ORIGINAL ARTICLE

Past, present, and future geographic range of an oro-Mediterranean Tertiary relict: The *juniperus drupacea* case study

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Abstract

Juniperus drupacea is a unique relict species found in the mountains of southern Greece, southern Turkey, and western Syria and Lebanon. The aim of this study was to describe the natural range of this juniper by determining the current locations of its populations and to predict a theoretical range for the species based on current, past, and future climatic conditions. We used data from the literature, herbarium materials, and our unpublished field notes (about 500 georeferenced points in total) to determine the current natural distribution of *J. drupacea* (realized niche). To predict suitable conditions with the program MaxEnt, we used data from the WordClim database, which allowed estimation of the potential niche. The potential niche of *J. drupacea* was much wider during the Last Glacial Maximum (LGM) and was severely restricted during the Eemian interglacial period. Depending on the climate scenario, this species could become endangered in the future due to climate changes. Considering the relatively restricted geographic range of *J. drupacea* and the decreasing numbers of localities where it is found, conservation strategies should be adopted to allow for preservation of its genetic and morphological diversity.

Editor: Wolfgang Cramer.

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Introduction

The Syrian juniper (*Juniperus drupacea* Labill.) is a Tertiary relict (Palamarev 1989) that currently occurs in a restricted area (Browicz 1982). This exceptional tree is the only representative of the section *Caryocedrus* Endl. of the genus *Juniperus* L. (Adams 2014) and is conspicuous with extremely large seed cones and connected seeds that form a drupe-like structure (Eliçin 1977; Boratyński and Browicz 1982; Maerki and Frankis 2015). This feature was the motivation for placing *J. drupacea* in its own genus *Arceuthos* Antoine & Kotschy; however, this is now generally treated as a synonym of *Juniperus* L. (Coode and Cullen 1965; Gaussen 1968; Christensen 1997; Farjon 2005; Adams 2014).

Juniperus drupacea is a tree that generally grows to a height of about 15–20 m with a stem reaching 60–80-cm diameter (Yaltırık 1993; Christensen 1997), though one individual was measured at 40 m in height (Karaca 1994). The current geographical range of *J. drupacea* covers the southern Peloponnese in Europe (Boratyński and Browicz 1982; Tan et al. 1999; Maerki and Frankis 2015), southern Turkey, western Syria, Lebanon, and the northernmost region of Israel in Asia (Mouterde 1966; Browicz 1982; Yaltırık 1993; Talhouk et al. 2001). The species is a component of *Abies cephalonica* Loudon forests in the mountains of Peloponnese in Europe and *Abies cilicica* (Antoine & Kotschy) Carrière, *Pinus nigra* Arnold, and *Cedrus libani* A. Rich. forests in the mountains of Asia. In the supra-Mediterranean layer of Lebanon, it is found with *Quercus coccifera* L., *Q. infectoria* Oliv., and *Q. cerris* L. (Abi-Saleh et al. 1996). In addition, it forms woodlands with other juniper species in areas previously occupied by forests or on abandoned fields (Zohary 1973; Browicz 1982; Mayer and Aksoy 1986). The occurrence of *J. drupacea* in the Asiatic part of its geographic range is discontinuous, with most localities found in areas recognized as refugia of Tertiary floras, including Central and East Taurus, Amanos, and the Lebanon mountains (Médail and Diadema 2009, p. 1336). This pattern of distribution underlines the relict's tertiary origin. The ancestor of *J. drupacea* probably diverged between the Eocene and Oligocene epochs (Mao et al. 2010). During the late Tertiary and early Quaternary, it was probably a component of the Tethyan and, subsequently, the Mediterranean sclerophyll flora (Palamarev 1989; Kvaček 2002; Palamarev et al. 2005); however, its palaeo-remnants are very scarce (Stockey et al. 2005). It was affected by relatively high temperatures and water deficits during the Messinian salt crisis, and afterward, during the Pliocene and Pleistocene, exposed to climate cooling and oscillations in temperature, which finally reduced its geographic range to the current area.

As a component of oro-Mediterranean communities, *J. drupacea* is a light-demanding tree and only young seedlings survive in shade. The species is moderately thermophilic (Zohary 1973; Yaltırık 1993), but less drought-tolerant than other junipers (Douaihy et al. 2017). These properties allowed *J. drupacea* to survive the Pleistocene climate oscillations in mountainous regions where it migrated to lower elevations during the cold glacial stages and to higher elevations during the warm interglacial periods, as did many other tree species (Hewitt 2004; Eastwood 2004; Thompson 2005). Its numbers most likely decreased during more humid periods due to competition with more moisture-demanding trees, but might have increased during drier periods, as described for other juniper species (Carrión et al. 2001; Carrión 2002; Hajar et al. 2008; Orland et al. 2012). It is also possible that reduction of fir and cedar forests by humans, together with other human activities during recent millennia, allowed for the extension of juniper woodlands with *J. drupacea* (Talhouk et al. 2001; Fady et al. 2008; Douaihy et al. 2011, 2012, 2013; Awad et al. 2014).

Recently, the geographic pattern of genetic and morphological structures of *J. drupacea* has been surveyed (Sobierajska et al. 2016), with identification of six groups of populations which differed genetically: two European, three Turkish, and one Lebanese. This could imply the possible origin from another region and/or long-lasting spatial isolation, together with different reaction of populations from these parts of the species geographic range to the environmental conditions. The differences between European, Turkish, and Lebanese *J. drupacea* were also detected in their essential oil compositions (Adams et al. 2017).

According to the International Union for Conservation of Nature (IUCN), *J. drupacea* is a species of "least concern," with a stable population trends at the global scale (Gardner 2013); however, the European (Gardner 2017) and Lebanese populations (Bou Dagher, personal communication) are considered threatened. Studies of *J. drupacea* distribution on the Peloponnese indicate that their conservation status was vulnerable due to very slow regeneration (Maerki, personal communication).

In Lebanon, cutting of *J. drupacea* is forbidden by law. In that country, it is present in cedar biosphere reserves at Jabal Moussa and Shouf, as well as in other areas under protection. The main current threat in Lebanon is an outbreak of the dwarf mistletoe *Arceuthobium oxycedri* (DC.) Bieb. (Douaihy et al. 2017; Gardner 2013). In addition, the difficulty in germinating *J. drupacea* seed means that it is not a component of forest restoration activities in Lebanon.

