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Conservation and restoration strategies to preserve the variability of cork oak *Quercus suber* — a Mediterranean forest species — under global warming

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ABSTRACT: Climate change effects on forest ecosystems are a matter of debate within the scientific community, given their implications for biodiversity conservation and management. Coupling environmental data and modelling techniques with new advances on species resistance to disturbances, resilience, and new potential colonization areas provides insights that can used in rehabilitation, reconstruction, reclamation, and replacement. Here, we investigated an economically relevant evergreen oak, *Quercus suber* L. that is naturally distributed in the central-western Mediterranean Basin. Ecological niche modeling (ENM) was applied to statistically forecast the suitability areas of 4 haplotypes, as detected in previous studies. Combining these results with past reconstructions of climatically favourable regions, we identified 22 putative refugia and their climate characteristics that could host cork oak haplotypes. Different responses were observed among haplotypes: some of them were foreseen to expand their range over the next century, others to retreat. Overall, coastal mountains appeared to play a crucial role in the species' conservation. Notably, future scenarios call for a differential type of management for cork oak, considering local conditions and human disturbances. For 3 examples (Apulia, Kabylie and Peloponnese), we analyzed conservation, enrichment, localized reforestation, and assisted migration as strategies to mitigate or prevent the loss of genetic diversity and the extinction risk driven by global warming. The implementation of advanced forest nursery technologies for high quality seedling production are factors recommended for the successful preservation and extension of cork oak presence in the Mediterranean under future climate change.

KEY WORDS: *Quercus suber* · Ecological niche modelling · Haplotype forecasting · Putative refugia · Assisted migration · Mediterranean Basin

1. INTRODUCTION

There has been a very high rate of change in climate conditions in the last decades. Global warming is the most outstanding of these changes. Future implications of climate change have been widely discussed in dedicated literature, and scientists have been striving to gain more knowledge on the mechanisms beyond the climate systems, so as to implement models to project future scenarios and address adequate answers or management decisions in a broad outline (Shao & Ditlevsen 2016). Current rapid climatic variations, which are in part human-based, exert a strong influence over the natural distribution of species and landscape composition (Pearson 2006). Forested ecosystems mirror the ongoing processes that affect the planet, due to the complex interactions that occur with their chemico-physical and biological

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components (Bonan 2008). Adaptation to climate change in forest management is becoming prominent at local levels (Seppala 2009, Keenan 2016).

Migration, genetic adaptation, phenotypic plasticity and other strategies commonly characterize plant species' aptitudes to face environmental alterations, but these may not be sufficient to guarantee a species' survival globally (Aitken et al. 2008, Feurdean et al. 2013, Bussotti et al. 2015, Rafferty et al. 2015). The ability to track future abrupt changes in climate is limited. Such events may cause massive extinctions in the future; this is especially true if there is no planning for human interventions to support forest restoration and species colonization capacity (Pearson 2006, Millar & Stephenson 2015, Fady et al. 2016).

Populations experiencing conditions at the edge of their physiological tolerances would be exposed to the strongest selective pressures in the forthcoming climate scenario, with drastic population reductions and even the risk of extinction (Alberto et al. 2013, Zhang et al. 2016). Hence, it is important to understand the range of different climate effects from the individual to the biome scale, and to consider which responses could occur (Bellard et al. 2012). In view of this, the information retrieved from the past can provide an assessment of palaeoclimates and insights into species responses, tolerance, and new potential colonization areas (Brayshaw et al. 2011). For example, pollen and fossil records have been useful in detecting migration pathways, extinction events, and putative refugia (Médail & Diadema 2009, Rull 2009). The latter are already acknowledged to be of paramount importance for long-term retention of plants, especially if they maintain an unchanged role in the future. In addition, areas that hosted a certain species in the past under a climate scenario similar to the one predicted for the future might be considered as sites for the species reintroduction, even outside of the present range (Millar et al. 2007, D'Orangeville et al. 2016).

A portfolio of forest restoration strategies have been conceived to ensure the conservation or recovery of ecological functions and biodiversity levels in forested ecosystems, with a special focus on degraded landscapes, protected areas, and refugial sites. According to their objectives, these restoration approaches can be classified as rehabilitation, reconstruction, reclamation, and replacement (Stanturf & Madsen 2002, Stanturf et al. 2014a,b, Dumroese et al. 2015a). Concerning long-term management plans, the uncertainty of the future climate scenario requires a strategy able to minimize the risk of a failure to achieve an enhancement of ecosystem resistance and resilience (Duveneck & Scheller 2016, Virah-Sawmy et al. 2016). The best approach with regards to climate hazards can sometimes be translocation, i.e. the movement of a species (or genotypes) from one location to another (Seddon 2010, Dumroese et al. 2015a). It is worth noting that when translocation is conducted by assisted species migration or managed relocation, a species can be moved far outside its current range to prevent its extinction due to climate change (Williams & Dumroese 2013, Dumroese et al. 2015a).

The preliminary step to successfully achieve a forest restoration plan, especially a replacement one, is to understand the target species' responses at spatial and temporal levels, as well as the bioclimatic envelope they are able to endure. There has been some progress in this, in particular regarding the potential suitability of species, assuming niche stability (Thuiller et al. 2003, Hidalgo et al. 2008). Here, we test the ecological niche modelling (ENM) approach, which usually explores environmental constraints on the suitable spatial range of a species over time. Despite a certain level of uncertainty due to modelling processes, especially in forecasting, statistical inference by testing several algorithms and emission scenarios is useful in reducing imprecision (Gould et al. 2014). Moreover, soil features, physiological limits and genetics information can be implemented within the niche models, when data is available and the spatial coverage matches with the climate variables (Valladares et al. 2014). Unfortunately, this is hard to achieve for tree species, due to a general lack of information on those basic aspects.

Many efforts have recently focused on biomes with a global conservation priority (Olson & Dinerstein 2002). Among them, the Mediterranean has received special attention, because projections foresee that this area is likely to face the most significant biodiversity loss of all terrestrial biomes, and already has a thousand-year history of human disturbance and landscape alteration (e.g. Klausmeyer & Shaw 2009).

Recent advances in model forested ecosystems have included studies on tree species regarding the characteristics of certain priority habitats, whether threatened or endemic. The volume of literature on this topic is rapidly increasing, showing the awareness of researchers and their ability to combine modelling approaches with forest management and restoration in the Mediterranean Basin (e.g. Vessella & Schirone 2013, Gaston et al. 2014, López-Tirado & Hidalgo 2016a).

