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The Quaternary range dynamics of *Noccaea iberidea* (Brassicaceae), a typical representative of subalpine/alpine steppe communities of Anatolian mountains

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The responses of Anatolian plants to global climate change have been poorly investigated. In this study, we aimed to understand how climatic oscillation during the Quaternary period helped to shape the current distribution patterns of the Anatolian endemic *Noccaea iberidea*, a typical representative of tragacanthic (thorny cushion) steppe communities of Anatolia. We used ecological niche modelling combined with statistical phylogeography, based on nuclear ribosomal ITS and plastidic *trnL-F* and *trnS-ycf9* regions. Both the structure of the haplotype networks and the results of the extended Bayesian skyline plot analysis clearly indicated that *N. iberidea* has been through a recent population expansion. This interpretation was also supported by ecological niche modelling analysis, which showed that the availability of areas of high suitability expanded from the Last Interglacial to the Last Glacial Maximum, suggesting that *N. iberidea* might have expanded its range during the glacial periods. In conclusion, the study improves our understanding of the demographic history and responses of steppe plant communities of Anatolia to global climate changes through the Late Quaternary glacial–interglacial cycles, which in turn might aid in the development of future conservation strategies.

ADDITIONAL KEYWORDS: Anatolia – *Noccaea iberidea* – plant demography – Pleistocene – steppe communities.

INTRODUCTION

Range shifts during the Quaternary climatic oscillations are assumed to have had an impact on biodiversity; thus, understanding the patterns of range shifts is crucial for conservation purposes (Hewitt, 1996; Angert *et al.*, 2011). The literature includes several studies revealing the spatiotemporal responses of species (e.g. range contractions and expansions) to the Quaternary climatic oscillations (Hewitt, 1996; Stewart *et al.*, 2010), which have been intensely focused in specific geographical regions, such as North America and the northern part of Europe (Feliner, 2014 and references therein). In contrast to the number of studies in these regions, the literature includes relatively few biogeographical studies in the Mediterranean region. Although a substantial increase in the number of studies in the western Mediterranean has occurred over recent years, the biogeographical patterns in the eastern Mediterranean have remained poorly investigated with respect to plant groups (Özüdoğru *et al.*, 2015).

A total of 36 biodiversity hotspots have been identified around the world. The remnant habitats in these biodiversity hotspots correspond to only 2.4% of the Earth's land surface, but still maintain > 50% of the world's endemic plant species and nearly 43% of the endemic amphibian, reptile, bird and mammal species (Conservation International, 2020). The Mediterranean Basin is considered one of the world's

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most important biodiversity hotspots, with high levels of endemism, particularly for plant species (Myers *et al.*, 2000; Feliner, 2014; Conservation International, 2020). Of the 24 000–25 000 plant species living in the Mediterranean Basin, 60% are endemic, and this richness can generally be attributed to the topographic and climatic heterogeneity of the Basin (Greuter, 1991; Médail & Diadema, 2009; Feliner, 2014; Euro+Med PlantBase, 2006).

Anatolia (the Asian part of Turkey) is one of the most floristically diverse regions in the world. It contains ~10 000 plant species and is also a hotspot for biological diversity in the Mediterranean Basin. Geographically, it is situated between the European and Asian continents and constitutes a crossroad for Euro-Siberian, Irano-Turanian and Mediterranean flora (Davis, 1965; Ansell *et al.*, 2011; Güner *et al.*, 2012). Owing to its complicated and unique tectonic history, Anatolia has complex topography and therefore a variety of climates within a relatively limited area (Şekercioğlu *et al.*, 2011). Another factor that has resulted in the high level of species diversity in Anatolia is its Quaternary history, wherein, unlike the northern parts of Europe and North America, only the high mountain peaks of Anatolia were covered by glaciers during the Quaternary (Atalay, 1996; Gür, 2017 and references therein), whereas the lowlands were covered by forest and steppe communities (Ansell *et al.*, 2011; Şenkul & Doğan, 2013). Thus, the glacial survival of temperate species could have been possible in these communities (Çıplak *et al.*, 2010; Gür 2017). Anatolia has already been suggested to be a refugium for temperate species (Hewitt, 1996). This hypothesis was tested on some organisms, e.g. the meadow grasshopper *Chorthippus parallelus* (Zetterstedt, 1821), and the potential role of Anatolia for the recolonization of Europe after the Last Glacial Maximum (LGM) was supported (Korkmaz *et al.*, 2014). Likewise, it was shown that the current lineages of *Microthlaspi erraticum* (Jord.) T.Ali & Thines originated from Balkans and Anatolia (Ali *et al.*, 2016). With regard to the some widespread plant species, including *Arabis alpina* L. and *Microthlaspi perfoliatum* (L.) F.K.Mey., Anatolia represents the highest genetic diversity and the centre of origin (Ansell *et al.*, 2011; Ali *et al.*, 2019). In the expansion of *Miniopterus schreibersii* (Kuhl, 1819) after the LGM from the Levantine refugium to Europe and the Caucasus, Anatolia played a crucial role in the stepping stone repopulation process (Bilgin *et al.*, 2016). For these reasons, Anatolia remains a biogeographically interesting but underexplored region (Ansell *et al.*, 2011).

Although the historical biogeography of Anatolia and adjoining areas has been relatively well represented in animals (e.g. Gür, 2013, 2017; Sağlam *et al.*, 2014; Perktaş *et al.*, 2015, 2019; Kaya & Çıplak, 2017; Asadi Aghbolaghi *et al.*, 2019), studies on plant groups in the region remain insufficient. Limited studies exist on the Quaternary history of plants, and the studies that do exist have generally been related to a genus rather than to individual species (e.g. *Heldreichia* Boiss., *Ricotia* L., *Centaurea* L.). However, there are also some species-level studies that focus mainly on the historical biogeography of Anatolia (Parolly *et al.*, 2010; Özüdoğru *et al.*, 2015; López-Pujol *et al.*, 2016).

