 was present in three populations and was shared with the outgroup species (*C. villosum*). The internal haplotype 2 was widely distributed across populations. Haplotypes 5, 7, 8, 9, 10 and 11 were exclusive to single populations.

3.2 | Genetic diversity and correlation analyses

Genetic diversity analyses and interpolated raster layers (Supporting Information Figure S2) showed similar spatial patterns across diversity indices within species. Genetic diversity was heterogeneous across the landscape, with the absence of latitudinal or longitudinal diversity gradients but a patchy distribution of high-diversity values (Supporting Information Figure S2). This pattern was observed in the three species.

Pairwise correlation values are shown in Figure 3 and Supporting Information Table S4. We found high positive correlation values among different cpDNA genetic diversity indices within each species ($r > 0.88$; $p < 0.05$). Moderate positive correlation values were found between diversity indices of different species from the same genus (*L. glacialis* and *L. nevadensis*; $0.18 < r < 0.47$; $p < 0.05$), particularly when the haplotype diversity index was used ($r = 0.46$). We also obtained moderate negative correlation values ($-0.10 < r < -0.47$; $p < 0.05$) between diversity indices of *C. glareosum* and those of *L. glacialis* (cpDNA) and *L. nevadensis*. We found significant positive correlation values between topographic variables and diversity indices of the two *Linaria* species ($0.03 < r < 0.1$; $p < 0.05$). In contrast, we found significant negative correlation values between topographic variables and diversity indices of *C. glareosum* ($-0.07 < r < -0.04$; $p < 0.05$).

3.3 | Neutrality/demography analyses

Results of neutrality tests can be found in Table 1. We observed significant negative values of the Tajima's *D* statistic for *C. glareosum* and *L. nevadensis*. These results indicate the presence of an excess of low-frequency alleles typical of positive selection or recent population expansion processes. We also observed significant negative values of the Fu and Li's *D* and *F* statistics for *C. glareosum*. This also suggests processes of long-term balancing selection or recent population expansion. Tajima's *D* and Fu and Li's *D* and *F* statistics did not identify any departures from neutrality or demographic instability for *L. glacialis*. The results of the mismatch distributions are shown in Supporting Information Figure S3. The observed mismatch distribution for *L. glacialis* fitted better to the distribution expected under the growth-decline model. The distributions for *L. nevadensis* and *C. glareosum* fitted equally well to the constant size and the growth–decline models.

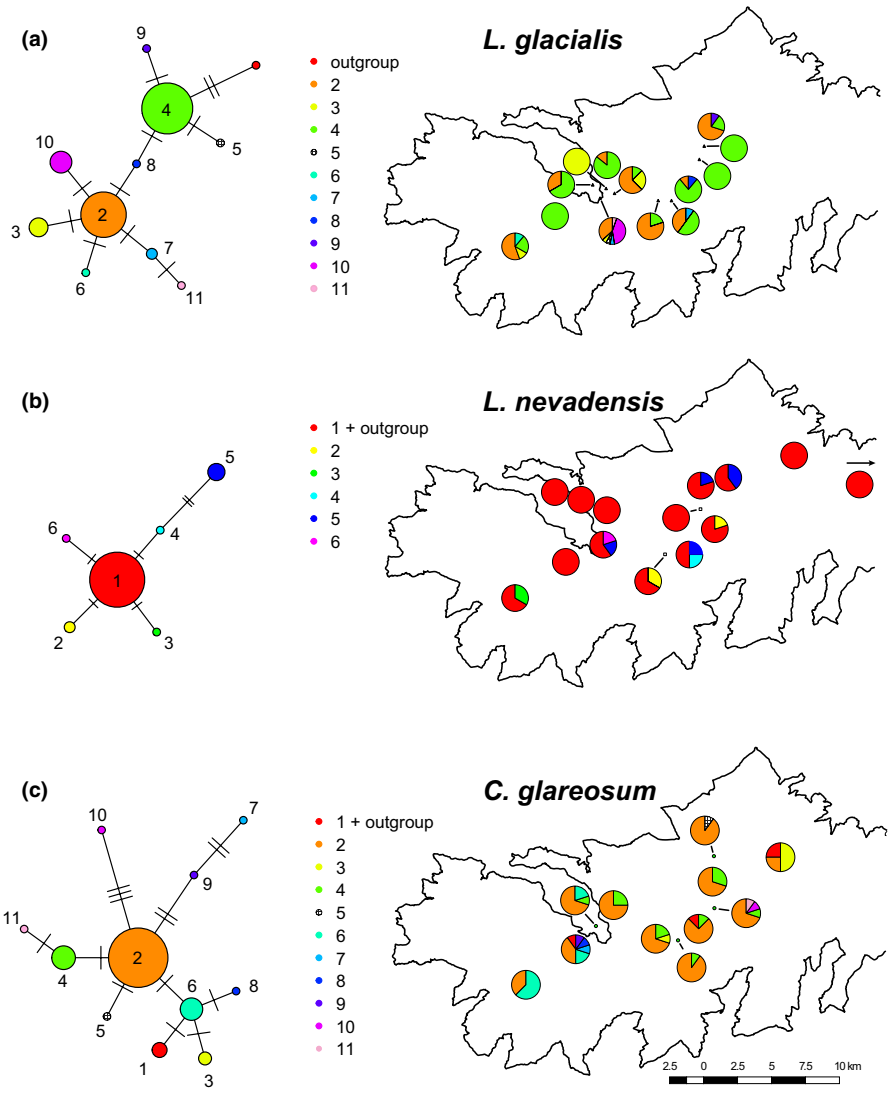

FIGURE 2 CpDNA haplotype networks for *Linaria glacialis*, *Linaria nevadensis* and *Chaenorhinum glareosum*, and spatial distribution of haplotypes in the Sierra Nevada National Park. Each haplotype is represented by both a number and a colour. Areas of circles in haplotype networks are proportional to the number of individuals displaying each haplotype. In the *L. glacialis* network, haplotype 1 (red) represents the outgroup species (*L. verticillata*). In the other two networks, haplotype 1 is shared between the outgroup (*L. amoi* for *L. nevadensis* and *C. villosum* for *C. glareosum*) and the study species [Colour figure can be viewed at wileyonlinelibrary.com]