The maintenance of *J. drupacea* in Turkey is also under forest legislation, which includes juniper species as protected elements of the forest. It is also conserved in 11 national parks established in the Mediterranean area of Turkey and therefore, there is no distinct threat in the Turkish territory. The use of the fleshy cones by local human populations for the production of pekmez does not threaten the species (Kani Işık, Tolga Ok, and Ali Dönmez personal communication).

Ongoing climate warming and aridization will influence the geographic range of organisms (Case and Lawler 2017; Tang et al. 2017). The influence of the climate warming on woody, long-lived species in the Mediterranean region was demonstrated for *Laurus nobilis* L. (Rodríguez-Sanchéz and Arroyo 2008) and *Cedrus atlantica* (Endl.) Manetti ex Carrière (Cheddadi et al. 2009). Similar studies were conducted with *Juniperus excelsa* M. Bieb. in the central part of Turkey (Özkan et al. 2015), *Q. coccifera* L. in the Levantine countries (Al-Qaddi et al. 2017), and *Taxus baccata* L. in Morocco (Romo et al. 2017). A potential impact of climate changes beginning in the Pliocene through modern times up to the end of the twenty-first century within the entire area of distribution was verified only for laurel and cedar. Impacts on *Laurus nobilis* were possible due to the relatively high number of subfossil remnants available and the large amount of accessible data on current localities. The subfossil data for *Cedrus atlantica*, although restricted, documented the species distribution in the mountains of north-western Africa and allowed for the approximation of palaeo-climate data and delineation of the species geographic range. Together with the climatic factors determining its current distribution, the region with favorable climate conditions for *C. atlantica* into the future was determined.

The subfossil data for junipers are very scarce due to their evolutionary origin and occurrence in arid regions, which reduces the probability of remnant conservation (e.g., Willis and McElwain 2002; Kvaček 2002; Palamarev et al. 2005; Stockey et al. 2005; Velitzelos et al. 2014). Additionally, pollen grains of juniper species are indistinguishable (e.g., Eastwood 2004; Tzedakis 2004). Thus, any retrospective evaluation and prediction of *J. drupacea*'s geographic range can only be based on its current distribution. Therefore, identification of *J. drupacea* occurrence is essential for monitoring demographic processes connected with climate change and for determining conservation needs. We aimed to (1) present the current distribution of *J. drupacea* and (2) define the bioclimatic parameters that determine its current localities. With this information, we (3) defined the geographic range of the species in the past and (4) predicted the potential impact of global climate change on its geographic range in the future. Taking into account the genetic and morphological differences between European (PEL), Turkish (AN), and Lebanese (LEB) populations of the species (Sobierajska et al. 2016; Adams et al. 2017), we intend also to verify its adaptation to local climate and reaction to climate changes.

Materials and methods

Data on the distribution of *J. drupacea* were extracted from the literature and the labels of herbarium materials. The most important collections are preserved in the herbaria of the British Museum (BM), the Botanical Garden of Edinburgh (E), Kew Gardens (K), the Istanbul Universities (ISTE and ISTO), the Universities of Ankara (ANK, HUB, and HUEF), the Naturhistorisches Museum Wien (W), the University of Patras (UPA), the Goulandris Natural History Museum (ATH), and the Institute of Dendrology Kórniks (KOR). Additionally, many field notes were made during the authors' expeditions, starting in the 1970s. When absent in the original documentation, the geographic coordinates (latitude, longitude, and altitude) were retrieved from Google Earth for every locality. Vague descriptions of locality, mostly historical in nature, which did not specify such information, were excluded from the analyses. We gathered more than 900 sets of location data, the great majority of them replicated in different herbaria and literature. From this data, we selected information for about 500 localities with sufficiently detailed geographic coordinates and altitudes (Supplementary Material, Table S1).

Bioclimatic variables were downloaded from the WorldClim database (Hijmans et al. 2005). We analyzed 19 variables (see Table 1) and altitude influences to determine the realized, retrospective, and predicted niches of *J. drupacea*; however, data concerning temperature and precipitation with altitude were generally recognized as the most important (Bradie and Leung 2017). Additionally, Emberger's pluviometric quotient (*Q*) (Emberger 1955) was calculated using the Environmental Rasters for Ecological Modeling (Envirem) R package (Title and Bemmels 2018) according to the formula:

$$Q = \frac{2000\,P}{(M + m + 546.4) \times (M - m)}$$

where *P* is the mean annual precipitation, *M* is the mean maximum temperature of the warmest month, and *m* is the mean minimum temperature of the coldest month.

Data from CAPE Last Interglacial Project (Otto-Bliesner et al. 2006) were used for the interglacial period (about 125 ka BP). For the Last Glacial Maximum (LGM, about 22 ka BP) and mid-Holocene (about 6 ka BP), data from Community Climate System Model (CCSM, Gent et al. 2010) were used. Data for past climate were downscaled and calibrated (bias corrected) using WorldClim 1.4 as the baseline "current" climate. The current and interglacial periods had 30-s (about 900 m at the equator) resolution, while the LGM, Holocene optimum, and future prevision used a 2.5-min (about 4.5 km at the equator) resolution. Two scenarios of future climate were selected as follows: RCP2.6 and RCP8.5 (Collins et al. 2013). The first scenario provided an increase of radiative forcing by 2.6 W m^{-2} before the year 2100 and an increase of average temperature by 1 °C before the year 2065, while RCP8.5 provided an increase of radiative forcing by 8.5 W m^{-2} before the year 2100 and an increase of average temperature by 2 °C before the year 2065.