The present study organism, *Noccaea iberidea* (Boiss.) Al-Shehbaz & Menke [= *Eunomia iberidea* Boiss. or *Aethionema iberideum* (Boiss.) Boiss.], is a caespitose (growing in dense tufts) semi-shrub, with long creeping rhizomes (Fig. 1). Recent phylogenetic studies have clearly shown that this species is located outside of *Aethionema* W.T.Aiton, but is a member of the genus *Noccaea* Moench or *Eunomia* DC., depending on the taxonomic treatments used, in the tribe Coluteocarpeae (Al-Shehbaz, 2014; BrassiBase, https://brassibase.cos.uni-heidelberg.de/; Kiefer *et al.*, 2014; Mohammadin *et al.*, 2017; Özüdoğru *et al.*, 2019). *Noccaea iberidea* is one of the typical elements of calcareous areas of the subalpine/alpine region in central Anatolia and the mountains surrounding the central Anatolian Plateau, including the Taurus and Anatolian Diagonal (running from the north-east of Turkey to the south-west and dividing inner Anatolia into two regions with different faunistic and floristic communities; Gür, 2016), and its distribution largely matches two of four endemism areas described recently (Fig. 1; Hedge, 1965; Gür, 2016; Noroozi *et al.*, 2019). Although it was recorded from Greece, literature and herbarium studies clearly showed that this species does not distribute out of Anatolia (Hedge, 1965; Al-Shehbaz, 2014); therefore, this species is endemic to Anatolia. *Noccaea iberidea* is well adapted to the high mountain vegetation of south Anatolia; however, most of the distribution of this species corresponds to the Irano-Turanian phytogeographical region, which is characterized by a continental climate and vegetation dominated by cushion-like xerophyte/dwarf shrubs (Manafzadeh *et al.*, 2014, 2016). Although there is no direct evidence for the dispersal strategy of *N. iberidea*, one can argue that this species is not able to disperse over long distances because of its non- mucilagineous seeds. The early flowering time of *N. iberidea* (May–June) at the higher elevation might also be an adaptation developed to avoid competition with other plants in terms of pollinators (Hedge, 1965). This species is highly associated with tragacanthic communities, which form a continuous layer of thorny cushion plants that are resistant to grazing and are found between 1300 and 2500 m a.s.l. (Hedge, 1965; Grace, 2010). Therefore, it might also represent a

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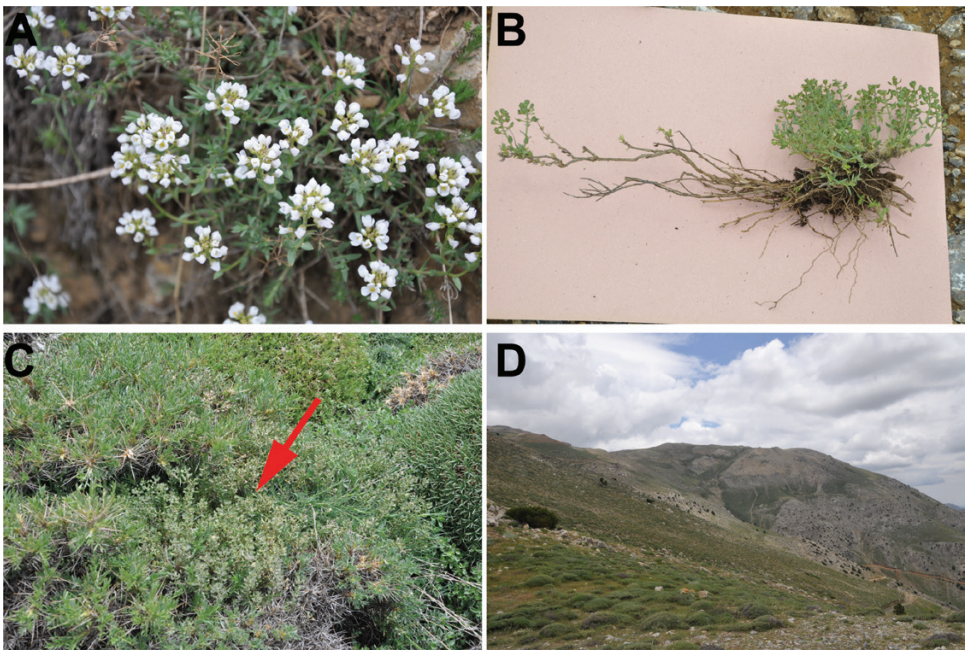

Figure 1. General view of *Noccaea iberidea* and its habitat. A, flowers. B, rhizomes. C, *N. iberidea* (marked by red arrow) with tragacanthic plants in its natural habitat. D, alpine habitat in Engizek Mountain in south Anatolia (Kahramanmaraş district).

model species to evaluate the responses of these plant communities to the Quaternary climatic oscillations and to ongoing and future global climate changes.

Herein, we present the first biogeographical study of *N. iberidea* across its distribution range in Anatolia. We wanted to understand how the Anatolian subalpine/alpine plant *N. iberidea* responded to global climate changes throughout the Quaternary glacial–interglacial cycles. Accordingly, the widely used ecological niche modelling (ENM) approach was combined with statistical phylogeography based on nuclear ribosomal internal transcribed spacer (ITS; from 85 individuals) and plastidic *trnL-F* and *trnS-ycf9* (from 83 individuals) regions. Specifically, the following questions were addressed:

Are there any genetic structures among the *N. iberidea* populations?

Which climatic or historical factors were responsible for shaping the genetic diversity of *N. iberidea*?

MATERIAL AND METHODS

Molecular phylogeography

Leaf materials of 42 accessions and 103 individuals, representing the entire geographical distribution area of *N. iberidea*, were used (Table 1). ITS regions (including ITS1 and ITS2) and the 5.8S gene of nuclear ribosomal DNA (hereafter called ITS) were amplified using primers ITS 1 and ITS 4 (White *et al.*, 1990). Plastidic *trnL-F* and *trnS-ycf9* regions were amplified using the primer pairs c/e of Taberlet *et al.* (1991) and the forward and reverse primers of Koch *et al.* (2016), respectively. Amplification of the ITS, *trnL-F* and *trnS-ycf9* followed the protocols of Warwick *et al.* (2004), Ansell *et al.* (2007) and Koch *et al.* (2016), respectively. Purification and sequencing were performed by BM Laboratuvar Sistemleri (Ankara, Turkey). All of the fragments were sequenced in both forward and reverse directions and edited using CodonCode Aligner (Dedham, MA, USA), aligned with MUSCLE v.3.6 (Edgar, 2004). Sequences from the two plastid DNA regions [*trnL-F* and *trnS-ycf9*, hereafter called the chloroplast DNA (cpDNA) data set] were concatenated into a single matrix for all the analyses. Alignments of both the ITS ribotype and cpDNA haplotype data sets are provided in the Supporting Information (Appendices S1 and S2).

Nucleotide and haplotype diversity (HD) and the number of polymorphic (segregating) sites (S) and unique haplotypes (H) of the ITS and cpDNA data sets were estimated. Additionally, to determine the selective neutrality of the genetic markers, Tajimas's D (Tajima, 1989) and Fu's F_S (Fu, 1997) tests were conducted. All these analyses were performed using DnaSP v.5.10 (Librado & Rozas, 2009).