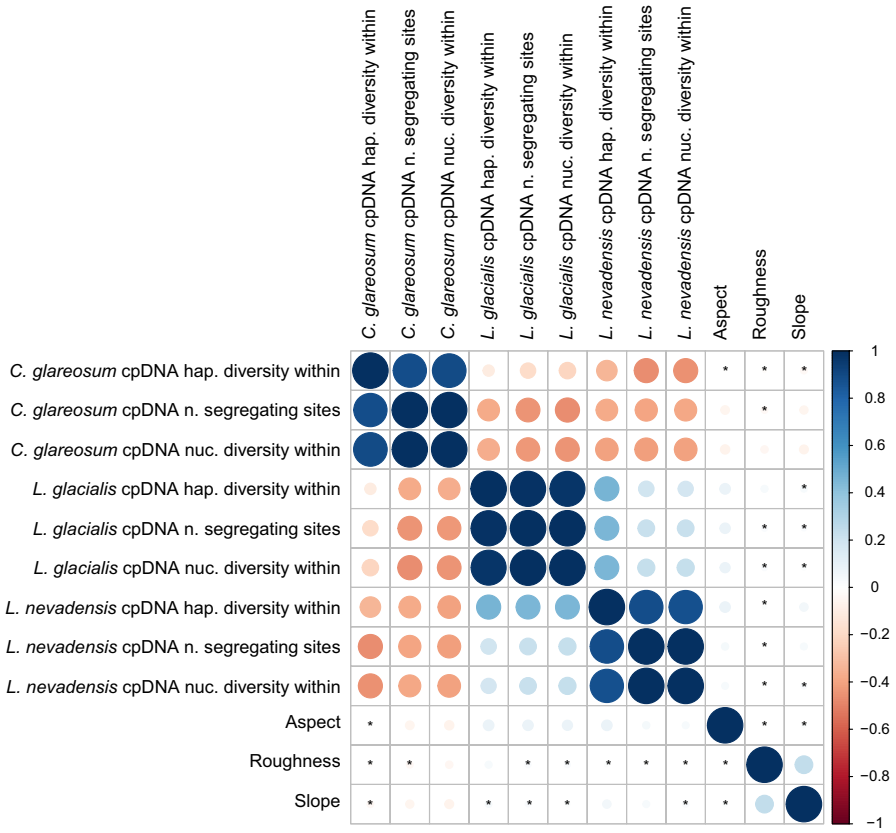

FIGURE 3 Correlation table displaying results of pairwise correlation tests among different species, genetic indices and topographic variables. Positive Pearson's correlation (*r*) values are represented in blue, and negative correlation values are represented in red. *, Nonsignificant (*p*-value > 0.05) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Neutrality/demography tests carried out using cpDNA data sets of *Linaria glacialis*, *Linaria nevadensis* and *Chaenorhinum glareosum*

	Tajima's *D*	Fu and Li's *D*	Fu and Li's *F*
L. glacialis[a]	5.40×10^{-2} Ns	−0.579 Ns	−0.432 Ns
L. nevadensis	−1.433 (*p*-value = 0.04)	−0.655 Ns	−1.008 Ns
C. glareosum	−1.877 (*p*-value = 0.002)	−3.079 (*p*-value = 0.006)	−3.159 (*p*-value = 0.003)

Notes. Ns, nonsignificant (*p*-value > 0.05).
[a]See Blanco-Pastor et al. (2013).

The BSPs (Figure 4) show similar effective population sizes (Ne) at present for the three species (2×10^5–5×10^5, median values). All of them showed a general trend of Ne increase/stabilization in the late Pleistocene, particularly since the last glacial maximum (LGM; c. 21 kya, Würm glaciation).

3.4 | Bayesian phylogeographical analyses

Discrete phylogeographical analyses estimated area B as the most likely ancestral location (i.e., location for the most recent common ancestor of all ingroup samples) for *L. glacialis* (PP = 0.74; Figure 5a). Diffusion routes from B to A and C received the highest support according to BF values (BF > 10). Area D was estimated as the most likely ancestral location for both *L. nevadensis* (PP = 0.63; Figure 5b) and *C. glareosum* (PP = 0.72; Figure 5c). Diffusion routes from D to B and C received high support for both species (BF > 10; Figure 5b,c). In addition, diffusion routes from D to A received high support for *C. glareosum*.

3.5 | Species distribution modelling

Current potential distributions inferred by distribution models essentially matched the known distribution ranges of the three species for both WorldClim- and CHELSA-based analyses, with small differences (Figure 6). Accordingly, the potential range of *L. glacialis* is restricted to the highest peaks of Sierra Nevada, while *L. nevadensis* inhabits a slightly wider altitudinal range and *C. glareosum* occupies an intermediate range. In WorldClim-based analyses, the environmental variables with the highest percent contributions to the models were bio6 for *L. glacialis* (76.3%) and bio12 for *L. nevadensis* (60.1%) and *C. glareosum* (81.3%). The average AUC for the replicate runs was 0.998 for *L. glacialis*, 0.994 for *L. nevadensis* and 0.997 for *C. glareosum*. In CHELSA-based analyses, the variables with the highest percent contributions were bio3 for *L. glacialis* (83.1%) and *L. nevadensis* (44.1%), and bio5 for *C. glareosum* (77.5%). The average AUC was 0.997 for *L. glacialis*, 0.994 for *L. nevadensis* and 0.994 for *C. glareosum*.

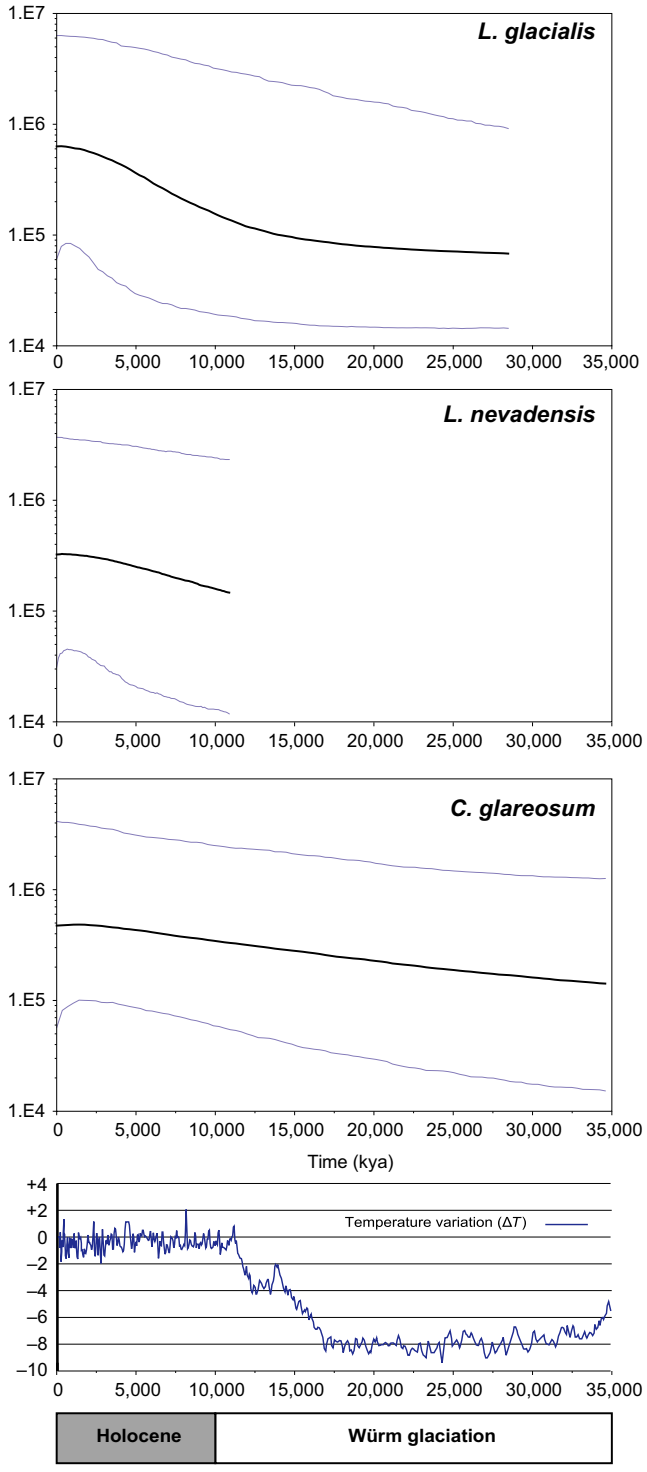

FIGURE 4 Bayesian skyline plots (BSPs) representing the demographic history of *Linaria glacialis*, *Linaria nevadensis* and *Chaenorhinum glareosum* in the past c.28, c.10 and c.35 thousand years, respectively, in the alpine areas of Sierra Nevada (Spain). The *X*-axis represents time; the *Y*-axis represents effective population size estimated from cpDNA data sets. The bottom graph represents temperature variation measured from the Vostok (Antarctica) ice core, modified from Petit et al. (1999) [Colour figure can be viewed at wileyonlinelibrary.com]

