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Dedicated to the Professor Adam Boratyński

Demographic history and range modelling of the East Mediterranean *Abies cilicica*

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Abstract. The Mediterranean Basin is one of the 36 global hotspots of biodiversity and it is rich in endemic tree species. The complex geological history of the region throughout the Neogene and Quaternary periods that were marked with several palaeoclimatic transformations was a major factor triggering the genetic divergence of lineages in tree species in the region. The ongoing global climate change is the main factor threatening Mediterranean biodiversity. The risk of population decline related to aridization is the highest in the case of endemics, especially for cold-adapted conifers, such as *Abies cilicica*. The Cilician fir grows in the East Mediterranean mountains that constitute a local centre of endemism within the region. The species range is fragmented and small-size populations prevail. Previous studies have suggested that the last glacial cycle led to a significant reduction in the species range and might have initiated genetic divergence. As a result, two lineages are currently recognized at the subspecies level, *A. cilicica* subsp. *isaurica* (Turkey) and *A. cilicica* subsp. *cilicica* (Turkey, Syria, and Lebanon). The predictions about the impact of future climate changes in the East Mediterranean suggest a profound reduction of precipitation and overall warming that may put the remnant populations of *A. cilicica* at a risk of decline. Here, we used the Bayesian approach to investigate the demographic history of endemic *A. cilicica*. Specifically, we estimated the probable time of the intraspecies divergence to verify previous assumptions about the species' evolutionary history. Additionally, niche modelling was used to outline the potential range of changes in the past and to indicate glacial refugia in where the species persisted climate crisis. This approach was also used to explore the possible influence of the future climate changes on the distribution of *A. cilicica* in the region. Our results demonstrate that the divergence between the Lebanese and the Turkish populations that occurred ~220 ka years BP coincided with the Riss glaciation. According to palaeoecological data, in the East Mediterranean, that glacial period caused a severe reduction in the populations of woody species due to the aridity of the climate. At that time, the Lebanese-Syrian part of the range was likely disconnected from the main range. The second split was induced by the last glacial cycle ~60 ka years BP and led to the separation of the Central Taurus and East Taurus population and, consequently, to the formation of the two subspecies. Niche modelling for the last glacial maximum has allowed us to locate the probable refugia for *A. cilicica* in the western Anatolia and Syria-Lebanon area. A projection of the future possible distribution of the species indicates a serious reduction of the range during this century.

Key words: Cilician fir, demographic scenarios, endemics, future range, genetic divergence, refugia

Introduction

The Mediterranean biome covers ~20% of the Earth's surface (Medail & Quezel 1997). Among the five Mediterranean climate regions worldwide, the Mediterranean Basin constitutes the largest domain comprising ~25,000 plant species of which more than half are endemic (Medail & Quezel 1997). Trees are a crucial component of the high plant richness in the Mediterranean. For example, while in temperate Europe 30 tree species have been found, 245 species and subspecies have been recorded in the Mediterranean (Médail et al. 2019). This outstanding biodiversity has made this region one of the global hotspots of biodiversity which are the priority in large-scale strategies of

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nature conservation (Mittenmeier et al. 2011; Albassatneh et al. 2021).

Recent reports and projections about global climate changes have defined the reduction of precipitation as the main factor threatening the stability of most natural ecosystems, with strong implications for human societies (IPPC, 2014). Nearly all regions in the world will experience drought events of different scales and intensities. In this matter, the Mediterranean Basin has been recognized as one of the most vulnerable regions to future climate warming. It has been even defined as the hotspot of climate change (Hoerling et al. 2012; Spinoni et al. 2018). Drought periods are likely to appear more frequently in the future, may last longer, and be more severe. Throughout 1960–2005, which does not include the last, most critical decade, the precipitation trend in the Mediterranean basin was –22 mm per decade (Mariotti et al. 2008). The pattern is not fully consistent as some areas of the Mediterranean will experience further loss of precipitation by the end of this century while others may gain more precipitation (Zittis 2018). The maintenance of this dry trend in the Mediterranean is one of the major concerns in the context of the survival of many endemic plant species in the region, which already have a narrow and fragmented distribution and/or occur in specific habitats. In this regard, cold-adapted and temperate tree species growing in the mountain belts of the Mediterranean, like coniferous species, may be at a high risk of decline (Ruiz-Labourdette et al. 2013; Marqués et al. 2016; Navarro-Cerrillo et al. 2020).

The level of endemism and biodiversity is not equally distributed within the Mediterranean and several local hotspots have been defined, such as the East Mediterranean which is the richest regional hotspot (Medail & Quezel 1997). The Mediterranean part of Turkey has been found to have the highest species variability, with a level of endemism reaching 31%. Similarly, high endemism is found also in the Syria-Lebanon area. Comparative studies have indicated that genetic diversity is also unequally distributed, and the eastern part of the Mediterranean harbours a significantly higher within-population genetic diversity of coniferous species (Fady & Conord 2010). One of the causes discussed of the observed east-west gradient of diversity is the impact of the last glacial cycle on the demographic history of the populations and repeated intraspecies divergence events that took place during their isolation in refugia. Accordingly, the higher diversity noted in the East Mediterranean may reflect the existence of more stable and milder conditions during the Last Glacial Maximum (LGM) in that area, that supposes the maintenance of a large effective size of tree populations in comparison to the West Mediterranean or southern Europe (Fady-Welterlen 2005; Fady & Conord 2010).

In the Northern Hemisphere, the last glacial cycle is the most frequently invoked factor responsible for the directions and the rates of the microevolution of woody species (e.g., Hewitt 2000; Petit et al. 2002; Roberts & Hamann 2015; Bagnoli et al. 2015; Dering et al. 2017). While this interpretation of the causative agents of intraspecific diversity and its spatial attributes predominates, some studies have identified the events of intraspecific divergence as having occurred earlier than the last glacial cycle. For example, the spatial distribution of the chloroplast variability in *Quercus suber* reflects the palaeoenvironmental changes in the West Mediterranean during the Oligocene – Miocene period (Magri et al. 2007). The adaptive divergence and split into western and eastern genetic pools of *Taxus baccata* was dated to ~2 Myr and it was attributed mostly to the interglacial periods (Mayol et al. 2015). On the other hand, investigations have revealed that intraspecific divergence may have occurred more recently – at the onset of the Holocene, when species expanded after the LGM and adapted to new habitats. Such a scenario was recently provided for *Pinus nigra* (Scotti-Saintagne et al. 2019).