Prediction of range was performed using the MaxEnt 3.3.3k software (Phillips et al. 2006). It used data related to sites of species localities. To estimate the probability of occurrence of a species outside the known area of distribution and to evaluate habitat suitability, the program used the maximum entropy model. For MaxEnt operation, the maximum number of iterations was set to 10,000, the convergence threshold to 10^{-5}, and the number of replicates to 10. The output format was logistic. A bootstrap run type and the "random seed" option were applied to provide random test partition (Phillips et al. 2006). To evaluate the results of the models, we used receiver operating characteristic (ROC) curves (Wang et al. 2007; Mas et al. 2013). Area under the curve (AUC) values lower than 0.6 meant that the result of the prediction was not much better than random, and a value of 1.0 indicated that the model prediction was excellent. We performed this procedure for the whole data set and subsequently separately for each of the three main groups of localities from the different parts of the species geographic range: (1) European (Peloponnese, PEL), (2) Turkish (Taurus, Anti-Taurus and Amanos mountains, AN), and (3) Lebanese (including Syrian and Israeli, LEB). The populations of *J. drupacea* from these three geographic regions exhibited significant genetic, morphological, and biochemical differentiations (Sobierajska et al. 2016; Adams et al. 2017). All predictions and the most important climatic variables were visualized in QGIS 2.14.21'Lyon' (QGIS Development Team 2012). The influence of particular environmental factors to the distribution of *J. drupacea* was verified using principal component analysis (PCA) implemented in R software.

Results

Present geographic range

The data allowed for an analysis of the relationship between the realized niche (Fig. 1) and recent climatic factors (Table 1). The important information from a geographic point of view was the altitudinal range of the species, which in Peloponnese appeared lower than in Turkey and in Lebanon (Fig. 2). Climatic factors related to the current distribution of *J. drupacea* are intercorrelated, frequently at statistically significant levels. The correlation of realized niche of *J. drupacea* with individual climate variables differed among the different regions of the species occurrence (Supplementary Materials, Table S2).

Evaluation of the MaxEnt model indicated that the realized niche prediction (Fig. 3a) for *J. drupacea* was very high. The average test AUC for the replicate runs was 0.980 for the whole range, 0.990 for Turkey, 0.992 for Europe, and 0.998 for Lebanon. The most important factor determining the

current geographic range of *J. drupacea* was precipitation quantity in the coldest quarter (Table 1). This variable contributed 41% for the whole range of the species, 47.5% for PEL, and 26.7% for ANA, but interestingly, as much as 85.7% for LEB. Climate variables that contributed across the whole range were precipitation seasonality (18.7%), precipitation in the warmest quarter (9.6%), temperature seasonality (9.5%), and mean temperature of the wettest quarter (6.6%). For PEL, the second most important variable influencing the range prediction was temperature seasonality (23.1%); however, precipitation seasonality (11.1%) and precipitation in the driest month (4.7%) were also relatively large contributing variables. For LEB, the most significant factor except for the precipitation in the coldest quarter was the precipitation in the wettest month (4.4%). For AN, the mean temperature of the wettest quarter (19.3%), the precipitation of the driest quarter (14.9%), precipitation seasonality (10.2%), and temperature seasonality (9.6%) were all large contributing variables. Generally, temperature variables had a smaller impact on range relative to precipitation (Table 1).

Cartographic analysis indicated that *J. drupacea* had a broader potential than realized niche (compare Figs. 1 and 3a). Interestingly, when analyzed separately, climate conditions for each of the three parts of the geographic range (PEL, AN, and LEB) detected different areas with conditions potentially conducive for range expansion (Fig. 3). The analysis using climate conditions from AN found no area in PEL where the climate was suitable for *J. drupacea* (Fig. 3c). The analyses using parameters from the PEL and LEB localities found no suitable climate conditions outside of these two regions (Fig. 3b, d).

Past and future geographic range

Suitable climate conditions for *J. drupacea* colonization have changed drastically in the past. During the Riss-Würm (Eemian) interglacial about 130–115 ka BP, the species could theoretically only find favorable climate conditions in a restricted area close to the Mediterranean Sea in Turkey and substantially less suitable conditions prevailed on the Peloponnese in Europe and a narrow belt in the Lebanon mountains (Fig. 4a). Particularly favorable climate conditions for *J. drupacea* occurred during the LGM, ca 20 ka BP, and provided an area for colonization almost three times as large as that available currently (Fig. 4b). By contrast, climate conditions in the mid-Holocene (about 6000 years BP) reduced the potential distributional area to one-third that currently available (Table 2).

Climate warming of 1 °C or 2 °C in the future will cause a reduction of the species' potential niche to 50% or 17%, respectively, of the contemporary area (Fig. 4e, f and Table 2).

Fig. 1 Geographical distribution of *Juniperus drupacea* on the basis of georeferenced data (Supplementary Materials, Table 1)

Table 1 Contribution [%] of bioclimatic variables and altitude for predicted habitat suitable for *Juniperus drupacea* on the data from the entire (ENT) and three different parts of the species geographic range: European (PEL), Turkish (AN) and Lebanese (LEB)

Bioclimatic factor	ENT	PEL	AN	LEB
BIO1 = Annual Mean Temperature	0.1	0.0	0.0	0.0
BIO2 = Mean Diurnal Range [Mean of monthly (max temp - min temp)]	0.1	0.1	0.4	0.0
BIO3 = Isothermality (BIO2/BIO7) (* 100)	1.2	0.4	1.4	0.1
BIO4 = Temperature Seasonality (standard deviation *100)	9.5	**23.1**	9.6	0.1
BIO5 = Max Temperature of Warmest Month	0.1	0.1	0.0	0.0
BIO6 = Min Temperature of Coldest Month	0.2	0.1	0.0	0.0
BIO7 = Temperature Annual Range (BIO5-BIO6)	0.4	0.4	0.4	0.1
BIO8 = Mean Temperature of Wettest Quarter	6.6	0.0	**19.3**	0.2
BIO9 = Mean Temperature of Driest Quarter	0.0	0.0	0.0	0.0
BIO10 = Mean Temperature of Warmest Quarter	0.1	1.2	0.1	0.0
BIO11 = Mean Temperature of Coldest Quarter	0.1	0.0	0.0	0.0
BIO12 = Annual Precipitation	2.7	0.0	1.3	0.0
BIO13 = Precipitation of Wettest Month	0.2	4.3	0.2	4.4
BIO14 = Precipitation of Driest Month	0.4	4.7	5.0	2.0
BIO15 = Precipitation Seasonality (Coefficient of Variation)	**18.7**	11.1	10.2	4.3
BIO16 = Precipitation of Wettest Quarter	0.2	0.0	0.2	0.0
BIO17 = Precipitation of Driest Quarter	0.5	0.0	**14.9**	1.1
BIO18 = Precipitation of Warmest Quarter	9.6	2.7	7.1	0.4
BIO19 = Precipitation of Coldest Quarter	**41.0**	**47.5**	**26.7**	**85.7**
Altitude	5.6	4.0	3.2	1.6