For *L. glacialis* and *C. glareosum*, potential distributions revealed by projections to the LIG and MH under WorldClim data were broader than the current ones (Figure 6). For the LGM, CMIP5 (WorldClim) layers and

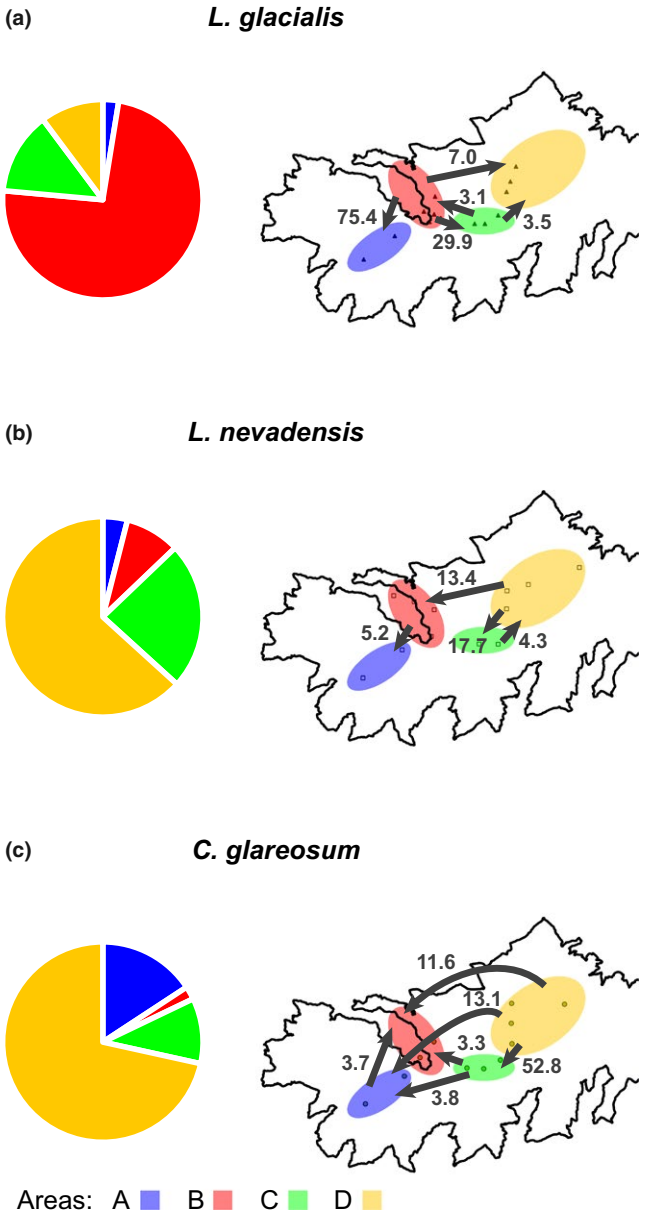

FIGURE 5 Results of Bayesian discrete phylogeographical analyses (DPAs). Analyses are based on cpDNA sequences of *Linaria glacialis*, *Linaria nevadensis* and *Chaenorhinum glareosum*. Arrows represent spread routes supported by Bayes factors (BF > 3). Bayes factor values are shown. Pie charts represent probabilities of ancestral location [Colour figure can be viewed at wileyonlinelibrary.com]

PMIP3 (CHELSA) layers recovered no potential distribution of these two species, while PMIP2 (WorldClim) layers recovered relatively broad distributions. For *L. nevadensis*, projections displayed little variation in the extent of potential distribution through time in WorldClim-based analyses. In the CHELSA-based analysis, projection to the LGM under PMIP3 data displayed a widespread distribution, even including lowlands surrounding Sierra Nevada. To visualize the effect of single variables on the LGM projections, we compared variables used under different models. Our analyses suggest that the joint effect of several variables, rather than a single variable, should be invoked to explain the anomalous projections obtained with the WorldClim CMIP5 data set and the CHELSA-PMIP3