Abies cilicica (Cilician fir) is an endemic fir species known from the mountains of the East Mediterranean region where it has been reported in three main distributional domains (Fig. 1). It occurs in the Central Taurus, East Taurus, and Amanus Mountains in Turkey, the Jbel Ansariye in Syria (Alawi Mountain Range or Syrian Coastal Mountain Range), and Jabal Ammoua and Ehden in Lebanon (Mount Lebanon Range) (Awad et al. 2014). This disjunct distribution is also reflected in taxonomical assessments because populations from the Central Taurus have been recognized as *A. cilicica* subsp. *isaurica*, while the remaining stands of this fir have been described as *A. cilicica* subsp. *cilicica* (Farjon 2010). In Turkey, Cilician fir grows at elevations between 1,150 and 2,000 m on the north- and 1,450 and 1,550 m on the south-facing slopes of the Taurus Mts. (Kaya & Raynal 2001). The species forms pure or mixed stands with *Pinus nigra* and *Cedrus libani* (Kaya & Raynal 2001; Kavgaci et al. 2010). Additionally, *Juniperus excelsa*, *Juniperus foetidissima*, and *Juniperus drupacea*, have been recognized as components of the fir forests (Kavgaci et al. 2010). *Abies cilicica* is at risk in its lower elevation localities due to the adridization of the local climates (Aussenac 2002; Gardner & Knees 2013) and is a near-threatened species in Lebanon (Talhouk et al. 2003; Awad et al. 2014) where fir forests reach their southernmost distribution.

Genetic studies have revealed significant differences between different distributional areas and almost a lack of intraspecific gene flow (Sękiewicz et al. 2016; Litkowiec et al. 2021). A low historical admixture suggests profound genetic isolation and rather an ancient split between the range fragments. However, details about the timing of the genetic divergence in this species are not known, and Pleistocene climatic oscillations have been hypothesised as the most probable factor contribution to intraspecific divergence (Sękiewicz et al. 2015). In this paper, we have used genetic data generated previously for this species based on nuclear microsatellite markers to answer the question about the most likely time of the intraspecific differentiation in Cilician fir. Considering the significant morphological differentiation between the subspecies of *A. cilicica*, reduced gene flow, and geographic isolation, we hypothesise that the very first divergence appeared between *A. cilicica* subsp. *isaurica* (Central Taurus) and *A. cilicica* subsp. *cilicica* (East Taurus) while the split

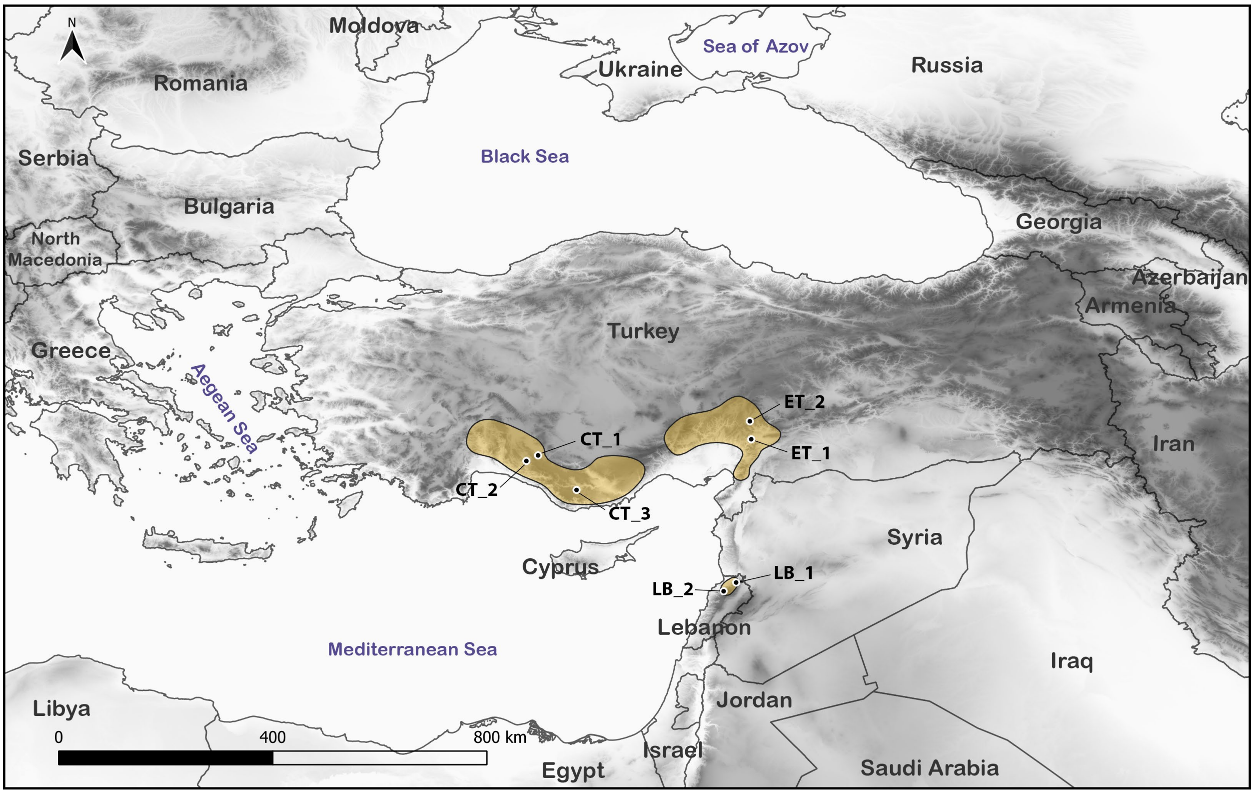

Figure 1. Location of studied populations of Cilician fir and the natural range of the species outlined with yellow color. Acronyms as in Table 1.

between the Lebanese and East Taurus genetic pools might have taken place later. To this end, we tested different demographic scenarios with a Bayesian approach. To refer the possible demographic to past changes of the natural range, we modelled the species range boundaries during the LGM using niche modelling. Next, considering the ecological requirements of the species in terms of precipitation and predictions about further aridization of the East Mediterranean region (Bucchignani et al. 2018), we investigated possible changes in species occurrence in the future, in reference to the possible risk of species decline.