To understand the relationships between the haplotypes and ribotypes, statistical parsimony

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Table 1. Collection and haplotype/ribotype information for samples used in this study

Voucher (herbarium code)	Locality, elevation, coordinates* (if possible) and collection date	Number of samples	Haplotypes/ribotypes†	GenBank accession numbers (*trnL-F*, *trnS-ycf9*/ITS)
B.Özüdoğru 4453 & K.Özgişi (HUB)‡	Kahramanmaraş, Berit Mountain, 2060 m, 38.01954/36.82456, 8 June 2016	6	H17, H18 (4)/R2 (5)	MN879504, MN895060, MN879505, MN895061/MN871752
B.Özüdoğru 4715 & K.Özgişi (HUB)	Kayseri, Dededağı, 2550 m, 37.92587/35.288, 6 August 2016	3	H16 (3)/–	MN879503, MN895059
B.Özüdoğru 4571 (HUB)	Çankırı, Ilgaz Mountain, 2140 m, 41.071459/33.83043, 20 June 2016	4	H15 (3)/R2, R8, R14, R15	MN879502, MN895058/MN871752, MN871750, MN871751, MN871749
B.Özüdoğru 4449 & K.Özgişi (HUB)	Kahramanmaraş, Engizek Mountain, 2220 m, 37.7937/37.09648, 8 June 2016	5	H3 (4)/R2 (3)	MN879501, MN895057/MN871752
B.Özüdoğru 4512 & K.Özgişi (HUB)	Adıyaman, Nemrut Mountain, 2060 m, 37.98232/38.74326, 13 June 2016	4	H14 (3), H19/R2 (4)	MN879499, MN895055, MN879500, MN895056/MN871752
B.Özüdoğru 3876 (HUB)	Kırıkkale, Çelebi Mountain, 1160 m, 39.447224/33.512529, 8 April 2016	3	H9 (3)/R2, R6 (2)	MN879498, MN895054/MN871752, MN871748
B.Özüdoğru 4171 (HUB)	Kırşehir, Kervansaray Mountain, 1527 m, 39.196073/34.228012, 18 May 2016	4	H3 (3)/R2, R6, R13 (2)	MN879501, MN895057/MN871752, MN871748, MN871747
B.Özüdoğru 4476 & K.Özgişi (HUB)	Sivas, Çamlıbel Pass, 1800 m, 39.96379/36.54159, 10 June 2016	5	H6 (5)/R2 (5)	MN879497, MN895053/MN871752
K.Özgişi 1217 (HUB)	Isparta, Kızıldağ National Park, 1570 m, 38.01194/31.44167, 26 June 2016	5	H3 (4)/R2 (3), R12	MN879501, MN895057/MN871752, MN871746
B.Özüdoğru 3653 & K.Özgişi (HUB)	Kahramanmaraş, Kaman Mountain, 1740 m, 37.97955/36.59709, 1 July 2015	4	H7 (4)/R2 (4)	MN879496, MN895052/MN871752
B.Özüdoğru 3579 & K.Özgişi (HUB)	Antalya, Gazipaşa, Şahinler Hill, 1780 m, 36.45552/32.440062, 22 June 2015	4	H5 (3)/R2 (3), R11	MN879495, MN895051/MN871752, MN871745
B.Özüdoğru 3993 & K.Özgişi (HUB)	Kayseri, Sarız, 1813 m, 38.55779/36.45042, 30 April 2016	5	H3 (4), R2 (5)	MN879501, MN895057/MN871752
B.Özüdoğru 4504 & K.Özgişi (HUB)	Malatya, Beydağı, 2270 m, 38.25488/38.38203, 13 June 2016	5	H13 (5), R10 (5)	MN879494, MN895050/MN871744
B.Özüdoğru 4475 & K.Özgişi (HUB)	Sivas, Şarkışla, 2070 m, 39.49956/36.12598, 10 June 2016	5	H12 (4), R2 (5)	MN879493, MN895049/MN871752
B.Özüdoğru 3941 (HUB)	Çankırı, Eldivan Mountain, 1780 m, 40.463227/33.476408, 15 April 2016	5	H10 (4), H11/R9 (3), R2, R8	MN879491, MN895047, MN879492, MN895048/MN871743, MN871752, MN871750
B.Özüdoğru 4459 & K.Özgişi (HUB)	Adana, Saimbeyli, Bozoğlan Hill, 1830 m, 38.05819/36.05404, 9 June 2016	5	H3 (5)/R2 (5)	MN879501, MN895057/MN871752
B.Özüdoğru 3927 (HUB)	Kırşehir, Kaman, 1400 m, 39.32265/34.002935298, 14 April 2016	4	H9 (4)/R6 (2), R2, R7	MN879498, MN895054/MN871748, MN871752, MN871742
K.Özgişi 1190 (HUB)	Eskişehir, Zeyköy, 1467 m, 39.6075/31.515, 17 June 2016	1	H3/R5	MN879501, MN895057/MN871741