This paper aims to review the findings on hindcasting and forecasting of cork oak *Quercus suber* L., a very important species both from an ecological

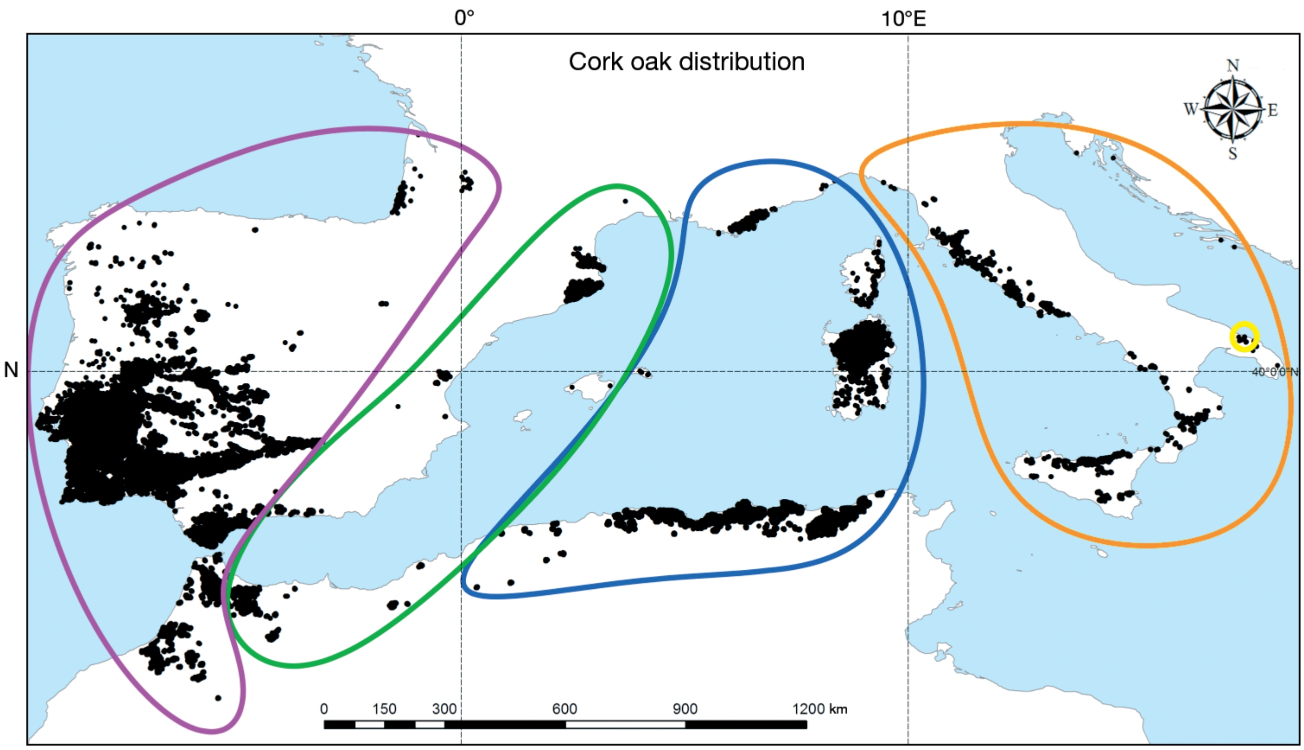

Fig. 1. Cork oak *Quercus suber* distribution and haplotype domains. Colored lines define the geographical zones where each haplotype (referred to here as yellow, orange, blue, green, and purple) has been detected according to Simeone et al. (2009)

and economic perspective. This species is typical of many agro-forestry landscapes in the central-western Mediterranean. It sustains a rich biodiversity and provides many ecoservices, including the maintenance of traditional livelihoods, water retention, carbon storage, and soil preservation; in addition, its bark is used in the manufacturing of many products (Bugalho et al. 2009, Costa & Oliveira 2015, Demertzi et al. 2016). It is also a keystone species of the Mediterranean bioclimate (sensu Rivas-Martínez et al. 2004). Here, we (1) focus on understanding the potential of the species to endure outside of its actual range, (2) identify refugial areas for the species in order to ensure their protection, (3) point out the critical points related to marginal areas and haplotypes, and (4) suggest appropriate restoration locations; in particular, detecting putative sites outside of the current species range in which to experiment with forest translocation strategies.

2. MATERIALS AND METHODS

In the present study, we focused on the global distribution of cork oak, which currently encompasses the central-western Mediterranean region including the Iberian Peninsula, France, Italy and Maghreb (Fig. 1). A fine-scale distribution of cork oak was assessed after merging pre-existing inventories (national and regional) with field surveys and remote sensing analyses. The final dataset resulted in 155 209 polygons stored in a GIS geodatabase (Arc GIS 9.3.1; ESRI). The ecological niche characterization obtained from previous work required conversion of the original polygons into a raster grid of 30 arc-seconds resolution to avoid pseudo-replication, lessen the effect of variation in sampling effort, and match the pedoclimatic variables' raster resolution, as basic requirements for the modelling algorithms to function correctly. This led to 75 028 spatially unique points representing the data source of hindcasting and forecasting approaches (Vessella et al. 2015). Past cork oak potential distribution was calculated for 3 temporal slices (Last Interglacial, Last Glacial Maximum, and Mid-Holocene), covering a period of ca. 130 k yr. A total of 14 climate variables from the WorldClim 1.4 repository and 7 modelling techniques were employed to produce 3 weighted average maps related to the abovementioned time periods using openModeller 1.5.0 (de Souza Muñoz et al. 2011). Present potential distribution and forecasting projections were similarly obtained. In particular, the future suitable areas for cork oak were calculated using an average climate model from 13 General

Table 1. Environmental variables and summary of General Circulation Models (GCMs) used in this study. Raster data has 30 arc-seconds resolution. The source for all the variables in this table is WorldClim, except for the Emberger index, which is sourced from the present study