Fig. 2 Percent of georeferenced localities of *Juniperus drupacea* in the mountains of Turkey (AN), Lebanon (LEB), and Greece (PEL)
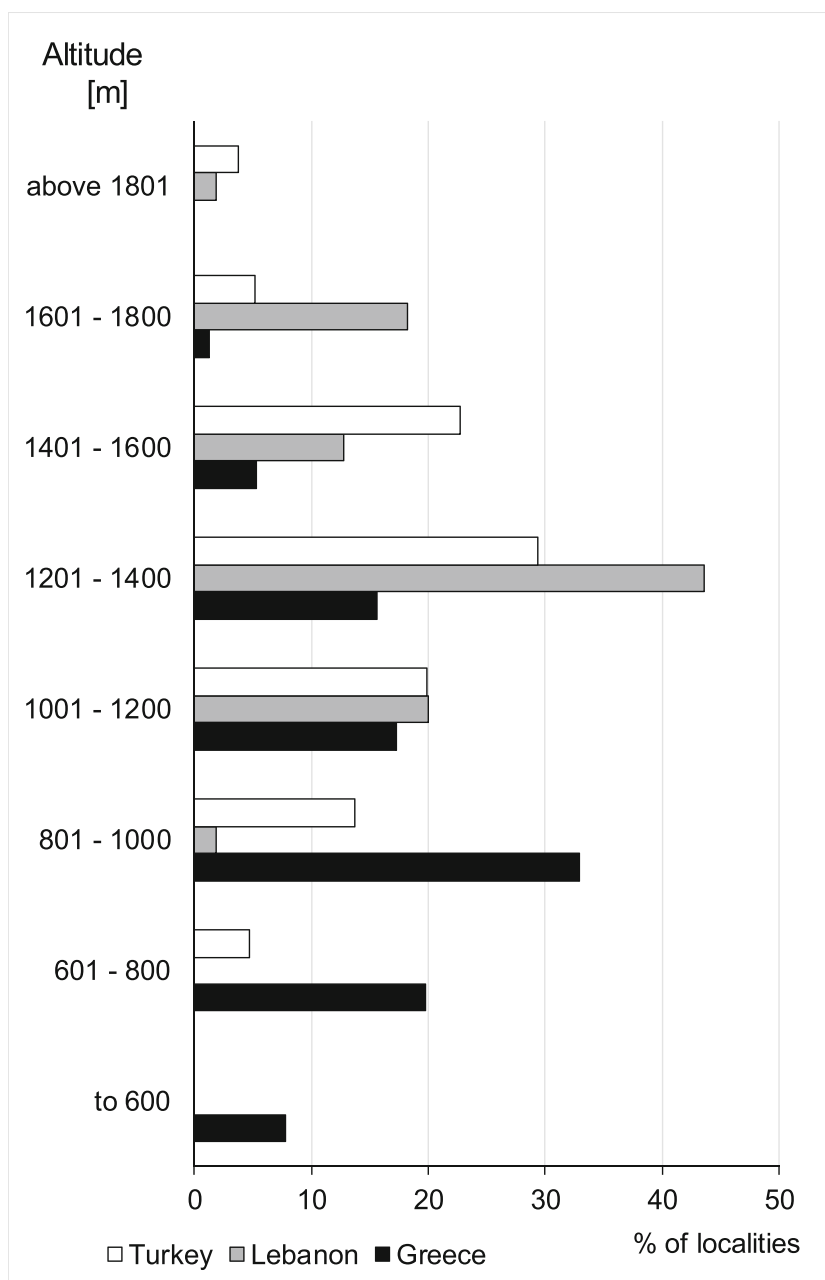

Discussion

Geographic range

The geographic range of *J. drupacea* was originally presented by Schmucker (1942). Coode and Cullen (1965) and Eliçin (1974) published the species' geographic range in Turkey and Lebanon in a simplified manner, but with localities marked on maps. Browicz (1982) published the first map highlighting the entire range of *J. drupacea*. Wazen and Fady (2015) redrew Browicz's (1982) map, adding the species' occurrence in

northern Iraq. This latter locality is difficult to reconcile with the climatic conditions found there and was likely a misidentification (Blakelock 1966; Liu et al. 2018).