Materials and methods

Plant material and genotyping

Seven natural populations of *Abies cilicica* from the East Mediterranean were included in this study (Table 1, Fig. 1). They were sampled in a natural range covering Turkey and Lebanon in 2009. Three populations were located in the Central Taurus (CT_1, CT_2 and CT_3) and represented *A. cilicica* subsp. *isaurica*. Two other populations in the East Taurus (ET_1 and ET_2) and two in Mount Lebanon (LB_1 and LB_2) represented *A. cilicica* subsp. *cilicica.* In each of the populations, 30 individuals were sampled, except for LB_2. The details about sampling scheme are presented in Sękiewicz et al. (2015). In total, 192 mature individuals were subjected to statistical analyses performed in this work. The genotypes for all individuals were obtained from Sękiewicz et al. (2015). Genotyping was performed with six nuclear microsatellite markers (nSSRs) originally developed for *A. alba*: SFb5, SF333, SF1, SF_239, SF78, and SFb4 (Cremer et al. 2006). The details of genetic analysis are presented in Sękiewicz et al. (2015).

Demographic history

Demographic scenarios of *A. cilicica* population divergence were tested through the Approximate Bayesian Computation (ABC) using DIYABC 2.1.0 (Cornuet et al. 2014). To reduce the complexity of simulations, the investigated populations were assembled into three groups revealed by STRUCTURE results presented in Sękiewicz et al. (2015). Genepool 1 (Pop1) contained populations ET_1 and ET_2, genepool 2 (Pop2) consisted of populations LB_1 and LB_2, and genepool 3 (Pop3) – CT_1-CT_3. Three scenarios regarding the topology of

Table 1. Locations of the studied populations of Cilician fir.

Population	N	Taxon	Location (N/E)	Altitude (a.s.l.)
CT_1	30	*Abies cilicica* subsp. *isaurica*	37°13′25″ 32°00′34″	1700 m
CT_2	30	*Abies cilicica* subsp. *isaurica*	37°06′12″ 31°45′30″	1400 m
CT_3	30	*Abies cilicica* subsp. *isaurica*	36°28′55″ 32°50′07″	1430 m
ET_1	30	*Abies cilicica* subsp. *cilicica*	37°34′12″ 36°35′05″	1300 m
ET_2	30	*Abies cilicica* subsp. *cilicica*	37°57′20″ 36°33′19″	1500 m
LB_1	30	*Abies cilicica* subsp. *cilicica*	34°29′44″ 36°15′40″	1565 m
LB_2	12	*Abies cilicica* subsp. *cilicica*	34°18′27″ 35°59′32″	1565 m

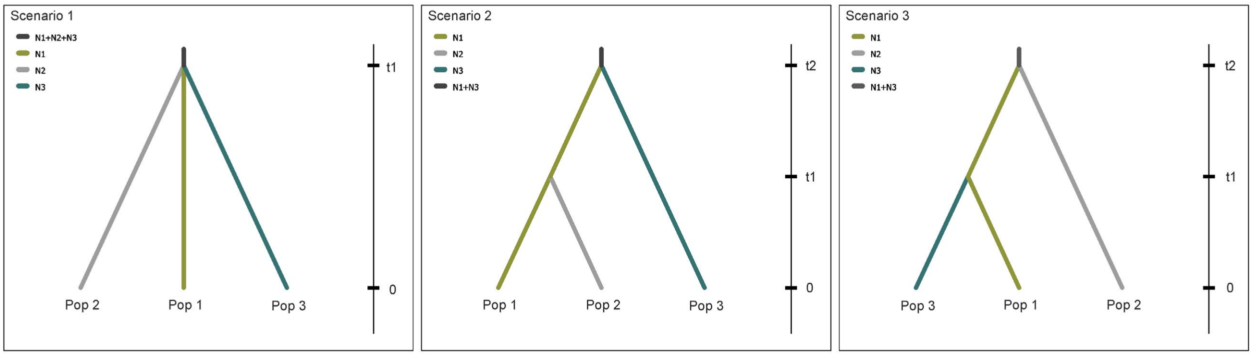

Figure 2. The topography of three demographic scenarios tested in DIYABC for Cilician fir. N1–N3 is for effective population sizes and refers to the genepools denoted as Pop 1–Pop 3. The time is not scaled: t1 and t2 denote time of the demographic event (here divergence), 0 states current time.

population ancestry were created based on the patterns of genetic differentiation revealed in Sękiewicz et al. (2015) and the evolutionary history of the genus *Abies* in Europe described by Linares (2011). Accordingly, the results of Sękiewicz et al. (2015) indicated that the current taxonomic division of the species was a result of the fragmentation of a previously more continuous ancestral range, while Linares (2011) assumed the existence of a single ancestor for the modern *Abies* species in the Mediterranean. Consequently, three scenarios (scenarios 1–3) mirror the possible intra-species divergence with the primary assumption of the existence of a common ancestor for both subspecies (Fig. 2).

The details of the DIYABC procedure, i.e., the prior distributions, are given in Table 2. We performed 6×10^5 coalescent simulations for the tested scenarios and scenario-prior combinations were evaluated using Principal Component Analysis (PCA) to test the fit between priors and observed data. The selection of the optimal scenario was done by calculating the posterior probabilities of each scenario using a logistic regression on the 1% of simulated data closest to the observed data. The confidence in the scenario choice was evaluated by generating 1,000 data sets from priors and by computing Type I (proportion of data sets simulated under the best scenario assigned to other scenarios) and Type II (proportion of data sets simulated under other scenarios assigned to the best scenario) errors. The posterior distributions of the genetic and demographic parameters were estimated using a local linear regression approach on the 1% of the simulated data closest to our observed data set after logit transformation of the parameters.

