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Ecology and potential distribution of the Cretan endemic tree species *Zelkova abelicea*

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Abstract

Mediterranean mountain forests feature woody species relicts such as *Zelkova abelicea*, an endemic tree species confined to six spatially and genetically distinct populations in Crete (S Aegean, Greece). We used species distribution modelling to predict the potential distribution of *Zelkova abelicea*. Comparison of coordinate-based geodata extractions for climate and topography revealed pronounced environmental differences for the metapopulations. Main factors for species distribution models were altitude and temperature seasonality (proxy for west-east gradient) whereas topographic conditions had surprisingly little influence on our models. While the most extensive *Zelkova* metapopulations were found to occur under locally fairly mesic conditions and comprising a wider ecological spectrum, the smaller populations comprising narrower ecological range occurred at lower elevations and further east. For further extrapolation with similar models for known populations, only similar site conditions allowed for a prediction. Differentiated site conditions in the mountains, genetic distinctness and possible environmental adaptations of isolated populations are to be considered in conservation and management.

Introduction

A particularity of Mediterranean forests is the conspicuous rate of endemic tree taxa, some of which are considered as relicts of a widespread and rich tertiary flora (Mai 1987). As especially isolation by topography is a driving factor for endemism (Steinbauer et al. 2013; Trigas et al. 2013; Steinbauer et al. 2016), Mediterranean mountains and the major Mediterranean islands host many relict tree and shrub populations. For instance, *Cedrus libanii* subsp. *brevifolia is* restricted to Cyprus; *Abies nebrodensis, Celtis tournefortii* subsp. *aetnensis* and *Rhamnus lojaconoi* occur only in the Sicilian mountains (Quézel & Médail 2003). Other prominent examples refer to the genus *Zelkova* (Ulmaceae). Widely distributed under favourable pre-Quaternary climate conditions (Garfi 1997; Quézel & Médail 2003), *Zelkova* died out in Central Italy in late Pleistocene, after repeated increase and decline along glacial-interglacial cycles (Follieri et al. 1986). Today two out of six species of the genus worldwide are represented in the Mediterranean basin: *Zelkova abelicea* in the mountains of Crete and *Zelkova sicula* in south-eastern Sicily (Di Pasquale et al. 1992; Garfì et al. 2011). Chloroplast and nuclear marker analyses revealed close relation of the two Mediterranean species

(Christe et al. 2014). *Z. abelicea* is listed Endangered by IUCN (Kozlowski et al. 2012), and *Z. sicula* which occurs in only two single spots is considered Critically endangered (Garfì 2006). Depending on browsing impact and climatic constraints (Garfì et al. 2002), they may grow as tree, treelet or shrub. Compared to co-occurring woody species, both *Zelkova* species take up a rather distinct ecological niche (Søndergaard & Egli 2006; Garfì et al. 2011). Local climate seems to be crucial, as *Zelkova* populations of both species are restricted to topographically or edaphically relatively favourable sites where evapotranspiration is rather low and water-supply satisfactory (Søndergaard & Egli 2006; Garfì et al. 2011). Cretan *Zelkova abelicea* grows in several isolated mountains between 900 m a.s.l. up to the tree line at about 1800 m a.s.l. (Kozlowski et al. 2012); *Z. sicula* occurs at lower elevation (320 to 520 m a.s.l.) but is confined to gullies, suggesting that this microtopographic position compensates for inadequate rainfall amounts and helps the species to withstand seasonal water stress (Garfì et al. 2011).

Isolated narrow-range plant populations may be genetically impoverished (Booy et al. 2000; Honnay & Jacquemyn 2007) or may show (unexpected) genetic diversity (Mousadik & Petit 1996; Bucci et al. 1997; Parducci et al. 2001; Liu et al. 2006; LaBonte et al. 2017). For example, Spanish populations of widespread European *Ulmus* species show high genetic variation compared to northern occurrences (Fuentes-Utrilla et al. 2014). This is interpreted as indicating relict populations, with higher genetic diversity compared to those originating from post-glacial colonisation. Relict populations are thus important for genetic diversity conservation and underline the need to protect glacial refugia in the Mediterranean and elsewhere. Broad genetic diversity also applies to *Zelkova abelicea.* Isolated subpopulations were found to be genetically differentiated (Christe et al. 2014). Haplotypes, the haploid genotype of individual samples, show distinct intraspecific patterns with a strong separation of lineages from different mountain ranges. This supports the assumption of long-term geographical isolation.

This study aims to illuminate the relation among ecology, distribution patterns and isolation of *Z. abelicea* through species distribution modelling. Toolsets for species distribution modelling can support a clearer understanding of species ecology on landscape scale. This approach helps to assess potential and actual distribution areas of species and can be used to explain past and recent range patterns (Elith et al. 2006; Svenning et al. 2011). Furthermore modelling allows to predict suitable sites under changing climate conditions (Skov & Svenning 2004; Keenan et al. 2011; Garcia et al. 2013). Species distribution modelling may complement molecular research or support targeted sampling; it is also useful for conservation and restoration and may even help to reveal hitherto unrecorded populations and cryptic taxa (Dick et al. 2003; Sattler et al. 2007; Rissler & Apodaca 2007). The present study addresses the following questions: How much do isolated populations of *Zelkova abelicea* differ in ecology, as expressed by abiotic variables? Are these differences related to known genetic patterns? Which environmental factors influence species distribution models most? How do predicted distribution patterns relate to known records? Do combined metapopulation samples improve the predictive value for known neighbouring populations? Consequences for biogeography and management are discussed.

Study area

Crete is among the largest islands of the Mediterranean and topographically outstanding with alternating high mountain ranges and lowland plains. Three mountain ranges rise over 2000 m and all are rather isolated, in the geological past even separated by shallow seas. Hard Triassic metamorphic limestones prevail in the high mountains. Mediterranean lowland climate, with mild winters and hot and dry summers, is modified in the mountains, with precipitation increasing, temperatures decreasing, and evapotranspiration reduced (Barry 2008). This favours hardy species adapted to rather mesic conditions. The prevailing westerlies bring about moist air masses which, in combination with a pronounced relief, cause rain shadow effects on the east sides. Northern strong dry etesian winds, called meltemi, occur regularly during summer. The rugged relief, shaped by tectonic events and erosion, promotes mesoclimatic variation (Barry & Blanken 2016). Sheltered sites in poljes, dolines, gorges and below cliffs support a specialised flora (Egli 1989; Egli et al. 1990; Hedderson & Blockeel 2013). Such local-climate conditions in otherwise sun- and wind-exposed environments favour xero-mesic taxa such as *Zelkova*.

Methods

Coordinates of *Zelkova abelicea* individuals were obtained from collections and field surveys (Tab. 1). Identical coordinates were reduced to one. Occurrences of *Zelkova* in isolated mountain ranges were considered as (meta)populations. Most records by far are in the west

Tab. 1 Data resources for *Zelkova abelicea* populations of Crete. Additional unpublished records are also included.