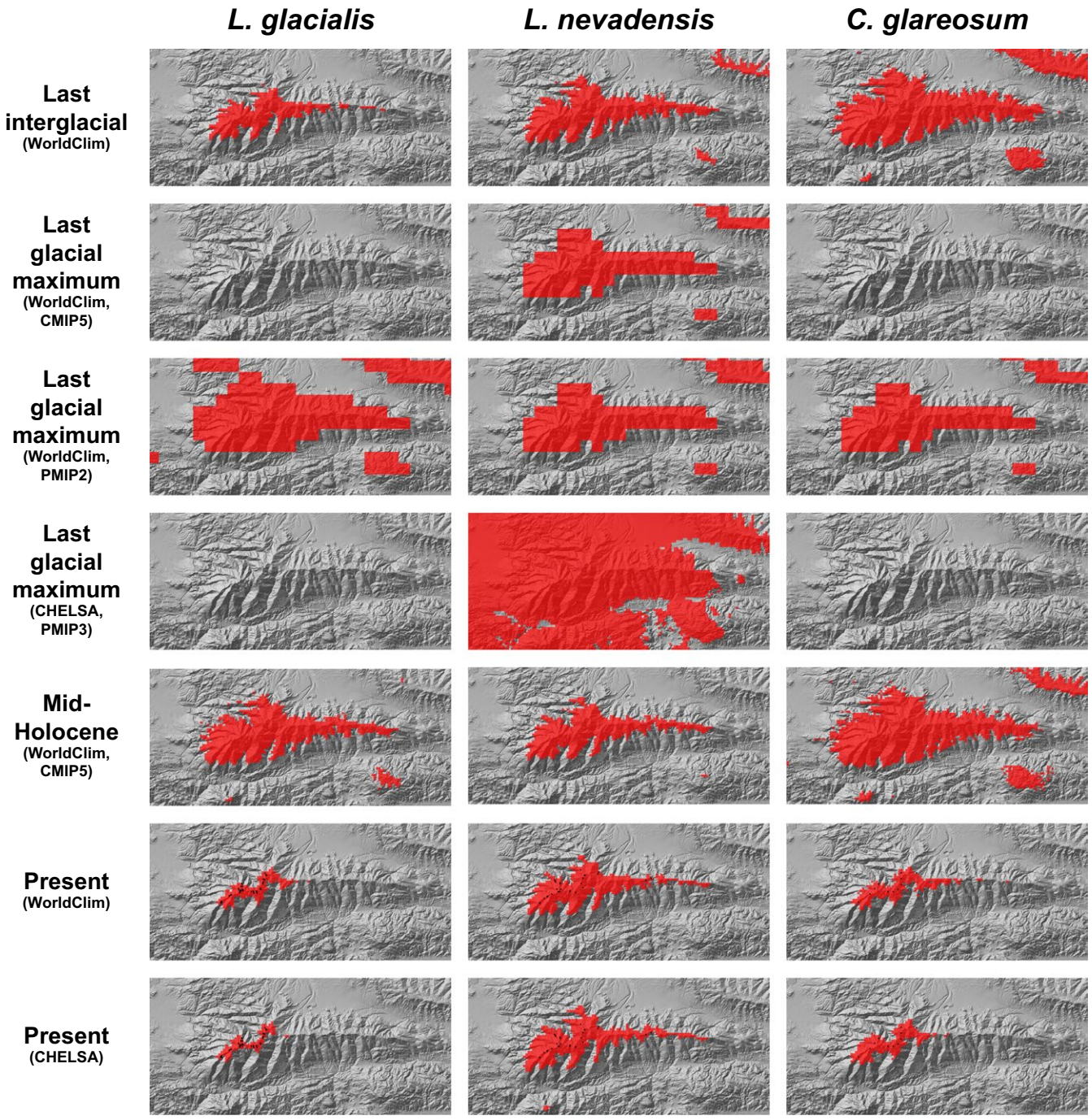

FIGURE 6 Results of species distribution modelling for *Linaria glacialis*, *Linaria nevadensis* and *Chaenorhinum glareosum* using the maximum entropy algorithm, as implemented in MAXENT. Analyses are based on WorldClim and CHELSA variables, and projected to past conditions: last interglacial (LIG, c. 120–140 kya), last glacial maximum (LGM, c. 21 kya) and mid-Holocene (MH, c. 6 kya). The presence/absence was estimated using the maximum training sensitivity plus specificity logistic threshold [Colour figure can be viewed at wileyonlinelibrary.com]

data set (i.e., no suitable habitat for *L. glacialis* and *C. glareosum* during the LGM; see Supporting Information Figure S4).

4 | DISCUSSION

Climate change will cause severe effects on biodiversity of Mediterranean mountain biomes. Given the high degree of endemism on Mediterranean summits, special conservation efforts must be focused on these particular habitats. This is especially true for small mountain ranges, such as Sierra Nevada, where a high number of threatened species are found. Specifically, the flora of Sierra Nevada includes 90 taxa that are threatened (or extinct) in the mountain range (IUCN categories VU, EN, CR and EX), of which 35 are endemic (Blanca et al., 1998). To set conservation priorities in this exceptionally fragile and rich environment, it is essential to understand

how species responded to past environmental constraints, and the mechanisms that led to the current distribution of genetic diversity.

4.1 | Historical factors cannot explain the spatial pattern of genetic diversity

In our study, we observed a positive correlation between the distribution of genetic diversity of two *Linaria* species (*L. glacialis* and *L. nevadensis*). In contrast, we observed negative correlation values when comparing the distribution of genetic diversity of these two *Linaria* species with that of one species of the related genus *Chaenorhinum* (*C. glareosum*; Figure 3). Fu and Li's *D* and *F* and Tajima's *D* statistics (Table 1), mismatch distributions (Supporting Information Figure S3) and BSPs (Figure 4) strongly suggest that population sizes have increased for all three species over the last 21 kyr. This suggests that the three investigated species responded similarly to large-scale environmental changes of the last millennia. As a consequence, historical demographic events are unlikely to be responsible for the uncoupled spatial patterns of genetic diversity between the two *Linaria* species and *C. glareosum*. Older demographic events not captured by our cpDNA data might explain these differences (e.g., an older bottleneck of *C. glareosum* caused by population extinctions in the central summits of Sierra Nevada), but this is unlikely given that, under population size increase, c. 35 kyr (Figure 4) should be enough time for gene flow to homogenize spatial patterns of genetic diversity at such small spatial scales. In addition, differences in the way populations expanded (e.g., differences in seed dispersal ability among species) might have been relevant for the generation of spatial patterns of genetic diversity. Although both, the wingless seeds of *C. glareosum* and the winged seeds of *Linaria*, can disperse long distances (Blanco-Pastor & Vargas, 2013; Fernández-Mazuecos & Vargas, 2011), further research on seed dispersal capacity of these species at small spatial scales may be necessary to reinforce our conclusions.

We consider that projected LGM distributions based on WorldClim CMIP5 and CHELSA variables are unlikely given the apparent absence (in *L. glacialis* and *C. glareosum*) or excess (in *L. nevadensis* for CHELSA results) of potential area recovered (Figure 6). Extent of glaciers in Sierra Nevada during the LGM cannot explain an absence of *L. glacialis* and *C. glareosum* during that period. This is because the mountain range was covered with glaciers above c. 2,500 m only, while large areas remained free of permanent ice (Gómez-Ortiz, Schulte, & Salvador-Franch, 1996). More important, molecular dating estimates, obtained from BSP analyses, disagree with an absence of *L. glacialis* and *C. glareosum* in Sierra Nevada during the LGM. Instead, BSP analyses indicate population expansion for these species during the LGM, which agrees with projected LGM distributions based on WorldClim PMIP2 variables (i.e., broad distributions across Sierra Nevada). Climate layers based on alternative climate modelling projects are highly variable for mountainous regions, and especially for the alpine belt, because of the strong influence of topographic factors. The key role of topography in altering climate projections to the LGM has been already documented (Pausata, Li, Wettstein, Kageyama, & Nisancioglu, 2011; Ullman, Legrande, Carlson, Anslow, & Licciardi, 2014). Different handling of ice sheet topography in the PMIP2, PMIP3 and CMIP5 projects (Abe-Ouchi et al., 2015) may be responsible for the differences observed here.

Overall, Bayesian skyline plots and SDM analyses point to a limited effect of range dynamics on demographic trends of the three study species. Initially, the significant increase of Ne throughout the Holocene (Figure 4) was somehow unexpected, given the SDM inference of range contraction to high altitudes spanning from the LGM (according to PMIP2 variables) to present time (Figure 6). However, range contraction of cold-adapted species to high altitude locations does not have to be accompanied by a decrease in Ne. In our study, WorldClim PMIP2 results can fit with BSP results if we consider that a reduction in range size since the LGM was not accompanied by a reduction, but by an increase in genetic diversity (Ne), a pattern that was already found and discussed in detail for *L. glacialis* (Blanco-Pastor et al., 2013). In short, this pattern is favoured by high gene flow rates among demes. Indeed, the observed unstructured distribution of haplotypes across the landscape (Figure 2) and the DPA analyses (Figure 5) of the three species suggest high dispersal rates among noncontiguous areas in Sierra Nevada for all three species.

Finally, diffusion patterns of the three species cannot explain the contrasting spatial patterns of genetic diversity found between the two *Linaria* species and *C. glareosum*. Westward diffusion is predominant for *L. nevadensis* and *C. glareosum*, while *L. glacialis* displays an alternative pattern with an ancestral area differing from that of the other two species. This result suggests that similar spatial patterns of genetic diversity have arisen in *L. glacialis* and *L. nevadensis* despite different diffusion patterns.