Range modelling

The theoretical range of *A. cilicica* in the East Mediterranean region was estimated in MAXENT 3.3.2 (Phillips et al. 2004, Elith et al. 2011). A dataset of 70 occurrence points (one point per grid cell of 1×1 km) that included our own information, published locations, and the GBIF database (Global Biodiversity Information Facility, 2020) were used. All data were checked in terms of reliability using the GoogleEarth application. Initially, a set of 19 bioclimatic variables, downloaded from the CHELSA database for near current conditions (for a climatological period from 1979–2013) and the CCSM4 Last Maximum Glaciation model (Gent et al. 2011; Karger et al. 2017) were employed with a 30 arc-sec resolution. We used this climatic dataset because of its high prediction accuracy and ability to reflect mountain-specific climatic conditions, particularly in terms of precipitation-related

Table 2. Prior distribution of estimated parameters used for demographic analysis in Cilician fir.

Parameters	Distribution	Min–Max	Mean	Shape
Genetic parameters				
Mean mutation rate	Log uniform	10^{-4}–10^{-3}		
Individual mutation rate	Gamma	10^{-5}–10^{-2}	Mean mutation rate	2
Mean coefficient P	Uniform	0.1–3.00		
Individual locus coefficient P	Gamma	0.1–9.00	Mean coefficient P	2
Mean SNI rate	Log-U	10^{-8}–10^{-5}		
Individual locus SNI rate	Gamma	10^{-9}–10^{-4}	Mean_u_SNI	2
Historical parameters				
N1 East Taurus (Pop1)		10–10000		
N2 Mount Lebanon (Pop2)		10–10000		
N3 Central Taurus (Pop3)		10–10000		
t1		10–10000		
t2		10–10000		
Conditions	t2>t1			

N1–N3 – effective population sizes; Coefficient P – parameter of the geometric distribution in Generalized Stepwise Mutation model used in ABC procedure; SNI rate – rate of insertion/deletion of a single microsatellite repeat; t1 and t2 – the time of the divergence events in the past estimated in number of generations.

variables (Karger et al. 2017). The correlation between climatic variables among the 19 used was evaluated with the *raster.cor* function from the ENMTools package in R 3.4.3. (R Core Team, 2013). To reduce collinearity between variables, several variables had to be dismissed (BIO1 – annual mean temperature, BIO2 – mean diurnal range, BIO4 – temperature seasonality, BIO5 – max. temperature of the warmest month, BIO10 – mean temperature of the warmest quarter, BIO11 – mean temperature of the coldest quarter, BIO12 – annual precipitation, BIO13 – precipitation of the wettest month, BIO14 – precipitation of the driest month, BIO16 – precipitation of the wettest quarter, and BIO17 – precipitation of the driest quarter) and not used in the final analyses.

The following analyses of the distributional changes of *A. cilicica* were performed: i) for the current conditions, ii) for the LGM, iii) for the future under RCP 4.5, and iv) for the future under RCP 8.5. Representative Concentration Pathways (RCPs) are scenarios of different global changes induced by carbon emissions. RPC 4.5 is frequently described as an intermediate scenario and assumes a peak of the CO_2 emission in 2040, which then declines leading to a global warming of 2–3°C by 2100, relative to pre-industrial temperatures (before 1850). We resigned to investigate the range changes under RCP 2.6, because it predicts the decrease in carbon emission starting from 2020, which is unrealistic, since global emissions are still rising (https://climate.nasa.gov/vital-signs/carbon-dioxide/). RCP 8.5 refers to the concentration of carbon that delivers global warming of about 4.3˚C by 2100: the worst scenario. A bootstrap procedure with 100 replicates with a 'random seed' option was used; 20% of data were used as test points for model evaluation. The output was set to logistic, convergence threshold to 0.00001, and maximum iterations were set to 10,000. The AUC (Value of Area Under the Curve) was used to evaluate the final model performance (Wang et al. 2007). The results were visualized in QGIS 3.4.8 'Madeira' (QGIS.org, 2021 Development Team, 2012).

Results

Demographic history

The PCA-based analysis in the DIYABC run under the tested scenarios showed that the coalescent simulations constructed with the selected prior assumptions were the best to sufficiently reproduce the observed genetic data (Fig. 3), and scenario 3 (Fig. 4) obtained the highest posterior probability equal to 0.7298 [95% CI: 0.7048 – 0.7548]. The proportion of incorrectly identified scenarios over 1,000 test data sets for the logistic approach (the posterior predictive error) was 0.32. The Type I error for scenario 3 was 0.297, and the Type II errors were 0.207 and 0.078 for scenarios 1 and 2, respectively. The PCA results for simulated data overlapped with the PCA results for the data observed in scenario 3, proving the reliability of our simulations (Fig. 5).

The detailed values of the estimated demographic parameters are given in Table 3. DIY ABC provides the time for divergence in number of generations that have past that is converted into calendar years based on the assumed generation time. For dating the differentiation points in *Abies cilicica*, we assumed 60 years to be the generation time. We adopted this time based on suggestions made by Hrivnák et al. (2017) for other East Mediterranean fir species. According to the selected Scenario 3, both intraspecies divergence events in *A. cilicica* preceded the LGM that occurred during Pleistocene. The first divergence was dated to 220,200 years BP [95% CI: 63,600–549,000] and involved a split between the Lebanese and the Turkish genepools. The second split mirrored the divergence between the Central and East Taurus (Fig. 2C) which likely occurred 60,000 years BP [95% CI: 15,400–171,000]. The median values of the effective population sizes for this scenario were 7940 for Pop1, 3630 for Pop2, and 4210 for Pop3.