Collector	Publication	Timespan	Number of records
L. Fazan et al.	Fazan et al. 2012; Fazan 2014	2010 - 2016	218
B. Egli	Egli 1998, 2000	1993 - 1999	50
E. Bergmeier	Bergmeier 2012	1999 - 2012	13
R. Jahn	-	1988 - 2014	11
various	Literature + herbarium specimen	1988 - 2014	39
total			**331**

of Crete (Fig. 1, Tab. 2). The majority of records are from the western Lefka Ori (W), fewer from the eastern Lefka Ori (E), including the lowest known site near Imbros. The Kedros population (K) is isolated on a single mountain massif in the western central part of Crete. Further east, on Psiloritis (P), only one small population occurs in the Rouvas forest. The east central mountain Dikti (D) harbours the second largest population, comprising 31 scattered records of one to few trees. The smallest number of records is from Thrypti (T), the easternmost mountain range. Coordinates from GPS measures as well as raster data for climate and geomorphology were processed in ArcGIS (ESRI 2013) (Tab. 3, Tab. 4). A grid resolution of 397 m was used for modelling, amounting to about 102,000 grid cells. Multiple records per grid cell were used. Further plotting of results and statistical tests were performed in R 3.4.0 (R Development Core Team 2017). For initially 30 environmental variables Spearman correlations were applied (Tab. 4, *psych* package, Revelle 2017). Collinear pairs were reduced to one for $R^2 > 0.6$ with priority on geomorphology and mean values, leaving 7 variables for final analysis (Tab. 3). For these variables coordinate-based geodata extractions were calculated for all records and plotted for populations. Additionally, Kruskal-Wallis tests were performed to reveal significant differences (*pgirmess* package, Giraudoux 2016). MaxEnt software version 3.4.0 was used to compute species distribution models (Phillips et al. 2006). Models based on multiple correlations were compiled for a set of environmental variables, resulting in relative habitat suitability for each grid cell, with or without prior *Zelkova* records. We applied standard settings which provided results similar to when manually modified. Models were improved by jackknife tests, therewith quantifying the contributions of single variables in models. This resulted in the exclusion of *mean annual precipitation*, as the latter

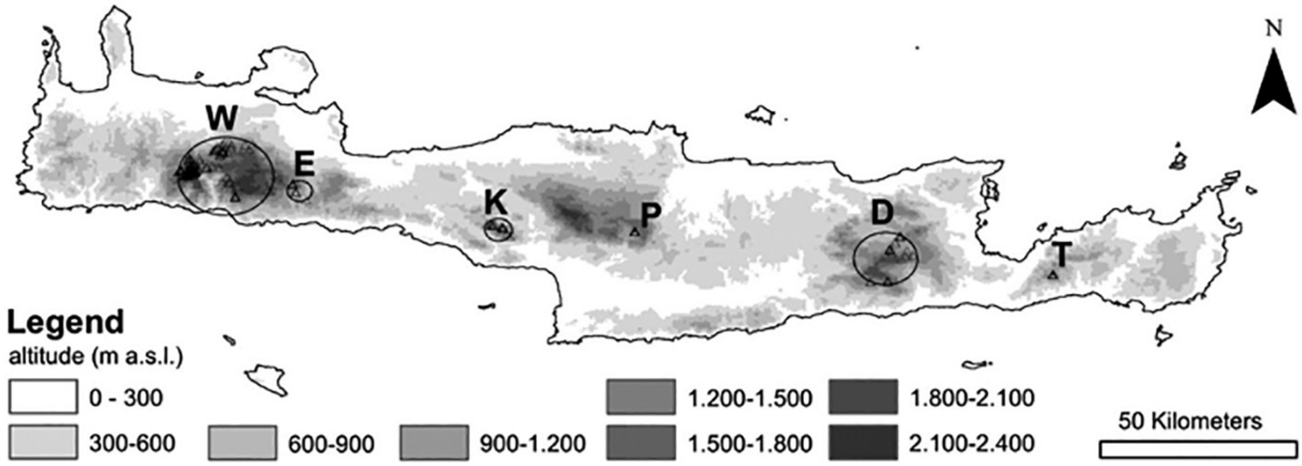

Fig. 1 Map of distribution and altitudinal patterns for the *Zelkova abelicea* metapopulations in Crete. Circles circumscribe areas with records, but records in P and T are given as single points.

Tab. 2 Metapopulations of *Zelkova abelicea* in the Cretan mountains with spatial extent, number of records and occupied grid cells (397 m x 397 m).

Population	Mountain range	Longitude	Latitude	Records	Grid cells
W	West Lefka Ori	23.88-24.06°	35.26-35.39°	256	114
E	East Lefka Ori (East Imbros)	24.09-24.18°	35.25-35.29°	14	5
K	Kedros	24.59-24.64°	35.17-35.20°	18	11
P	Psiloritis	24.93°	35.18°	7	1
D	Dikti	25.47-25.57°	35.06-35.17°	31	18
T	Thrypti	25.89°	35.08°	6	3

Tab. 3 Environmental factors used as variables to predict species distribution.

Data source	Original resolution	Variables
Chelsa climate data 1.1 (Karger et al. 2016)	30 ArcSec = ~1 km	1. *mean annual precipitation* (mm) 2. Bio2/ *temperature mean diurnal range* (standard deviation *100) 3. Bio4/ *temperature seasonality* (mean of monthly (max - min))
Digital Elevation Modell over Europe (EEA 2015)	30 m	4. *altitude* (m a.s.l.) **Derived thereof:** 5. *slope* (°, Burrough & McDonell 1998) 6. *heatload* (McCune & Keon 2002) 7. *cti* (compound topographic index, Moore et al. 1993, Gessler et al. 1995)

Tab. 4 Spearman correlations of environmental parameters, pairs with values ≥0.6 are reduced to one; selected variables in bold font (see Tab.3 for abbreviations), all further refer to macro-climate (Karger et al. 2016), prec= precipitation, temp= temperature, intanvar= inter-annual variation.