Variable	GCM	Source
Annual mean temperature	Access 1-0	https://confluence.csiro.au/display/ACCESS
Mean diurnal range	BCC-CSM 1-1	http://forecast.bcccsm.ncc-cma.net/
Isothermality	CCSM4	www.cesm.ucar.edu/models/ccsm4.0/
Temperature seasonality	CNRM-CM5	www.cnrm-game-meteo.fr/spip.php?article126&lang=fr
Max. temperature of warmest month	GFDL-CM3	www.gfdl.noaa.gov/coupled-physical-model-cm3/
Min. temperature of coldest month	GISS-E2-R	http://data.giss.nasa.gov/modelE/ar5/
Temperature annual range	HadGEM2-ES	https://verc.enes.org/models/earthsystem-models/ metoffice-hadley-centre/hadgem2-es
Mean temperature of wettest quarter	INM-CM4	http://140.109.172.249/xms/content/show.php?id=3443
Mean temperature of driest quarter	IPSL-CM5A-LR	https://verc.enes.org/models/earthsystem-models/ipsl/ipslesm
Mean temperature of warmest quarter	MIROC5	www.icesfoundation.org/Pages/ScienceItemDetails.aspx?siid=181
Mean temperature of coldest quarter	MPI-ESM-LR	www.mpimet.mpg.de/en/science/models/mpi-esm/
Annual precipitation	MRI-CGCM3	http://cmip-pcmdi.llnl.gov/cmip5/availability.html
Precipitation of wettest month	NorESM1-M	https://verc.enes.org/models/earthsystem-models/ncc/noresm
Precipitation of driest month		
Precipitation seasonality		
Precipitation of wettest quarter		
Precipitation of driest quarter		
Precipitation of warmest quarter		
Precipitation of coldest quarter		
Emberger index		

Circulation Models (GCMs) for 2 different emissions scenarios based on Representative Concentration Pathways (RCPs). The first achieves an impact of 4.5 W m^{-2} by 2100, comparable with the Special Report on Emissions and Scenarios (SRES) B1 'intermediate emissions scenario'; the second accomplishes an increase of 8.5 W m^{-2} by the same period, consistent with the SRES A1FI 'high emissions scenario' (IPCC 2014). Predictions for these scenarios and subsequent forecasting projections of cork oak suitability areas were analyzed in 2 temporal slices: 2050 (average for 2041–2060) and 2070 (average for 2061–2080). Details of the GCMs and variables used in this study are summarized in Table 1.

Previous works on cork oak hindcasting have already identified areas where the species would have been able to persist over time (Vessella et al. 2015); those areas were assumed to include putative glacial refugia during the last 130 k yr. Similar investigations have been conducted for the present and future as well, using different statistical approaches and GCMs (Thuiller et al. 2003, Hidalgo et al. 2008, Vessella & Schirone 2013). Here, we overlap an implemented forecasting study with previously gathered results to verify if past putative refugia could be spatially confirmed under an intermediate and pessimistic climatic scenario throughout the 21st century. In addition, the chloroplast DNA variation identified in Simeone et al. (2009) serves as a basis to encompass the spatial extent of the detected haplotypes (Fig. 1), and we model and count their future suitable areas, and overlap their geographical domain with the distribution of putative refugia. Following the same methods of hindcasting and forecasting at the species level, the 4 haplotypes of cork oak were mapped, and the theoretical suitable areas detected. An additional haplotype occurs in a single population in Apulia, and although it represents an important relic feature, it was not considered in the analysis because the models require multiple presence points. In addition, we performed a jackknife test with 10000 bootstrap replicates to measure variable importance that could discriminate each haplotype projection. The combination of genetic information and niche modelling can provide further information about the risk of extinction at the haplotypic level, and help to guide proper solutions to safeguard intraspecific diversity.

In order to obtain more reliable results, current land cover and soil types were used as restriction parameters for a subset of the refugial areas that were determined to be suitable for the whole genetic diversity of cork oak, thus obtaining appropriate areas for the species' conservation and/or expansion. Data were retrieved from the European Environment Agency (EEA; Corine Land Cover v.13; www.eea.

europa.eu) and World Soil Information (ISRIC; SoilGrids System, 1 km^2 resolution; www.isric.org). Urban areas, croplands, and areas used for high-value agrifood cultivation or containing highly calcareous soils were subtracted from the available surface area of those putative refugia. The latter soil parameter was excluded because cork oak thrives mostly in acidic soils.

3. RESULTS

Hindcasting has provided a global overview of cork oak putative refugia across space and time, encompassing the last 130 k yr of the species history, while forecasting identifies those potentially suitable areas in the near future. Based on this coupled data, we were able to detect major areas for the species' persistence based on both intermediate and pessimistic emission scenarios. The locations of these putative refugia lie mainly within the current cork oak range (i.e. the central-western Mediterranean Basin), with the exception of the Peloponnese, Crete, and the Aegean Islands (Fig. 2). Overall, we identified a set of 22 major refugial areas under the intermediate emission scenario by 2050, which was decreased to 17 by the end of the century; under the pessimistic scenario, 18 refugia were identified by the middle of the century, with a reduction to 15 by 2070 (Fig. 2, Table 2). Among these regions, there were 2 large areas of >1 million ha in southern Portugal–Eastern Andalusia, and the islands of Corsica and Sardinia. The remaining refugia differed in size, from a few thousand to 100s of 1000s of ha, comprising a heterogeneous mosaic of potential zones where the species' survival can potentially be safeguarded. Spatio-temporal analysis revealed 2 features worthy of mention. (1) All the refugia are predicted to undergo a reduction in extent over time (with the exception of the small area of Var, France) under both the intermediate and pessimistic scenarios, or disappear entirely (e.g. many North African zones and Apulia around 2070 in the worst scenario). (2) The reduction in area is often associated with fragmentation (e.g. southern Portugal, Sardinia, and Campania-Calabria, among others). The magnitude of such change also varies, with significant surface loss of >50%, especially under the pessimistic scenario.

Table 2. Major theoretical putative refugia for cork oak *Quercus suber* obtained by overlapping its past 130 ka occurrence with 21st century projections under 'intermediate' and 'pessimistic' greenhouses gas emission scenarios. See Figs. 2 & 3 for site numbers. (–) Putative refugia lost in the second half of the 21st century or not identified under the 'pessimistic scenario'

Site no.	Label	Location	Area (ha) Intermediate scenario 2050	Intermediate scenario 2070	Pessimistic scenario 2050	Pessimistic scenario 2070
1	Alentejo-Algarve-West Andalusia	Portugal-Spain	5 396 551	2 516 634	3 744 689	570 863
2	Douro Valley	Portugal	40 503	40 503	40 503	12 941
3	Serrania de Ronda	Spain	128 267	21 020	40 394	3143
4	Balearic Islands	Spain	493 322	435 328	483 316	257 901
5	Catalonian coast	Spain	116 715	48 285	62 615	31 512
6	West Anti-Atlas	Morocco	17 448	–	395	–
7	West Middle-Atlas	Morocco	337 785	–	–	–
8	Rif Mountains	Morocco	141 085	50 509	75 853	22 306
9	Oran-Tell Atlas	Algeria	59 926	–	–	–
10	Mostaganem	Algeria	10 605	–	–	–
11	Kabylie	Algeria	118 118	5861	17 873	689
12	Skikda	Algeria	60 215	137	3979	–
13	Bizerte	Tunisia	6348	–	–	–
14	Var	France	6035	6035	6035	6035
15	Corse-Sardinia	France-Italy	1 619 873	1 480 224	1 602 886	862 546
16	Tyrrhenian coast	Italy	154 920	151 954	153 657	3042
17	Campania-Calabria	Italy	910 087	557 295	646 181	211 849
18	Sicily	Italy	395 672	214 940	280 231	97 255
19	Apulia	Italy	99 185	24 538	78 626	–
20	Peloponnese	Greece	292 930	103 850	159 877	43 663
21	Crete	Greece	196 395	91 849	88 247	67 282
22	Cyclades	Greece	8993	4602	8415	3457
TOTAL			10 603 750	5 735 564	7 493 772	2 194 484