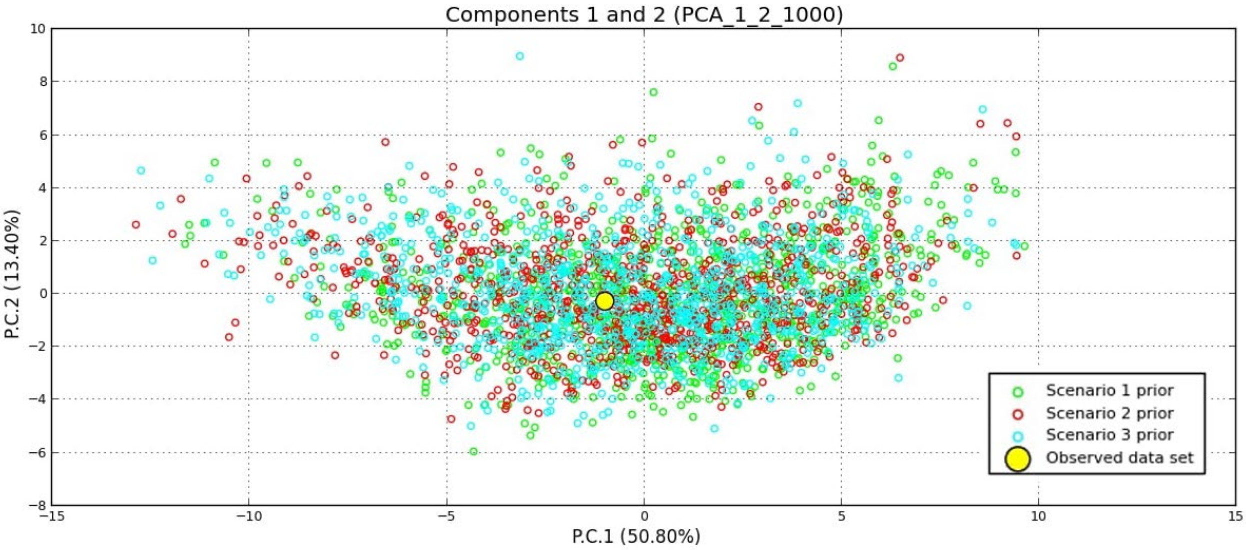

Figure 3. Principal Component Analysis (PCA) to evaluate the simulated data sets to test for the scenarios of divergence. Each color dot represents simulated data for each of the scenarios tested while the big yellow dot represents the observed data set.

Table 3. Demographic parameters estimated for Cilician fir according to Scenario 3. The topology of Scenario 3 is presented in Fig. 2.

Parameter	Median	Q5%	Q95%
N1 East Taurus (Pop1)	7.94×10^{3}	4.07×10^{3}	9.89×10^{3}
N2 Mount Lebanon (Pop2)	3.63×10^{3}	1.13×10^{3}	8.58×10^{3}
N3 Central Taurus (Pop3)	4.21×10^{3}	1.12×10^{3}	9.08×10^{3}
t1	1.00×10^{3}	2.58×10^{2}	2.85×10^{3}
t2	3.67×10^{3}	1.06×10^{3}	9.15×10^{3}
µmic	4.33×10^{-4}	2.50×10^{-4}	9.68×10^{-4}
Pmic	7.75×10^{-1}	1.45×10^{-1}	2.87
SNImic	3.50×10^{-7}	1.23×10^{-8}	7.85×10^{-6}

N1–N3 – effective population sizes; µmic – mutation rate; Pmic – coefficient P, a parameter of the geometric distribution in Generalized Stepwise Mutation model used in ABC procedure; SNImic – rate of insertion/deletion of a single microsatellite repeat.

Niche modelling

The climatic space suitable for *A. cilicica* is defined by a set of variables listed in Table 4. The most significant variable was BIO19 (Precipitation of Coldest Quarter) followed by BIO8 (Precipitation of Warmest Quarter). The current theoretical geographic distribution presented in Fig. 6A is broader in comparison to the observed range, which is especially clear for the *A. cilicica* subsp. *isaurica* in the West Taurus. MAXENT also predicted a wider distribution of *A. cilicica* subsp. *cilicica* in Lebanon and Syria with high habitat suitability. A projection of the probable LGM natural range indicated that the range of *A. cilicica* subsp. *isaurica* might have covered not only the Central Taurus range, but also West Turkey over the Aegean Sea (Fig. 6B). According to our simulations, the range of *A. cilicica* subsp. *cilicica* in the East Taurus shifted southward during the LGM to areas presently covering the territory of Syria, while the Lebanese part of the range remained largely unchanged. In terms of future predictions, both considered scenarios presented a reduction of the species range (Fig. 6C–D). Future climatic refugia are likely to become reduced to the central parts of the East Taurus and Lebanon. The current range in the East Taurus is predicted to become almost completely lost by the year 2070.

Discussion

Genetic divergence

In the Northern Hemisphere, the range-wide patterns of differentiation reflect the rate and directions of the microevolutionary processes primarily controlled by the last glaciation (Hewitt 2000; Magri 2008; Dering et al. 2017). The locations of refugia during the LGM and re-colonization routes were of crucial significance for the current genetic structure of many European tree species (Havrdová et al. 2015; Tollefsrud et al. 2015). The model of vicariance in distinct and genetically isolated refugia that existed during the last glacial period predominated as a major mechanism of intraspecies divergence and only a handful of studies have provided data that proved the earlier intraspecies diversification (e.g., Mayol et al. 2015).

Here, we have provided the first insights into the demographic history of East Mediterranean *Abies cilicica*, an important component of the mountainous forest ecosystems of Southern Anatolia. The common ancestor of *A. cilicica* was likely present during the Miocene-Pliocene (23–5.3 Ma) period in the eastern part of the Parathetys together with the ancestors of the modern *A. alba* and *A. cephalonica* (Linares 2011). According to the hypothesis of the east-west speciation sequence proposed for the genus *Abies*, the ancestor of *A. cilicica* might have been the first taxon to diverge (Linares 2011). The likely impulse for diversification in *Abies* in the East Mediterranean region was the palaeogeographical and climatic transformation of the region related to the Alpine orogeny and the formation of the Mediterranean Sea (Popov et al. 2006). Those events led to the uplift of the major mountain belts in the region which offered new habitats for cold-adapted firs at the time of the progressing climate aridization and set what is now defined as the Mediterranean climate. While the progenitor of a current *A. alba* spread in a westward direction widely colonizing new territories on the European continent, *A. cilicica* spread locally and occupied the southern fringes of the Asia Minor Peninsula, including the Taurus Mts., the Syrian Coastal Mountain Range, and Mount Lebanon. Surprisingly, the split between the Central Taurus and East Taurus lineages that are also morphologically very distinct occurred earlier than the divergence within *A. cilicica* subsp. *cilicica*. According to our ABC analysis, the very

Table 4. Contribution of the environmental variables in the tested climate models. The climatic variables with the highest contribution to model are bolded.