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Table 1. Continued

Voucher (herbarium code)	Locality, elevation, coordinates* (if possible) and collection date	Number of samples	Haplotypes/ribotypes†	GenBank accession numbers (*trnL-F*, *trnS-ycf9*/ITS)
Ş.Yıldırımlı 1650 (HUB)	Erzincan, Kemah, Maksutuşağı Köyü, 1700–2300 m, 27 May 1979	1	H8/R2	MN879490, MN895046/MN871752
B.Yıldız 1647 (HUB)	Kahramanmaraş, Göksun, Fındık Village, 1600 m, 23 April 1978	1	H7/R2	MN879496, MN895052/MN895052
M.Vural & Ü.Kol 4527 (HUB)	Nevşehir, Zelve, Akdağ, 1350 m, 38.65912/34.872738, 20 April 1989	1	H6/R2	MN879497, MN895053/MN895052
H.Sümbül 2141 (HUB)	Mersin, Anamur, Akine Village, 1900–2200 m, 20 June 1983	1	H5/R2	MN879495, MN895051/MN895052
A.A.Dönmez 13638 (HUB)	Antalya, Alanya, Koçdavud pass, 1261 m, 36.553759/32.328721, 14 June 2006	1	H5/R2	MN879495, MN895051/MN895052
B.Yıldız 2559 (HUB)	Kahramanmereş, Göksun, Fındıklı-Bostandere, 1800 m, 30 May 1981	1	H3/R2	MN879501, MN895057/MN895052
H.Sümbül 1751 (HUB)	Antalya, Gazipaşa, Sugözü Village,1900–2000 m, 17 May 1983	1	H5/R4	MN879495, MN895051/MN871740
H.Sümbül 3346 (HUB)	Antalya, Akseki, 1550 m, 27 June 1989	1	H3/R2	MN879501, MN895057/MN895052
Z.Aytaç & H.Duman 3500 (HUB)	Kahramanmaraş, Ahır Mountain, 1900–2000 m, 2 May 1991	1	H3/R2	MN879501, MN895057/MN895052
Ş.Yıldırımlı 3066 (HUB)	Erzincan, Kemaliye, Yeşilyamaç Village, 1680 m, 39.25919/38.556619, 21 May 1980	1	H3/R3	MN879501, MN895057/MN871739
M.Koyuncu 6025 & S.Erik (HUB)	Antalya, Gündoğmuş, 1700 m, 25 May 1983	1	H4/R2	MN879489, MN895045/MN895052
M.Koyuncu 4300 & S.Erik (HUB)	Adana, Saimbeyli, 1400–1850 m, 2 June 1981	1	H3/R2	MN879501, MN895057/MN895052
B.Yıldız 2774 (HUB)	Kahramanmaraş, Süleymanlı, 2000 m, 15 June 1981	1	H2/R2	MN879488, MN895044/MN895052
Okan Ürker (HUB)	Mersin, Sertavul Pass, 1590 m, 36.935155/33.170464, 16 April 2016	1	H1/–	MN879487, MN895043/–
N.Çelik 1150 (HUB)	Kayseri, Akkışla, 1800 m, 39.036606/36.311213, 19 May 1980	1	–/R1	–/MN871738

*Longitude (E)/latitude (N).
† If there is more than one haplotype/ribotype present per population, the number of individuals carrying the haplotypes/ribotypes is given in paratheses.
‡ Herbarium of Hacettepe University, Department of Biology.

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networks were generated for the ITS and cpDNA using POPART (Leigh & Bryant, 2015). All the haplotypes and ribotypes defined in DNASP were used in the phylogenetic analyses to reveal the intraspecific lineages within *N. iberidea*. *Noccaea oppositifolia* (Pers.) Al-Shehbaz & Menke was used as an outgroup in these analyses because of its close relationship to *N. iberidea*, as a member of the *Eunomia/Vania* clade described by Özüdoğru *et al.* (2019). Phylogenetic analyses were conducted using MRBAYES v.3.2.7 (Ronquist *et al.*, 2012). Before the analyses, the best-fitting substitution models were selected using MEGA6 (Tamura *et al.*, 2013) and set as JC and HKY for the ITS and cpDNA (*trnL-F* and *trnS-ycf9*) data sets, respectively. Two simultaneous runs of Metropolis-coupled Markov chain Monte Carlo (MCMC) were performed for ten million generations, and one tree was sampled every 1000 generations, using a default of three heated chains and one cold chain and a random starting tree. Bayesian posterior probabilities were obtained from the majority rule consensus of the trees. All these analyses were performed for the haplotype and ribotype data sets separately.

DEMOGRAPHY

Historical population expansions in *N. iberidea* were evaluated using the mismatch distribution of the observed haplotype pairwise differences under the sudden population expansion model of Rogers & Harpending (1992). Changes in the effective population size (N_{ef}) over time were evaluated further using extended Bayesian skyline plots (EBSPs; Heled & Drummond, 2008). The EBSP uses MCMC sampling and generates a posterior distribution of the N_{ef} over time. This analysis was implemented in BEAST v.2.5 (Bouckaert *et al.*, 2014). Before the EBSP analysis, the best-fitting substitution models were selected using MEGA6 (Tamura *et al.*, 2013), as in the phylogenetic analyses, and set as JC and HKY for the ITS and cpDNA (*trnL-F* and *trnS-ycf9*) data sets, respectively.

Given that there has been no reliable mutation rate for *N. iberidea* reported in the literature, the rates for nuclear ITS and plastidic *trnL-F* were estimated based on the following strategies. Representatives of each *Noccaea s.l.* clade (according to Özüdoğru *et al.*, 2019) plus some representatives of other Brassicaceae lineages (see Supporting Information, Appendix S3) were used in this analyses, and *Aethionema saxatile* (L.) W.T.Aiton served as an outgroup for the core Brassicaceae. The crown ages of the Brassicaceae and core Brassicaceae (excluding *Aethionema*) were set to 34.9 ± 0.3 and 25.1 ± 0.3 Mya, to take into account the variation of different results of the age estimations presented in various studies (Couvreur *et al.*, 2010; Hohmann *et al.*, 2015; Huang *et al.*, 2016, 2020; Guo *et al.*, 2017).

The MCMC analysis was run for 100 million generations (sampling every 10 000 generations), of which the first 10% was discarded as the burn-in. All the analyses were conducted under the strict clock prior by taking into consideration clock-like trees, which were obtained from both the ITS and *trnL-F* analyses. Results were checked using TRACER v.1.5 (Rambaut & Drummond, 2007) for a sufficient effective sample size (ESS > 200 for all of the estimated parameters, as suggested by the developers). The EBSP was visualized using R (R Core Team, 2019).

ECOLOGICAL NICHE MODELLING

For the Anatolian subalpine/alpine plant *N. iberidea*, 50 species occurrence records were obtained from the field and herbarium studies. To eliminate a potential bias of the clustered records, the occurrence records were filtered spatially by removing records that were within 10 km of one another, resulting in 46 records (Fig. 2).

Bioclimatic data were downloaded from the WorldClim database (Hijmans *et al.*, 2005; http://www.worldclim.org) for the Last Interglacial (LIG; ~140–120 kya), LGM (~22 kya) and present (~1960–1990) bioclimatic conditions and used at a spatial resolution of 30 arc s. The reconstructed LIG and LGM bioclimatic data were based on one (CCSM3) and three (CCSM4, MIROC-ESM and MPI-ESM-P) global climate models, respectively (for detailed information, see the WorldClim database). The bioclimatic data included 19 bioclimatic variables derived from monthly temperature and precipitation values (for detailed descriptions of the bioclimatic variables, see the WorldClim database) and represented annual trends (e.g. annual mean temperature and precipitation), seasonality (e.g. temperature and precipitation seasonality) and limiting factors (e.g. temperature of the warmest and coldest months and precipitation of the wettest and driest months). Four bioclimatic variables (i.e. the mean temperature of the wettest and driest quarters and precipitation of the warmest and coldest quarters) were removed from the bioclimatic data owing to known spatial artefacts. All the other bioclimatic variables were masked to include only the study area (Fig. 2). The study area was defined by a minimum convex polygon that was created from the occurrence records, to which a 150 km buffer was applied.