We believe that the map presented here (Fig. 1) is the most comprehensive and up to date. This map resulted from a wide range of data including historical information from classic herbarium collections and basic floras, verified data from new collections, and unpublished field notes. The highest elevation localities of the species in Europe were at 1790 m near Refugio Parnonas, while those at the lowest elevation were at 300 m below Moni Elonis, both in the Parnon Oros (Maerki
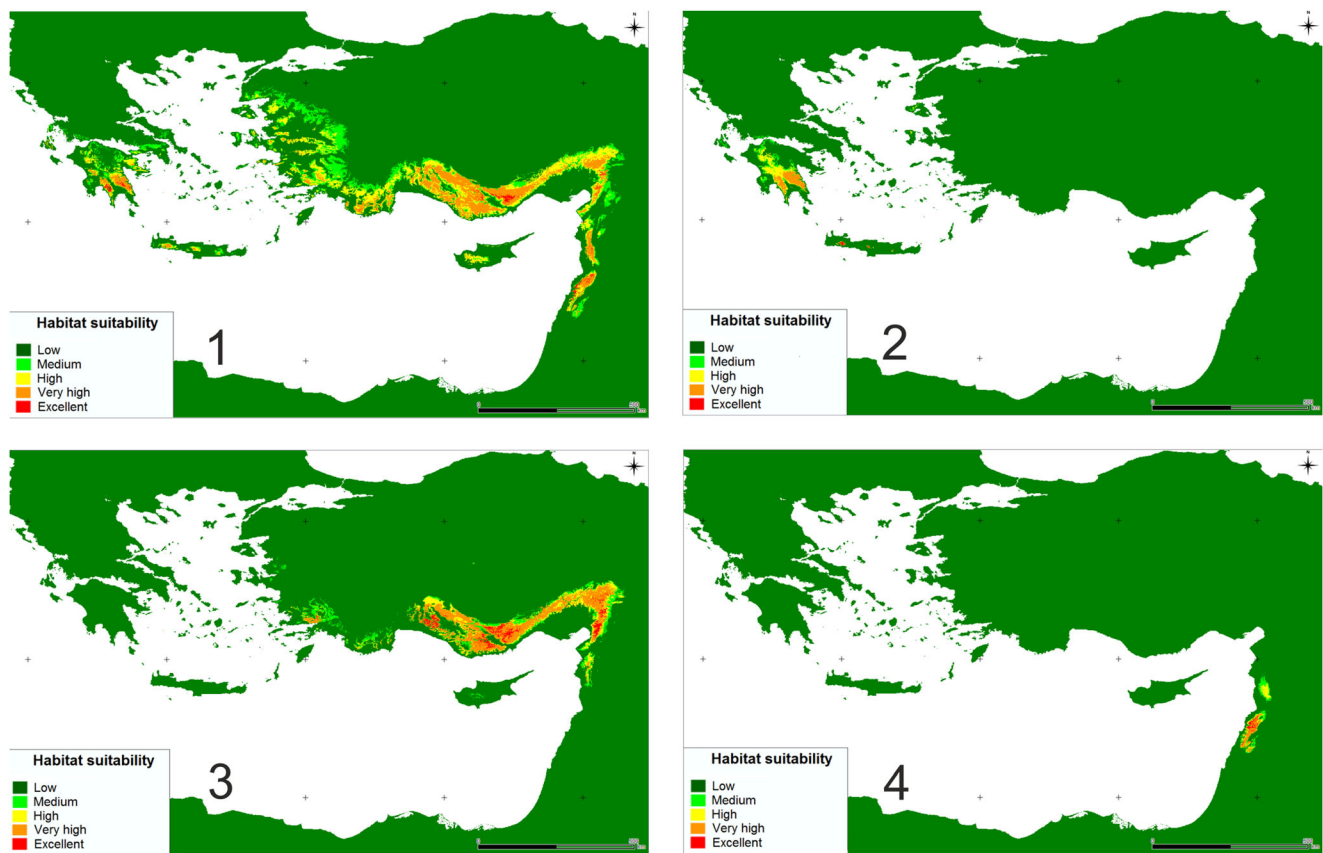
Fig. 3 Climate habitat suitability maps for the contemporary occurrence of *Juniperus drupacea*. **a** Data from the entire geographic range. **b** Data from European (PEL). **c** Data from Turkish (AN). **d** Data from Lebanese (including Syrian) (LEB) portions of the geographic range

and Frankis 2015). In Turkey, the highest elevation stands were recorded at 2050 m in Aladağlar (Schiechtl et al. 1965) and 2000 m in Ahır Dağı, while the lowest elevation stand was reported at about 650–700 m (Kocakulak 2007). The prevalence of localities in Europe was between 800 and 1000 m, while in Turkey and Lebanon, they were between 1200 and 1400 m (Fig. 2), which could be interpreted as indicating that optimal conditions in the Asiatic mountains were at a higher altitude. These data were consistent with the work of Abi-Saleh et al. (1996) who found that the optimal altitudinal range of the species in Lebanon was 1250–1500 m.

Climatic determinants of geographic range

From the 19 verified factors relating to climate conditions, precipitation in the coldest 3 months appeared to be the most influential with regard to the realized niche of *J. drupacea*. Surprisingly, temperature variables, which are very influential to the geographic ranges of most organisms (Bradie and Leung 2017), played only a limited role in the Syrian juniper distribution (Supplementary Materials, Fig. S1). The weak influence of temperature may in part result from a high level of adaptation by the species to a broad range of temperatures, with high diurnal and annual amplitudes. From the range of

variables relating to temperature, only mean temperature in the wettest quarter and temperature seasonality had an influence on the species' realized niche, and even so, the dependence was not as strong as for the precipitation variables (Table 1).