Variables	*Model*	Current	LGM	RCP 4.5	RCP 8.5
	AUC	0.980	0.980	0.981	0.981
BIO3	Isothermality	0.6	0.7	1.1	1.0
BIO6	Min Temperature of Coldest Month	6.8	5.3	5.7	5.0
BIO7	Temperature Annual Range	**10.7**	**10.7**	9.7	9.9
BIO8	Mean Temperature of Wettest Quarter	16.1	17.2	16.9	18.9
BIO9	Mean Temperature of Driest Quarter	10.4	10.1	12.1	10.4
BIO15	Precipitation Seasonality	8.3	9.6	8.0	9.4
BIO18	Precipitation of Warmest Quarter	**10.8**	**10.9**	**10.3**	9.8
BIO19	Precipitation of Coldest Quarter	36.2	35.5	36.2	35.7

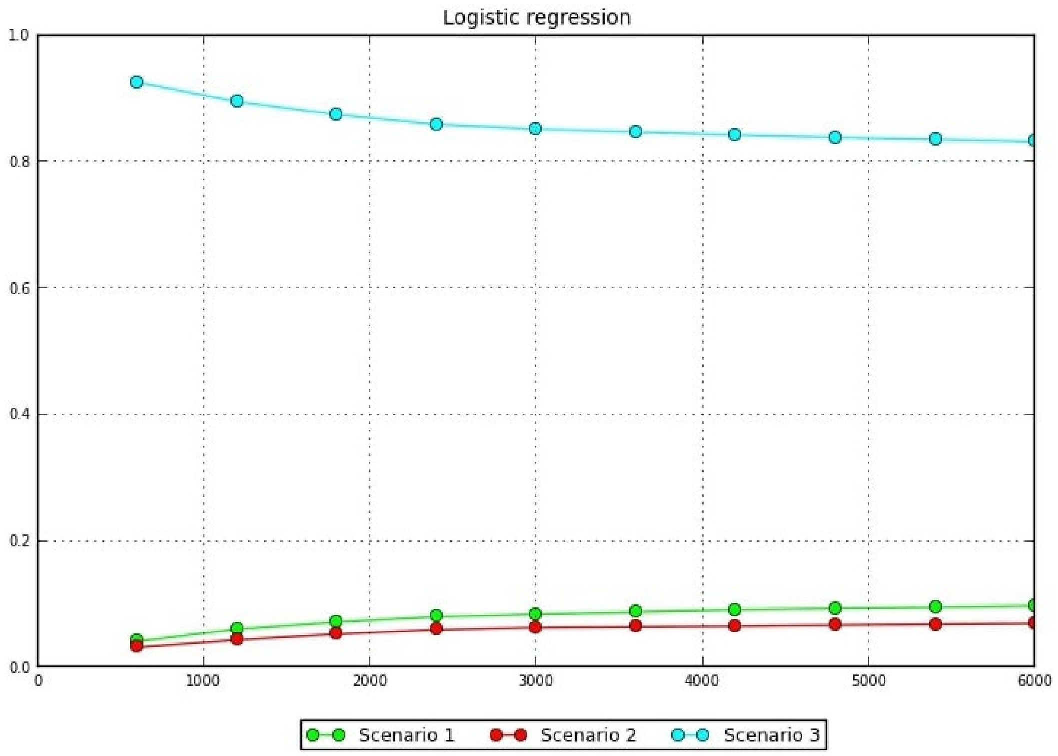

Figure 4. Posterior probability of scenarios of divergence – a logistic regression – indicating Scenario 3 as the most probable demographic scenario.

first diversification within *A. cilicica* occurred over 220 ka years BP and involved the separation of two genetic pools – one currently related to the populations distributed in Mount Lebanon and the second one in the East Taurus Range. The reduction of the range of *Pinus pinea*, also growing in the East Mediterranean domain, has been shown to have occurred as a result of the Riss glaciation (Jaramillo-Correa et al. 2020). The reconstruction of the vegetation in Asia Minor from that time revealed the predominance in the pollen spectra species typical for desert-steppe communities which suggests a period of strong aridity (Pickarski & Litt 2017). At the same time, the palaeoclimatic data from Lebanon pointed to optimal conditions for tree growth, including that of fir, the pollen of which was found abundantly in the pollen assemblies (Gasse et al. 2011). In summary, the fragmentation of the previously wider range, and probably also the altitudinal migration in response to the climate deterioration in Asia Minor, led at first to the isolation of the southernmost distributional area of *A. cilicica*. This ancient separation also finds strong support in genetic differentiation. The admixture between populations from the East Taurus and Mount Lebanon was found to be very limited and the pairwise differentiations between populations were quite high, reaching even a value of Fst = 0.25 (Sękiewicz et al. 2016; Litkowiec et al. 2021). However, the long-term