4.2 | Topography as a key factor to explain the distribution of genetic diversity

Neither dispersal syndrome, nor demographic trends (Figure 4), nor dispersal routes (Figure 5), nor ancestral range dynamics (Figure 6), can explain the differences in spatial patterns of genetic diversity between the two *Linaria* species and *C. glareosum*. This suggests that factors other than historical large-scale dispersal constraints should be invoked to explain the observed complementary patterns. The two *Linaria* species are presumably not interfertile, as hybrids have not been found in the field despite individuals of the two species being commonly found inhabiting the same localities. Therefore, their similar spatial patterns of genetic diversity can hardly be attributed to interspecific hybridization. We inferred an increase in genetic diversity (effective population size) during range contraction and upward migration for *L. glacialis* and *C. glareosum*, and to a lesser extent for *L. nevadensis* (range contraction was less evident in this species), suggesting that the highest altitudes of Sierra Nevada provide highly favourable habitats for the three species. However, microhabitat features in the small area of the alpine belt of Sierra Nevada may provide different opportunities for the survival of the two genera. It has been observed that *L. glacialis* and *L. nevadensis* are usually more abundant on rocky soils (Sáez & Bernal, 2009)

while *C. glareosum* prefers rock fissures and less developed soils (Benedí & Güemes, 2009). Favourable microhabitat features may have enabled maintenance of genetic diversity in the same areas for the two *Linaria* species. Still, these particular small-scale environmental conditions may not be equally favourable for *C. glareosum* despite its close relationship with *Linaria*. This is supported by the contrasting correlation values between diversity indices and topographic variables found in the two *Linaria* species and *C. glareosum* (Figure 3). These differences are more evident for the "aspect" variable, representing the azimuth that slopes are facing. Plant populations predominantly inhabiting shaded rock fissures, such as those of *C. glareosum*, may require higher levels of direct sunshine for their survival and persistence. Contrarily, more exposed populations, such as those of the two *Linaria* species, may be favoured on north-facing slopes, thus avoiding episodes of heat stress during summer. This may partly explain the observed spatial pattern of genetic diversity in our study system.

Topography is a key determinant of climatic variation at small spatial scales (from microsites of a few square metres to hundreds of square kilometres), especially in treeless areas such as alpine regions (Graae et al., 2018; Scherrer & Körner, 2011). We point to an association between topographic microniche variation and the spatial distribution of genetic diversity of plant species in this heterogeneous alpine landscape. The observed spatial structure of cpDNA diversity is tightly linked to plant colonization success (Crawford & Whitney, 2010; Hughes et al., 2008). In our system, high gene flow across Sierra Nevada summits would tend to homogenize the spatial patterns of genetic diversity, but microhabitat preferences would prevent a full homogenization of genetic diversity patterns across the species ranges. The three species inhabit the same areas and have similar dispersal syndromes, but these microhabitat preferences may have been important for the differential establishment of seeds under the harsh environmental conditions of the alpine belt of Sierra Nevada.

4.3 | Topographically complex areas: a priority for conservation in alpine environments

Mediterranean mountains are important biodiversity hotspots because they allowed altitudinal shifts or the in situ persistence of species during past climate changes (Beug, 1975; Médail & Diadema, 2009). During Quaternary climatic cycles, the Spanish Sierra Nevada mountains were glaciated only above c. 2,500 m, and large areas remained free of permanent ice (Gómez-Ortiz et al., 1996), favouring the persistence and diversification of local alpine plant lineages (Kropf et al., 2006). Still, the alpine ecosystem of Sierra Nevada consists of a limited area. Specifically, the uppermost vegetation belt (alpine or cryoromediterranean belt) has an extension of 3,875 ha and harbours at least 185 plant taxa (Fernández Calzado & Molero, 2011). The diversification and long-term survival of this large number of species in this remarkably small environment may have been possible thanks to the locally high diversity of ecological microniches and topographical conditions, notably: (a) sheltered and relatively humid gullies vs. exposed and relatively dry ridges, (b) south- vs. north-facing slopes and (c) different altitudinal locations (Médail & Diadema, 2009). The two *Linaria* species may have different "large-scale" niches (e.g., *L. nevadensis* inhabits areas at lower altitude and variables with the highest contribution to distribution models are different for each species) but similar microniches, which allowed a concentration of genetic diversity in the same areas for both species. We suggest that climate variables might be appropriate factors to explain the distribution of species, while topographic features should be considered to explain the distribution of genetic diversity. We also suggest that microniche partitioning and maintenance of high genetic diversity in these microhabitats may have been linked to species survival and diversification during Quaternary climate changes. In particular, this may have been true for the two *Linaria* and one *Chaenorhinum* species studied here during the warming period from the LGM (21 kya) to the present, including the last decades. This conclusion lies within the theoretical framework developed by Graae et al. (2018), who hypothesized that populations and communities in topographically complex landscapes should be more resistant and resilient to climate change.

5 | CONCLUDING REMARKS

In this study, we used comparative phylogeography to evaluate historical factors responsible for differences in the distribution of genetic diversity among closely related species. Our results provide insights into the processes responsible for the generation and maintenance of biodiversity in the remarkably species-diverse high mountain hot spot of Sierra Nevada. We highlight the important role of microhabitat heterogeneity for the maintenance of distinct phylogenetic lineages, species and genetic diversity in high mountain biodiversity hotspots. We also propose that areas with high topographical diversity should be especially considered for conservation in Mediterranean summits given the expected fast temperature increase in the near future.

ACKNOWLEDGEMENTS

We wish to thank Javier Valverde, Jesús Gómez, Miguel Ángel Rodríguez-Gironés, Concepción Ornosa, Ana Otero, Javier Freijanes, Daniel Romero, Ignacio Flores and Antonio Gómez for field work assistance. Emilio Cano, Fátima Durán, Guillermo Sanjuanbenito and Gemma Andreu provided laboratory work assistance. We also thank three anonymous reviewers for their constructive comments that improved the quality of this manuscript. This study was supported by a research project of the Spanish Ministry for Environment, and Rural and Marine Affairs (MARM; reference 005/2008). J.L.B-P. was supported by a JAEpre fellowship (Spanish National Research Council, CSIC). M.F-M. was supported by a FPU fellowship (Spanish Ministry of Education, reference AP2007-01841) and a Juan de la Cierva fellowship (Spanish Ministry of Economy and Competitivity,

reference IJCI-2015-23459). A.J.C. was supported by a FPU fellowship (Spanish Ministry of Education, reference FPU16/05681).

DATA ACCESSIBILITY

Newly generated sequence data is stored in GenBank under the accession numbers: MG962547–MG962858.

ORCID

José Luis Blanco-Pastor http://orcid.org/0000-0002-7708-1342

REFERENCES

Abe-Ouchi, A., Saito, F., Kageyama, M., Braconnot, P., Harrison, S. P., Lambeck, K., … Takahashi, K. (2015). Ice-sheet configuration in the CMIP5/PMIP3 Last Glacial Maximum experiments. *Geoscientific Model Development*, *8*, 3621–3637. https://doi.org/10.5194/gmd-8-3621-2015

Alvarez, N., Thiel-Egenter, C., Tribsch, A., Holderegger, R., Manel, S., Schönswetter, P., … Gugerli, F. (2009). History or ecology? Substrate type as a major driver of patial genetic structure in Alpine plants. *Ecology Letters*, *12*, 632–640. https://doi.org/10.1111/j.1461-0248.2009.01312.x

Avise, J. C. (1987). Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, *18*, 489–522. https://doi.org/10.1146/annurev.es.18.110187.002421

Avise, J. C. (2009). Phylogeography: Retrospect and prospect. *Journal of Biogeography*, *36*, 3–15. https://doi.org/10.1111/j.1365-2699.2008.02032.x

Benedí, C., & Güemes, J. (2009). *Chaenorhinum* (DC.) Rchb. *Flora Iberica*, *13*, 167–198.