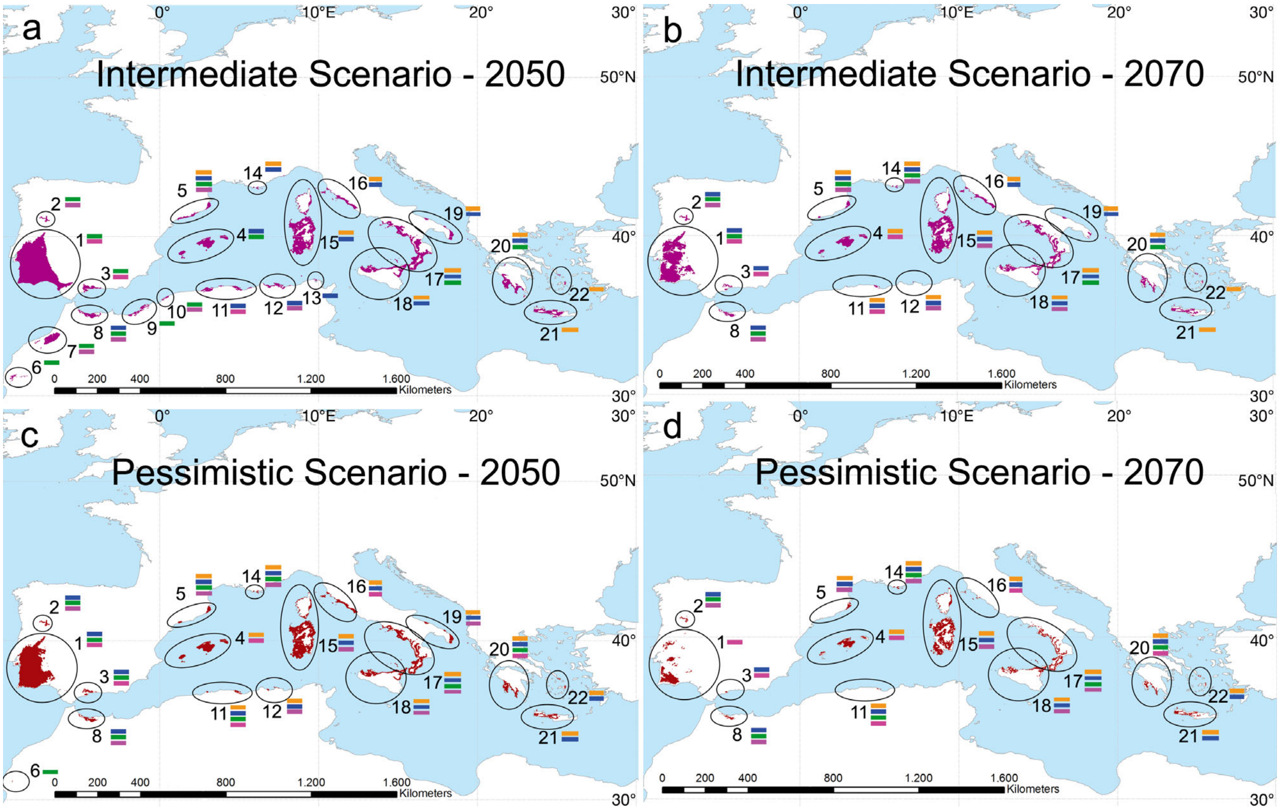

Fig. 2. Putative cork oak *Quercus suber* refugia identified after overlapping present results with hindcastings of Vessella et al. (2015). Haplotype suitability shown according to model outputs of this study under (a,b) intermediate and (c,d) pessimistic greenhouses emissions scenarios for (a,c) 2050 and (b,d) 2070. Colored bars close to site numbers refer to haplotypes, as outlined in Fig. 1

The overlapping results of the modelling analysis at the haplotype level led to the identification of pertinent locations that can define the range of survival for each haplotype. Data analyses allowed for the extraction of ranges of the bioclimatic variables of each haplotype, in order to describe the climatic framework where they presently occur and the potential conditions in the next century (see Table S1 in the Supplement at www.int-res.com/articles/suppl/c071p171_supp.pdf). Hence, it is possible that some genetic components might undergo a drastic reduction in their persistence in the future, or an expansion of their actual distribution (Fig. 2, Table 3). For example, the orange haplotype, originally endemic to the Italian peninsula (see also Simeone et al. 2009), would spread westward in Sardinia, Provence, and Catalonia, and eastward in Greece and the Aegean Islands. At the end of the century, it would reach the African coasts and the Baleares. Under the pessimistic scenario, the same haplotype would follow a similar pathway, except for North Africa due to the disappearance of most refugial areas in the second half of the century. A comparable pattern would occur for the purple and blue haplotypes as well; in those cases, they could become more ubiquitous across time, spanning from the Atlantic to the Aegean. On the other hand, the green haplotype appears to undergo a gradual erosion from its refugia, and a displacement into small enclaves towards the west (Douro Valley and Rif), in Provence, and towards the east (i.e. South Italy and Peloponnese).

Focusing on single areas, under the intermediate scenario, some putative refugia would appear to increase the number of hosted haplotypes (e.g. Var, Sardinia, Sicily, Kabylie, Alentejo-Algarve-West Andalusia, Douro Valley), while in other areas the change in suitable conditions would promote replacement (e.g. green and blue components in 2050, substituted by orange and purple in 2070 in the Baleares). Different patterns would occur under the pessimistic scenario. Here, the progressive erosion of suitable areas across the century would lead to a depletion of the genetic components within the remaining refugia (e.g. Alentejo-Algarve-West Andalusia).