	slope	**heatload**	**cti**	**altitude**	temp annual mean	temp intanvar	temp July	temp January	**annual mean prec**	prec intanvar	bio9	bio8	bio7	bio6	bio5	**bio4**	bio3	**bio2**	bio19	bio17	bio16	bio15	bio14	bio13	bio12	bio11	bio10	bio1	prec July	prec January
slope	1.00																													
heatload	-0.02	1.00																												
cti	-0.39	-0.02	1.00																											
altitude	0.36	-0.03	-0.16	1.00																										
temp annual mean	-0.24	0.02	0.10	-0.73	1.00																									
temp intanvar	-0.25	-0.17	0.16	-0.14	0.31	1.00																								
temp July	-0.28	0.01	0.11	-0.71	0.98	0.40	1.00																							
temp January	-0.24	0.04	0.09	-0.75	1.00	0.28	0.97	1.00																						
annual mean prec	0.27	-0.27	-0.02	0.14	-0.31	-0.18	-0.36	-0.28	1.00																					
prec intanvar	0.25	-0.18	-0.06	0.17	-0.33	-0.31	-0.41	-0.31	0.89	1.00																				
bio9	-0.25	-0.01	0.07	-0.70	0.95	0.47	0.97	0.94	-0.36	-0.44	1.00																			
bio8	-0.31	0.01	0.10	-0.72	0.91	0.42	0.91	0.91	-0.37	-0.42	0.93	1.00																		
bio7	-0.27	-0.10	0.20	-0.22	0.43	0.73	0.52	0.40	-0.34	-0.51	0.56	0.52	1.00																	
bio6	-0.24	0.03	0.05	-0.75	0.97	0.38	0.97	0.97	-0.32	-0.37	0.98	0.94	0.47	1.00																
bio5	-0.24	-0.01	0.08	-0.70	0.95	0.46	0.98	0.94	-0.36	-0.43	1.00	0.93	0.56	0.98	1.00															
bio4	-0.30	0.01	0.11	-0.37	0.63	0.54	0.70	0.60	-0.50	-0.59	0.72	0.64	0.87	0.66	0.72	1.00														
bio3	0.19	0.00	-0.11	0.22	-0.41	-0.22	-0.47	-0.37	0.58	0.72	-0.49	-0.35	-0.59	-0.41	-0.48	-0.73	1.00													
bio2	-0.09	0.06	-0.03	-0.22	0.19	0.23	0.16	0.23	0.34	0.20	0.18	0.29	0.19	0.22	0.18	0.02	0.39	1.00												
bio19	0.30	-0.23	-0.06	0.19	-0.32	-0.21	-0.38	-0.30	0.99	0.89	-0.38	-0.40	-0.36	-0.33	-0.37	-0.51	0.59	0.34	1.00											
bio17	0.03	-0.06	0.05	-0.22	0.07	-0.23	-0.02	0.11	0.68	0.79	-0.07	-0.05	-0.37	0.02	-0.07	-0.29	0.46	0.22	0.64	1.00										
bio16	0.32	-0.22	-0.05	0.22	-0.36	-0.20	-0.41	-0.33	0.98	0.88	-0.40	-0.43	-0.36	-0.36	-0.40	-0.53	0.59	0.32	0.99	0.60	1.00									
bio15	0.18	-0.09	0.04	0.63	-0.61	0.17	-0.52	-0.65	-0.03	-0.11	-0.46	-0.55	0.08	-0.56	-0.46	-0.15	0.03	-0.31	0.02	-0.52	0.08	1.00								
bio14	0.04	-0.05	0.03	-0.25	0.08	-0.30	-0.03	0.11	0.59	0.71	-0.07	-0.04	-0.45	0.03	-0.07	-0.31	0.40	0.11	0.56	0.95	0.52	-0.54	1.00							
bio13	0.29	-0.25	-0.05	0.18	-0.34	-0.22	-0.40	-0.31	0.99	0.89	-0.40	-0.42	-0.36	-0.35	-0.39	-0.51	0.56	0.29	0.99	0.64	0.99	0.02	0.56	1.00						
bio12	0.25	-0.27	-0.02	0.11	-0.27	-0.18	-0.33	-0.24	1.00	0.90	-0.33	-0.34	-0.32	-0.28	-0.33	-0.47	0.57	0.34	0.98	0.70	0.97	-0.07	0.61	0.99	1.00					
bio11	-0.24	0.02	0.05	-0.75	0.97	0.38	0.97	0.97	-0.32	-0.37	0.98	0.94	0.47	1.00	0.98	0.66	-0.42	0.22	-0.33	0.02	-0.36	-0.56	0.03	-0.35	-0.28	1.00				
bio10	-0.25	-0.01	0.07	-0.70	0.95	0.47	0.97	0.94	-0.36	-0.44	1.00	0.93	0.56	0.98	1.00	0.72	-0.49	0.18	-0.38	-0.07	-0.40	-0.46	-0.07	-0.40	-0.33	0.98	1.00			
bio1	-0.25	0.01	0.06	-0.72	0.96	0.43	0.98	0.95	-0.36	-0.43	1.00	0.93	0.52	0.99	1.00	0.70	-0.47	0.19	-0.38	-0.05	-0.40	-0.50	-0.03	-0.40	-0.33	0.99	1.00	1.00		
prec July	0.06	-0.05	0.05	-0.21	0.03	-0.36	-0.07	0.07	0.61	0.73	-0.11	-0.08	-0.48	-0.01	-0.11	-0.34	0.37	0.06	0.57	0.95	0.53	-0.53	0.98	0.57	0.63	-0.01	-0.11	-0.07	1.00	
prec January	0.35	-0.21	-0.07	0.25	-0.40	-0.22	-0.45	-0.37	0.95	0.86	-0.43	-0.46	-0.38	-0.39	-0.42	-0.56	0.62	0.31	0.96	0.54	0.99	0.13	0.46	0.96	0.94	-0.39	-0.43	-0.43	0.48	1.00

data layer was covered by other values, and did not add further value to the models. Cross-validation with geographically distinct metapopulations was preferred to random test sample selection. One species distribution model was performed using all known records, to achieve a robust evaluation of the present *Zelkova* distribution. Extrapolation performance was tested further with combined metapopulations, leaving out the test population. Combinations resulting in sample sizes of n < 80 were excluded, as such sample numbers constrain internal handling of environmental features in MaxEnt and therefore render model outputs hardly comparable (Phillips & Dudík 2008; Morales et al. 2017). As for some populations only few records were available, metapopulation W with the largest sample number was always included. The general modelling performance according to Area-under-the-Curve (AUC) test was high, with values close to the maximum, but the measure was not suitable to predict extrapolation performance (Lobo et al. 2008). Hence regularised sample predictions were used for the evaluation of test data, the values of which maximize towards 1, and to describe environmental suitability (Merow et al. 2013). These values were visualised in maps; with values above 0.6 species occurrence is likely.

Results

Environmental comparison of populations

In total 332 *Zelkova* records were used, from (meta) populations ranging between 6 (T) to 256 (W) trees. The six metapopulations of *Zelkova abelicea* differed in their environmental characteristics (Fig.2). As revealed by the amplitude of abiotic values, within the Lefka Ori the largest metapopulation (W) displayed