Bermingham, E., & Moritz, C. (1998). Comparative phylogeography: Concepts and applications. *Molecular Ecology*, *7*, 367–369. https://doi.org/10.1046/j.1365-294x.1998.00424.x

Beug, H. J. (1975). Changes of climate and vegetation belts in the mountains of Mediterranean Europe during the Holocene. *Bulletin of Geology*, *10*, 101–110.

Bielejec, F., Baele, G., Vrancken, B., Suchard, M. A., Rambaut, A., & Lemey, P. (2016). Sprea D3: Interactive visualization of spatiotemporal history and trait evolutionary processes. *Molecular Biology and Evolution*, *33*, 2167–2169. https://doi.org/10.1093/molbev/msw082

Blanca, G., Cueto, M., Martinez-Lirola, M. J., Molero-Mesa, J., Martínez-Lirola, M. J., & Molero-Mesa, J. (1998). Threatened vascular flora of Sierra Nevada (southern Spain). *Biological Conservation*, *85*, 269–285. https://doi.org/10.1016/S0006-3207(97)00169-9

Blanco-Pastor, J. L. L., Fernández-Mazuecos, M., & Vargas, P. (2013). Past and future demographic dynamics of alpine species: Limited genetic consequences despite dramatic range contraction in a plant from the Spanish Sierra Nevada. *Molecular Ecology*, *22*, 4177–4195. https://doi.org/10.1111/mec.12383

Blanco-Pastor, J. L. L., & Vargas, P. (2013). Autecological traits determined two evolutionary strategies in Mediterranean plants during the Quaternary: Low differentiation and range expansion versus geographical speciation in *Linaria*. *Molecular Ecology*, *22*, 5651–5668. https://doi.org/10.1111/mec.12518

Blanco-Pastor, J. L., Vargas, P., & Pfeil, B. E. (2012). Coalescent simulations reveal hybridization and incomplete lineage sorting in Mediterranean *Linaria*. *PLoS ONE*, *7*, e39089. https://doi.org/10.1371/journal.pone.0039089

Bobrowski, M., & Udo, S. (2017). Why input matters: Selection of climate data sets for modelling the potential distribution of a treeline species in the Himalayan region. *Ecological Modelling*, *359*, 92–102.

Bos, D. H., & Sites, J. W. (2001). Phylogeography and conservation genetics of the Columbia spotted frog (*Rana luteiventris*; Amphibia, Ranidae). *Molecular Ecology*, *10*, 1499–1513. https://doi.org/10.1046/j.1365-294X.2001.01295.x

Cañadas, E. M., Fenu, G., Peñas, J., Lorite, J., Mattana, E., & Bacchetta, G. (2014). Hotspots within hotspots: Endemic plant richness, environmental drivers, and implications for conservation. *Biological Conservation*, *170*, 282–291. https://doi.org/10.1016/j.biocon.2013.12.007

Corriveau, J. L., & Coleman, A. W. (1988). Rapid screening method to detect potential biparental inheritance of plastid DNA and results for over 200 angiosperm species. *American Journal of Botany*, *75*, 1443–1458. https://doi.org/10.1002/j.1537-2197.1988.tb11219.x

Crawford, K. M., & Whitney, K. D. (2010). Population genetic diversity influences colonization success. *Molecular Ecology*, *19*, 1253–1263. https://doi.org/10.1111/j.1365-294X.2010.04550.x

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods*, *9*, 772. https://doi.org/10.1038/nmeth.2109

De Maio, N., Wu, C. H., O'Reilly, K. M., & Wilson, D. (2015). New routes to phylogeography: A Bayesian structured coalescent approximation. *PLoS Genetics*, *11*, 1–22.

Drummond, A. J., & Bouckaert, R. R. (2015). *Bayesian evolutionary analysis with BEAST*. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9781139095112

Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, *7*, 214. https://doi.org/10.1186/1471-2148-7-214

Drummond, A. J., Rambaut, A., Shapiro, B., & Pybus, O. G. (2005). Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution*, *22*, 1185–1192. https://doi.org/10.1093/molbev/msi103

Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., AraúJo, M. B., … Guisan, A. (2011). 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, *17*, 2330–2341. https://doi.org/10.1111/j.1365-2486.2010.02393.x

Fernández Calzado, M. R., & Molero, Mesa J. (2011). The cartography of vegetation in the cryoromediterranean belt of Sierra Nevada: A tool for biodiversity conservation. *LAZAROA*, *32*, 101–115.

Fernández-Mazuecos, M., & Vargas, P. (2011). Historical isolation versus recent long-distance connections between Europe and Africa in bifid toadflaxes (*Linaria* sect. *Versicolores*). *PLoS ONE*, *6*, e22234. https://doi.org/10.1371/journal.pone.0022234

Fisher, R. A. (1930). *The genetical theory of natural selection*. Oxford, UK: Oxford University Press. https://doi.org/10.5962/bhl.title.27468

Fu, Y. X., & Li, W. H. (1993). Statistical tests of neutrality of mutations. *Genetics*, *133*, 693–709.

García-Fernández, A., Iriondo, J. M., Escudero, A., Aguilar, J. F., & Feliner, G. N. (2013). Genetic patterns of habitat fragmentation and past climate-change effects in the Mediterranean high-mountain plant *Armeria caespitosa* (Plumbaginaceae). *American Journal of Botany*, *100*, 1641–1650. https://doi.org/10.3732/ajb.1200653

Gómez-Ortiz, A., Schulte, L., & Salvador-Franch, F. (1996). Contribución al conocimiento de la deglaciación reciente y morfología asociada del Corral del Veleta (Sierra Nevada). *Cuadernos do Laboratorio Xeolóxico de Laxe*, *21*, 543–558.

González-Sampériz, P., Leroy, S. A. G., Carrión, J. S., Fernández, S., García-Antón, M., Gil-García, M. J., … Figueiral, I. (2010). Steppes, savannahs, forests and phytodiversity reservoirs during the Pleistocene in the Iberian Peninsula. *Review of Palaeobotany and Palynology*, *162*, 427–457. https://doi.org/10.1016/j.revpalbo.2010.03.009

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L. J. L., … Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, *2*, 111–115. https://doi.org/10.1038/nclimate1329

Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J. C., Hylander, K., … Lenoir, J. (2018). Stay or go – How topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics*, *30*, 41–50. https://doi.org/10.1016/j.ppees.2017.09.008

Gugerli, F., Englisch, T., Niklfeld, H., Tribsch, A., Mirek, Z., Ronikier, M., … Taberlet, P. (2008). Relationships among levels of biodiversity and the relevance of intraspecific diversity in conservation – A project synopsis. *Perspectives in Plant Ecology, Evolution and Systematics*, *10*, 259–281. https://doi.org/10.1016/j.ppees.2008.07.001

Gugerli, F., & Holderegger, R. (2001). Nunatak survival, tabula rasa and the influence of the Pleistocene ice-ages on plant evolution in mountain areas. *Trends in Plant Science*, *6*, 397–398. https://doi.org/10.1016/S1360-1385(01)02053-2

Guzmán, B., Gómez, J. M., & Vargas, P. (2015). Bees and evolution of occluded corollas in snapdragons and relatives (Antirrhineae). *Perspectives in Plant Ecology, Evolution and Systematics*, *17*, 467–475. https://doi.org/10.1016/j.ppees.2015.07.003

Hamming, R. W. (1950). Error detecting and error correcting codes. *Bell Labs Technical Journal*, *29*, 147–160. https://doi.org/10.1002/j.1538-7305.1950.tb00463.x

Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, *58*, 247–276. https://doi.org/10.1111/j.1095-8312.1996.tb01434.x

Hewitt, G. (2000). The genetic legacy of the quaternary ice ages. *Nature*, *405*, 907–913. https://doi.org/10.1038/35016000

Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *359*, 183–195. https://doi.org/10.1098/rstb.2003.1388

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. https://doi.org/10.1002/(ISSN)1097-0088

Hijmans, R. J., & van Etten, J. (2014). *raster: Geographic data analysis and modeling*. R Packag. version. 2:15.