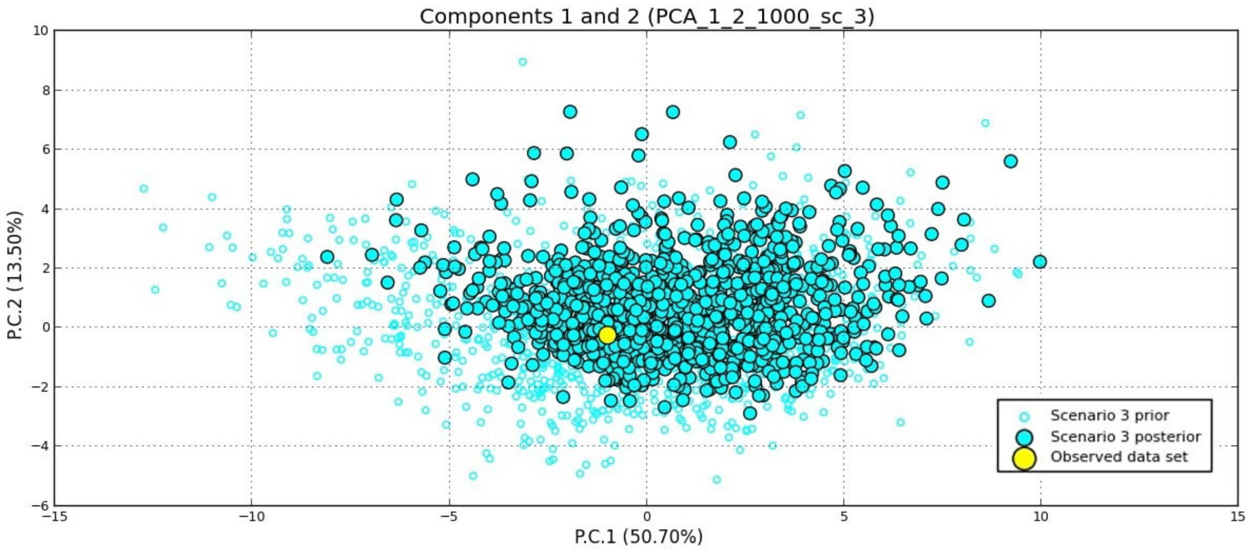

Figure 5. Model checking for the Scenario 3 indicated as the most probable scenario of divergence for current data.

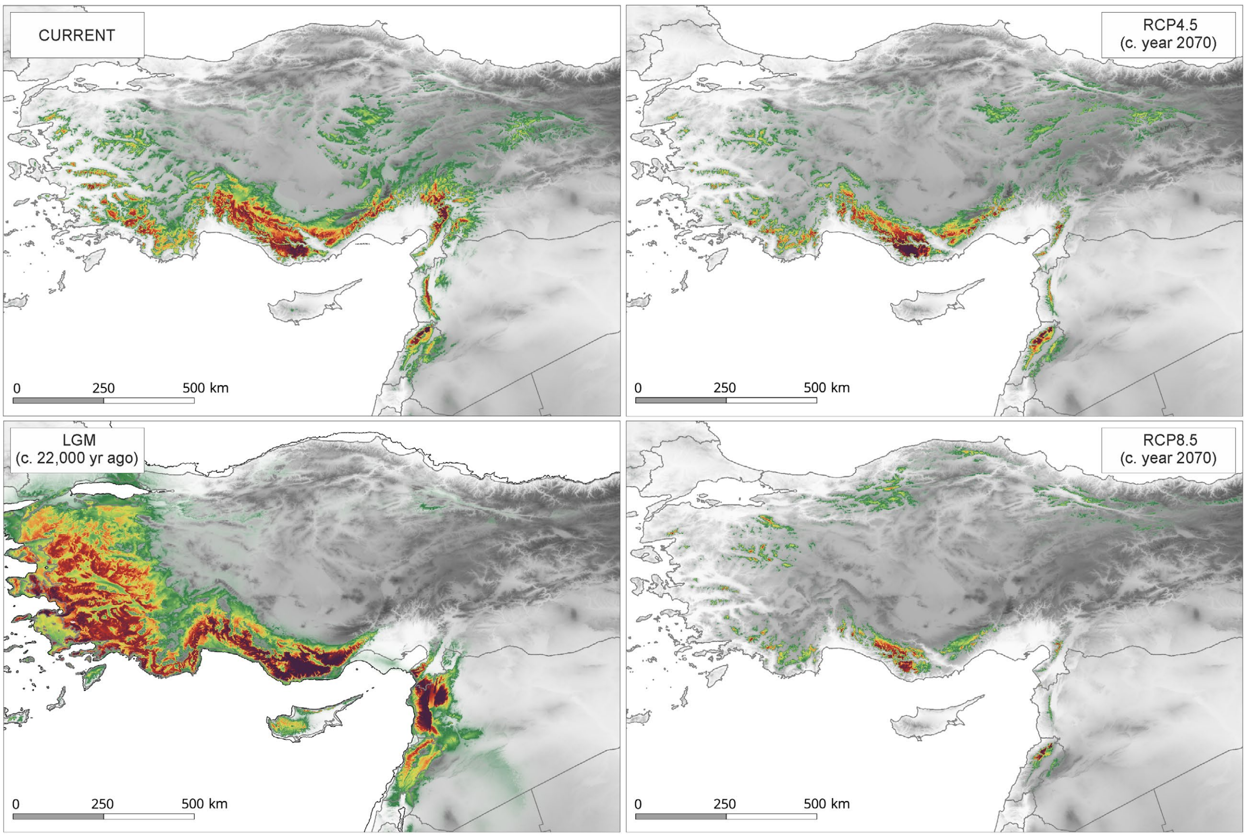

Figure 6. Theoretical range of Cilician fir in the East Mediterranean in different time periods estimated with using MAXENT based on raster data from CHELSA database: current theoretical range, LGM (c. 22,000 years ago), future (c. 2070) range according to scenario RCP4.5 and scenario RCP8.5. Map prepared with QGIS.

genetic isolation between populations of *A. cilicica* from both range domains is less evident at the morphological level and may be referred to as having adapted to shared environmental conditions (Boratyńska et al. 2015). A similar pattern of divergence was also revealed for *Juniperus drupacea* (Sobierajska et al. 2016) and between the Turkish and Lebanese populations of *Cedrus libani* (Fady et al. 2008), *Juniperus excelsa* (Douaihy et al. 2011), and *Quercus cerris* (Bagnoli et al. 2015). Such congruent phylogeographic patterns are a strong premise for the existing shared evolutionary factors of woody species in the East Mediterranean.