MAXENT v.3.4.1 (Phillips *et al.*, 2017) and SDMTOOLBOX v.2.2b (Brown *et al.*, 2017) software implemented in ARCGIS v.10.2.2 software were used to predict bioclimatic suitability for *N. iberidea* under LIG, LGM and present bioclimatic conditions. MAXENT was run with the following settings. A minimum convex polygon was created from the occurrence records, to which a 50 km buffer was applied (note that when a 100 km buffer was applied, the results did not change;

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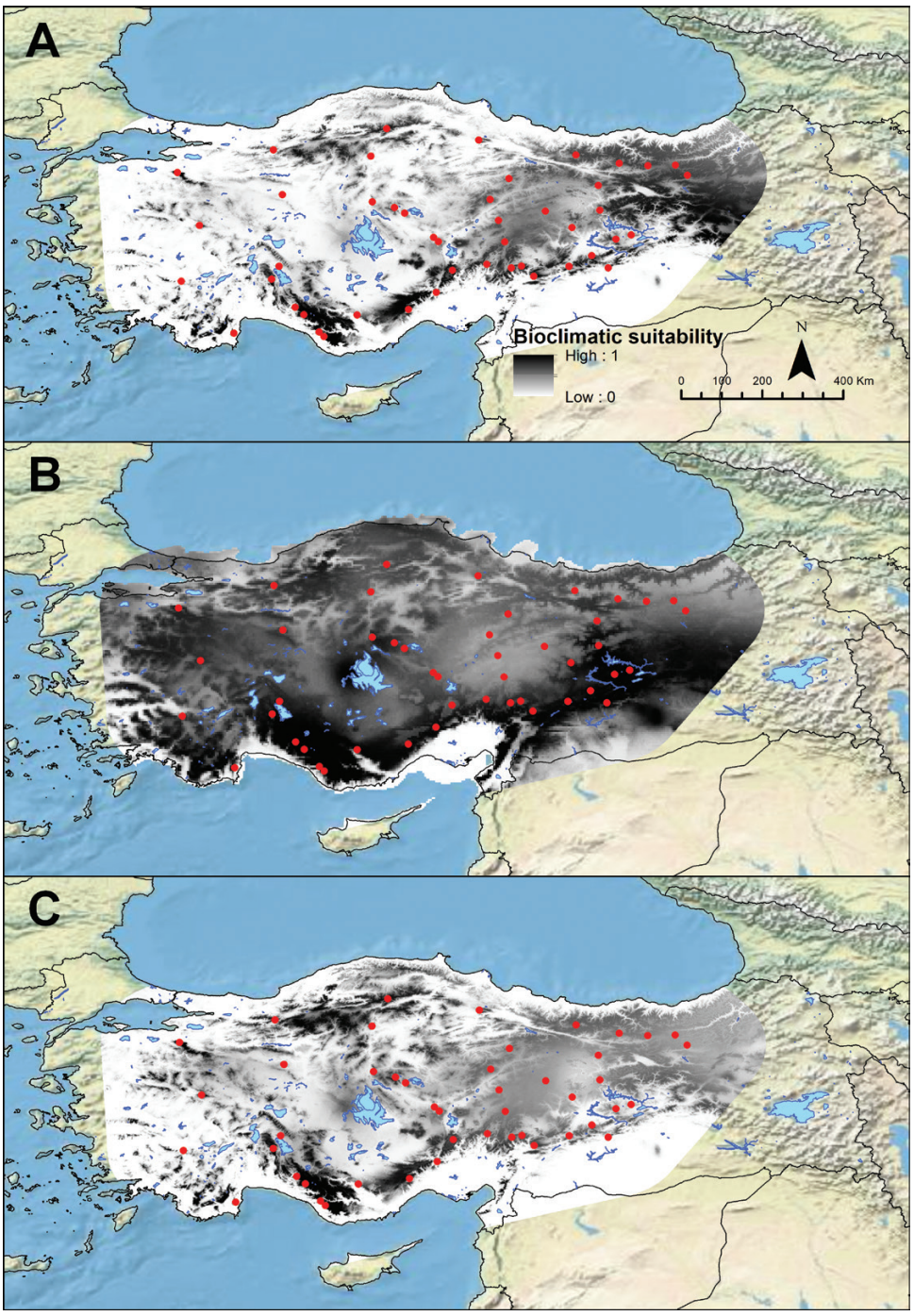

Figure 2. Bioclimatic suitability for Anatolian alpine plant *Noccaea iberidea* in the present bioclimatic conditions (A), the Last Glacial Maximum (B) and the Last Interglacial (C). Red circles indicate the 46 occurrence records used for ecological niche modelling.

not shown). This area was used to sample 10 000 background points randomly, which might reduce issues associated with background selection (for a discussion on background selection, see Elith *et al.*, 2011; Merow *et al.*, 2013). The contributions of the bioclimatic variables to a final model were determined using the jackknife test. Using all combinations of the following feature classes: (1) linear; (2) linear and quadratic; (3) hinge; (4) linear, quadratic and hinge; and (5) linear, quadratic, hinge and product; and

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regularization multipliers (classes 1–5 in increments of one), different models were tested to optimize the model complexity (for a discussion on features and regularization, see Elith *et al.*, 2011; Merow *et al.*, 2013). These models were calibrated using spatial jackknifing (or geographically structured k-fold cross-validation, $k = 3$). The model with the highest area under the curve (AUC) of a receiver operating characteristic (ROC) plot was selected as the best model. After the optimal model parameters were determined, a final model was developed using all the occurrence records together (for more details, see Brown *et al.*, 2017). This model was then projected to the LIG and LGM bioclimatic conditions. Three predictions under three different global climate models were averaged to generate a final summary prediction for the LGM. Clamping and extrapolation were performed because the multivariate environmental similarity surface (MESS) maps (Elith *et al.*, 2010) showed that projecting the model onto non-analog bioclimatic conditions was necessary. Model performance and significance were evaluated by a partial ROC analysis (Peterson *et al.*, 2008), as implemented in the NICHETOOLBOX (Osorio-Olvera, 2016). Moreover, the response curves were examined if they were biologically logical.

RESULTS

None of the phylogenetic analyses of the ITS and cpDNA data sets resulted in a well-resolved tree, and statistically supported clades were not obtained. Therefore, all the genetic diversity parameters were estimated for the complete ITS and cpDNA data sets, ignoring any population groups.