Holland, B. S., & Hadfield, M. G. (2002). Islands within an island: Phylogeography and conservation genetics of the endangered Hawaiian tree snail *Achatinella mustelina*. *Molecular Ecology*, *11*, 365–375. https://doi.org/10.1046/j.1365-294X.2002.01464.x

Hudson, R. R., Slatkin, M., & Maddison, W. (1992). Estimation of levels of gene flow from DNA sequence data. *Genetics*, *132*, 583–589.

Hughes, A. R., Inouye, B. D., Johnson, M. T. J., Underwood, N., & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecology Letters*, *11*, 609–623. https://doi.org/10.1111/j.1461-0248.2008.01179.x

IGME (2006). *Mapa litoestratigráfico y de permeabilidades de España 1/200.000*. Madrid, Spain: Instituto Geológico y Minero de España

Jay, F., Manel, S., Alvarez, N., Durand, E. Y., Thuiller, W., Holderegger, R., … François, O. (2012). Forecasting changes in population genetic structure of alpine plants in response to global warming. *Molecular Ecology*, *21*, 2354–2368. https://doi.org/10.1111/j.1365-294X.2012.05541.x

Kalan, K., Ivovic, V., Glasnovic, P., & Buzan, E. (2017). Presence and potential distribution of *Aedes albopictus* and *Aedes japonicus japonicus* (Diptera: Culicidae) in Slovenia. *Journal of Medical Entomology*, *54*, 1510–1518. https://doi.org/10.1093/jme/tjx150

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., … Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 170122. https://doi.org/10.1038/sdata.2017.122

Karl, S. A., Castro, A. L. F., Lopez, J. A., Charvet, P., & Burgess, G. H. (2011). Phylogeography and conservation of the bull shark (*Carcharhinus leucas*) inferred from mitochondrial and microsatellite DNA. *Conservation Genetics*, *12*, 371–382. https://doi.org/10.1007/s10592-010-0145-1

Katoh, K., Misawa, K., Kuma, K., & Miyata, T. (2002). MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, *30*, 3059–3066. https://doi.org/10.1093/nar/gkf436

Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*, *30*, 772–780. https://doi.org/10.1093/molbev/mst010

Kropf, M., Comes, H. P., & Kadereit, J. W. (2006). Long-distance dispersal vs vicariance: The origin and genetic diversity of alpine plants in the Spanish Sierra Nevada. *New Phytologist*, *172*, 169–184. https://doi.org/10.1111/j.1469-8137.2006.01795.x

Lemey, P., Rambaut, A., Drummond, A. J., & Suchard, M. A. (2009). Bayesian phylogeography finds its roots. *PLoS Computational Biology*, *5*, e1000520.

Librado, P., & Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, *25*, 1451–1452. https://doi.org/10.1093/bioinformatics/btp187

Magri, D., Vendramin, G. G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D., … De Beaulieu, J.-L. J. L. (2006). A new scenario for the Quaternary history of European beech populations: Palaeobotanical evidence and genetic consequences. *New Phytologist*, *171*, 199–221. https://doi.org/10.1111/j.1469-8137.2006.01740.x

Médail, F., & Diadema, K. (2009). Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography*, *36*, 1333–1345. https://doi.org/10.1111/j.1365-2699.2008.02051.x

Miraldo, A., Li, S., Borregaard, M. K., Flórez-Rodríguez, A., Gopalakrishnan, S., Rizvanovic, M., … Nogués-Bravo, D. (2016). An Anthropocene map of genetic diversity. *Science*, *353*, 1532–1535. https://doi.org/10.1126/science.aaf4381

Moreno, J. C. (2010). *Lista Roja de la Flora Vascular Española 2008*. Actualizacion con los datos del Adenda 2010 al Atlas y Libro Rojo de la Flora Vascular Amenazada Española. Madrid, Spain: Dirección General de Medio Natural y Política Forestal (Ministerio de Medio Ambiente, y Medio Rural y Marino, y Sociedad Española de Biología de la Conservación de Plantas).

Moritz, C., & Faith, D. P. (1998). Comparative phylogeography and the identification of genetically divergent areas for conservation. *Molecular Ecology*, *7*, 419–429. https://doi.org/10.1046/j.1365-294x.1998.00317.x

Mráz, P., Gaudeul, M., Rioux, D., Gielly, L., Choler, P., & Taberlet, P. (2007). Genetic structure of *Hypochaeris uniflora* (Asteraceae) suggests vicariance in the Carpathians and rapid post-glacial colonization of the Alps from an eastern Alpine refugium. *Journal of Biogeography*, *34*, 2100–2114. https://doi.org/10.1111/j.1365-2699.2007.01765.x

Nersting, L. G., & Arctander, P. (2001). Phylogeography and conservation of impala and greater kudu. *Molecular Ecology*, *10*, 711–719.

Nieto Feliner, G. (2014). Patterns and processes in plant phylogeography in the Mediterranean Basin. A review. *Perspectives in Plant Ecology, Evolution and Systematics*, *16*, 265–278. https://doi.org/10.1016/j.ppees.2014.07.002

Otto-Bliesner, B. L., Marshall, S. J., Overpeck, J. T., Miller, G. H., Hu, A., & Members C.L.I.P. (2006). Simulating arctic climate warmth and icefield retreat in the Last Interglaciation. *Science*, *311*, 1751–1753. https://doi.org/10.1126/science.1120808

Pachschwöll, C., García, P. E., Winkler, M., Schneeweiss, G. M., Schönswetter, P., Escobar, García P., … Schönswetter, P. (2015). Polyploidisation and geographic differentiation drive diversification in a European high mountain plant group (*Doronicum clusii* aggregate, Asteraceae). *PLoS ONE*, *10*, e0118197. https://doi.org/10.1371/journal.pone.0118197

Paradis, E. (2010). pegas: An R package for population genetics with an integrated–modular approach. *Bioinformatics*, *26*, 419–420. https://doi.org/10.1093/bioinformatics/btp696

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, *37*, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B., … Grabherr, G. (2012). Recent plant diversity changes on Europe's mountain summits. *Science*, *336*, 353–355. https://doi.org/10.1126/science.1219033

Pauli, H., Gottfried, M., & Grabherr, G. (1996). Effects of climate change on mountain ecosystems – Upward shifting of alpine plants. *World Resource Review*, *8*, 382–390.