The Central and East Taurus populations of *A. cilicica* are genetically and morphologically different and this distinctiveness also found a taxonomical implication (Boratyńska et al. 2015; Farjon 2015; Sękiewicz et al. 2016; Hrivnák et al. 2017). The needles of *A. cilicica* subsp. *cilicica* tend to be smaller in comparison to *A. cilicica* subsp. *isaurica* which may be ascribed to its adaptation to drier habitats. The analysis of the spatial genetic structure points to a limited gene flow among both subspecies (Sękiewicz et al. 2016). The genetic divergence between populations in the West/Central and East Taurus have also been described for other tree species such as *Cupressus sempervirens* (Sękiewicz et al. 2018) and *J. drupacea* (Sobierajska et al. 2016). The genetic split between populations in the Central and East Taurus revealed in our analysis falls into the last glacial cycle, but long before its culmination. However, the climate deterioration in Asia Minor started as soon as 70 ka years BP. An especially high variability in the relative abundances of the arboreal pollen has been recorded in the period ~61–28 ka years BP (Pickarski et al. 2015). It seems that aridization and cooling caused a profound reduction in the tree populations in the whole of Anatolia. The periods of pronounced climate aridization and cooling noted in Anatolia reflect stadial-interstadial patterns correlated with Heinrich events (stadials) and Dansgaard-Oeschger events (interstadials). The inferred time of probable divergence in *A. cilicica* in the Taurus Mts., which was dated with the ABC procedure to have occurred ~60 ka years BP, matches one of such stadial episodes that brought more severe dryness to the region (Pickarski et al. 2015). In the second part of the last glacial cycle, a general trend of aridization and cooling dominated in the region with the culmination during the LGM characterized by very low percentages (<10%) of tree pollen (Pickarski et al. 2015). The temporal regional moisture availability noted after the LGM was secondarily limited during the Younger Dryas climate reversal that, again, significantly reduced the arboreal vegetation. In summary, the intraspecific divergence revealed in *A. cilicica* was tightly related to the climatic changes in the region, but not strictly attributed to the LGM, as frequently assumed for many tree species in the North Hemisphere.

Range formation in the past and predictions of future distributions

The current theoretical distribution of Cilician fir developed by MAXENT is much wider than the realized distribution. Nowadays, the species persists within fragmented forest patches, especially the Lebanese stands (Awad et al. 2014). Beyond the known areas of species occurrence, the model indicated highly suitable habitats on the Aegean coast of the Asia Minor Peninsula where the species is currently absent. The discrepancy between the currently observed distribution and the theoretical one should be referred to as being due to the human impact on the region. The development and spread of the agro-pastoral activities that required forest clearance and fires induced profound changes in the vegetation of the East Mediterranean and the Middle East, also affecting the genetic diversity of tree populations (Dagher-Kharrat et al. 2007; Dusar et al. 2011; Kaniewski et al. 2007). The Lebanese populations are the best example of how the development of early human societies has changed the natural habitats, mostly forests, due to land use. Indeed, those populations are currently the most reduced and fragmented populations of the species because of overexploitation (Awad et al. 2014). Consequently, their genetic variability is low (Awad et al. 2014) putting at risk their adaptability and hence, the long-term persistence of the species in the face of future climate changes.

The most important climatic variable in our model was the precipitation of the coldest quarter (BIO19). It reflects the adaptation of the precipitation to a seasonal pattern in the region, while the thermal requirements of the species are reflected in the input of the second important variable – the mean temperature of the wettest quarter (BIO8). *Abies cilicica* occupies the Oro-Mediterranean climatic zone with precipitation available during the winter season. It grows on southern and northern slopes of the Taurus Mts. (1200–2200 m a.s.l) even with precipitation as low as 800 mm/year, but with significant precipitation coming from the extensive fog that builds up in the upper parts of the mountain belts (Atalay et al. 2014; Aussenac 2002).

The theoretical distribution of *A. cilicica* reconstructed for the period of the LGM covers a much wider area. Interestingly, the Lebanese domain remained spatially stable. The range might have covered approximately the same area in Lebanon as suggested for the current theoretical range. The most striking result of the past range projection denotes a southward shift of the current East Taurus range to the areas currently referred to as Syria. If such a LGM range shift occurred, we would expect the gene flow to have taken place, while genetic studies instead contradict such a possibility (Sękiewicz et al. 2016; Litkowiec et al. 2021). The possible solution of this perplexing inconsistency between genetic and ecological data may lie in the methodological limitations of niche modelling procedures that may lead to an overestimation of past ranges. The modelling based only on climatic variables does not consider other factors having a great impact on the species' distribution pattern, for example, interspecies competition. We can imagine that this type of interaction might be quite intensive in the refugial areas, leading to a much narrower and/or patchy distribution of *A. cilicica*, all while reducing or preventing intensive gene flow. However, a similar location of the glacial refugial has also been indicated for the other oroMediterranean species, *J. drupacea* (Walas et al. 2019), potentially suggesting the existence of some regional refugium in the Syrian mountains.

The prediction of the future changes of climate for the East Mediterranean is expected to bring about drier conditions and more events of extreme dryness (Lelieveld et al. 2012). One of the recent and detailed predictions suggests that one of the most impacted areas might be the high-altitude habitats in Turkey (Bucchignani et al. 2018). If such extreme dry conditions arise, then this climatic trajectory will certainly negatively affect the remnant populations of Cilician fir. Our prediction of the future range of *A. cilicica* clearly indicates that the species is under real threat from the ongoing climate changes, especially populations in the East Taurus. In this situation, it is critically important to undertake conservation activities aiming to mitigate the risk of species decline or extinction from some areas. The Cilician fir is a significant timber source in the region and past overexploitation has led to the genetic depletion of some populations, especially those in Lebanon (Awad et al. 2014). However, the excess of the homozygosity and a bottleneck effect have been confirmed for almost all stands included in this study that were also analyzed by Sękiewicz et al. (2015). These results, referring to the genetic structure of the population in the context of the expected deterioration of the climate and ongoing exploitation of the Cilician fir forests put this species at great risk of reduction. Hence, *in situ* and *ex situ* conservation activities should be launched immediately.

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