Average climate conditions across the geographic range of *J. drupacea* were characterized by relatively high precipitation during the coldest quarter (the winter months of December–February), which was frequently associated with snow that could sometimes be intense but not persistent. Snow cover can last up to a few weeks in localities above 1000 m in the Parnon Oros on Peloponnese and above 1200–1300 m in the Taurus and Lebanon mountains (Türkeş 2003; Lionello 2012; Atalay et al. 2014). The total precipitation for the coldest 3 months was usually 400–500 mm and sometimes up to 600 mm (Fig. 5). Precipitation during the driest months was also a positive influence on the geographic range of the Syrian juniper in Turkey. There was high interannual variability in precipitation during the summer months (Thompson 2005; Lionello 2012; Atalay et al. 2014), and while there was on average 100–150 mm annually, there was more than 200 mm in some years. Regions with a more continental type of the climate in Turkey, where precipitation seasonality and
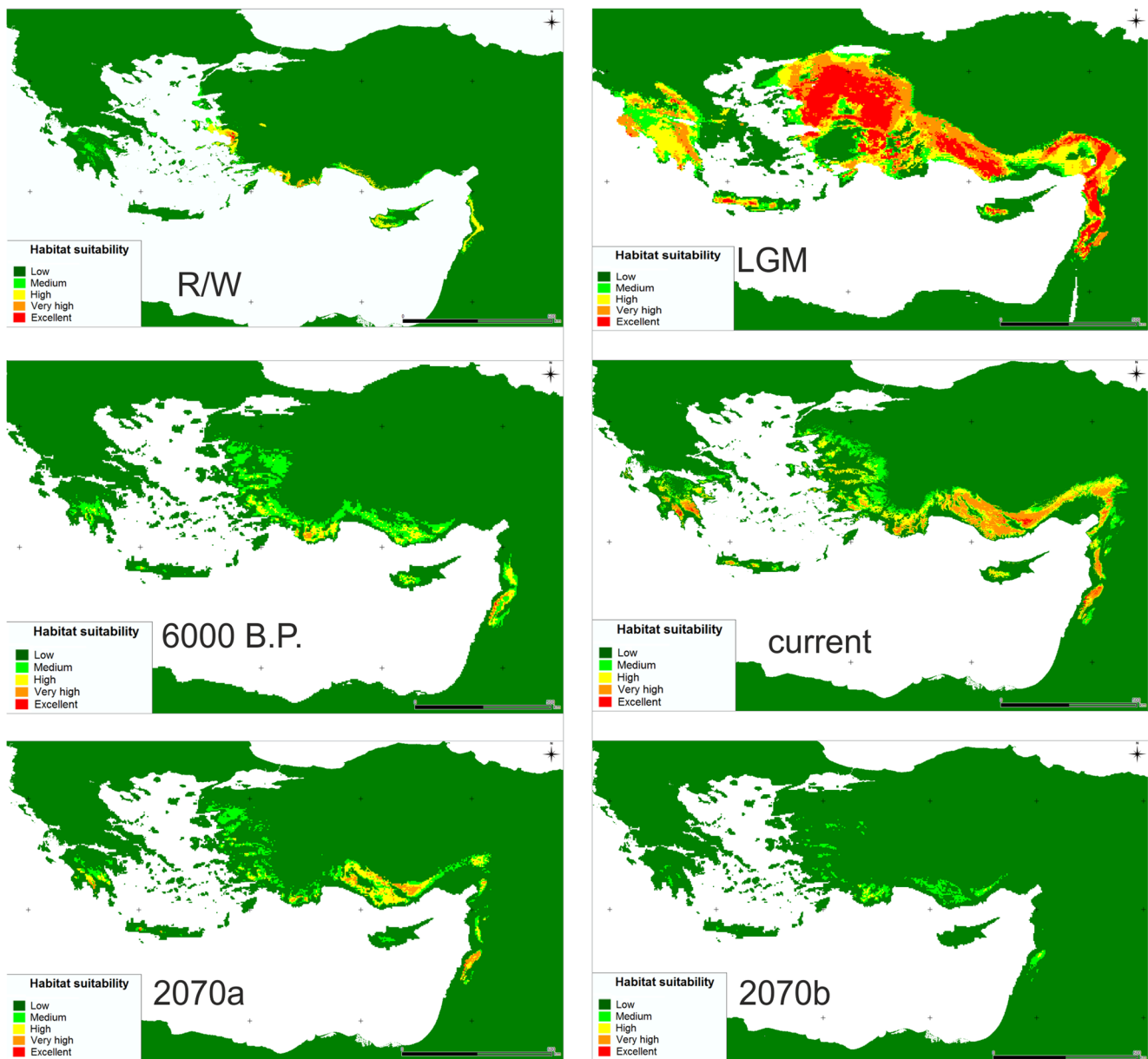
Fig. 4 Climatically suitable habitat maps for *Juniperus drupacea*. **a** During the Eemian about 125 ka BP. **b** During the Late Glacial Maximum about 20 ka BP. **c** During the Holocene climate optimum about 6000 BP. **d** In current climate conditions. **e** In 2070 for low climate warming (2.6 W m^{-2}). **f** In 2070 for high climate warming (8.5 W m^{-2})

Table 2 Estimated area of potential distribution of *Juniperus drupacea*.

Model	Predicted area (km^2)	Difference with respect to the present (km^2 and %)
Present	103 301	-
Eemian interstadial about 130 ka BP	21 670	81 631 (-79%)
Late Glacial Maximum about 20 ka BP	286 395	183 094 (+177%)
Holocene climate optimum about 6 ka BP	68 908	34 393 (-33%)
Future - low climate warming (2.6 W/m^2)	54 975	54 975 (-47%)
Future - higher climate warming (8.5 W/m^2)	17 286	86 015 (-83%)

Emberger's quotients have lower values, do not have *J. drupacea* (compare Figs. 1 and 5).

The greater aridity in the Eastern part of the Peloponnese compared with the mountains of Turkey (Türkeş 2003; Ünal et al. 2003; Panagiotis et al. 2013; Paparrizos et al. 2016) did not seem to influence the species' geographic range; however, it did affect absolute numbers, with just single dead individuals of *J. drupacea* observed on the shallow soil (Maerki, personal communication).

The impact of high precipitation seasonality and low precipitation during summer months on *J. drupacea*