Paun, O., SchÖnswetter, P., Winkler, M., & Tribsch, A. (2008). Historical divergence vs. contemporary gene flow: Evolutionary history of the calcicole *Ranunculus alpestris* group (Ranunculaceae) in the European Alps and the Carpathians. *Molecular Ecology*, *17*, 4263–4275. https://doi.org/10.1111/j.1365-294X.2008.03908.x

Pausata, F. S. R., Li, C., Wettstein, J. J., Kageyama, M., & Nisancioglu, K. H. (2011). The key role of topography in altering North Atlantic atmospheric circulation during the last glacial period. *Climate of the Past*, *7*, 1089–1101. https://doi.org/10.5194/cp-7-1089-2011

Petit, R. J., Aguinagalde, I., de Beaulieu, J.-L., Bittkau, C., Brewer, S., Cheddadi, R., … Vendramin, G. G. (2003). Glacial Refugia: Hotspots but not melting pots of genetic diversity. *Science*, *300*, 1563–1565. https://doi.org/10.1126/science.1083264

Petit, J.-R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davis, M., & Delaygue G. (1999). Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature*, *399*, 429–436.

Pfeifer, B., Wittelsbürger, U., Ramos-Onsins, S. E., & Lercher, M. J. (2014). PopGenome: An efficient Swiss army knife for population genomic analyses in R. *Molecular Biology and Evolution*, *31*, 1929–1936. https://doi.org/10.1093/molbev/msu136

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

QGIS Development Team (2016). *QGIS Geographic Information System. Open Source Geospatial Foundation Project*. Retrieved from http://www.qgis.org/

R Development Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

Rambaut, A., & Drummond, A. J. (2016). *Tracer version 1.6*. Retrieved from http://tree.bio.ed.ac.uk/software/tracer/

Rogers, A. R., & Harpending, H. (1992). Population growth makes waves in the distribution of pairwise genetic differences. *Molecular Biology and Evolution*, *9*, 552–569.

Ronikier, M., Cieślak, E., & Korbecka, G. (2008). High genetic differentiation in the alpine plant *Campanula alpina* Jacq. (Campanulaceae): Evidence for glacial survival in several Carpathian regions and long-term isolation between the Carpathians and the Alps. *Molecular Ecology*, *17*, 1763–1775. https://doi.org/10.1111/j.1365-294X.2008.03664.x

Sáez, L., & Bernal, M. (2009). *Linaria* Mill. In S. Castroviejo, A. Herrero, C. Benedí, E. Rico, & J. Güemes (Eds.), *Flora Iberica 13* (pp. 232–324). Madrid, Spain: CSIC.

Scherrer, D., & Körner, C. (2011). Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, *38*, 406–416. https://doi.org/10.1111/j.1365-2699.2010.02407.x

Schönswetter, P., Stehlik, I., Holderegger, R., & Tribsch, A. (2005). Molecular evidence for glacial refugia of mountain plants in the European Alps. *Molecular Ecology*, *14*, 3547–3555. https://doi.org/10.1111/j.1365-294X.2005.02683.x

Schwartz, M. K., Luikart, G., & Waples, R. S. (2007). Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology & Evolution*, *22*, 25–33. https://doi.org/10.1016/j.tree.2006.08.009

Shaffer, H. B., Fellers, G. M., Randal, Voss S., Oliver, J. C., & Pauly, G. B. (2004). Species boundaries, phylogeography and conservation genetics of the red-legged frog (*Rana aurora/draytonii*) complex. *Molecular Ecology*, *13*, 2667–2677. https://doi.org/10.1111/j.1365-294X.2004.02285.x

Shaw, J., Lickey, E. B., Schilling, E. E., & Small, R. L. (2007). Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: The Tortoise and the hare III. *American Journal of Botany*, *94*, 275–288. https://doi.org/10.3732/ajb.94.3.275

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., … Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, *556*, 231–234. https://doi.org/10.1038/s41586-018-0005-6

Surina, B., Schneeweiss, G. M., Glasnovic, P., & Schönswetter, P. (2014). Testing the efficiency of nested barriers to dispersal in the Mediterranean high mountain plant *Edraianthus graminifolius* (Campanulaceae). *Molecular Ecology*, *23*, 2861–2875. https://doi.org/10.1111/mec.12779

Taberlet, P. (1998). Biodiversity at the intraspecific level: The comparative phylogeographic approach. *Journal of Biotechnology*, *64*, 91–100. https://doi.org/10.1016/S0168-1656(98)00106-0

Tajima, F. (1989). Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, *123*, 585–595.

Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 8245–8250. https://doi.org/10.1073/pnas.0409902102

Ullman, D. J., Legrande, A. N., Carlson, A. E., Anslow, F. S., & Licciardi, J. M. (2014). Assessing the impact of laurentide ice sheet topography on glacial climate. *Climate of the Past*, *10*, 487–507. https://doi.org/10.5194/cp-10-487-2014

Vargas, P. (2003). Molecular evidence for multiple diversification patterns of alpine plants in Mediterranean Europe. *Taxon*, *52*, 463–476. https://doi.org/10.2307/3647446

Vargas, P., Valente, L. M. L. M., Blanco-Pastor, J. L. J. L., Liberal, I., Guzmán, B., Cano, E., … Fernández-Mazuecos, M. (2014). Testing the biogeographical congruence of palaeofloras using molecular phylogenetics: Snapdragons and the Madrean-Tethyan flora. *Journal of Biogeography*, *41*, 932–943. https://doi.org/10.1111/jbi.12253

Wakeley, J. (1996). The variance of pairwise nucleotide differences in two populations with migration. *Theoretical Population Biology*, *49*, 39–57. https://doi.org/10.1006/tpbi.1996.0002

Walther, G.-R., Beißner, S., & Burga, C. A. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, *16*, 541–548. https://doi.org/10.1111/j.1654-1103.2005.tb02394.x

Wei, T., & Simko, V. (2013). *corrplot: Visualization of a correlation matrix*. R Packag. version 0.73. 230:11.

Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., & Grehan, A. J. (2007). Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Marine Geodesy*, *30*, 3–35. https://doi.org/10.1080/01490410701295962

Wolfe, K. H., Li, W. H., & Sharp, P. M. (1987). Rates of nucleotide substitution vary greatly among plant mitochondrial, chloroplast, and nuclear DNAs. *Proceedings of the National Academy of Sciences of the United States of America*, *84*, 9054–9058. https://doi.org/10.1073/pnas.84.24.9054

BIOSKETCH

José Luis Blanco-Pastor's main scientific goal is to study *the evolution and diversity of species, populations and genes*. Specifically, his research is focussed on the study of the effect of past climate changes on plant evolution, gene flow and adaptation to environmental factors. He is particularly interested in the use of this information to help plant species to adapt to future climatic conditions.

Authors' contributions: J.L.B-P. and P.V. conceived the ideas; J.L.B-P., M.F-M., J.P. and P.V. collected the data; J.L.B-P., M.F-M. and A.J.C. analysed the data; J.L.B-P., M.F-M., A.J.C. and P.V. interpreted results. J.L.B-P. led the writing, and J.L.B-P., M.F-M., A.J.C. and P.V. participated in the edition of the manuscript.

SUPPORTING INFORMATION

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

How to cite this article: Blanco-Pastor JL, Fernández-Mazuecos M, Coello AJ, Pastor J, Vargas P. Topography explains the distribution of genetic diversity in one of the most fragile European hotspots *Divers Distrib*. 2019;25:74–89. https://doi.org/10.1111/ddi.12836