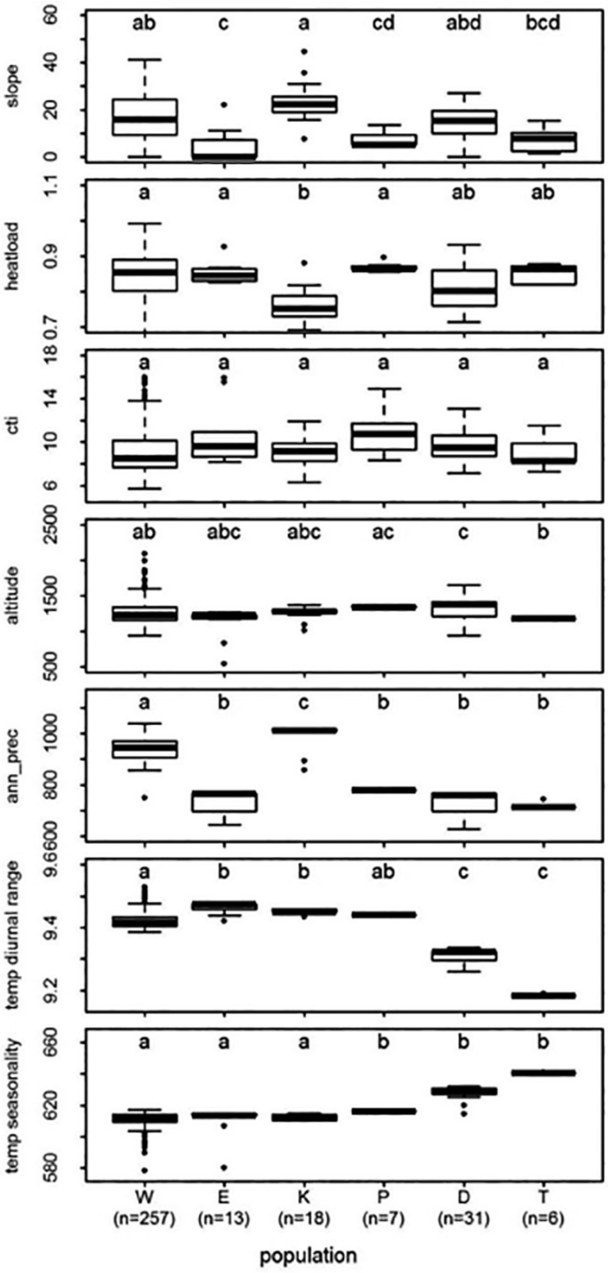

Fig. 2 Site conditions for six metapopulations of *Zelkova abelicea*. Values from coordinate-based geodata extractions; W= W Lefka Ori, E= E Lefka Ori (i.e., east of Imbros gorge), K= Kedros, P= Psiloritis (Rouvas Forest), D= Dikti, T= Thrypti; dissimilar letters (a, b, c, d) indicate significant differences in ranks of the Kruskal-Wallis-Test (p-value = 0.05).

the broadest ecological range. The smaller metapopulations covered narrower ecological amplitudes. Steep sloping terrain was a characteristic of *Zelkova* populations in the western Lefka Ori (W), Kedros (K) and Dikti (D). *Heatload* differed among the metapopulations, with lowest values for K. Compound topographic index (*cti*), indicating relief position preferences, was indifferent among metapopulations. The diurnal range of temperatures was highest in the populations of central Crete, while daily differences were attenuated for the two eastern populations. Temperature seasonality was higher in the three eastern populations Psiloritis (P), Dikti (D) and Thrypti (T). From the western to the eastern populations *mean annual precipitation* according to rain shadow effects decreased from 900 - 1000 mm to 700 - 800 mm per year.

Models and prediction values

In jackknife tests *altitude* and *temperature seasonality* were influencing models most, followed by *temperature diurnal range*, while the other variables contributed to a lesser extent. For a model that included all *Zelkova abelicea* records the maximum prediction value for any single metapopulation was found for W (Tab. 5). The wide environmental range of the W metapopulation was nevertheless not fully covered by this general model. As some records were poorly predicted (minimum values), a lower mean prediction value resulted.

The best mean values for the extrapolation tests added up for population K (Tab. 6). With only few good predictions with values above 0.6, and all other populations below this prediction threshold, the model poorly qualified. W was included in all extrapolation models, thus it could not be tested and its overall influence remained high. Combinations with neighbouring metapopulations modified the extrapolation performance slightly. The best results in mean and maximum sample prediction values were obtained from the combination WEPDT, followed by WEPD, WEDT and WED. The poorest results were from WT.

Predicted populations in maps

Mapped distribution patterns visualise the model-specific site conditions and their suitability for *Zelkova* (Fig. 3). Favourable conditions and thus high occurrence propability of *Zelkova* were indicated by higher values (0.6 is frequently used as presence-absence threshold). The three maps exemplify repeatedly occurring predictions for modelled metapopulation combinations: while the distribution patterns of W and K,

Tab. 5 Sample predictions with tested populations for a species distribution model based on all *Zelkova* records (mx = maximum, mn = mean, sd = standard deviation).

Population	W	E	K	P	D	F
mx	0.963	0.730	0.863	0.642	0.406	0.652
mn	0.723	0.578	0.717	0.596	0.332	0.516
sd	0.234	0.242	0.153	0.029	0.081	0.060

derived from W, were well predicted, the others were not (Fig. 3a). The map in Fig. 3b, based on WEKPT, did not predict population D but it predicted population T, though with rather low values. With all populations included (Fig. 3c), rather different prediction values applied, some of which were low (D). Populations E, D and T were predicted with low to very low sample prediction values in all three maps. Also in all maps predictions of the *Zelkova* range were locally overestimated and did not correspond to recent records, for example areas neighbouring west (Apopighadhi range) and east (around Kastro mountain) of the main Lefka Ori metapopulation (W), topmost Agathes mountains east of E and large parts of the Psiloritis range.

Tab. 6 Sample prediction values for combinations of populations (rows) excluding the tested population (columns; mx=maximum, mn=mean, sd=standard deviation); prediction values >0.6 in bold; *as map in Fig.3.

Population	E			K			P			D			T		
	mx	mn	sd	mx	mn	sd	mx	mn	sd	mx	mn	sd	mx	mn	sd
W*	0.463	0.247	0.119	**0.778**	0.550	0.113	0.505	0.499	0.010	0.060	0.020	0.008	0.000	0.000	0.000
WE				0.764	0.575	0.118	0.492	0.467	0.016	0.067	0.022	0.009	0.000	0.000	0.000
WK	0.596	0.282	0.151				0.496	0.481	0.025	0.053	0.017	0.007	0.000	0.000	0.000
WP	0.463	0.247	0.119	**0.778**	0.550	0.113				0.060	0.020	0.008	0.000	0.000	0.000
WD	0.491	0.250	0.116	**0.795**	0.560	0.129	0.439	0.432	0.010				0.007	0.006	0.001
WT	0.452	0.244	0.111	**0.779**	0.539	0.129	0.441	0.433	0.012	0.083	0.034	0.019			
WEK							0.535	0.515	0.012	0.057	0.018	0.008	0.000	0.000	0.000
WEP				**0.773**	0.598	0.120				0.065	0.022	0.009	0.000	0.000	0.000
WED				**0.814**	**0.630**	0.137	0.553	0.500	0.034				0.006	0.006	0.001
WET				**0.790**	**0.604**	0.131	0.545	0.493	0.033	0.090	0.035	0.021			
WKP	**0.612**	0.298	0.161							0.050	0.016	0.007	0.000	0.000	0.000
WKD	**0.648**	0.307	0.159				0.516	0.509	0.011				0.006	0.006	0.001
WKT	**0.624**	0.310	0.159				0.510	0.504	0.010	0.076	0.032	0.017			
WPD	0.534	0.284	0.133	**0.810**	0.598	0.133							0.007	0.006	0.001
WPT	0.483	0.270	0.124	**0.795**	0.562	0.123				0.094	0.036	0.023			
WDT	0.499	0.256	0.118	**0.794**	0.564	0.136	0.447	0.441	0.010						
WEKP										0.056	0.018	0.008	0.000	0.000	0.000
WEKD							**0.638**	0.588	0.032				0.006	0.006	0.001
WEKT							0.564	0.532	0.021	0.079	0.033	0.018			
WEPD				**0.821**	**0.655**	0.139							0.006	0.005	0.001
WEPT				**0.797**	**0.627**	0.134				0.098	0.036	0.024			
WEDT				**0.806**	**0.633**	0.142	0.546	0.503	0.027						
WKPD	**0.651**	0.322	0.165										0.007	0.007	0.001
WKPT	**0.639**	0.330	0.168							0.065	0.031	0.014			
WKDT	**0.648**	0.316	0.159				0.526	0.520	0.009						
WPDT	0.534	0.286	0.133	**0.810**	**0.605**	0.138									
WEKPD													0.006	0.006	0.001
WEKPT										0.065	0.029	0.015			
WEKDT							0.595	0.548	0.030						
WEPDT*				**0.844**	**0.708**	0.146									
WKPDT	**0.655**	0.332	0.166												