NUCLEAR ITS SEQUENCE VARIATION AND RIBOTYPE DISTRIBUTION

A total of 15 (R1–R15) different ITS ribotypes were detected from 85 individuals. The length of the ITS data set was 624 bp, 12 of which were variable and six potentially parsimony informative. The frequency of one ribotype (R2) was very high and observed in 59 individuals. This common ribotype was evenly spread throughout the distribution area of *N. iberidea*, and the remaining ribotypes were seperated from it by one or two mutational steps, except for R9 (three mutational steps) (Fig. 3). Both the ribotype (0.514) and nucleotide diversity (0.00151) were relatively low in the data set. Tajima's D and Fu's F_S values for the ITS data set were negative (–1.8578 and –13.028) and significantly different from zero.

PLASTID DNA SEQUENCE VARIATION AND HAPLOTYPE DISTRIBUTION

The length of the concatenated plastid data set was 1186 bp, 24 of which were variable and 16 potentially parsimony informative. A total of 19 haplotypes were found in the data set (from 83 individuals), and one haplotype (H3) was found at higher frequencies (detected in 26 individuals), as observed in the ITS data set. A similar distribution pattern of the common haplotype was detected in the cpDNA data set, and this haplotype was observed in most of the distribution areas of *N. iberidea* (Fig. 4). Contrary to the ITS data set, HD was high in the cpDNA data set (0.876), whereas nucleotide diversity (0.00200) was low. Both the Tajima's D (–1.71630) and Fu's F_S (–9.446) values of the cpDNA data set were negative, as in the ITS data set, and they were not statistically different from zero.

DEMOGRAPHIC HISTORY

A significant population expansion was supported by multiple tests. The sudden expansion model was not rejected by the separate mismatch distribution analyses based on the ITS and cpDNA data sets (the raggedness index, $r = 0.0411$; $P > 0.05$ and Ramos-Onsins and Rozas' test statistic $R^2 = 0.0424$, $P > 0.05$ in the cpDNA, $r = 0.0710$; $P > 0.05$ and $R^2 = 0.0363$, $P > 0.05$ in the ITS), and both distributions were Unimodal (Figs 3, 4).

In the age estimation analyses (not presented here), the rates of ITS and *trnL-F* were estimated as 0.0046/Myr (between 0.0009 and 0.002/Myr) and 0.0013/Myr (between 0.0004 and 0.0032/Myr), respectively. Based on these rates, the EBSP indicated a clear population expansion beginning before the LIG period (~200 kya), and this expansion might have continued during the Last Glacial period, including the LGM. However, a very slight contraction after the LGM was detected by the EBSP (Fig. 5).

ECOLOGICAL NICHE MODELLING

Herein, 250 different models were tested based on different model parameters (feature classes and regularization multipliers) and training/test partitions (spatial jackknifing). The final model was developed using the linear and quadratic feature classes, and a regularization multiplier of one. This model performed better than the random prediction ($N = 1000$, mean AUC ratio = 1.74 ± 0.05, 1.58–1.87, $P < 0.001$).

In the present bioclimatic conditions, areas of high suitability were predicted mainly across the mountain ranges surrounding the central Anatolian plain. The explain tool in MAXENT (to explore what drives a high

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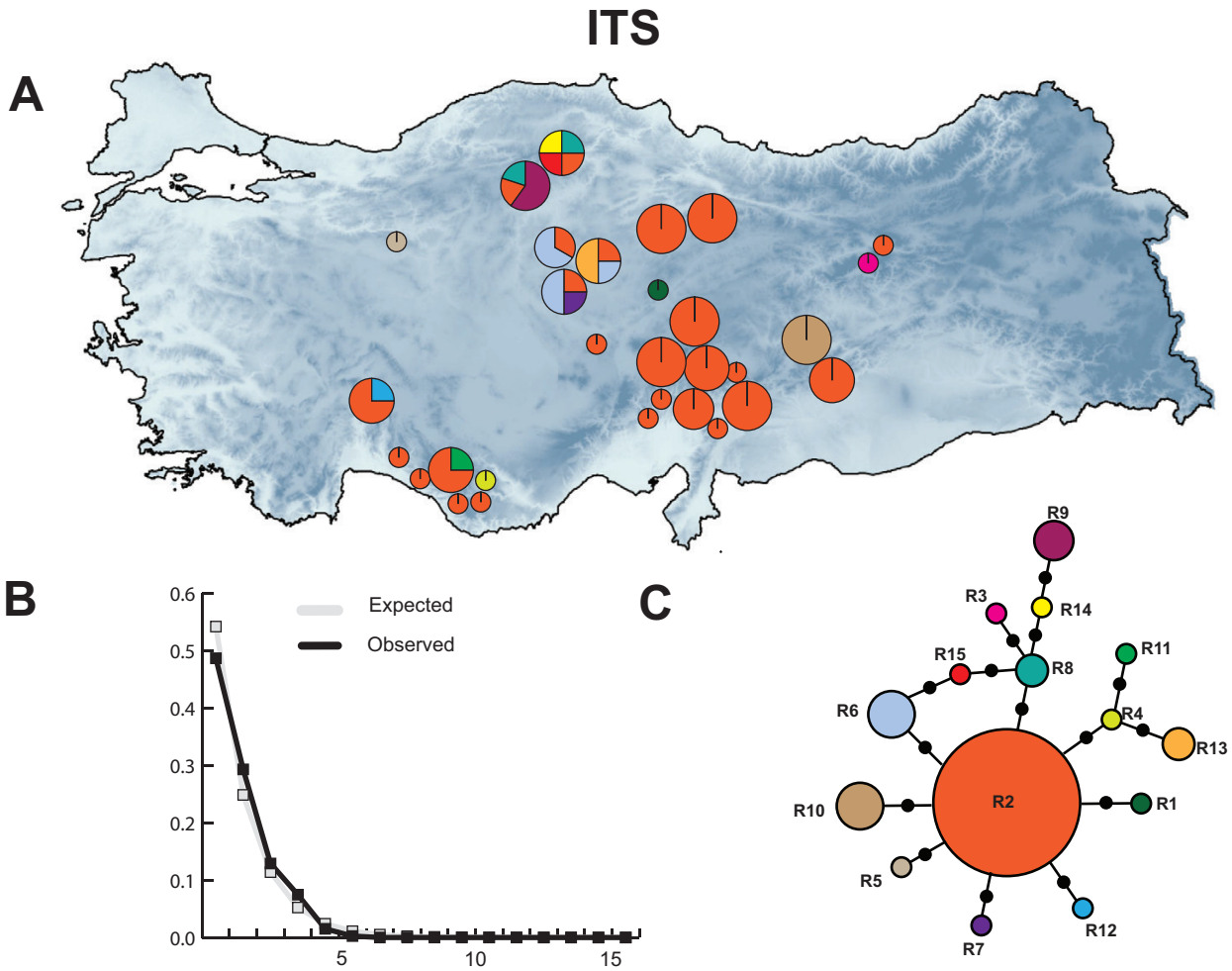