distribution may be diminished in the Taurus Mountains by mist at elevations of about 1000–1200 m (Atalay et al. 2014). The effect of mist in the mountains may be comparable to the beneficial influence of mistiness on the northern slopes of the Rif Mountains in northern Africa on the occurrence of *Abies marocana* Trab. (Esteban et al. 2010) and *Taxus baccata* L. (Romo et al. 2017). However, both of these species are more susceptible to a lack of humidity than *J. drupacea*. Though, *J. drupacea* is somewhat more drought resistant, which explains its distribution and occurrence in moderately thermophilic plant communities (Zohary 1973;
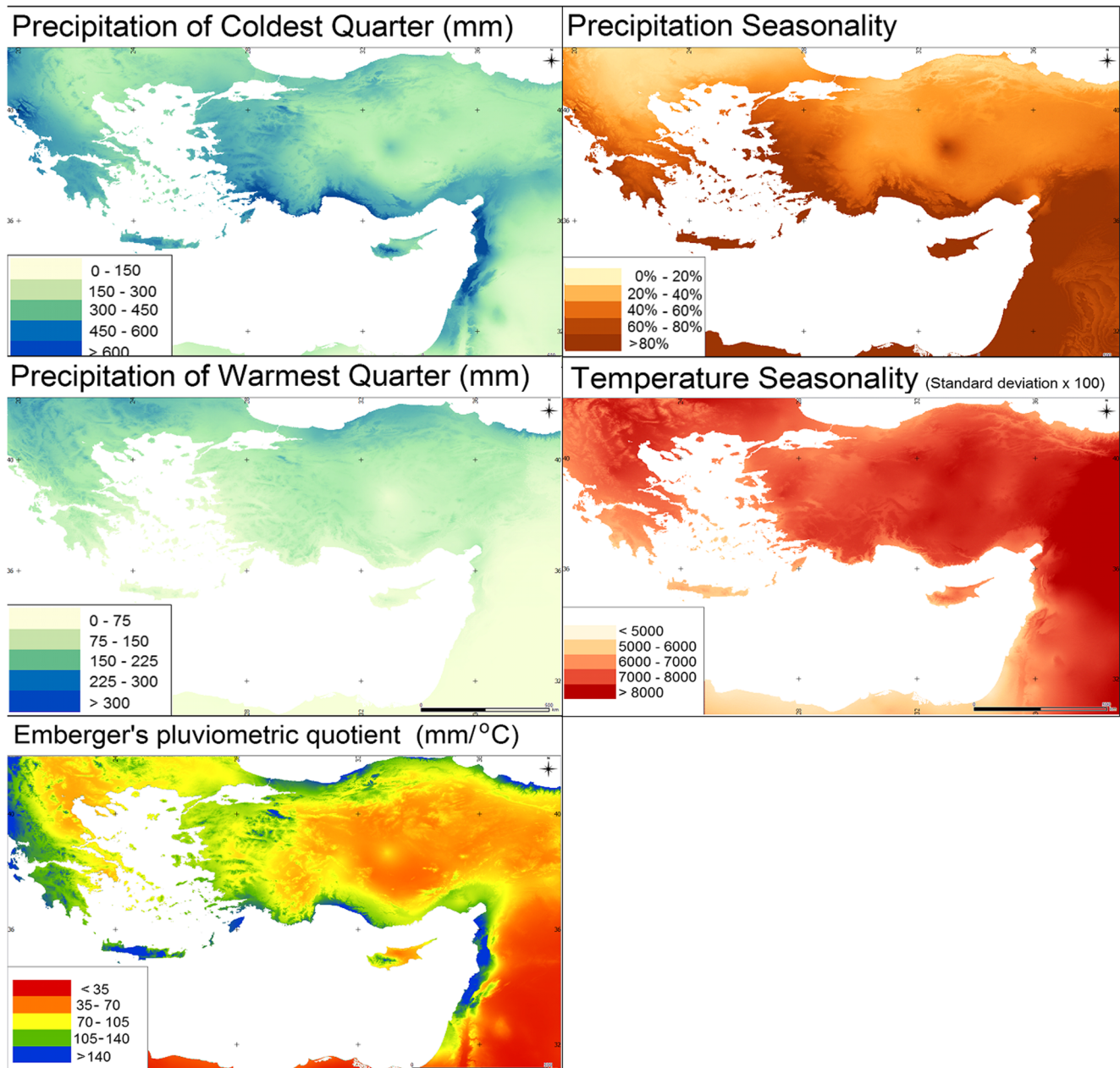

Fig. 5 Distribution of the bioclimatic variables with the greatest degree of influence on the occurrence of *Juniperus drupacea*

Mayer and Aksoy 1986; Talhouk et al. 2001; Bergmeier 2002; Atalay et al. 2014).

Juniperus drupacea occurred in the oro-Mediterranean climate with high precipitation during the cold months. The temperature during these months did not generally exceed 5–6 °C (Fig. 5c) and on some days could drop to − 5 °C or even − 10 °C (Orcan et al. 2004, p. 310; Bakker et al. 2013, p. 63). Conversely, during the dry period (June to August), the average temperature reached 20–21 °C (Quézel and Médail 2003; Orcan et al. 2004; Rivas-Martínez et al. 2004; Giannakopoulos et al. 2009; Lionello 2012; Atalay et al. 2014: 795; Robinson et al. 2006; Roberts et al. 2011). In spite of that, temperatures only influenced the current geographic range of the species to a limited extent (Table 1). Among temperature variables, the most influential was the mean temperature of the wettest quarter, which for the area of *J. drupacea* occurrence was the coldest quarter, December–February. It was noteworthy that low temperatures combined with the lower precipitation above the cloud level appeared as a restricting factor for the species' occurrence in the high mountains.

The European, Turkish, and Lebanese populations evolved in slightly different climatic conditions (Table 1). The separate analysis of the conditions for the European part of the geographic range of *J. drupacea* did not detect suitable conditions in any other part of the current species geographic range, but did indicate highly propitious climatic conditions in the mountains of Crete. Similarly, the climate conditions analyzed for the Lebanese part of species range did not find other suitable areas in Anatolia or in Europe (Fig. 3). Different climate conditions in different parts of a geographic range containing different genetic lineages were also detected for the lizard *Phrynosoma platyrhinos* (Jezkova et al. 2016), for rodents from the genus *Nephelomys* Thomas (Anderson and Raza 2010), and for *Cornus florida* L. (Call et al. 2016). This was interpreted as resulting from different niches in the past and due to spatial isolation within different parts of the geographic range. Subsequent genetic comparisons detected differences between subranges of both, *Phrynosoma platyrhinos* and *Nephelomys* (Anderson and Raza 2010; Jezkova et al. 2016).

Species niche modeling is affected by parameterization with only a partial distribution as was shown, for example, with the Carbonell's wall lizard (*Podarcis carbonelli* Perez Mellado; Carretero and Sillero 2016). The distribution of *P. carbonelli* is elongated, scattered, and divided into four parts. An analysis of niche conditions for the central part of the geographic range allowed the prediction of the entire distributional area; however, this was not possible when using information from the three other parts (Carretero and Sillero 2016). In our study, no niche in the three verified parts of *J. drupacea*'s geographic range allowed the prediction of the entire distribution of the species. Even the largest (AN subrange) predicted only the Turkish niches and parts of the Syrian niches (Fig. 3). Consequently, the adaptation of

European, Turkish, and Lebanese populations to local climates was at least part of the reason for the genetic and morphological differentiation detected by Sobierajska et al. (2016) and by Adams et al. (2017). These populations are considered independent biogeographic units.