Results from jackknife resampling highlighted 10 out of 20 climatic factors that mostly explain the different haplotypes' projections (Table 4). Those variables showed a correlation with the cork oak haplotypes, and their range of influence spread to different genetic groups in some cases. Specifically, we observed how annual range of temperature, minimum temperature of the coldest month, and the Emberger index mainly contributed to the Italian haplotype's (i.e. the 'orange' haplotype's) future distribution. Seasonal precipitation (warmest and coldest quarters), precipitation of the driest month and temperature seasonality (standard deviation of mean seasonal temperatures) affected the 'blue' haplotype. Annual temperature and temperature seasonality, as well as the thermopluviometric regimes during the coldest season influenced the 'green' haplotype. Finally, annual precipitation, annual mean temperature, the Emberger index and temperature seasonality influenced the forecasting results for the 'purple' haplotype.

Overall, the future scenarios investigated here highlight different possibilities for the putative refugia to host single or multiple haplotypes, as mentioned above. In particular, the projections highlight how the Rif Mountains, Kabylie, Catalonian Coast, Var, Sicily, South Italy, and the Peloponnese could maintain or expand their suitability for the totality of cork oak genetic diversity (Fig. 2). Those areas could be considered of paramount importance for conservation purposes; however, the transition from theory to reality, in terms of the use of restriction parameters, leads to a reduction in available area for cork oak survival, exacerbating the fragmentation (Table 5). In some sites, human exploitation could seriously reduce the suitability for cork oak projected by the theoretical models. For example, in Catalonia and Var, the presence of extensive urbanization left <40% of the original area intact; the same pattern was observed in many European refugia, where humans precipitated a high level of landscape transformation through the development of extensive agricultural and urban networks.

The case of Apulia is worthy of mention. Presently the easternmost boundary of the species range (where cork oak largely occurred in the past), it was progressively reduced to 30 isolated stands, with a total surface area of 117 ha. The presence of human civilizations since the Palaeolithic and the diffusion of agriculture represented 2 driving forces that marginalized the species into small enclaves, most of them <15 ha (Benazzi et al. 2011, Schirone et al. 2015b). This explains why the usable area in Table 5 is limited to <10% of the theoretical one; in addition, for a pessimistic scenario cork oak would disappear by 2070.

4. DISCUSSION

Much attention has been paid to global warming effects on terrestrial and marine biomes during the

Table 3. Cork oak *Quercus suber* haplotype occurrence over space and time on the detected putative refugial areas. Crosses indicate haplotype presence in each site; see Table 2 for extended labels. Representative Concentration Pathways RCP45 and RCP85 correspond to 'intermediate' and 'pessimistic' emission scenarios, respectively

Haplotype	Time slice	Site No. 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Orange	RCP45 2050					X									X	X	X	X	X	X	X	X	X
	RCP45 2070				X	X						X	X		X	X	X	X	X	X	X	X	X
	RCP85 2050				X	X						X	X		X	X	X	X	X	X	X	X	X
	RCP85 2070				X	X						X			X	X	X	X	X		X	X	X
Blue	RCP45 2050				X	X			X			X	X	X	X	X	X	X	X	X	X		
	RCP45 2070	X	X	X		X			X			X	X		X	X	X	X	X	X	X		
	RCP85 2050	X	X	X		X			X			X	X		X	X	X	X	X	X	X	X	X
	RCP85 2070		X	X		X			X			X			X	X	X	X	X		X	X	X
Green	RCP45 2050	X	X	X	X	X	X	X	X	X	X							X			X		
	RCP45 2070	X	X			X			X						X			X			X		
	RCP85 2050	X	X	X		X	X		X			X			X			X			X		
	RCP85 2070		X						X			X			X			X			X		
Purple	RCP45 2050	X	X	X		X		X	X		X	X	X										
	RCP45 2070	X	X	X	X	X			X			X	X		X	X			X				
	RCP85 2050	X	X	X	X	X			X			X	X		X	X	X	X	X	X	X		
	RCP85 2070	X	X	X	X	X			X			X			X	X	X	X	X		X		

Table 4. Relative contributions of the environmental variables to cork oak *Quercus suber* haplotype projections (haplotype colors refer to areas outlined in Fig. 1). Values shown are averages over 25 runs after 10 000 bootstrap iterations. Variables with highest contribution per haplotype (over 10 %) are in **bold**

Variable	Percent contribution Orange	Blue	Green	Purple
Annual mean temperature	1.3	0.2	**13.9**	**20**
Mean diurnal range	0	0.1	0	0
Isothermality	0	0	0.1	0
Temperature seasonality	1.3	**11**	**18.4**	**19.1**
Max. temp of warmest month	3.1	0.1	0.4	0.3
Min. temp of coldest month	**22.7**	0.1	0	3.5
Temperature annual range	**29.1**	0.2	0	1.6
Mean temp. of wettest quarter	0.3	0	0.4	0
Mean temp. of driest quarter	8.7	0.5	0.1	0
Mean temp. of warmest quarter	2.7	0	6	0
Mean temp. of coldest quarter	0.1	3.9	**15.9**	0
Annual precipitation	0	0	4.5	**28.4**
Precipitation of wettest month	4.2	0	0.2	0
Precipitation of driest month	1	**19.6**	1	0.4
Precipitation seasonality	0	0.4	1.2	6.4
Precipitation of wettest quarter	1.3	0.4	1.9	2.3
Precipitation of driest quarter	1.2	0.2	8	4
Precipitation of warmest quarter	5.1	**13.5**	0.1	1
Precipitation of coldest quarter	7.9	**44.1**	**21.3**	0.7
Emberger index	**10**	5.7	6.6	**12.3**

last decades. Efforts to predict changes and future dynamics of many life forms is considered of paramount importance, even for human survival on Earth. The development of advanced techniques, statistical approaches, algorithms, powerful software and computers have provided the basis for modelling approaches such as those used in this study. Despite the general robustness of the methods, the data input represented by the forecasting climatic scenarios, GCMs, and species occurrence have imperfections, and are often divergent or under debate (Araújo & New 2007, Buisson et al. 2010). In view of this, we consider our findings a starting point for the discussion of feasible strategies of forest restoration in a dynamic and changing environment, applied to a key species in the Mediterranean biome. Here, we analyzed the changes of climate in the current century without projecting forward to future centuries, thus avoiding many uncertainties (Stainforth et al. 2005). Moreover, we focused on the fundamental (i.e. the potential area and resources an oganism is capable of us-

Table 5. Surface availability within the putative cork oak *Quercus suber* refugia after the application of land cover and soil types which do not allow cork oak occurrence. Parentheses: proportion with respect to correspon-ding areas in Table 2