Figure 3. Ribotype distribution, network and mismatch distribution analyses of pairwise ribotype differences. A, location of the *Noccaea iberidea* populations sampled throughout its distribution range. Each pie chart on the map represents an ITS ribotype, and the size of the pie is proportional to the number of individuals. B, distribution of pairwise differences among ITS ribotypes. C, haplotype network of the obtained ITS ribotypes. Each ribotype is represented by colour, and the size of pie is proportional, as in the map. Black dots represent one mutational step between ribotypes.

or low prediction at any given site in geographical space; Elith *et al.*, 2010) indicated that low suitability in the central Anatolian plain was mainly attributable to high temperatures. The temperature variables dominated over the precipitation variables, suggesting that temperature might have been a more important driver of the distribution patterns of *N. iberidea*. Areas of high suitability expanded (i.e. shifted towards lower elevations) from the LIG to the LGM and contracted (i.e. shifted towards higher elevations) from the LGM to the present, suggesting that *N. iberidea* might have expanded its range during the glacial periods (Fig. 2).

The results of the ENM were also in agreement with those of the molecular phylogeography, in that *N. iberidea* expanded its range in the LGM and contracted its range in the present interglacial period (Figs 2–5).

DISCUSSION

The effect of Quaternary climatic oscillations on the distribution patterns of plants has been revealed in different parts of the world, including the Alps, Qinghai-Tibetan Plateau and North America (Hewitt, 2004; Li *et al.*, 2018; Park & Donoghue, 2019). Although the remarkable impact of the mountains on the rich flora of Anatolia is well known, the biogeographical and phylogeographical history of alpine plants has been poorly studied in this region, and only a limited

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Figure 4. Haplotype distribution, network and mismatch distribution analyses of pairwise haplotype differences. A, location of the *Noccaea iberidea* populations sampled throughout its distribution range. Each pie chart on the map represents a chloroplast DNA (cpDNA) haplotype, and the size of the pie is proportional to the number of individuals. B, distribution of pairwise differences among cpDNA haplotypes. C, haplotype network of the obtained cpDNA haplotypes. Each haplotype is represented by colour, and the size of pie is proportional, as in the map. Black dots represent one mutational step between haplotypes.

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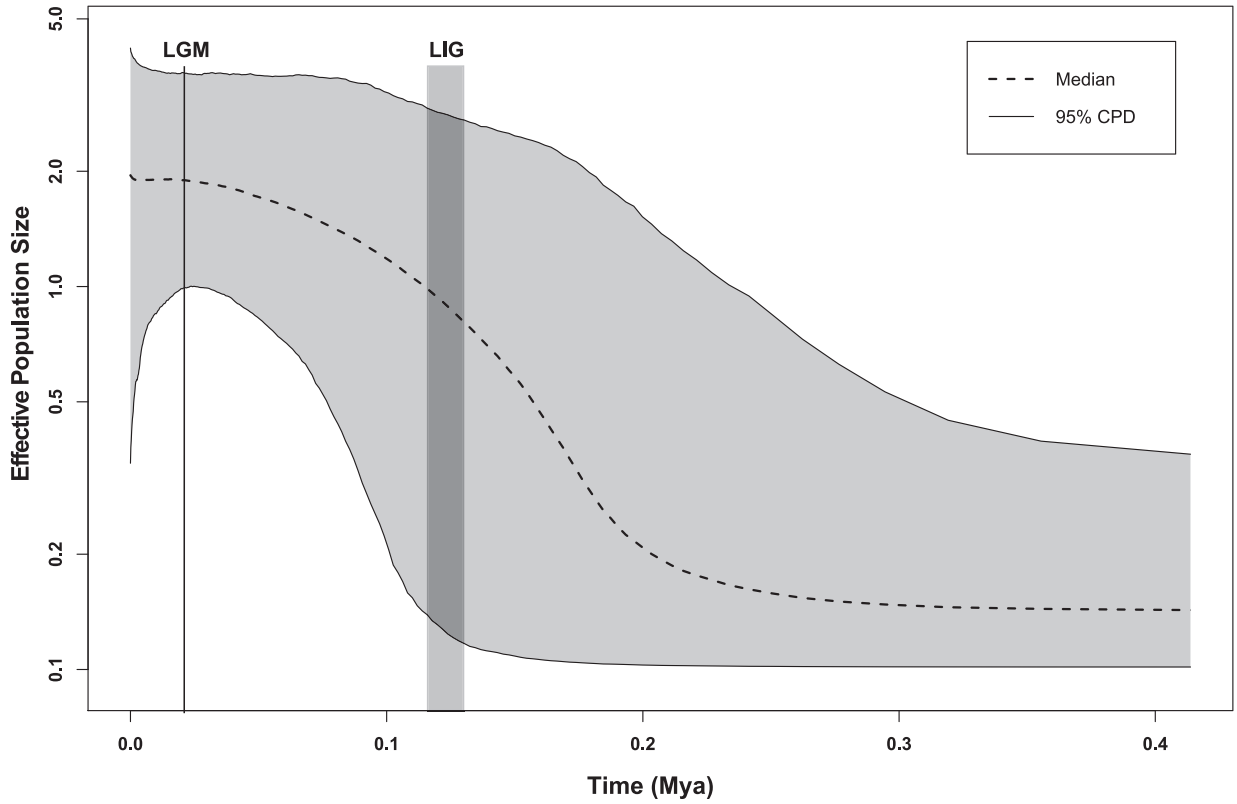

Figure 5. Extended Bayesian skyline plots showing changes in effective population size over time. The Last Interglacial (LIG) and Last Glacial Maximum (LGM) are indicated by vertical bars.

number of biogeographical studies have included demographic analyses or the ENM approach (Ansell *et al.*, 2011; Koch *et al.*, 2016; López-Pujol *et al.*, 2016; Smýkal *et al.*, 2017). The present study represents the first integrating study of Anatolian subalpine/alpine plants based on ENM and demographic analyses.