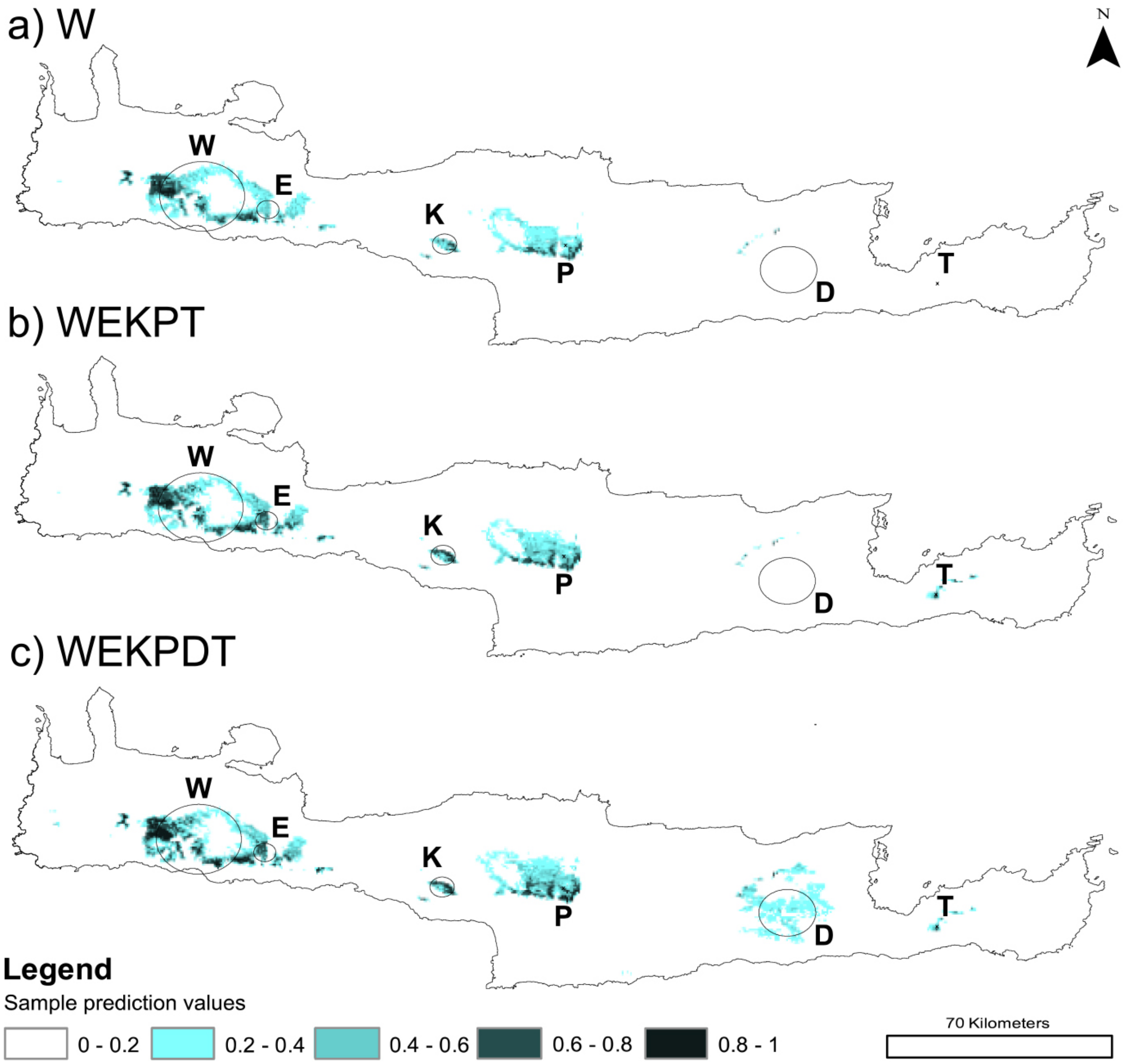

Fig. 3 Result maps of species distribution modelling (regularised training gain) based on various combinations of neighbouring metapopulations by using the same set of environmental variables; model based on (a) W, (b) WEKPT and (c) all six metapopulations; values > 0.6 imply favourable site conditions according to model parameters and occurrence probability; x (single spot) or surrounding circles indicate metapopulations.

Discussion

Ecology of populations

Zelkova abelicea needs specific environmental conditions typical for high altitudinal woodlands (Bauer & Bergmeier 2011). Fairly mesic conditions are crucial (Søndergaard & Egli 2006). Such environments are common in the west but less so eastwards due to decreasing rates of precipitation. Beside elevation, a longitudinal gradient is regarded by *temperature seasonality* in distribution models. We assume less favourable climate conditions towards east to be responsible for scattered or small populations, with frequently dwarfed *Zelkova* plants. Thus topography-driven climate conditions (topoclimate, mesoclimate) may compensate for less than perfect macro-climatic conditions by mitigating, e.g., irradiation and water stress (Lipscomp and Nilsen 1990a, 1990b; Scherrer et al. 2011). *Zelkova abelicea* is known for a general preference for such woodland sites (Søndergaard & Egli 2006). The present study even revealed pronounced affinity to low *heatload* values for the eastern *Zelkova* populations. As long as there are locally favourable conditions, environments with raised *temperature seasonality* and lower *mean annual precipitation* are occupied. The closely related *Z. sicula* is linked to specific topoclimate too (Garfi et al. 2011). Low *heatload* values as found in Kedros are induced by the orientation of the mountain range, hosting the main population on the windward northern side. The vital Kedros population grows in evergreen woodlands on steep shaded slopes with relatively high precipitation and high potential water run-off (or rather raised percolation). The main *Zelkova* metapopulation in the western Lefka Ori, an area which receives more precipitation than the other Cretan mountains, is associated with the widest spectrum of site conditions among all populations. Precipitation can be high and steep slopes are colonised there as well. It may be deduced that, together with generally more humid environments, slopes with high potential run-off and permeable soils are preferred by *Zelkova abelicea*, supporting sizable populations and a broader environmental niche. In drier environments, in contrast, usually moderately sloped or flat terrain, with consequently lower potential water run-off and shaded mountain sides, are preferred. As a general rule, populations of *Zelkova abelicea* were found to be associated with complex but predictable environmental gradients but site condition spectra differ between metapopulations.