Site no.	Label	Area, ha (proportion, %) Intermediate scenario 2050	Intermediate scenario 2070	Pessimistic scenario 2050	Pessimistic scenario 2070
1	Alentejo-Algarve-West Andalusia	3 677 770 (68.1)	1 837 866 (73)	2 626 272 (70.1)	450 306 (78.9)
2	Douro Valley	34 964 (86.3)	33 612 (82.9)	33 612 (82.9)	11 157 (86.2)
3	Serrania de Ronda	66 530 (51.9)	12 703 (60.4)	21 385 (52.9)	2929 (93.2)
4	Balearic Islands	301 576 (61.1)	265 513 (61)	291 899 (60.4)	168 391 (65.3)
5	Catalonian coast	44 761 (38.3)	16 002 (33.1)	26 845 (42.9)	17 709 (56.2)
6	West Anti-Atlas	15 808 (90.6)	–	158 (40)	–
7	West Middle-Atlas	335 583 (99.3)	–	–	–
8	Rif Mountains	136 262 (96.6)	50 314 (99.6)	75 570 (99.6)	221 76 (99.4)
9	Oran-Tell Atlas	57 764 (96.4)	–	–	–
10	Mostaganem	10 402 (98.1)	–	–	–
11	Kabylie	91 373 (77.3)	5723 (97.6)	14 789 (82.7)	–
12	Skikda	51 678 (85.8)	137 (100)	3903 (98.1)	–
13	Bizerte	2722 (42.9)	–	–	–
14	Var	1554 (25.7)	1537 (25.5)	1537 (25.5)	1537 (25.5)
15	Corse-Sardinia	831 848 (51.3)	759 185 (51.3)	813 154 (50.7)	513 602 (59.5)
16	Tyrrhenian coast	85 145 (54.9)	82 915 (54.6)	83 645 (54.3)	2985 (98.1)
17	Campania-Calabria	653 353 (71.8)	445 054 (79.8)	514 460 (79.6)	186 348 (88)
18	Sicily	231 472 (58.5)	133 199 (62)	167 117 (59.6)	61 841 (63.6)
19	Apulia	6318 (6.4)	6199 (25.3)	6459 (8.21)	–
20	Peloponnese	235 320 (80.3)	91 790 (88.4)	142 174 (88.9)	37 581 (86.1)
21	Crete	134 947 (68.7)	70 565 (76.8)	69 431 (78.7)	54 245 (80.6)
22	Cyclades	6302 (70.1)	3132 (68.1)	5971 (70.9)	2615 (75.6)
TOTAL		7 013 452 (66.1)	381 5 446 (66.5)	4 898 381 (65.4)	1 533 422 (69.9)

ing) instead of the realized niche of cork oak, hence moving into theoretical predictions — although doing so resulted in a lack of factors such as species competition, thus rendering difficult or unfeasible to make projections at a coarse scale (Soberon & Townsend Peterson 2005). In addition, possible hybridization phenomena could potentially increase the probability of species enduring in certain locations, in addition to crosspollination between haplotypes sharing the same area.

The temporal framework investigated here revealed that the fundamental niche for cork oak might undergo a strong reduction, with upward and pole-ward shifts (Vessella & Schirone 2013, López-Tirado & Hidalgo 2016b). However, models are simply indicators of the spatial variations of suitable climatic conditions for the species' persistence. A realized migration (especially pole-ward) to those areas is almost impossible; this is because of the reduced time period investigated (<1 century), generation time, reproduction, long-distance dispersal capacity, site accessibility, and geographical barriers (Petit & Hampe 2006, Delzon et al. 2013). On the other hand, the complete and rapid disappearance of cork oak from many areas already occupied can be mitigated by the species' ecophysiology (i.e. its capacity to resist adverse conditions). In fact, cork oak has a good resprouting capacity and fire resistance, 2 features that could increase its capacity to successfully face a warmer climate (Ciampi et al. 1977, Catry et al. 2009, Moreira et al. 2009). Cork oak can also exhibit 'flexible' reproductive cycles, with annual or biennial acorn maturation (the latter if adverse climatic conditions such as severe drought or winter cold stress occur). Episodes of biennial fruit maturation used to occur at the outer edges of the species range, as in Apulia (Corti 1955, Francini Corti 1960, Elena-Rosselló et al. 1993, Schirone et al. 2015a). In addition, cork oak may conserve its genetic heritage into 'biological' refugia through hybridization. Such a behaviour has been observed with *Quercus cerris* L. (forming the hybrid *Q. x crenata* Lam.), *Q. ilex* L. (*Q. x morisii* Borzi), and *Q. canariensis* Willd. (*Q. afares* Pomel) (Bellarosa et al. 1996, Schirone & Piovesan 1998, Mir et al. 2006), aiding the survival of the species' genome in cooler or drier conditions.

Overall, the effects of climate change could overcome and reduce the species' resilience, for example by the occurrence of more extreme events such as heat waves and hotter drought, which have recently become more frequent in Europe. Mega disturbances (e.g. large and frequent forest fires, or massive insect and pathogen attacks) could even lead the species to a survival tipping point (Adams 2013, Reyer et al. 2015, Allen et al. 2015). In this view, *Phytophtora cinnamomi* invasion on cork oak and other forests, favoured by global warming, is already a matter of concern (Brasier 1996, Scanu et al. 2013). Thus, worthy of attention are those areas where site accessibility and complex orography on a local scale might facilitate cork oak survival in microrefugia, for example in Kabylie, Moroccan Rif, South Italy, and Catalonia (Dobrowski 2011). Herein, our findings evidenced many putative refugia characterized by coastal mountains and heterogeneous topography, where cork oak might find favourable local climatic conditions.

The importance of the detected putative refugia includes the value of control areas to monitor the species' biology and ecology. These are regions that appear to maintain climatic characteristics suitable for the species over time, although they may be reduced in area, mainly due to the severity of warming conditions during the second half of the 21st century (Meehl & Tebaldi 2004, IPCC 2014). Those areas are already occupied by cork oak populations, with the exception of the Peloponnese, which represents the only case of extra-zonal refugia with respect to the current species distribution.