Mountains play a key role as cradles, bridges, barriers for species and reservoirs of biodiversity, and their high species richness is a product of the interaction of topographic heterogeneity with climate ((Antonelli *et al.*, 2018; Perrigo *et al.*, 2019; Salariato *et al.*, 2020). As a result of their complex topographic and climatic features, the Anatolian Mountains maintain high floral diversity and contain many micro-refugia (Ansell *et al.*, 2011; Şekercioğlu *et al.*, 2011). It is well known that a species can find its optimal niche by moving very short distances along a mountain gradient, unlike lowland environments. This phenomenon is especially true for the Anatolian Mountains, and cold-adaptive alpine populations would have been isolated at the higher elevations of these mountains. Thus, the Anatolian Mountains represent a complex refugial system (Çıplak, 2008; Korkmaz *et al.*, 2014; Perrigo *et al.*, 2019).

Taking into account that the distribution areas of alpine plants during the glacial periods were broader than during the interglacial periods (Schönswetter *et al.*, 2005; Kajtoch *et al.*, 2016), the results herein were in accordance with this hypothesis exemplified by many alpine taxa (Anderson *et al.*, 2006; Opgenoorth *et al.*, 2010; Gao *et al.*, 2015). The historical distribution patterns predicted by the ENM revealed that *N. iberidea* had a potentially large distribution area throughout Anatolia during the LGM (Fig. 2B), as expected for a cold-adapted/cold-tolerant species.

Population expansion during the LGM was supported by haplotype networks. One haplotype (H3/R2) was found at a higher frequency, and the other haplotypes were generally separated from this haplotype by one or two mutation steps in both networks (Figs 3, 4). Thus, both networks were typically star-like and indicated a recent population expansion. Additionally, this pattern more or less matched the Avise's phylogeographical category V (Avise, 2000), which included a widespread

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haplotype and closely related private haplotypes. Hence, it can be interpreted that populations were connected during glacial periods but isolated during interglacial periods (including the present). A possible reason for the current or past interglacial breaks seemed to be the presence of deep valleys among Anatolian Mountains (Atalay, 1996).

Noccaea iberidea has winged but dehiscent fruit; therefore, the fruit opens during maturation (Mummenhoff *et al.*, 2009; Bhattacharya *et al.*, 2019). Owing to the anatomical structure of *N. iberidea* fruit, wind dispersal does not seem a likely mechanism, either for the fruit or for its wingless seeds. Therefore, long-distance dispersal might not be a mechanism to explain the distribution pattern of this species. The most plausible explanation of the genetic relationships of populations might be a gradual expansion during glacial periods, rather than long-distance dispersal, because the seeds of *N. iberidea* do not seem to be able to cross deep valleys during interglacial periods. This is also congruent with the hypothesis for the present and past interglacial breaks.

An expansion revealed by the haplotype networks was supported by the unimodal mismatch distributions presented in Figures 3 and 4. Apart from the northern part of the distribution area of *N. iberidea* and some individual mountains, such as Beydağı (H13), common haplotypes can be observed in the whole distribution area of the species (Fig. 3). In the ribotype network, a common ribotype (R2) was also observed in the northern part of the species distribution area. However, maternally inherited cpDNA showed pronounced haplotype diversity along with a large number of geographically localized haplotypes. At this point, two distinct models, Pioneer and Phalanx, which explain the consequences of population expansion on genetic legacy, can be mentioned (Hewitt, 2004). The Pioneer model is characterized by a decrease of genetic diversity along latitudes as a result of a founder effect during interglacial periods, whereas the Phalanx expansion model supposes elevational range shifts owing to climatic oscillations, often without the loss of allelic diversity (Hewitt, 2004; Yan *et al.*, 2012; Shao *et al.*, 2017). Following the prediction of the Phalanx expansion model, one can argue that populations, like islands, would form at the higher elevations of the Taurus and Anatolian Diagonal during interglacial periods, and these mountains might create a complex refugial system in Anatolia (Çıplak, 2004, 2008). Consequently, this type of elevational range shift would result in multiple centres of diversity, as in the case of *N. iberidea* and the Anatolian population of *Arabis alpina* (Ansell *et al.*, 2011).

Differences in the frequency and distribution between the haplotypes and ribotypes can be explained by the differences in the rate of evolution. Despite the low mutation rate (see the Results section), the cpDNA data set resulted in a higher HD (0.876 vs. 0.514), as observed in the crucifer genus *Aubrieta* (Koch *et al.*, 2016), but this can be associated with its longer sequence length (1186 vs. 624 bp).

The results of the neutrality tests and the unimodal mismatch distribution of both the ITS and plastid data sets also corroborated a rapid expansion. An expansion that started ~200 kya and continued between the LIG and LGM was detected by the EBSP in accordance with those of the ENM results. A similar expansion pattern was also observed in different crucifer species. The expansion of *Arabis alpina* populations or the major haplogroups of the genus *Aubrieta* was dated long before the LGM, but still in the Quaternary period (Ansell *et al.*, 2011; Koch *et al.*, 2016). Contrary to the results of these studies, no phylogeographical structure with highly supported phylogenetic clades in *N. iberidea* has been observed, and this can be linked to large effective population sizes, which have limited genetic drift (Crow, 1986).

However, the ENM results indicated fewer suitable areas for the present time than during the LGM, and this could be an indication of a recent population contraction. The EBSPs, based on both the ITS and cpDNA data sets, were not able to detect a recent contraction, which was clearly detected by the ENM after the LGM. Therefore, it was tentatively concluded either that 20 kya was too short a time to reveal such a contraction event in the population history of *N. iberidea* or that the markers used in this study might not have had sufficient variation.

An expansion in the distribution of the habitat suitability for *N. iberidea* in the LGM presumably accompanied an expansion in the distribution of steppe areas in inner, southern and eastern Anatolia, because this species is strictly associated with steppe communities. Owing to the co-occurrence of the members of these communities and the fact that they have similar life-history traits, including a perennial life cycle, resistance to disturbance via below ground structure, etc., it was concluded that *N. iberidea* can mirror the biogeographical history of tragacanthic plant communities throughout the Anatolian Mountains. To test this idea, some representatives of these plant communities, such as *Astragalus* spp., could be subjected to similar studies for further conclusions. Such research might contribute to our understanding of the responses of these communities to climate change and also aid in the development of conservation strategies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

AppendixS1. Alignment of ITS ribotypes.
Appendix S2. Alignment of cpDNA haplotypes.
Appendix S3. GenBank accession numbers for the sequences (*trnL-F* region including *trnL(UAA)* gene, *trnL-F* spacer) used in the phylogenetic analyses.

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