Ecological and genetic patterns

Knowledge about regional ecological and genetic variation is required for many applications (Petit et al. 2004; Khadari et al. 2005; Vander Mijnsbrugge et al. 2010) and may inspire biogeographic and evolutionary research (Thompson 1999). Along environmental gradients, differentiated physiological reactions were recognised for distinct populations of Mediterranean *Quercus ilex* (Martin-StPaul et al. 2013) and high-Andean pines (Sáenz-Romero et al. 2013), assuming relations between ecology, physiology and genetic variability. Other studies showed that geographic isolation is a driver for species evolution, followed by ecological adaptations of isolated populations (Peterson et al. 1999; Wiens 2004). For *Zelkova abelicea*, indeed, several genetic markers suggest local patterns of isolated populations (Christe et al. 2014). The authors found that western populations (W, E) are genetically heterogeneous, central populations (K, P) are different but share similarities with that of D, and the easternmost population (T) is genetically more pronouncedly separated. We assume that the individual genetic structure of populations may be linked to environmental adaptations. High genetic diversity of the western population corresponds to high diversity of the occupied sites, and a strong genetic separation of the eastern populations comes along with their relative ecological distinctness. Conceivable may be either *in situ* adaptation to local site conditions or ancient colonisation from genetically and ecologically different lineages. Further research on comparative ecology and functional genetics within and between metapopulations of *Zelkova abelicea* are necessary.

Environmental variables in models

Main factors for species distribution models were *altitude* and *temperature seasonality.* Topographic conditions had surprisingly little influence on our models; their importance for general distribution was low, though populations showed individual differences. The clear preference of *Zelkova abelicea* for high elevations supports model compilation. In Mediterranean high mountains specific environmental factors act upon plants, such as low temperatures, snow cover, etc. (Körner 2014), supporting many hardy xero-mesic species such as *Zelkova abelicea*, many of which being narrow endemics and absent from the lowlands (Bergmeier 2002). *Temperature seasonality* is known for its fundamental influence on biological processes (Vazquez et al. 2017) and, within the models, expresses an east-west gradient. *Annual mean precipitation* is based on extrapolation of climate station records and the algorithm comprises a correction for elevation and topographic lee-side effects, but it reduces model performance and was outperformed by the two above mentioned parameters. A reason could be low relevance of overall precipitation patterns for *Zelkova abelicea,* perhaps due to its preference for topoclimatic (mesoclimatic) conditions with factors such as cloud and dew formation, water condensation, snow cover, frost protection, etc. Another reason for weak performance of the dataset can be unreliable or unsuitable *annual mean precipitation* values for the study area. Climate stations for data extrapolation in the mountains of Crete are lacking. Poor data quality can also be due to underestimated terrain complexity in the algorithm or variability in origins of climatic influences. Coarse grained climate data have been criticised as unsuitable for fine-scale studies like ours (Nadeau et al. 2017).

Distribution maps and extrapolation performance

Suitable habitats for *Zelkova abelicea* are scarce in the Cretan mountains and the species is probably declining, boosted by human impact (Egli 1997). Its range may have been less fragmented during more humid periods in the past. In our models the potential distribution range of *Zelkova abelicea* appears to be overestimated, as especially in western to central Crete some mountains without actual records have been assigned high occurrence probability. Local prediction errors such as near population E may be due to dry lee-side conditions. Further, erroneous distribution gaps cannot be ruled out. Near Imbros *Zelkova* has only recently been recorded, and especially dwarfed and browsed individuals are easily overlooked. The Psiloritis distribution gap, however, is likely to be actual, and is supported by our models that predict low occurrence probability for most of the mountain range, except for the south-eastern part (Rouvas), where population P occurs in mixed and sheltered stands with *Acer sempervirens* and *Quercus coccifera* (Bauer & Bergmeier 2011).

Heikkinen et al. (2012) reported for MaxEnt models high prediction accuracy for range extrapolations over large areas. This is only partly confirmed by our local study. Scale differences clearly matter, and while the tested model with all records is fairly close in predicting the general distribution pattern, extrapolations fail for populations with markedly different environmental conditions. We assume that marginal ecological conditions deviate too much from the mean and thus hamper model extrapolation. Low prediction accuracy can be due to unbalanced sampling or too simplistic model, as few parameters were included. Our model approximates site conditions but only roughly, while complex environmental conditions may influence mountain plants in many ways, such as by acting upon seedling growth through frost damage (Viveros-Viveros et al. 2009). Low prediction accuracy can thus be due to a lack of environmental as well as biotic data such as of soil parameters, mist and cloud cover frequency, surrounding vegetation, wildfires, grazing intensity and other historical and recent land management.

Biogeographical implications

Due to repeated climate change during the Pleistocene and Holocene, changes in plant population numbers, species range and vegetation composition occurred throughout Europe and the Mediterranean (Huntley 1990). As a result of cyclic climate development Mediterranean forests expanded and declined (Combourieu-Nebout 1993). For *Zelkova abelicea*, as a consequence of changing growth conditions during these cycles, shifts in altitudinal range, retreat to refugia and forest expansion may be assumed. Even so, distinct genetic patterns suggest long-term isolation and limited genetic exchange between metapopulations to the present day (Christe et al. 2014). Similarly, our results show, underlined by prediction patterns, metapopulations in each mountain range to be rather varying in terms of occupied site conditions. Specific abiotic combinations even for nearby metapopulations support the hypothesis of their long-term isolation. This corresponds with the concept of elevation-driven ecological isolation (Steinbauer et al. 2013), enhanced by mountain-specific conditions.

Concluding remarks

Along an east-west gradient in Crete, *Zelkova abelicea* shows surprising genetic and site variation. As spectra of site conditions vary among mountains inhabited by *Zelkova*, metapopulations differ in the range and degree of abiotic parameters. From a methodological point of view, the mountain-specific habitat heterogeneity of *Zelkova* metapopulations hampers good overall performance of species distribution models. In all *Zelkova* sites specific topoclimatic conditions are involved that mitigate to some extent unfavourable macroclimatic conditions. Suitable sites are rather rare and require special attention in conservation and forest management. In the Cretan mountains, as emphasised by Bauer & Bergmeier (2011), current woodland and rangeland degradation as a result of overgrazing is arguably the most fatal impact and counter measures are urgently needed. In spite of the patchy distribution of *Zelkova*, it is crucial to protect mountain ranges in total, covering complex abiotic conditions, thereby taking account of distributional shift under climate change.

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References

Barry, R.G. 2008. Mountain weather and climate. Cambridge University Press, Cambridge, New York, USA.

Barry, R.G., Blanken, P. 2016. Microclimate and local climate. Cambridge University Press, New York, NY, USA.

Bauer, E.-M., Bergmeier, E. 2011. The mountain woodlands of western Crete - plant communities, forest goods, grazing impact and conservation. Phytocoenologia 41: 73–105.

Bergmeier, E. 2002. The vegetation of the high mountains of Crete - a revision and multivariate analysis. Phytocoenologia 32: 205–249.

Bergmeier, E. 2012. KRITI - the vegetation of Crete database. Biodiversity & Ecology 4: 384.

Booy, G., Hendriks, R.J.J., Smulders, M.J.M., Groenendael, J.M., Vosman, B. 2000. Genetic diversity and the survival of populations. Plant Biology 2: 379–395.

Bucci, G., Vendramin, G.G., Lelli, L., Vicario, F. 1997. Assessing the genetic divergence of Pinus leucodermis Ant. endangered populations. Use of molecular markers for conservation purposes. Theoretical and Applied Genetics 95: 1138–1146.

Burrough, P.A., McDonell, R.A. 1998. Principles of Geographical Information Systems. Oxford University Press, New York, USA.