The results show how every haplotype will face important changes in suitable area availability, but individual responses are linked to specific climatic variables, thus we can argue that global warming will act differently, favouring or penalizing the spread of each haplotype. Such a pattern is supported by many investigations about past environmental changes shaping the modern genetic diversity of plant species (e.g. Cheddadi et al. 2006, Lavergne et al. 2010). In the case of cork oak, we observed 3 different responses from the haplotypes investigated: (1) a large spread of the purple and blue haplotypes (westward for the former, east and westward for the latter); (2) an extent of the orange domain, but constrained westward up to Catalonia; (3) a reduction of the green haplotype in the west due to the disappearance of several refugia, and its probable survival in those areas with local conditions of humidity (e.g. the Douro Valley) or mountainous contexts characterized by milder local climate (e.g. Moroccan Rif, South Italian Apennines). Each haplotype forecasting is specifically affected by a restricted number of environmental variables. The seasonal ranges of temperature and precipitation were found to be important for all the groups (cf. Table 4), in addition to annual variation and some extreme values (e.g. temperature of the coldest month and precipitation of the driest month). Therefore, the orange haplotype showed a more thermophilous behaviour, while the green appeared to be more dependent on humidity and cool environments. In fact, the former presently occurs in the central Mediterranean and will spread east and west, benefitting from more arid conditions; the latter would disappear from many refugia, surviving only northward and in coastal mountains higher in altitude (cf. Table 3, Fig. 2).

Two areas are worthy of further consideration: Kabylie and Apulia. The former will notably decline in extent, but will play a crucial role in safeguarding the North African species remnants (together with Moroccan Rif), being the refuge for the whole haplotypic assemblage. The latter contains the easternmost extent of *Q. suber* in Europe, isolated in respect to the species' core range. Those very fragmented populations will follow the same changes as the other areas, including disappearance in the most pessimistic scenario at the end of the century. However, Apulia is a notable area, hosting a rare haplotype found in only a few stands (Bellarosa et al. 1993, 1996, Simeone et al. 2009). Thus, the loss of that area includes the loss of that genetic component of cork oak.

Moving onto topics of forest restoration and biodiversity conservation, it could be argued that cork oak and its genetic components should be safeguarded by driving specific actions, according to the multiple abovementioned responses and to the strategies suggested by experts in the field (cf. Stanturf et al. 2014a, Dumroese et al. 2015a). Among them, of particular importance could be relic population preservation (e.g. in Kabylie, Serrania de Ronda and Var); localized reforestation (Tyrrhenian coast, Rif Mountains); defragmentation towards tree lines or reconnection of closing stands (Apulia, Algarve-Alentejo-West Andalusia); and species diffusion into parks and gardens, where the effects of climate change can be mitigated by human care (arboreta).

An interesting study area would be the Kabylie (see Fig. 2), where cork oak forms pure or mixed stands along the mountain coasts facing the Mediterranean, with *Cedrus atlantica* (Endl.) G. Manetti ex Carrière, *Q. ilex* L., *Q. afares* Pomel, *Q. canariensis* Willd., *Pinus halepensis* Mill., *P. pinaster* Aiton, *Tetraclinis articulata* (Vahl) Mast., *Olea europaea* L., and many shrub species (Louni 1994, Messaoudène & Merouani 2009).

Aerial photographs (Fig. 3a; the example of Bejaia District, Region of Kabylie) reveal a high degree of forest integrity. Evident processes of forest fragmentation due to heavy urbanization and infrastructure are mostly absent, although official Algerian statistics (BNEDER 2008) highlight an ongoing reduction in cork oak area due to frequent forest fires, land abandonment, inadequate silvicultural management and incorrect cork harvesting procedures, overgrazing, and *Platypus cylindrus* attacks (Branco & Ramos 2009). Hence, all strategies related to cork oak conservation in Kabylie could be focused on site protection where the species already occurs, and move towards the implementation of a national legislation devoted to forest management (e.g. foundation of parks or natural reserves). Disturbances should be limited by strict control of the area, and the evolution of forest coenoses could be monitored by local experts. These activities are not hard to achieve, as the University Mouloud Mammeri of Tizi-Ouzu already works in that district with skilled foresters and researchers. In addition, traditional active restoration strategies could be adopted following Aronson et al. (2009).

In the case of Apulia (cf. Site no. 19 in Table 2; see Figs. 2 & 3), cork oak is found with other oak species like *Q. trojana* Webb and *Q. ithaburensis* subsp. *macrolepis* (Kotschy) Hedge & Yalt., which meet at the westernmost limit of their range, attesting to the importance of such a region for the biogeographic history of oaks in the Mediterranean (Schirone & Spada 1995). In some cork oak populations, *Q. x morisii* is also present (Scarascia Mugnozza & Schirone 1983). Presently, the conditions for *Q. suber* in Apulia are very compromised, as shown in Fig. 3b and in the Italian soil use database (www.soilmonitor.it). Fragmentation caused by extensive urbanization and intensive agriculture has led to small, scattered and highly isolated cork oak remnants, so that the species might be considered to be at risk of extinction (Saunders et al. 1991, Pirnat & Hladnik 2016). All this being considered, the species' persistence in Apulia appears to be at risk — which implies a loss of the haplotype that is probably the most drought resistant, due to its geographic position and frequent biennial acorn production.

Species conservation in Apulia often requires human intervention, as was recently carried out by the regional government towards implementation of specific legislation and a campaign to increase public awareness. Projects devoted to mitigating the effects of the extensive fragmentation have been done in the neighbourhood of natural stands (e.g. reforestation of 50 ha), despite the difficulty in finding available bare lands. However, these actions should be combined with reconnection programs, for example by using tree lines along private fields, which are usually de-