Past and future geographic range

The site conditions of Syrian juniper localities allowed the classification of the species as tolerating average monthly temperatures of 0–22 °C (Hijmans et al. 2005), but it did not respond in a significant way to lower extremal daily temperatures (Table 1). Despite higher precipitation, its ecological characteristics probably allowed it to survive in Anatolia during the last interglacial in some areas, likely a result of higher insolation (Abrantes et al. 2012, but see also discussion in Bar-Matthews et al. 1997 and Cheddadi and Khater 2016).

Direct use of palynological data for reconstructing *J. drupacea*'s geographic range is impossible because the pollen grains of juniper species are indistinguishable (e.g., Carrión et al. 2001). However, *J. drupacea* distribution contemporary follows *Cedrus libani*, so the pollen of cedar could also indicate the presence of Syrian juniper during the LGM or at least at the Late Glacial (e.g., Vermoere et al. 1999; Hajar et al. 2010; Touchan et al. 2014; Cheddadi and Khater 2016), which coincides with our result (Fig. 4b). There may have even been compensatory factors, such as a reduction in broadleaved tree occurrence to small patchy areas that could have reduced light competition and resulted in a broader distribution of *J. drupacea* (e.g., Carrión et al. 2001; Carrión 2002; but see also the percentage of *Quercus* pollen in Vermoere et al. 1999).

Considering the current thermal conditions at the upper altitudinal limit of *J. drupacea* together with the temperature lapse rate in the mountains (6.5 °C km^{-1}, Barry and Chorley 1987) during LGM, the species would have had appropriate thermal conditions for growth at altitudes of about 1200–1400 m lower than at present. Consequently, its geographic range could have covered a larger area (Dean et al. 2015). The area where *J. drupacea* occurred in the Taurus Mountains after the LGM, even during the first millennia of the Holocene, could also have been somewhat below the present altitudinal range because of the prolonged deglaciation of the highest parts of the mountains (Sarıkaya et al. 2011).

The response of *J. drupacea* tree-ring increments to climate conditions would be interesting, but has not yet been analyzed. However, the co-occurrence of this species with *Cedrus libani*, *Abies cilicica*, *Pinus nigra*, and *A. cephalonica* suggests that it would respond similarly to climatic changes. *Cedrus libani*, *Abies cilicica*, *Pinus nigra*, and *A. cephalonica* are included into a group of species that react positively to May–June precipitation (Touchan et al. 2014), which was detected as important for *J. drupacea*, though mostly for the

Anatolian portion of its geographic range (BIO17 and BIO18 in Table 1).

During the Holocene climate optimum about 6000 years ago, higher temperatures, but also higher precipitation, shifted the area with climate conditions suitable for *J. drupacea* to the higher altitudes (Fig. 4c). We should expect an even greater restriction on the species occurrence though due to the expansion of forest-forming broadleaved trees, primarily oaks, which influence junipers through light competition (Carrión 2002). *Juniperus drupacea*, as other juniper species, likely escaped from lower locations to higher altitudes or other places inaccessible to broadleaved trees, such as steep slopes, rocks, and rocky ridges. However, this is only a working hypothesis with no confirmatory paleo data.

The effect of future climate conditions depends on the scenario. While a 1 °C temperature increase (scenario RCP2.6) would dramatically reduce the area with conditions suitable for *J. drupacea*, conservation of the species genetic variation in situ would still be ensured. By contrast with a 2 °C increase (scenario RCP8.5), the species would not find suitable conditions in most of its current geographic range (compare Fig. 4f and Fig. 1), due in part to higher temperatures, but also due to less precipitation and greater evapotranspiration (Lionello 2012).

Threats

Precipitation is a crucial factor for many Mediterranean tree species (Thompson 2005; Allen et al. 2010). Unfortunately, this region is threatened by droughts in the future. Precipitation in the coldest quarter may be reduced by 15–25% within *J. drupacea*'s range (Giorgi and Lionello 2008). This variable was identified as the most important for the species, and such extensive drying in a short time will pose a great threat to natural populations. The lack of rain during the growing season additionally deepens the water deficit and increases fire risk. These effects were observed in recent years, when after long periods without rain, the death of individual trees was observed in the locations with shallow soils (Maerki, personal communication).

The Anti-Taurus Mountains with their broad distribution of *J. drupacea* may lose conditions suitable for the species. The Anti-Taurian populations differ genetically from all the others in Turkey (Sobierajska et al. 2016) and therefore, the loss of this population will diminish species variation. Populations from the Turkish portion of the species' geographic range should be monitored carefully despite the lack of a current threat. Surprisingly, the most conducive climate conditions will be retained in a small area of the Lebanon Mountains. In the Peloponnese, the current major threat for *J. drupacea* is fire. Elevated temperatures could increase the fire risk substantially.

The scattered populations of *J. drupacea*, especially in regions with fragmented forests, may be endangered due to a lack of pollination and fertilization, leading to production of empty seeds. This problem was detected in other dioecious junipers (Juan et al. 2003; Tylkowski 2009, 2010; Rodríguez-Garcia et al. 2017). Moreover, the presence of a reserve of dormant seeds in the soil (Owens and Schliesing 1995) that can stabilize population dynamics by spreading out risk and diminishing large fluctuations in response to short-term environmental perturbations (Leishman et al. 2000) is threatened by climate change. Litter decomposition and the organisms involved in this key process are also affected by drought (Kinloch and Friedel 2005; Li et al. 2017).

There is a necessity to conserve the widest possible range of genetic diversity considering that *J. drupacea* is an exceptional relict species within the genus. The populations from the Peloponnese, different parts of the Taurus in Turkey, and the Syria and the Lebanon mountains should be preserved in the form of conservation plantations and seed orchards. Additionally, the biology of seed dormancy requires further study in order to use the species in forest restoration programs, and in particular taking into consideration the gender balance. Ex situ conservation of seeds should also be developed. As of 2019, such species conservation activities have not been initiated; however, *J. drupacea* is planted as a forest tree in Turkey (Tolga Ok, personal communication). In Lebanon, some efforts were made to limit dye back of *J. drupacea* resulting from *Arceuthobium oxycedri* M. Bieb. infestation and to propagate the species vegetatively within a program that plans to plant 40 million trees (Magda Bou Dagher, personal communication).

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