Christe, C., Kozlowski, G., Frey, D., Bétrisey, S., Maharramova, E., Garfì, G., Pirintsos, S., Naciri, Y. 2014. Footprints of past intensive diversification and structuring in the genus Zelkova (Ulmaceae) in south-western Eurasia. Journal of Biogeography 41: 1081–1093.

Combourieu-Nebout, N. 1993. Vegetation response to upper Pliocene glacial/ interglacial cyclicity in the Central Mediterranean. Quaternary Research 40: 228–236.

Di Pasquale, G., Garfi, G., Quézel, P. 1992. Sur la présence d’un Zelkova nouveau en Sicile sud orientale (Ulmaceae). Biocosme Mésogéen 8–9: 401–409.

Dick, C.W., Abdul-Salim, K., Bermingham, E. 2003. Molecular systematic analysis reveals cryptic tertiary diversification of a widespread tropical rain forest tree. The American naturalist 162: 691–703.

EEA 2015. Digital Elevation Model over Europe (EU-DEM). URL: http://www.eea.europa.eu/data-and-maps/data/eu-dem (last check: 14th March 2017).

Egli, B.R. 1989. Ecology of dolines in the mountains of Crete (Greece). Bielefelder Ökologische Beiträge 4: 59–63.

Egli, B.R. 1997. A project for the preservation of Zelkova abelicea (Ulmaceae), a threatened endemic tree species from the mountains of Crete. Bocconea 5: 505–510.

Egli, B.R. 1998. Effects of grazing on the natural forests of western Crete. In: V.P. Papanastasis and D. Peter (eds.), Ecological Basis of Livestock grazing in Mediterranean Ecosystems: 103–106.

Egli, B.R. 2000. Forest vegetation of Western Crete. Botanika Chronika 13: 1–21.

Egli, B.R., Gerstberger, P., Greuter, W., Risse, H. 1990. Horstrissea dolinicola, a new genus and species of umbels (Umbelliferae, Apiaceae) from Kriti (Greece). Willdenowia 19: 389–399.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Townsend Peterson, A., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S.E., Wisz, M.S., Zimmermann, N.E. 2006. Novel methods improve prediction of species’ distributions from occurrence data. Ecography 29: 129–151.

ESRI 2013. ArcGIS for Desktop: Release 10.2 Redlands, CA: Environmental Systems Research Institute.

Fazan, L. 2014. Investigating the response to climate in two Mediterranean tree species growing in the mountains of Crete (Greece): Zelkova abelicea and Cupressus sempervirens. Msc-thesis, Université de Genève, Switzerland.

Fazan, L., Stoffel, M., Frey, D.J., Pirintsos, S., Kozlowski, G. 2012. Small does not mean young. Age estimation of severely browsed trees in anthropogenic Mediterranean landscapes. Biological Conservation 153: 97–100.

Follieri, M., Magri, D., Sadori, L. 1986. Late Pleistocene Zelkova extinction in Central Italy. New Phytologist 103: 269–273.

Fuentes-Utrilla, P., Venturas, M., Hollingsworth, P.M., Squirrell, J., Collada, C., Stone, G.N., Gil, L. 2014. Extending glacial refugia for a European tree: genetic markers show that Iberian populations of white elm are native relicts and not introductions. Heredity 112: 105–113.

Garcia, K., Lasco, R., Ines, A., Lyon, B., Pulhin, F. 2013. Predicting geographic distribution and habitat suitability due to climate change of selected threatened forest tree species in the Philippines. Applied Geography 44: 12–22.

Garfì, G. 1997. Première contribution à l’étude de Zelkova sicula (Ulmaceae), une relique de la flore tertiaire, endémique de la Sicile sud-orientale. PhD-Thesis, University of Aix-Marseille III, France.

Garfì, G., Barbero, M., Tessier, L. 2002. Architecture and growth patterns of Zelkova sicula (Ulmaceae) in south-east Sicily as a response to environmental conditions. Journal of Mediterranean Ecology 3: 65–76.

Garfì, G. 2006. The IUCN Red List of Threatened Species. Zelkova sicula. URL: http://www.iucnredlist.org/details/61678/0 (last check: 17th March 2017).

Garfì, G., Carimi, F., Pasta, S., Rühl, J., Trigila, S. 2011. Additional insights on the ecology of the relict tree Zelkova sicula di Pasquale, Garfì et Quézel (Ulmaceae) after the finding of a new population. Flora 206: 407–417.

Gessler, P.E., Moore, I.D., McKenzie, N.J., Ryan, P.J. 1995. Soil-landscape modelling and spatial prediction of soil attributes. International journal of geographical information systems 9: 421–432.

Giraudoux, P. 2016. pgirmess. A package for data analysis in ecology. URL: http://giraudoux.pagesperso-orange.fr/ (last check: 17th March 2017).

Hedderson, T.A., Blockeel, T.L. 2013. Oncophorus dendrophilus, a new moss species from Cyprus and Crete. Journal of Bryology 28: 357–359.

Heikkinen, R.K., Marmion, M., Luoto, M. 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability? Ecography 35: 276–288.

Honnay, O., Jacquemyn, H. 2007. Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. Conservation Biology 21: 823–831.

Huntley, B. 1990. European post-glacial forests: compositional changes in response to climatic change. Journal of Vegetation Science 1: 507–518.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N., Zimmermann, N.E., Kessler, M. 2016. CHELSA climatologies at high resolution for the earth‘s land surface areas (Version 1.0). URL: http://chelsa-climate.org/ (last check: 17th March 2017).

Keenan, T., Maria Serra, J., Lloret, F., Ninyerola, M., Sabate, S. 2011. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models. CO2 matters! Global Change Biology 17: 565–579.

Khadari, B., Grout, C., Santoni, S., Kjellberg, F. 2005. Contrasted genetic diversity and differentiation among Mediterranean populations of Ficus carica L.: A study using mtDNA RFLP. Genetic Resources and Crop Evolution 52: 97–109.

Körner, C. 2014. Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems. Springer, Berlin, Germany.

Kozlowski, G., Frey, D., Fazan, L., Egli, B., Pirintsos, S. 2012. IUCN Red List of Threatened Species. Zelkova abelicea. URL: http://www.iucnredlist.org/details/30319/0 (last check: 17th March 2017).

LaBonte, N., Tonos, J., Hartel, C., Woeste, K.E. 2017. Genetic diversity and differentiation of yellowwood [Cladrastis kentukea (Dum.Cours.) Rudd] growing in the wild and in planted populations outside the natural range. New Forests 9: 12pp. online. URL: http://link.springer.com/article/10.1007/s11056-017-9566-8 (last check: 17th March 2017).

Lipscomp, M.V., Nilsen, E.T. 1990a. Environmental and physiological factors influencing the natural distribution of evergreen and deciduous ericaceous shrubs on northeast- and southwest- facing slopes of the Southern Appalachian mountains. I. Irradiance tolerance. American Journal of Botany 77: 108–115.

Lipscomp, M.V., Nilsen, E.T. 1990b. Environmental and physiological factors influencing the natural distribution of evergreen and deciduous ericaceous shrubs on northeast- and southwest- facing slopes of the Southern Appalachian mountains. II. Water relations. American Journal of Botany 77: 517–526.