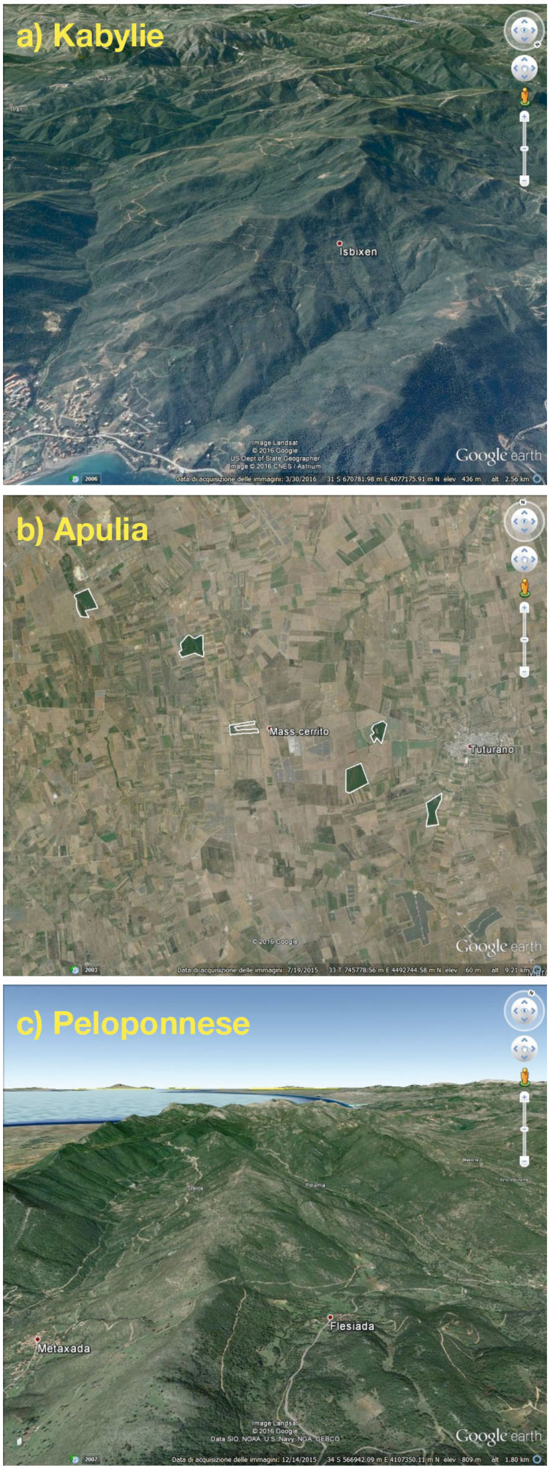

Fig. 3. Overview of 3 areas, as key examples within putative cork oak *Quercus suber* refugia, where different forest management and restoration approaches should be followed. Intact natural cork oak forests at (a) Bejaia district in Kabylie, Algeria; (b) highly fragmented remnants of cork oak stands in Brindisi Province, Apulia, Italy; (c) suitable valleys for cork oak assisted migration in central Messenie Region, south-west Peloponnese, Greece

limited with dry stone walls. The main advantage of tree lines is that they provide 'linear' stands that are not space demanding, but are economically profitable because of the supplementary income provided from cork harvesting. Coupling tree lines with dry stone walls (already common in the area) acts as natural condenser of dew and air humidity in arid regions, and might be worthy of interest for biodiversity conservation (Beysens & Milimouk 2000). Furthermore, the ornamental value of cork oak has increased by recent awareness campaigns, and the species' recruitment at forest nurseries is even easier, so that its diffusion into parks and gardens is becoming an additional mechanism to avoid species extinction. Finally, a biotechnological approach should be considered as well (Dumroese et al. 2015a). DNA samples of all the Apulian provenances and many others from the Mediterranean have already been collected and stored at the University of Tuscia (Italy), for a possible cisgenic lines production.

However, these actions may not be enough to guarantee a full conservation program; thus, it might also be important to implement assisted migration. According to previous studies (Schirone & Spada 1995, Simeone et al. 2009, Schirone et al. 2015b), the Apulian edge population of cork oak is the remnant of a recent westward retreat of the species range, which previously extended to the eastern Mediterranean Basin. Therefore, it would be particularly useful if the assisted migration took place in Greece (from Site nos. 19 to 20; see Table 2, Figs 2 & 3), where the species was present until the 19th or early 20th century (Schirone et al. 2015b and references therein, Vessella et al. 2015), and especially in the Peloponnese, as this was shown as a potential refugium from our findings. On the other hand, attempts at assisted migration have been successfully made in the Ionian Islands and in eastern Bulgaria, demonstrating the possibility of locating cork oak even in the eastern Mediterranean (Dafis 2000, Alexandrov & Dobrev 2012). Cork translocation in the Peloponnese, in particular that of the orange haplotype, would represent an assisted migration sensu stricto, because there is no possibility for the species to naturally re-occur in Greece due to the geographical barrier of the Adriatic sea. In detail, a reliable area for the assisted migration of Apulian haplotypes might be the southwestern part of the Peloponnese (Messenie region; Fig. 3c), which is characterized by wide zones with absent vegetation or sparse Mediterranean maquis. Even the blue haplotype might find suitable areas (if a pessimistic scenario occurs), especially at higher altitudes or where favourable wetter microclimates persist. Thus, a cork oak reintroduction could take place without altering the current land use. The current climate in the Messenie region is also comparable to the Apulia climate (cf. www.climate-data.org; www.worldclim.org), but a deeper investigation should focus on soil properties at a fine scale (Serrasolses et al. 2009). On a broad scale, the soil characteristics in that area are comparable with those of Apulia, i.e. a limestone bedrock with an upper layer of terra-rossa. pH values in Messenie, between Pilos and Kalamata, range between 6.6 and 7 (Panagos et al. 2012), which is less than that of the Apulian cork oak stands (7.1) (Scarascia Mugnozza & Schirone 1983). On the other hand, Serrasolses et al. (2009) pointed out that cork oak, which is usually considered acidophilous, can occur even on limestone by reducing the pH of the rizospheric soil. Such a capacity might even be favoured by human interventions, e.g. by adding soil amendments during plantation. The same assisted migration could benefit even the less calcifugous natural hybrids of cork oak still occurring in the Balkans (Schirone et al. 2015b and references therein). At the economic level, the species' reintroduction might be supported through integrated projects, which could also include crops (Marras et al. 2014).

6. CONCLUSIONS

This study represents, to our knowledge, the first attempt of a conservation plan on a broad scale to focus on the germplasm of a Mediterranean species, which includes the possibility of assisted migration of selected haplotypes under 2 global warming scenarios. Two issues are worthy of closing remarks. These investigations were based on a niche modelling approach, analyzing a time window of approximately 130 k yr (from the Last Intergracial to present) as reported in Vessella et al. (2015); this allowed us to detect some putative refugia for cork oak — including areas in Greece, where the species occurred until the beginning of the 20^{th} century (Schirone et al. 2015b). Presently, natural cork oak forests are absent in Greece and the Balkans, possibly due to an excessive anthropic impact coupled with a phase of past climate change — natural (Frisia et al. 2006) or human-based (Zennaro et al. 2015). In view of this, cork oak assisted migration in Greece would mean bringing the species back into its competency area, keeping safe the principle of 'restoration history based' (cf. Dumroese et al. 2015b, Hart et al. 2015a,b). Finally, high quality cork oak seedling production requires specific expertise due to the recalcitrant behaviour of its seeds (Almeida et al. 2009). Managing and organizing traditional nursery activity in Greece for cork oak production could therefore be difficult, especially considering that forest nurseries will also face challenges related to climate change and typical plant production (Williams & Dumroese 2014; Dumroese et al. 2015a). A solution might potentially come from new technologies, such as the creation of robotized nurseries for indoor seedling production (like the Zephyr Project products; www.zephyr-project.eu), which could be placed near plantation sites.

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