Liu, Y., Wang, Y., Hongwen, H. 2006. High interpopulation genetic differnetiation and unidirectional linear migration patterns in Myricaria laxiflora (Tamaricaceae), an endemic riparian plant in the Three Gorges Valley of the Yangtze river. American Journal of Botany 93: 206–215.

Lobo, J.M., Jiménez-Valverde, A., Real, R. 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17: 145–151.

Magri, D. 1999. Late Quaternary vegetation history at Lagaccione near Lago di Bolsena (central Italy). Review of Palaeobotany and Palynology 106: 171–208.

Mai, D.H. 1987. Development and regional differentiation of the European vegetation during the Tertiary. Plant Systematics and Evolution 162: 79–91.

Martin-StPaul, N.K., Limousin, J.-M., Rodríguez-Calcerrada, J., Ruffault, J., Rambal, S., Letts, M.G., Misson, L. 2013. Photosynthetic sensitivity to drought varies among populations of Quercus ilex along a rainfall gradient. Functional Plant Biology 39: 25–37.

McCune, B., Keon, D. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13: 603–606.

Merow, C., Smith, M.J., Silander, J.A. 2013. A practical guide to MaxEnt for modeling species’ distributions. What it does, and why inputs and settings matter. Ecography 36: 1058–1069.

Moore, I.D., Gessler, P.E., Nielsen, G.A., Peterson, G.A. 1993. Soil attribute prediction using terrain analysis. Soil Science Society of America Journal 57: 443–447.

Morales, N.S., Fernandez, I.C., Baca-Gonzalez, V. 2017. MaxEnt‘s parameter configuration and small samples: are we paying attention to recommendations? A systematic review. PeerJ 5: 16pp. URL: https://peerj.com/articles/3093/ (last check: 17th March 2017).

Mousadik, A.E., Petit, R.J. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree Argania spinosa (L.) Skeels endemic to Morocco. Theoretical and Applied Genetics 92: 832–839.

Nadeau, C.P., Urban, M.C., Bridle, J.R. 2017. Coarse climate change projections for species living in a fine-scaled world. Global Change Biology 23: 12–24.

Parducci, L., Szmidt, A.E., Madaghiele, A., Anzidei, M., Vendramin, G.G. 2001. Genetic variation at chloroplast microsatellites (cpSSRs) in Abies nebrodensis (Lojac.) Mattei and three neighboring Abies species. Theoretical and Applied Genetics 102: 733–740.

Peterson, A.T., Soberón, J., Sánchez-Cordero, V. 1999. Conservatism of Ecological Niches in Evolutionary Time. Science 285: 1265–1267.

Petit, R.J., Bialozyt, R., Garnier-Géré, P., Hampe, A. 2004. Ecology and genetics of tree invasions: from recent introductions to Quaternary migrations. Forest Ecology and Management 197: 117–137.

Phillips, S.J., Anderson, R.P., Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–259.

Phillips, S.J., Dudík, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31: 161–175.

Quézel, P., Médail, F. 2003. Écologie et biogéographie des forêts du bassin méditerranéen. Elsevier, Paris, France.

R Development Core Team 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org (last check: 17th March 2017).

Revelle, W. 2017. psych. A package for personality, psychometric, and psychological research. URL: http://personality-project.org/r/psych/ (last check: 17th March 2017).

Rissler, L.J., Apodaca, J.J. 2007. Adding more ecology into species delimitation: ecological niche models and phylogeography help define cryptic species in the black salamander (Aneides flavipunctatus). Systematic Biology 56: 924–942.

Sáenz-Romero, C., Lamy, J.-B., Loya-Rebollar, E., Plaza-Aguilar, A., Burlett, R., Lobit, P., Delzon, S. 2013. Genetic variation of drought-induced cavitation resistance among Pinus hartwegii populations from an altitudinal gradient. Acta Physiologiae Plantarum 35: 2905–2913.

Sattler, T., Bontadina, F., Hirzel, A.H., Arlettaz, R. 2007. Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. Journal of Applied Ecology 44: 1188–1199.

Scherrer, D., Schmid, S., Körner, C. 2011. Elevational species shifts in a warmer climate are overestimated when based on weather station data. International Journal of Biometeorology 55: 645–654.

Skov, F., Svenning, J.-C. 2004. Potential impact of climatic change on the distribution of forest herbs in Europe. Ecography 27: 366–380.

Søndergaard, P., Egli, B.R. 2006. Zelkova abelicea (Ulmaceae) in Crete: floristics, ecology, propagation and threats. Willdenowia 36: 317–322.

Steinbauer, M.J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., Birks, H.J.B., Borges, P.A.V., Cardoso, P., Chou, C.-H., Sanctis, M. de, Sequeira, M.M.d., Duarte, M.C., Elias, R.B., Fernández-Palacios, J.M., Gabriel, R., Gereau, R.E., Gillespie, R.G., Greimler, J., Harter, D.E.V., Huang, T.-J., Irl, S.D.H., Jeanmonod, D., Jentsch, A., Jump, A.S., Kueffer, C., Nogué, S., Otto, R., Price, J., Romeiras, M.M., Strasberg, D., Stuessy, T., Svenning, J.-C., Vetaas, O.R., Beierkuhnlein, C. 2016. Topography-driven isolation, speciation and a global increase of endemism with elevation. Global Ecology and Biogeography 25: 1097–1107.

Steinbauer, M.J., Irl, S., Beierkuhnlein, C. 2013. Elevation-driven ecological isolation promotes diversification on Mediterranean islands. Acta Oecologica 47: 52–56.

Svenning, J.-C., Fløjgaard, C., Marske, K.A., Nógues-Bravo, D., Normand, S. 2011. Applications of species distribution modeling to paleobiology. Quaternary Science Reviews 30: 2930–2947.

Thompson, J.D. 1999. Population differentiation in Mediterranean plants: insights into colonization history and the evolution and conservation of endemic species. Heredity 82: 229–236.

Trigas, P., Panitsa, M., Tsiftsis, S., Moreau, C.S. 2013. Elevational Gradient of Vascular Plant Species Richness and Endemism in Crete – The Effect of Post-Isolation Mountain Uplift on a Continental Island System. PLoS ONE 8: e59425, 13pp. URL: https://doi.org/10.1371/journal.pone.0059425 (last check: 17th March 2017).

Vander Mijnsbrugge, K., Bischoff, A., Smith, B. 2010. A question of origin: Where and how to collect seed for ecological restoration. Basic and Applied Ecology 11: 300–311.

Vazquez, D.P., Gianoli, E., Morris, W.F., Bozinovic, F. 2017. Ecological and evolutionary impacts of changing climatic variability. Biological Reviews of the Cambridge Philosophical Society 92: 22–42.

Viveros-Viveros, H., Sáenz-Romero, C., Vargas-Hernández, J.J., López-Upton, J., Ramírez-Valverde, G., Santacruz-Varela, A. 2009. Altitudinal genetic variation in Pinus hartwegii Lindl. I. Height growth, shoot phenology, and frost damage in seedlings. Forest Ecology and Management 257: 836–842.

Wiens, J.J. 2004. Speciation and ecology revisited. Phylogenetic niche conservatism and the origin of species. Evolution 58: 193–197.